

Life-history variation of wild reindeer (*Rangifer tarandus*) in the highly productive North Ottadalen region, Norway

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(Accepted 19 May 2004)

Abstract

Variation in life history is a central key to understanding population dynamics, and density dependence and climate are important factors in shaping life-history variation in ungulates. Early growth is often sensitive to adverse conditions and this may in turn affect juvenile survival and age at first reproduction. We report variation in body weight of 5079 reindeer *Rangifer tarandus* from North Ottadalen, a very productive reindeer area in Norway, sampled over 14 years in the period 1967–1989. The North Ottadalen reindeer herd was established in 1964 from a winter herd of some 500 semi-domestic reindeer, and allowed to grow to a peak of over 3300 reindeer in 1974, after which increased harvest decreased the population size. The proportion of lactating yearling females varied between 0% and 50%. Lactating females had lower autumn body weights than non-lactating females. A decline in body weight with age, i.e. senescence, was evident in both males and females from around 7 to 9 years of age. Body weights of all age and sex groups as well as the proportion of yearling females lactating decreased over time, and more so in younger than older males, although the population size declined markedly after the population peak in 1974. We found no effect of the North Atlantic Oscillation or local weather on body weight. The possible causes of the marked decline in performance with time in the North Ottadalen reindeer herd are discussed, and it is suggested that this may be related to the transition from being managed as semi-domestic to wild (i.e. hunted).

Key words: *Rangifer tarandus*, wild reindeer, life-history variation

INTRODUCTION

Density dependence and climate are both important in shaping variation in life-history traits and subsequent population dynamics in ungulates (Sæther, 1997; Gaillard *et al.*, 2000; Coulson *et al.*, 2001). The most sensitive parameter towards density and climatic conditions are typically early growth, which may in turn affect juvenile survival and age at first reproduction (Reimers, 1983b; Gaillard *et al.*, 2000). Early body weight is therefore an important life-history trait to study in order to understand population dynamics (Gaillard, Festa-Bianchet & Yoccoz, 1998; Gaillard *et al.*, 2000).

While the effects of increasing density on life-history traits are nearly always negative (Fowler, 1987; Gaillard *et al.*, 2000), there has been more discussion regarding patterns of life-history variation related to climate (Sæther, 1997; Weladji *et al.*, 2002; Mysterud *et al.*, 2003). In recent years, much attention has been paid to how the North Atlantic Oscillation (NAO), a climatic phenomenon

explaining a large proportion of the weather patterns in the North Atlantic region (Hurrell, 1995; Hurrell *et al.*, 2003), affects life-history variation and population dynamics of ungulates (Post *et al.*, 1997; Post & Stenseth, 1999; Mysterud *et al.*, 2001b; reviews in Stenseth *et al.*, 2002; Mysterud *et al.*, 2003). The winter-NAO is indexed from December through March, and may directly affect herbivores by mechanisms such as rainfall-induced mortality of soay sheep *Ovis aries* on St. Kilda (Catchpole *et al.*, 2000; Coulson *et al.*, 2001). Indirect effects of the NAO are also important, as winters with much snow lead to a spatially heterogeneous snow melt. This results in more variable plant flowering dates (Post & Stenseth, 1999) leading to newly emergent plants of high quality throughout the grazing season giving higher autumn body weights in herbivores (Mysterud *et al.*, 2001b).

While much has been published on the responses of northern temperate ungulates to the NAO (reviews in Ottersen *et al.*, 2001; Stenseth *et al.*, 2002; Mysterud *et al.*, 2003), little information is available for alpine ungulates. A negative correlation between adult female fecundity and the NAO was reported for reindeer *Rangifer*

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Table 1. An overview of sample sizes separated by year, age groups and sex

