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Effects of density-dependence and climate on the dynamics of a Svalbard reindeer population

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To determine the main factors affecting the population dynamics of Svalbard reindeer, we analysed 21 yr of annual censuses, including data on population size, recruitment rate (calves per female) and mortality (number of deaths), from the Reindalen reindeer population. In accordance with previous studies on population dynamics of Svalbard reindeer, we found large inter-annual variation in population size, mortality and recruitment rates within the study area. Population size decreased in years with low recruitment rate as well as high winter mortality and vice versa. Apparently, the fluctuations were due to both direct density-dependent food limitation and variation in winter climate associated with high precipitation and icing of the feeding range. We found no delayed density-dependence or effect of climatic conditions during summer on the population dynamics. The mortality during die-off years was mainly of calves and very old individuals, indicating that the population was more vulnerable to high die off in years following high recruitment rate. These results suggest an unstable interaction between the reindeer population and its food supply in these predator-free environments.

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Predation, human harvesting, density-dependence and stochastic variation in climate are the most important factors influencing the population dynamics of large herbivores (see Sæther 1997 and Gaillard et al. 1998, for recent reviews). In environments without predation and harvesting, many recently published long term studies have revealed a complex interplay between the effects of climate and density on population dynamics (e.g. Bousses et al. 1994, Clutton-Brock et al. 1997, Loison and Langvatn 1998, Post and Stenseth 1998, 1999, Forchhammer et al. 1998, Solberg et al. 1999). This contrasts with previously suggested characteristics of the population dynamics of the Svalbard reindeer *Rangifer tarandus platyrhynchus* Vrolik (Reimers 1977, 1982, Tyler 1987). Living further north than any other cervid species, this sub-species experiences almost no predation and negligible human harvesting, but has to cope with an extreme and variable environment (Reimers 1977, 1982, Tyler 1987, Aanes et al. 2000, see Klein 1991 for a general view). Extreme winter conditions with subsequent starvation of the animals, leading to a high die-off of individuals during some particular winters along with low fecundity the following summer, has been described as the main factor shaping their dynamics (Reimers 1977, 1982, Tyler 1987). These "bad winters" appear frequently and cause large fluctuations in population size, and seem to be independent of population density (Tyler 1987). Indeed, this apparent strong effect of climate made Alendal and Byrkjedal (1974) and Reimers (1977, 1982) suggest that some Svalbard reindeer populations, by the frequent effect of "bad winters", may be kept at densities well below any

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effects of density-dependence. Within such a scenario, the population should exhibit an approximate Brownian process without any regulatory mechanism. Previous studies, however, have been of short duration (e.g. Tyler 1987, 6 yr) and lacked reliable estimates of population density as well as information on the causal mechanisms making some winters "bad". For the latter, several mechanisms have commonly been suggested, including deep snow and icing of the feeding ground (Lønø 1959, Alendal and Byrkjedal 1974, Larsen 1976, Reimers 1977, 1982, Tyler 1987, Aanes et al. 2000, see also Adamczewski et al. 1988 for arctic Canada), but statistically testing for these effects has been constrained by crude meteorological data and limited length of study. Since these early studies, several longer series of census data have been collected (e.g. this study, Aanes et al. 2000), which may improve our understanding of the Svalbard reindeer population dynamics. Here, we explore the population dynamics pattern emerging from a 21 yr long time series of censuses of a Svalbard reindeer population, and examine the following three questions: 1) what are the patterns in the population dynamics and demography of a Svalbard reindeer population? 2) To what extent are those patterns explained by variation in climate? 3) How does variation in density influence the demography and population dynamics?

Study area and methods

Study area

The study was conducted in the following valleys: Reindalen, Semmeldalen, Colesdalen and Fardalen on the Nordenskiöld Land peninsula (78°N) on Svalbard (Fig. 1) in the period 1979–1999. The whole area is characterised by arctic tundra dominated by graminoids, mosses and herbs in the valley floors and slopes, and mainly barren on the summits separating the valleys (e.g. Loe 1999). The study area, as most of the Svalbard archipelago, can be described as a cold desert due to low temperatures and little precipitation (Førland et al. 1997).

Data sampling and estimation of demographic parameters

The censuses were conducted during late July and early August in the period 1982–1999, and in late June to