Year	1967	1968	1969	1970	1971	1972	1973	1974	1975	1976	1977	1983	1988	1989	Total
Female calves		1	3			1	3	40	47	44	37	6	7	19	208
Male calves			8			2		25	35	18	24	9	7	26	154
Yearling females	2	5	8	1	4	3	15	83	143	96	123	9	3	22	517
Yearling males	8	4	6	1	12	31	16	97	112	97	136	31	7	45	603
Adult females	7	20	11	6	68	39	84	405	414	356	490	44	19	97	2060
Adult males	102	67	3	19	75	84	49	229	368	177	211	41	14	98	1537
Proportion of yearling females lactating	1.0	0.20	0.50	0	0.25	0	0.20	0.19	0.17	0.23	0.21	0.11		0	

tarandus at Hardangervidda, Norway (Post & Stenseth, 1999). In the Pyrénées, the NAO partly accounted for cohort effects in survival in the alpine chamois *Rupicapra rupicapra*, while this was not found in the Alps (Loison, Jullien & Menaut, 1999). Individuals born after positive NAO winters (indicative of high temperature and low precipitation) exhibited a low adult winter survival in the Pyrénées. However, most of the information that is published on alpine and arctic ungulates is data on total population counts or some other population indices (Post & Stenseth, 1999; Aanes *et al.*, 2002; Forchhammer *et al.*, 2002; Post & Forchhammer, 2002), giving little insight into the population processes. In this study, we present analysis of earlier unpublished data on body weight from 362 calves, 1120 yearlings and 3597 adult reindeer from North Ottadalen in Norway (Table 1). For females, lactational status was also given, so that we could estimate variation in age of first reproduction. We test the predictions that: (1) body weights of reindeer calves and yearlings should be negatively affected by density (Skogland, 1990); (2) the NAO should be negatively related to weights (as fecundity was reported depressed on Hardangervidda, Norway; Post & Stenseth, 1999); (3) lactating females have a lower body mass than non-lactating females due to costs of reproduction (Reimers, 1983b; Sand, 1998; Finstad & Prichard, 2000); (4) there is senescence in body weight for the oldest age-classes (Mysterud *et al.*, 2001c).

MATERIAL AND METHODS

Study area

Data derive from the management area of the North Ottadalen wild reindeer, located in the North Ottadalen mountain range (approximately 62° N, 8–9° E) in southern part of Norway. The region covers an area of 3245 km², with peaks reaching above 2000 m a.s.l. The region is fairly undisturbed with little human infrastructure such as cabin areas and tourist trail systems. There is a varied climate due to its wide longitudinal extension. It is situated partly in a continental region with cold winters, warm summers and little precipitation, and partly in an oceanic region with heavy rainfall during summers and much snow during relatively mild winters. The rock composition lies within the north-western bedrock area, mainly consisting

of Precambrian gneisses with low levels of plant nutrition. There are some Quarternary deposits from the latest ice age, deposited as glacial fans, moraine material in the valley bottoms, and some moraines at the mountain plains. Apart from this, there is little soil overlying the bedrock. The plant cover in North Ottadalen is sparse due to the nutritional composition of the bedrock and the high altitude. The timberline is at approximately 1000 m a.s.l. and birch *Betula pubescens* is the borderline tree species. Willow *Salix* sp. is a major component of the vegetation, as are lichens and heather species (Abrahamsen *et al.*, 1977).

The North Ottadalen reindeer population

The reindeer in Ottadalen were semi-domesticated until 1964, when the semi-domestic reindeer company (Trio tamreinlag A/L) terminated their activity. A total of 402 calves and yearlings from the final gathering was released in 1964–65 in the north-western part of North Ottadalen, where they joined an estimated 100 wild reindeer (made up partly from animals lost from the Trio herd in previous years and partly from animals native to this area) (Reimers, 1972). The population was allowed to grow until hunting began in 1967 (Reimers, 1983a). Hunting quotas have ranged from a few hundred animals in the 1960s to more than 1000 animals in the 1980s and 1990s (Statistics Norway 1967–1990; Fig. 1a). The population size has fluctuated throughout the years peaking during 1974–75 at around 3300 animals (Fig. 1a). North Ottadalen is known as a productive reindeer area, with some females calving as yearlings (Reimers, 1983b; Reimers, 1997). Calving is also quite early, but has changed from May 6 during 1969–72 to May 12–14 during 1996–98 (Flydal & Reimers, 2002), compared to May 24–25 in other wild reindeer areas in Norway, such as Rondane and Hardangervidda (Reimers, Klein & Sørungård, 1983).

Reindeer data

Jawbones were collected from 362 calves, 1120 yearlings and 3597 adult reindeer during the annual harvest in August–September (years 1967–77, 1983, 1988–1989; i.e., 14 years) together with data on dressed weight (i.e. live weight minus head, skin, viscera, bleedable blood

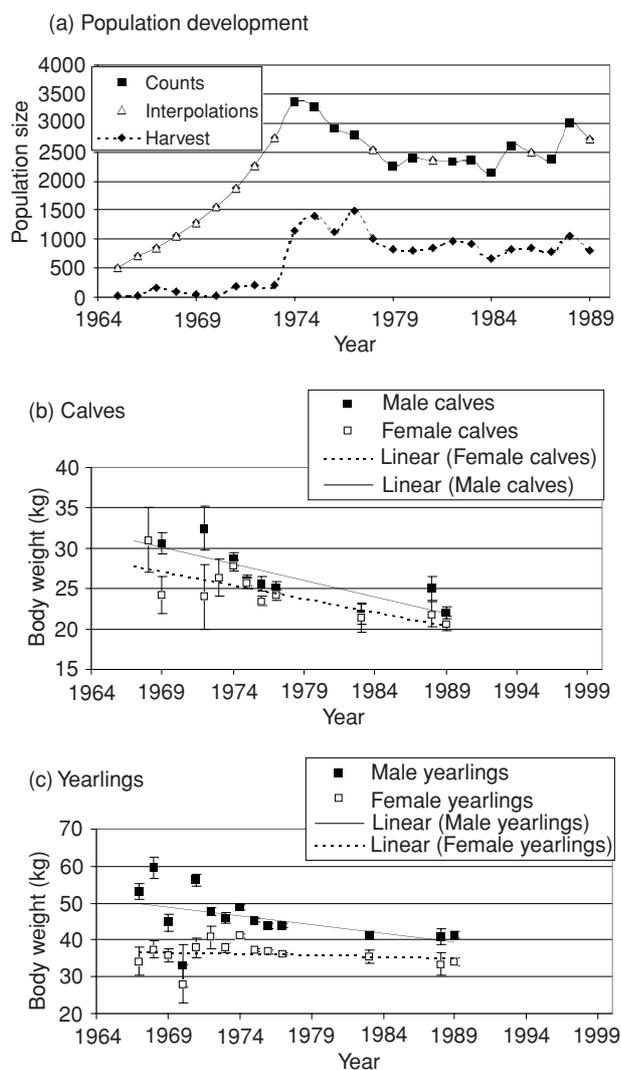


Fig. 1. (a) The development of the population size and harvest of the wild reindeer *Rangifer tarandus* herd in the North Ottadalen area, Norway, from its establishment in 1965 to 1989. Population sizes are either based on counts (very extensive surveys for years 1974–1988) or estimates that are mainly interpolations using information on size of the harvest. The average multiplication rate was estimated at 1.31 between 1965 and 1974. Weight development of male and female (b) calves and (c) yearlings as a function of time. Brackets are standard errors. The curves for males and females are not significantly different.

and metapodials) and female lactational status (Table 1). Lactational status in August–September probably underestimates female productivity in this area (see Reimers, 1997), as a number of females have ceased or reduced lactation to a level that may go undetected by the observer. The jawbones were sent to the State Game Research Institute for age analyses. Age was determined by tooth development in young animals and by counting annuli in tooth cementum in adults (Reimers & Nordby, 1968).

Estimates of population size were made in February–March each year by aerial counts of herds on their winter ranges, mainly in central and eastern parts of

the area (Fig. 1a). Experienced ground personnel assisted in locating the reindeer herds, which were flown over and photographed from fixed wing aircrafts. Generally, females and younger animals were found in 2 to 3 large herds, while the males frequently appeared in herds smaller than 100 animals. In 1975 the local game authorities carried out aerial counts on February 26 and March 21 and found 3250 and 3280 animals, respectively, indicating that surveys are relatively reliable and, at least, capture trends. While we are confident that the herds of females and younger animals were found, photographed and accurately counted in the different years, a small number of males may have been overlooked in some years. We do realize that they are minimum counts, and therefore refer to this as the minimum population size index. For the period 1964 to 1973, values are interpolated based on the known starting point (502 animals in 1964) and the count in 1974 (using the average multiplication rate of 1.31), and some simple interpolations between years were also done (Fig. 1a). From the peak in 1974 to 1990, there was a marginally significant linear (ln) decrease in population size over time when only including actual counts (linear regression, $r^2 = 0.271$, $T = -2.021$, $P = 0.068$), but a second-order polynomial for year gave a much better fit ($r^2 = 0.697$, $T = 3.752$, $P = 0.004$), as the population size was fairly stable (weak increase) between 1979 and 1989 (Fig. 1a, $r^2 = 0.255$, $T = 1.548$, $P = 0.165$).