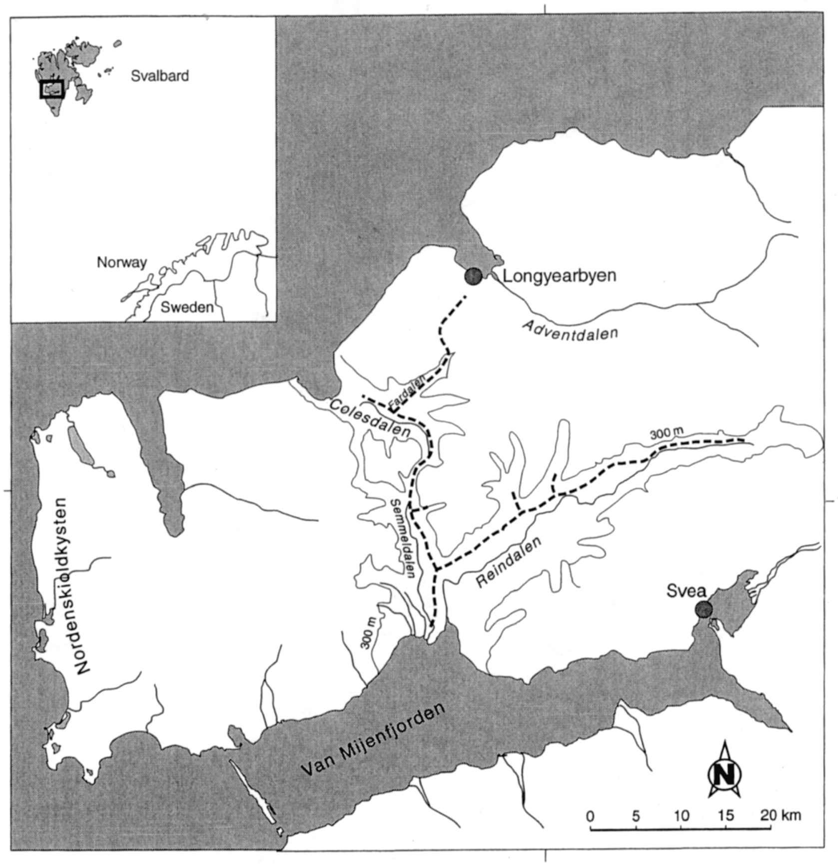

Fig. 1. The study area including the transect walked (stippled line) and the 300 m a.s.l. contour.

Table 1. The Pearson correlation coefficients for the relationship between population growth rate (above diagonal, $n = 17$) and calves per female (below diagonal, $n = 18$) among valleys in the study area.

	Reindalen	Semmeldalen	Colesdalen	Fardalen
Reindalen	–	0.71**	0.47	0.20
Semmeldalen	0.88***	–	0.48*	0.54*
Colesdalen	0.85***	0.76***	–	0.21
Fardalen	0.52*	0.58*	0.67**	–

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

early July in the period 1979–1981. With one exception (1988, see below), sampling consisted of two people walking a fixed transect through the valleys (Fig. 1), recording the number, group size, sex and age (calves, yearlings and adults 2 yr, and individuals unclassified to sex and age) of all individuals observed. The number of animals not possible to classify to age and sex never exceeded 14% (mean = 2.8, SD = 3.7). On average, 41% (SD = 7.0) of the reindeer were observed in Reindalen, 31% (5.6) in Semmeldalen, 19% (5.3) in Colesdalen, and 9% (2.7) in Fardalen. Animals found dead following the last winter were also recorded, and from most carcasses the lower jaws were collected for age determination (Reimers and Nordby 1968). The number of dead individuals recorded each year varied from zero (1987, 1999) to 68 (1991) individuals (mean = 10.8, SD = 16.7, Fig. 2), with the main part of the distribution < 10 individuals per year.

From the transect walked, the whole study area was viewed with binoculars and telescopes. The sedentary behaviour and small group size of the Svalbard reindeer (Tyler and Øritsland 1989) combined with the open habitat made reindeer easily observable, and it was assumed that the number recorded was close to the actual number of animals in the valleys at the present time. It is however important to note that the sampling procedure did not allow for computation of standard error of the estimates, but we do believe that the number of animals recorded represents a reliable estimate of the minimum number of animals present.

During the census of 1988, ca 60% of the sampling area was surveyed by helicopter in an attempt to improve the efficiency of the census method. Within the limits of available resources, however, this method was found less efficient and less precise than ground observations, as it generally underestimated the number of animals seen by the original procedure (Jordhøy and Strand unpubl.). This method was therefore not employed in the forthcoming censuses. Unfortunately, the original procedure was not repeated in the complete area covered by helicopter so that the population size estimated this year by all probability was an underestimate. For this year, we therefore based our population estimate on the reindeer observed by the original procedure in 40% of the area (85 animals), corrected by the annual mean proportion of reindeer observed in this part of the study area (28%) during the study period (85/0.28 = 304). In contrast, mortality data based on dead animals found this year was excluded from the analyses as this information was not location-specific and highly variable among years (see below).

From the observation data, we used four different variables: Population size – the total number of reindeer observed (n = 21 yr). Population growth rate – the total number of reindeer observed in year t divided by the number observed in year $t - 1$ (n = 20 yr). Calves per female – the number of calves observed per female two years and older (n = 21 yr). Mortality index – the number of dead animals recorded during the surveys divided by the total number of animals observed the previous year (n = 19 yr). All demographic variables were ln-transformed or analysed with logit link function.

Variation among valleys

The four valleys included in the study are connected and constitute a "natural" population unit on the Nordenskiold peninsula. However, interchange of animals may occur with the reindeer populations in the nearby Adventdalen in the north, the Nordenskiold coast in the west and the reindeer population living on the north shore of the van Mijen fjord in the south (Fig. 1).

To examine the assumption that the reindeer in the four valleys can be considered as one population, we performed cross correlation between similar demographic variables from the separate valleys. Mainly significant relationships existed among valleys for both population growth rate and calves per female (Table 1), indicating that similar factors affected the dynamics over the whole study area. Moreover, to further examine our assumption, we repeated all analyses on the pooled material from Reindalen and Semmeldalen, as these two valleys contained the largest portion of the population and may cover a more discrete area (Fig. 1). The analyses did not differ qualitatively from the analyses based on the complete data set, but as the number of observations was lower and because we only possessed 18 yr with information on observation location, the statistical power was generally lower. For the sake of simplicity and to gain as much power as possible, we therefore presented the results from the pooled data based on all four valleys only.

Climatic variables

The common assumption is that the variation in mortality and fecundity of the Svalbard reindeer is shaped by variation in winter climate, and in particular by the frequency of icing of the ground (Lønø 1959, Alendal and Byrkjedal 1974, Larsen 1976, Reimers 1977, 1982, 1983, Tyler 1987, Øritsland 1998). Being an island, all parts of Svalbard are close to the sea (and the North Atlantic (Gulf) current), which, despite the extreme northern latitude, may lead to quite mild temperatures even in midwinter, including short periods with temperature above zero. When such conditions are combined with rain, thin snow cover, and a subsequent decline in temperature, severe icing of the ground covering the vegetation may be the result (e.g. Forchhammer and Boertmann 1993). Despite the frequent reports of icing negatively affecting Svalbard reindeer population dynamics, we are not aware of any study trying to quantify either icing itself or its potential influence on Svalbard reindeer density fluctuations. Icing may therefore occur even without any mass death of reindeer.

Based on the climatic records, we constructed a crude variable assumed to index the icing condition; Icing index – the annual sum of precipitation during days with temperature above 0°C between 1 October and 31 May. The icing index may sometimes predict a harder snowpack rather than ice as mild temperatures and precipitation can lead to a wet snow layer, which hardens with a drop in temperature and (or) strong wind rather than becoming ice (see Parker et al. 1975). The consequence for reindeer would however be the same, i.e. they have to penetrate a hard snow- or ice-layer to find food. We also examined the variation in demographic variables in relation to the mean maximum monthly snow depth (Winter snow), and the mean monthly temperature during the period October–May (Winter temperature). Deep snow may have a detrimental effect on the feeding conditions and survival during winter (Fancy and White 1985, Adamczewski et al. 1988). Moreover, based on the significant relationship found by Aanes et al. (2000) between population growth rate and total winter precipitation (winter precipitation) in the nearby Brøgger reindeer population, we also examined the effect of this variable on the population dynamics in the present population. The effect of total winter precipitation (snow and rain) may differ from the effect of snow depth if high precipitation during winter is due to much precipitation as rain. This was partly supported by a positive, although not significant relationship between winter precipitation and the icing index ($r = 0.27$, $n = 21$, $p = 0.24$). The period from 1 October to 31 May was selected because the temperature during these months on average was below zero and the ground covered by snow. These months may consequently be assumed to constitute the harshest period during the year for the reindeer to survive.

In addition to these variables, we examined the possible effects of the North Atlantic Oscillation index (NAO) on the population dynamics. The NAO is based on the difference of normalised sea level pressures between Lisbon, Portugal and Stykkisholmur, Iceland (see Hurrell 1995 for a more detailed description), and has recently been found to relate to the population dynamics of a variety of cervids (Post et al. 1997, Forchhammer et al. 1998, Post and Stenseth 1999). The NAO index is available from the Climate Analysis Section on the World Wide Web: http://www.cgd.ucar.edu/cas/climind. Other indices of icing (e.g. number of rainy days during winter, icing index divided by total snow depth) and variables based on shorter periods during winter were examined, but were generally found to be closely correlated with the variables selected.

Cervid population dynamics may also be affected by variation in summer climate (Albon and Clutton-Brock 1988, Sæther 1997, Solberg et al. 1999), as climate induced variation in the summer feeding conditions may affect autumn body condition and subsequently the probability of ovulation. Such variation in body conditions may for instance follow large variation in quantity or quality of plants produced during summer, which for many temperate herbivores is associated with variation in summer temperature (e.g. Sæther 1997, see also Discussion). To index the conditions for plant growth we used the mean temperature (Summer temperature) and the sum of precipitation (Summer precipitation) in the period 1 June–31 August, the main period for plant growth (e.g. Wookey et al. 1995) at Svalbard. As for the winter variables, the monthly summer values were in general highly correlated with the values based on the whole period. No significant relationship existed between any combinations of the selected summer or winter climatic variables ($p > 0.06$). Because the underlying mechanisms for the effect of climate on the population demography was unknown we tested the effect of climate both on a logarithmic and absolute scale. In general the variance of the independent variable explained by climatic variables slightly increased after ln-transformation compared to nontransformed values, and the plot of the relationship appeared more linear. Accordingly we presented the results based on ln-transformed climatic variables (either directly or after adding a fixed number to get positive values).