Climate and local weather

The NAO is an alteration in air pressure difference between the sub-tropical high-pressure belt situated over the Azores and low-pressure belt situated over Iceland (Hurrell, 1995; Hurrell *et al.*, 2003), and its use in ecological studies is described in detail elsewhere (Ottersen *et al.*, 2001; Stenseth *et al.*, 2002; Myrsetrud *et al.*, 2003). The NAO is commonly indexed from December through March (available at <http://www.cgd.ucar.edu/~jhurrell/nao.html#winter>). In Norway, a positive value of the NAO index indicates warm winters with much precipitation. In coastal areas of Norway, the temperature during winter is frequently close to zero, and precipitation alters between snow and rain. The NAO index therefore has a negative correlation with snow depth at sea level and a positive correlation at higher altitudes (Myrsetrud *et al.*, 2000). The use of global climate indices like the NAO solves difficult problems of model selection often related to the large number of local weather parameters (Stenseth *et al.*, 2003). In addition to the commonly used winter index described, we also used the seasonal (winter: December–February; spring: March–May; summer: June–August) indices of the NAO based on principal component analysis (Hurrell *et al.*, 2003; available from <http://www.cgd.ucar.edu/~jhurrell/nao.pc.html>).

Data on local weather (monthly averages of temperature, precipitation and snow depth) were retrieved from the weather stations of the Norwegian Meteorological Institute (DNMI) surrounding the Ottadalen area. For

precipitation, we used stations at Preststulen (DNMI 14550) at 823 m a.s.l. and Vikhø (DNMI 15630) at 1140 m a.s.l. The correlation between the NAO and precipitation was weak at both Preststulen (Dec–Mar: $r = 0.095$) and Vikhø ($r = -0.282$). For snow depth, we used Preststulen. There was no correlation between the NAO and snow depth at Preststulen ($r = 0.202$). Data on temperature was available for the coastal station Tafjord (DNMI 60500) at 15 m a.s.l., but the NAO and air temperature was not correlated ($r = 0.004$).

To make local weather variables more tractable from a modelling perspective, we used principal component analysis (PCA) on monthly values of temperature, precipitation and snow depth for winter (December–March, as for the NAO index; Hurrell, 1995), spring (April–June) and summer (July and August) seasons. We used the first PCA (referred to as PCA1) for each season in the modelling. The PCA1 for winter (high value: cold/much snow/little correlation with precipitation; correlation with NAO: $r = 0.190$), spring (high value: warm/less precipitation and snow in April–May, more in June) and summer (high value: much precipitation/little correlation with temperature), explained, respectively 30.7%, 26.2% and 41.7% of the variance in local weather.

Statistical analyses

We used general linear mixed models (GLMM) to analyse variation in body weights (for applications, see Milner, Elston & Albon, 1999; Mysterud *et al.*, 2000), with ‘year’ as a random factor to account for the fact that individuals sampled in the same year cannot be treated as full replication when it comes to climatic effects or density (varying at the scale of years, and not between individuals sampled the same year). Separate models were used for calves, yearlings, and male and female adults. For yearlings, the analyses were performed both with sexes combined and separated. Analysing females separately was necessary in order to include reproductive status of females, while a combined model was necessary in order to evaluate possible sex specific effects of climate.

Fixed variables were sex, the minimum population size index, the NAO of the previous winter, and the NAO in the year of birth (called cohort-NAO) for yearlings and adults. Year was included as a continuous variable in order to quantify any time trends. Body weight was ln-transformed to stabilize the variance. In the models for adults, we explored non-linear relationships with age, first with general additive models (GAM; Hastie & Tibshirani, 1990), and then using higher order polynomials (e.g. Yoccoz *et al.*, 2002) or threshold models (e.g. Mysterud *et al.*, 2001a) in a GLMM. Only results from the latter are reported here, as results were consistent. We used model selection and the Akaike Information Criterion (AIC; Burnham & Anderson, 1998) for selecting an appropriate model for hypothesis testing. The AIC identifies the most parsimonious model, i.e. the best compromise between explaining most of the variation and simultaneously using

as few parameters as possible (Burnham & Anderson, 1998). The model with the lowest AIC value is the most parsimonious model. The detailed strategy for model selection is given in Tables 2, 3 & 4.