The meteorological data used in the analyses were collected at Svalbard airport (Longyearbyen) in the north and at the Svea mining town south-east of the study area (Fig. 1, Norwegian Meteorological Inst., Oslo, Norway). We used the mean of the values recorded in the two stations, except for snow depth during 1994–1999, when this variable was not available from Svalbard airport. For these years, snow depth is based on data from Svea only.

Data analyses

By the use of correlation and regression analyses, we first examined the inter-relationship between demographic parameters (population growth rate, calves per female, mortality index) and to what extent the variation in calves per female and mortality could explain the variation in population growth rate

The effects of population density on the different population variables were tested by regressing the demographic parameters on population size in year $t-1$. A significant negative relationship was considered as evidence of density-dependence. To examine the potential time lags in the population dynamics, we determined the partial autocorrelation function for the population growth rate.

To analyse the climatic effects on the variation in calves per female and the mortality index, we first examined the univariate relationship between the different climatic variables and the demographic parameters. Because calves per female and the mortality index were proportions estimated with varying precision from year to year, we used logistic regression analyses with binomial error models and logit link function (Crawley 1993).

To analyse the combined effect of climate and population size on the dependent variables, we used generalised linear models where the dependent variables (calves per female and mortality index) were analysed in relation to population density as a category variable (high; population size in year $t-1$ above the mean, low; below the mean) or as a covariate (population size), the climatic variables as covariates, and the 2-way interactions involving population density (as category variable) and climate. The 2-way interaction was included to test for different effects of climate at high compared to low density. Because we expected the effect of winter climate to be partly associated with the proportion of the range accessible for feeding, we predicted that the effect of winter climate should be more severe (steeper slope) at high compared to low density. The analyses were performed using the Proc Genmod in SAS (Anon. 1996).

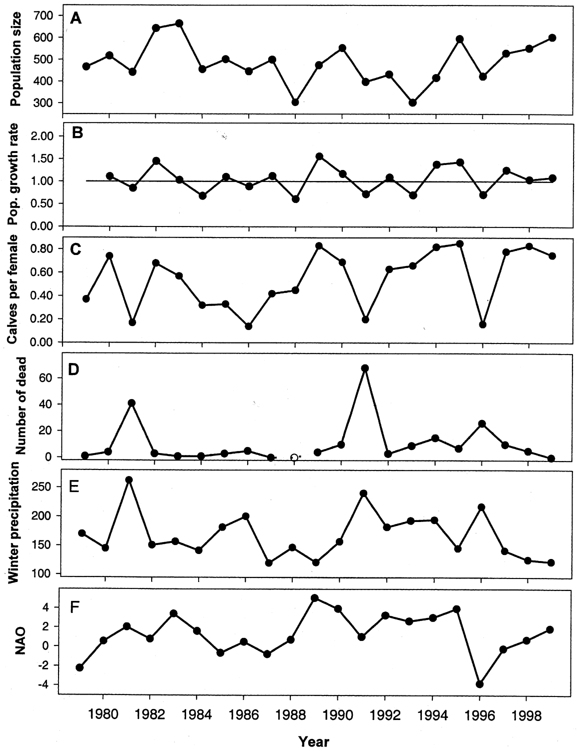

Fig. 2. Annual variation in demographic parameters and climate in the period 1979–1999. Open circles indicate data not included in the analyses (see Methods).

The contribution of independent variables was tested by using the likelihood ratio test and stepwise forward inclusion and alternate exclusion of independent variables. Only variables that significantly ($p < 0.05$) reduced the error deviance (D) were allowed to enter the model. The change in deviance between two nested models (e.g. $DH_0 - DH$) is approximately χ^2 distributed, with $p - p_0$ degrees of freedom where p and p_0 are the number of parameters under the models H and H_0, respectively. If the change in deviance is sufficiently large H_0 can be rejected in favour of the more general model H. However, because we had overdispersion (Eberhardt 1978, Tufto et al. 1998) in the data, this test statistic is not always sufficient. In these cases we used the recommended test statistics,

$$\frac{(D(H_0) - (DH))/(p - p_0)}{D(H_0)/(r - p_0)}, \qquad (1)$$

which is approximately F distributed with $p - p_0$ and $r - p_0$ (residual degrees of freedom) degrees of freedom (Anon. 1996, Tufto et al. 1998).

The univariate contribution of climate on population growth rate was analysed by linear regression analyses. To find the relative contribution of climate and variation in population size we applied a first and second order autoregression model to the population growth rate with the effect of climate incorporated in the model (Royama 1992). This model can mathematically be described as

$$R_t = a_0 + a_1R_{t-1} + a_2R_{t-2} + \ldots + a_dR_{t-d} + \omega_1U_t + \omega_2U_{t-1} + \ldots + \omega_kU_{t-k} + \varepsilon_t, \qquad (2)$$

where a_i are the auto-regressive coefficients (Box and Jenkins 1970), U_t the stochastic climatic term at different lags (only $t-1$ and $t-2$) and ε the random noise assumed to have zero mean and a constant variance. We estimated the auto-regressive coefficients with the

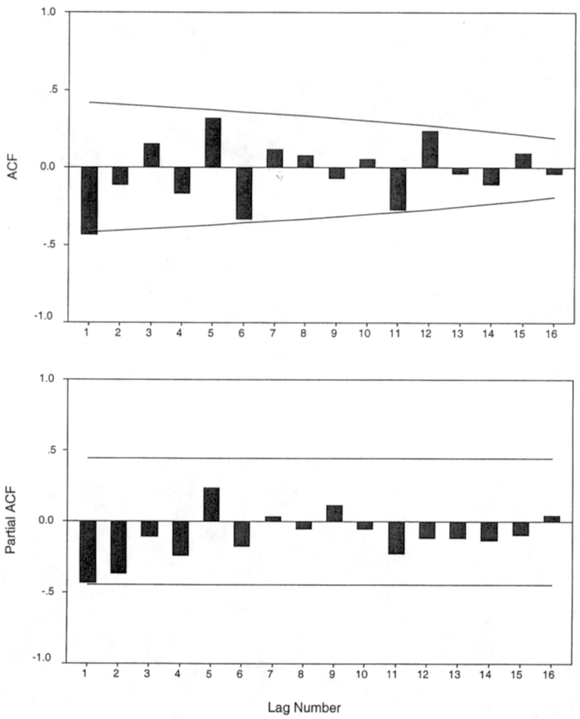

Fig. 3. The autocorrelation function (top) and partial autocorrelation function (bottom) of the population growth rate ($\ln(n_t/n_{t-1})$) in relation to the time lag during the period 1980–1999. Confidence limits indicate two standard errors.

AUTOREG procedure using maximum likelihood estimation (Anon. 1996) with lags from 1 to 3 yr. The most parsimonious model was selected by the corrected Akaike information criterion, AIC_c (Hurvich and Tsai 1989), the model with lowest AIC_c being considered most parsimonious (Sakamoto et al. 1986). All other statistics were performed using SPSS (Anon. 1999). All probabilities were 2-tailed.

The age structure of dead animals was determined based on the carcasses recovered in 1981 and 1991, the two major die off years (Fig. 2). In 1981 all dead animals were aged, whereas in 1991 the lower jaw was only collected for 65% of dead animals recorded as the others were either missing (e.g. removed with the head by scavengers) or because the jawbone was not collected. However, it is assumed that the collected sample is a random sample regarding the age structure. The age structure was not separated to sex as only a small fraction (20%) of the carcasses was sexed.

Results

Demographic patterns

Large fluctuations in population size occurred during the study period (Fig. 2A), with a maximum of 665 in 1983 and a minimum of 303 in 1993. Accordingly, there was large variation in population growth rate (Fig. 2B), calves per female and in the mortality index (Fig. 2C, D).

The population growth rate increased with calves per female ($r = 0.63$, $n = 20$, $p = 0.003$), but was not significantly related to the mortality index ($r = -0.16$, $n = 19$, $p = 0.53$). Accordingly, the annual variation in calves per female was neither significantly related to the mortality index ($r = -0.29$, $n = 19$, $p = 0.23$). Hence, despite our expectation of a close relationship between recruitment rate and mortality, this correlation was not very strong.

The effect of climate and population density

Based on the univariate relationships, only the icing index, winter precipitation and NAO were able to explain part of the variation in the demographic variables (Table 2, Fig. 4). Hence, "bad" winters were apparently a function of total precipitation, independent of whether this appeared as rain or snow. Similarly, the population size in year $t-1$ was inversely related to both the population growth rate (Table 2) and calves per female (Table 2), indicating density-dependence. No significant relationship existed between the mortality and population size (Table 2). In all regressions of density on demographic variables the residuals were independent of time ($p > 0.28$). Moreover, both the auto-correlation and the partial auto-correlation analyses of the population growth rate indicated a significant negative first order auto-correlation ($r = -0.43$, $n = 20$), but no significant auto-correlation at higher lags (Fig. 3). Hence, time delayed density-dependence was not very important in this population.

When examining the relative importance of climate and density in a multiple model, the best model explaining the variation in calves per female was population size, winter precipitation and NAO (Table 3). No other climatic variable or climate × density interaction were found to contribute significantly to the model. The model that best explained the variation in the mortality index included only winter precipitation (Table 3), whereas no other variable were even close to explaining a significant proportion ($p > 0.10$).

The best model explaining the variation in population growth rate included the first-order density effect (growth rate in year $t-1$) and winter precipitation (Table 4). A more general model including the first order effect, winter precipitation and the NAO did not differ extensively from the best model according to the AIC_c (Table 4), but was found to be less "attractive" based on the principle of minimising the number of variables in the model.