To assess interactions between 2 continuous predictors (such as the minimum population size index and year), we restricted the analysis to a multiplicative term of the standardized variables (termed st(Population size) and st(Year)). The predictor variables were standardized (mean 0, variance 1) to facilitate the interpretation of the interaction and polynomial terms (Mysterud *et al.*, 2001c). The NAO index is already standardized (Hurrell, 1995; Hurrell *et al.*, 2003).

Statistical analyses were performed in S-Plus (Venables & Ripley, 1994), except for logistic regression within a GLMM setting which was done in R (Lindsey, 1999) to explore relationship between lactational status of yearlings and time.

RESULTS

Calves and yearlings

The most parsimonious model for calves included both sex and year (Table 2). The most parsimonious model for yearlings included only sex (Table 2). However, the model including year was second best and the two models were far better than other models, and the latter model was therefore used for parameter estimation (Table 3). Male calves (average weight 24.9 kg, SE = 1.01) and yearlings (average weight = 44.2 kg, SE = 1.01) were heavier than female calves (average weight 24.2 kg, SE = 1.01; Table 3) and yearlings (average weight 37.0 kg, SE = 1.01; Table 3). Body weight decreased markedly over time for both calves and yearlings (Fig. 1b, Table 3). Including the minimum population size index, the winter-NAO for previous winter or in year of birth (cohort-NAO, yearlings only) or interactions resulted in much poorer models (Table 2). The same was the case when adding local (PCA-based) weather variables for winter, spring and summer seasons, or the PCA-based NAO indices for winter, spring and summer (Table 2), and when adding monthly values of temperature, precipitation or snow depth (results not shown).

The proportion of lactating female yearlings varied between 0 and 50% (Table 1, the year with 100% is built on only two individuals), and declined significantly over the time period considered (Intercept: l.s. mean = 242.83, SE = 85.617, $t = 2.836$, $P = 0.014$; year: l.s. mean = -0.1236 , SE = 0.043, $t = -2.852$, $P = 0.014$). Population size (ln-transformed) was not significant when added to the model (l.s. mean = 0.613, SE = 0.523, $t = -1.173$, $P = 0.262$). When analysing female yearlings separately (with year in the model), lactation had a negative effect on weights (l.s. mean = -0.058 , SE = 0.0079, $df = 476$, $t = -7.403$, $P < 0.001$). Mean weight of lactating females was 34.3 kg, while mean weight of non-lactating females was 38.2 kg.

Table 2. Results from model selection with AIC for calf and yearling reindeer *Rangifer tarandus* from North Ottadalen, Norway. x, term included in model. AIC, Akaike Information Criteria; Δ AIC, difference in AIC value between the AIC for the model given in that row and the most parsimonious model (lowest AIC; bolded). NAO, the commonly used station-based winter index of the North Atlantic Oscillations (Hurrell, 1995). cohortNAO, the station-based winter index of the NAO for the year of birth (for yearlings only). NAO – PCA, Principal Component based indices and for months December–February (DJF), March–May (MAM) and June–August (JJA). PCA1, first PCA axes per season for local measures of temperature, precipitation and snow depth (for winter and spring only). st, standardized variable (mean = 0, SD = 1)

Sex	Year (continuous)	st(Population size)	NAO	cohortNAO	Sex*Year	Sex*st(Population size)	Sex*NAO	Sex*cohortNAO	NAO*st(Population size)	PCA1 – winter climate	PCA1 – spring climate	PCA1 – summer climate	NAO – PCA - DJF	NAO – PCA - MAM	NAO – PCA - JJA	AIC	Δ AIC
A. Calves																	
x	x	x	x													- 238.1456	29.6551
x	x	x	x				x									- 228.6418	39.1589
x	x	x														- 247.2189	20.5818
x	x	x				x										- 230.4691	37.3316
x	x				x											- 256.2751	11.5256
x	x															- 266.0357	1.765
x	x	x	x						x							- 240.6262	27.1745
x	x									x						- 260.4704	7.3303
x	x										x					- 260.5723	7.2284
x	x											x				- 260.0958	7.7049
x	x												x			- 259.3969	8.4038
x	x													x		- 260.6714	7.1293
x	x														x	- 261.3149	6.4858
B. Yearlings																	
x	x	x	x	x												- 1149.283	40.418
x	x	x	x	x												- 1147.094	42.607
x	x	x	x													- 1156.226	33.475
x	x	x	x							x						- 1145.359	44.342
x	x	x														- 1164.323	25.378
x	x	x				x										- 1152.106	37.595
x	x				x											- 1174.639	15.062
x	x															- 1185.431	4.270
x	x															- 1189.701	0
x	x	x	x						x							- 1146.375	43.326
x	x									x						- 1177.108	12.593
x	x										x					- 1176.480	13.221
x	x											x				- 1176.998	12.703
x	x												x			- 1177.985	11.716
x	x													x		- 1177.870	11.831
x	x														x	- 1177.870	11.831