Age distribution of dead animals

The age distribution of dead animals was dominated by calves and older (> 6 yr) animals, whereas prime age animals from 1 to 6 yr of age were almost absent from the sample. The age structure was highly correlated between the two years (Fig. 5, $r = 0.93$, $n = 16$, $p < 0.001$). The proportion of calves observed in the population in the year prior to collections of dead (34% in 1980 and 26% in 1990) was less than (< 69%) the proportion calves in the sample of dead (Fig. 5). Similarly, given the fecundity and mortality pattern during the preceding years, the adult population during the

Table 2. Parameter estimates of the slope (B) and SE for the linear (population growth rate $\ln(n_t/n_{t-1})$) and logistic regression of demographic variables on the annual variation in climate (ln) and population size (ln) during the study period. Parameters in bold are statistically significant.

	Population growth rate N = 20	Calves per female N = 21	Mortality index N = 19
Icing index	B = −0.028 SE = 0.063	**B = −0.031** **SE = 0.011****	**B = 0.019** **SE = 0.009***
Winter precipitation	**B = −0.525** **SE = 0.255***	**B = −0.019** **SE = 0.005*****	**B = 0.023** **SE = 0.004*****
Winter snow depth	B = −0.026 SE = 0.128	B = 0.007 SE = 0.015	B = −0.017 SE = 0.019
Winter temperature	B = 2.369 SE = 3.201	B = 0.085 SE = 0.128	B = −0.096 SE = 0.174
NAO	B = 0.530 SE = 0.307	**B = 0.248** **SE = 0.106***	B = −0.070 SE = 0.138
Summer temperature in year t − 1	B = 0.112 SE = 0.445	B = −0.311 SE = 0.363	B = 0.672 SE = 0.448
Summer precipitation in year t − 1	B = 0.186 SE = 0.138	B = 1.906 SE = 1.101	B = −0.351 SE = 1.513
Population size in year t − 1	**B = −0.872** **SE = 0.242****	**B = −0.005** **SE = 0.003***	B = 0.001 SE = 0.003

* $p<0.05$, ** $p<0.01$, *** $p<0.001$.

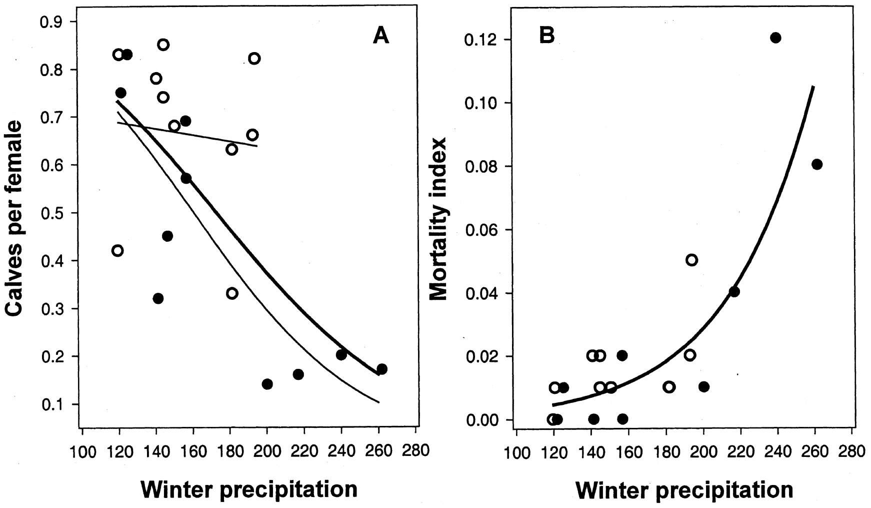

Fig. 4. Calves per female (A) and the mortality index (B, number of dead/population size in year t − 1) in relation to the winter precipitation at low (open circles) and high (filled circles) density. The curves were fitted to the logistic equation; $y = e^{(a+bx)}/(1 + e^{(a+bx)})$, where y is the calves per female or mortality index, a and b are constants and x is winter precipitation. Thick curves show the main effect of winter precipitation, whereas the upper and lower thin curves in A indicate the logistic relationship at low and high density (below and above the average density), respectively.

Table 3. The combined effects of climate (ln) and population size (ln) on the calves per female and mortality index. Parameter estimates are for the full selected model, whereas the Deviance shows the reduction in error deviance by adding successive variables to the model.

Dependent variable	Equation	χ^2 or t	p	Deviance
Calves per female	4.92 (intercept)	21.46	0.001	1058
	−0.018 winter precipitation	23.36	0.001	572
	+0.241 NAO	8.68	0.003	386
	−0.004 population size in t − 1	7.28	0.007	263
Mortality index	−8.134 (intercept)	100.25	0.001	315
	+0.023 winter precipitation	41.25	0.001	92

Table 4. The autoregressive models explaining the variation in population growth rate.

Dependent variable	Equation	t-value	p	R^2	AICc
Population growth rate	2.288	1.78	0.094	0.32	4.81
	-0.376 population growth rate in $t-1$	-1.81	0.090		
	-0.446 winter precipitation	-1.77	0.095		
Population growth rate	0.961	0.62	0.544	0.41	5.71
	-0.358 population growth rate in $t-1$	-1.77	0.096		
	-0.382 winter precipitation	-1.54	0.143		
	$+0.412$ NAO	1.44	0.170		

two high mortality years (1981, 1991) were unlikely to be dominated by old age-classes. Accordingly, despite our lack of data on the standing population age-structure, the pattern in the sample of dead animals indicated that calves and older animals have the highest mortality rates in this population during die-off years.

Discussion

In the present study, we found that the population dynamics of the Reindalen reindeer population to a large extent was determined by varying winter climate associated with precipitation and/or ice crust formation combined with density-dependence. Following such "bad" winters, the recruitment of calves to the population decreased and the mortality of calves and old animals increased with the consequence that the population size decreased. Ice crust formation is believed to restrict the access to food resources leading to the death of weak individuals by starvation (e.g. Reimers 1977, 1982). Accordingly, several other studies have reported extensive mortality in Svalbard reindeer and other high arctic ungulate populations following ice crust formation or deep snow accumulation (Skoog 1968, Alendal and Byrkjedal 1974, Parker et al. 1975, Larsen 1976, Reimers 1977, 1982, 1983, Tyler 1987, Forchhammer and Boertmann 1993, Øritsland 1998, Aanes et al. 2000). Moreover, reduced female body condition during "bad" winters may explain the following low recruitment rates, probably due to foetus absorption, abortion or neonatal mortality (e.g. Cameron et al. 1993, Andersen and Linnell 1998) with the consequence that large variation existed in the proportions of calves (7–34%) recruited to the population.

Recently, Aanes et al. (2000) examined the population dynamics of an introduced population of Svalbard reindeer. They found, as in the present study, that inter-annual variation in population growth rate was mainly guided through a negative correlation to the amount of precipitation during winter. A crude icing index, similar to the one used in the present study (Table 2), also influenced the population dynamics in their study, although less than precipitation itself. Moreover, the present study mirrors Aanes et al. (2000) as we found no effect of climatic conditions during summer on Svalbard reindeer population dynamics. Hence, there is now evidence from two independent populations of Svalbard reindeer studied for ≥ 20 yr that climatic variation during winter is the main factor leading to the observed fluctuations in population density and growth rate, while the effect of summer climate seems to be minor or absent. This result contrasts with studies on large herbivores in temperate areas, where summer climate, through an influence on forage quality and quantity, has been found to largely influence population dynamics and demography (e.g. Albon and Clutton-Brock 1988, Sæther 1997, Loison et al. 1999, Solberg et al. 1999). One reason for this striking difference might be that the strong direct negative effect of frequent "bad" winters result in population densities during summer that are below carrying capacity, giving sufficient resources to all animals in the population (Wegener and Odasz-Albrigtsen 1998). Alternatively, or working in synergy with the first, the warmer summer climate at lower latitudes may have a stronger impact on food quality compared to the climate on Svalbard. Because the early phenological phases of plant growth are associated with peak protein levels (Van Soest 1983)

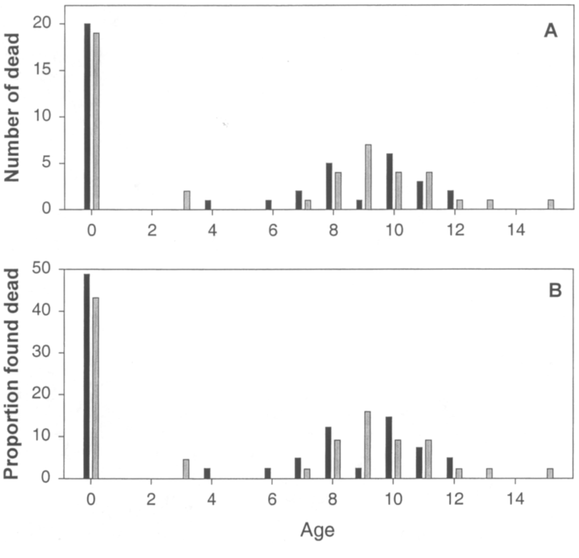

Fig. 5. The age-specific number (A) and proportion (B) of animals found dead in the study area following the preceding winter. Black column 1981 ($n = 41$), grey column 1991 ($n = 44$).

and high digestibility (Deinum 1984, Bennet and Mathias 1984, Wedin et al. 1984), long periods of plant growth, often associated with cool summers, are beneficial for body growth in temperate ungulates (Sæther 1985, Solberg and Sæther 1994, Langvatn et al. 1996, Solberg et al. 1999). In contrast, summer temperatures at Svalbard are low (e.g. mean temperature for July, the warmest month, in the period 1978–1999 in our study area; 6.26°C, SD = 0.86) and summers short, indicating that the complete summer is needed for plants to grow to their final phenological stage. This may suggest that summer feeding conditions are good and more stable in arctic areas than in more temperate environments (e.g. Van der Wal et al. 2000), making temperate ungulates relatively more vulnerable to "bad summers".