Adults

The most parsimonious model included age up to second order for females and a sixth order polynomial of age for males, as well as year for both sexes, and lactational status in females only and an interaction term between age and year in males only (Table 4). A threshold effect for age at 9 years in females resulted in a slightly less parsimonious model (even if giving a good visual fit), but the way age was modelled for females did not affect the estimate for other effects. Body weights of both sexes decreased markedly over the time period considered. Adult males lost more weight over time than females, and younger males

lost more than older males (Table 3, Fig. 2a). Lactating females were lighter than non-lactating females.

The senescence in body weight was significant when considering a separate analysis including only males aged 7 years or older (l.s. mean = - 0.016, SE = 0.0073, df = 103, $t = - 2.150$, $P = 0.034$) and females aged 9 years or older (l.s. mean = - 0.019, SE = 0.0072, df = 183, $t = - 2.671$, $P = 0.008$). For lactation, there was a significant age effect up to a second order term giving some evidence for reproductive senescence (Intercept: l.s. mean = 0.278, SE = 0.191, $t = 1.459$, $P = 0.167$; age: l.s. mean = 0.284, SE = 0.073, $t = 3.869$, $P = 0.002$; (age)²: l.s. mean = - 0.020, SE = 0.0057, $t = - 3.572$, $P = 0.003$).

Table 3. Parameter estimation with linear mixed models (with 'year' as random factor) for calf, yearling, adult male and female reindeer *Rangifer tarandus* from North Ottadalen, Norway. Note that 'year' (as a fixed factor below) refers to the linear effect of the term entered as a continuous variable. l.s. mean = least square mean

	L.s. mean	SE	df	<i>t</i>	<i>P</i>
Calves					
Intercept	31.416	5.827	350	5.391	< 0.001
Sex (M-F)	0.052	0.017	350	3.053	0.002
Year	-0.014	0.003	9	-4.845	0.001
Yearlings					
Intercept	20.985	4.738	1105	4.429	< 0.001
Sex (M-F)	0.193	0.009	1105	22.702	< 0.001
Year	-0.009	0.002	12	-3.667	0.003
Adult males					
Intercept	4.397	0.018	1516	244.833	< 0.001
Age	3.936	0.133	1516	29.542	< 0.001
(Age) ²	-3.107	0.129	1516	-24.072	< 0.001
(Age) ³	1.607	0.124	1516	12.921	< 0.001
(Age) ⁴	-0.580	0.129	1516	-4.492	< 0.001
(Age) ⁵	0.658	0.124	1516	5.317	< 0.001
(Age) ⁶	-0.196	0.124	1516	-1.577	0.115
st(Year)	-0.118	0.015	12	-7.983	< 0.001
Age*st(Year)	0.009	0.001	1516	6.433	< 0.001
Adult females					
Intercept	18.683	3.686	1941	5.069	< 0.001
Age	0.035	0.004	1941	8.506	< 0.001
(Age) ²	-0.002	0.000	1941	-7.198	< 0.001
Year	-0.008	0.002	12	-4.069	0.002
Lactational status	-0.132	0.006	1941	-21.125	< 0.001

However, tabular data suggest that the proportion of lactating females did not decline markedly with age (high up to 13 years of age), and sample size for females older than 13 years old are very small (Table 5).

DISCUSSION

We have reported variation in life-history traits as a possible function of climate, population size and time of reindeer from North Ottadalen, a very productive reindeer area in Norway. We found some interesting patterns: (1) a high proportion of yearlings were lactating, which incurred a weight cost; (2) senescence in body weight was evident in both males and females; (3) body weights of all age and sex groups and proportion of yearling females lactating decreased over time, although the minimum population size index declined markedly after the population peak in 1974; (4) there was no effect of either the NAO or local weather.