In addition to the effect of climate, population size decreased after years with high population density, probably related to starvation. The effect of density was mainly additive to the effects of winter precipitation, whereas no significant climate × density interaction were present. Given the pattern in Fig. 4, however, we suspect that inclusion of data from more years may reveal that the effects of winter precipitation is more severe during high-compared to low-density years. During winter, reindeer feed where wind allows the range to be uncovered or under shallow snow, which lead to a spaced out distribution (Nellemann 1996). Following wet weather, deep snow and/or ice crust formation, reindeer aggregate in smaller ice-free areas, typically on mountain slopes and at higher altitude (Hjeljord 1973, Alendal and Byrkjedal 1974) where food-competition is intensified, in particular when density is already high. Correspondingly, "bad" winters following summers with low population density should be expected to be less severe, as food competition, even within a restricted number of ice-free patches, may be relatively low.

The factors outlined above may possibly also be responsible for the general lack of delayed density-dependence in Svalbard reindeer (this study; Aanes et al. 2000). If individuals surviving a harsh winter are able to compensate during summer due to sufficient available resources and negligible competition, delayed density-dependence may be of minor importance in the dynamics. On the other hand, we expected the large variation in recruitment rate and mortality to have delayed effects on the future population growth rate due to the variation it imposes on the age-structure. Because "bad" winters affect two consecutive cohorts (high winter calf mortality and reduced fecundity), a subsequent delayed decrease in the number of breeding females and number of calves produced may be expected. However, no significant time delayed negative effect was found in the auto-correlation of the population growth rate (Fig. 3), possibly because of the swamping by the other factors that affected the dynamics.

Given the age-specific variation in mortality, particularly the high mortality rates of calves, an interacting effect may also exist between recruitment rate and mortality that may guide the outcome of subsequent climatic perturbations. For instance, as observed in Fig. 2, the high mortality years followed years with high fecundity, as if a large proportion of calves in the population was necessary for a large die-off. This makes sense given the general higher vulnerability of calves to severe winter conditions (Fig. 5, Gaillard et al. 1998). Moreover, high mortality years were also characterised by a larger proportion of adult females with calves at the onset of winter (the previous year), which, given the often observed higher energetic costs involved with lactating (Clutton-Brock et al. 1989, Aanes unpubl.), may enter winter with reduced fat reserves compared to years without maternal commitments. Accordingly, high fecundity years, irrespective of population density, may decrease the mean body condition in the population at the start of the winter, both because of high proportion calves with generally low fat reserves, and possibly because of on average lower fat reserves among females following lactation. Such a scenario may explain the relatively low number of carcasses recovered in 1986, despite the low fecundity observed during the summer, apparently due to a "bad" winter (Fig. 2). Because of the low proportion of calves produced in 1985 (15%), few calves were present during the following winter, while the condition of adult females at the onset of winter may have been relatively high because of low maternal commitments.

Based on the different variables derived from the observation data it is apparent that one or several of the annual population densities are biased. In particular this seems apparent for the high density observed in 1982, indicating a population increase of 44%. Despite the fact that this year was characterised by high recruitment rates and low mortality such growth rates are extremely high (Heard 1990) in consideration of the sex- and age distribution indicated by the observation data, even with a high average female to male sex ratio (mean = 2.03, SD = 1.05). Furthermore, the observed variation in sex ratio between years further indicates that the study might suffer from sample errors such as failure in determining correct sex and/or to count all groups of animals in some years. High growth rate may also be due to immigration, in particular during years of extreme winter conditions further west on the peninsula (e.g. in 1985 and 1994). Nevertheless, we argue that the effect of migration in the present study is likely to be low. Firstly, previous studies (e.g. Tyler and Øritsland 1989) have found Svalbard reindeer to be sedentary and non-migratory. The necessary food base is available within relative small areas throughout Svalbard (Tyler and Øritsland 1989), and the surrounding areas is therefore likely to contain the same amount of food per individual due to the reindeer's scattered distribution, which reduces the potential benefits of migration. Secondly, due to geographical barriers there are not many available areas to immigrate to or emigrate from. One such likely area might be Adventdalen, which is located ca 25 km further north. However, the population dynamics observed in the Adventdalen population (Tyler and Øritsland 1999) suggests that negligible migration occur between these two areas.

To conclude, we have shown that even in this relatively simple high-arctic ecosystem (few species and trophic levels), complex dynamics may appear due to the combination of density-dependence, environmental stochasticity and possibly population age-structure. The contribution of stochastic factors relative to deterministic variables (e.g. density dependence) to future population fluctuations awaits a stochastic modelling of the various processes described in this paper. We do however expect that the results of such modelling will show that a very unstable interaction exists between the reindeer population and its food resources.

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