Age at first reproduction and senescence

The proportion of lactating female yearlings varied between 0 and 50% (Table 1). This supports earlier and more fragmentary observations of pregnant calves, in both South and North Ottadalen (Reimers, 1983b). Lactating yearlings are not observed in less productive

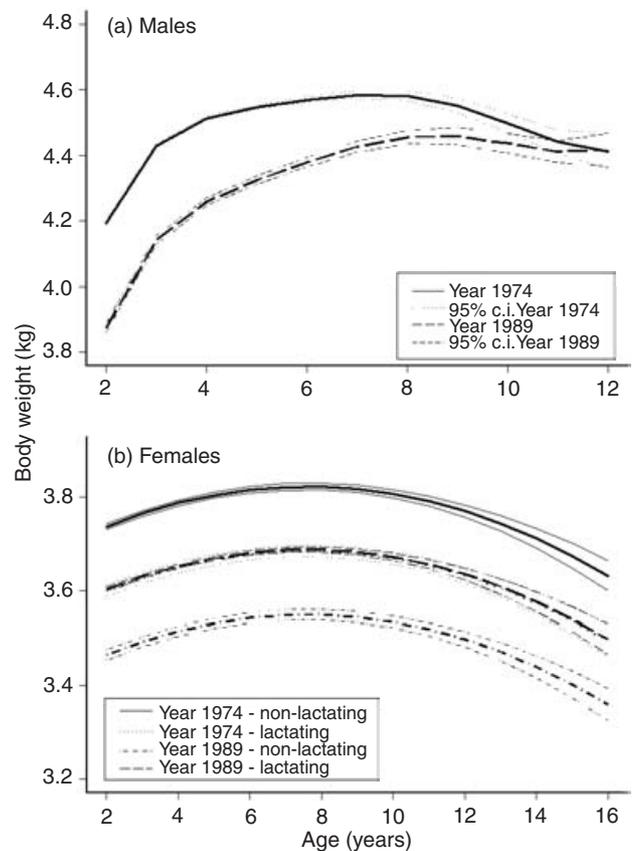


Fig. 2. The relationship between body weight and age in (a) male and (b) female reindeer *Rangifer tarandus* from the North Ottadalen, Norway. Weaker lines indicate standard errors. Note that lines for 1974 lactating and 1989 non-lactating overlaps in females.

reindeer areas in Norway, such as Hardangervidda and Snøhetta (Reimers, 1983b), but are reported in semi-domestic reindeer herds in southern Norway (Lenvik & Fjellheim, 1988; Ropstad *et al.*, 1991). Indeed, such a high proportion of females conceiving as calves and calving as yearlings is relatively rare among wild ungulates (Gaillard *et al.*, 2000), but it occurs frequently in soay sheep (Clutton-Brock *et al.*, 1997) and sometimes in smaller deer species, such as white-tailed deer *Odocoileus virginianus* (Cheatum & Morton, 1942) and black-tailed deer *Odocoileus hemionus* (McCullough, 1997). More commonly, age at first calving is at 2 years in reindeer (Reimers, 1997) and in caribou mostly at 3 years of age (Bergerud, 1980; Calef, 1980), and in ungulates in general first calving between 2 and 4 years is typical (Gaillard *et al.*, 2000). Reproduction in young female reindeer and caribou is a close function of body weight (Reimers, 1983b; Adams & Dale, 1998). Age at first reproduction is subsequently strongly dependent on factors governing growth and body composition and is thus frequently related to density (Albon, Mitchell & Staines, 1983) and climate (Langvatn *et al.*, 1996), and regarded as very important for population dynamics and stability (Clutton-Brock *et al.*, 1997). The early age of first reproduction incurred a cost to the reindeer females in North Ottadalen, as lactating yearling females were lighter than

Table 5. An overview of age distribution of adult male and female reindeer *Rangifer tarandus* and number of lactating and non-lactating female reindeer from North Ottadalen, Norway. Note that lactational status was established late (in autumn) and therefore probably represents an underestimate

Age (years)	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Males	352	444	316	198	110	51	32	12	8	9	3	1	1		
Females	515	404	326	245	165	124	87	59	66	29	19	11	5	4	1
Non-lactating	162	101	76	52	35	26	22	20	12	6	6	1	3	3	
Lactating	330	282	230	181	120	95	63	37	52	20	11	10		1	1

of age (Mysterud *et al.*, 2001c) and until 11 years of age in bighorn sheep *Ovis canadensis* (Bérubé, Festa-Bianchet & Jorgenson, 1999). Data on reproduction of older age classes were limited in our study, even though a second order term for age was significant, the proportion of lactating females seemed not to decline markedly with age (Table 5).

Decline in performance over time

Body weight of all sex and age groups and proportion of yearling females lactating declined markedly for the whole study period 1967–1989 (Fig. 1, Table 3), however, the decline was much more marked in younger than older males (Fig. 2a). This is consistent with the different evolutionary trajectories of the sexes, making growth a priority for young males (Clutton-Brock, Guinness & Albon, 1982), and they are therefore more sensitive to variation in environmental conditions. The decline in individual performance over time, despite a decline in the minimum population size index, may possibly be due to delayed negative effects, if carrying capacity was exceeded in the years when the population peaked. The North Ottadalen area covers 3245 km², and the minimum population size index suggested at least 3300 individuals in 1974. This gives a density of about one reindeer per km² that year, which is in the upper density scale among wild reindeer herds in Norway (Reimers, 1986). Density has remained mostly below 0.8 reindeer per km² since 1978. As lichen heaths were plentiful in the area and the summer grazing situation seems to be good (Reimers *et al.*, 1983), we therefore cannot substantiate that this decline in performance was due to overgrazing.

Another issue we regard as crucial, is that this population was ‘semi-domestic’ before it was changed to ‘wild’ by a management decision in 1964 (see above). The reindeer populations in Norway have a history from pure semi-domestic reindeer in some areas, via a good mix of wild and semi-domestic in other areas, to (close to) genetically wild in only a few areas (Røed, 1985, 1998). Most of the formerly semi-domestic population seem to have much larger body weights and better reproductive performance than many of the wild populations (Skogland, 1983; Reimers, 2002). We regard it as likely that the hunting pressure in Ottadalen may have changed the behaviour to a more alert and nervous type, imposing also a reduction in performance (Reimers, 1980). It is clearly established that populations with a

semi-domestic background are less shy than ‘pure’ wild reindeer in Norway (Reimers & Svela, 2001), but it is not known whether this is due to genetic or behavioural differences. Since there is no documented evidence of such behavioural changes within a population over time, the suggestion that the decreasing performance is related to behavioural changes in the transition from semi-domestic to wild therefore remains speculative at present. Active hunter selection for large phenotypes may also reduce performance over time. We would welcome studies addressing this in more detail.

Effects of global climate and local weather

Climate has repeatedly been reported to have an impact on population dynamics of ungulates, in particular influencing survival and reproduction of younger and older animals (Sæther, 1997; Gaillard *et al.*, 2000). In the North Ottadalen reindeer herd, there was no effect of the NAO on body weight of either calves or yearlings. This may not be surprising, considering that the NAO had a fairly low correlation with local weather in this region (see above). However, there was no relationship between reindeer performance and local weather patterns either. We therefore failed to find effects of either the NAO or local weather. Other studies have reported an effect of both the NAO and local weather for a range of different ungulates (reviews in Sæther, 1997; Stenseth *et al.*, 2002; Weladji *et al.*, 2002; Mysterud *et al.*, 2003), including a time series of equal length from reindeer on Hardangervidda (Post & Stenseth, 1999). Our study urges for some caution in extrapolating results of the NAO from one area to other areas, there may evidently be much spatial variation in responses. Our results may suggest that climatic effects are less important in herds in very good condition as they are in Ottadalen. Alternatively, it may also be that reindeer in this area can use spatial heterogeneity to find suitable habitats even though overall conditions are not ideal.

Acknowledgements

We thank our collaborators Rolf Sørungård and Øystein Mølmen and numerous hunters for logistic support and field assistance, and Jonathan Colman, Jean-Michel Gaillard, Øystein Holand, Anne Loison, Ivar Mysterud, Harald Steen and one anonymous referee for comments

to previous versions of the text. The climate work of AM is funded by the EcoClim-project (NFR).

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