

Relationships between sex ratio, climate and density in red deer: the importance of spatial scale

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Summary

1. Recently, contrasting evidence of density-dependent offspring sex ratio variation in red deer (*Cervus elaphus* L.) has been presented. Kruuk *et al.* (1999) reported that the proportion of male red deer born on the island of Rum, Scotland, each year declined with increasing population density and with winter rainfall, i.e. as nutritional stress in females increased. In contrast, Post *et al.* (1999a) reported increasing male-biased offspring sex ratios in Hordaland, Norway, with both rising numbers of hinds and increasing values of the North Atlantic Oscillation (NAO), which they regarded an index of severe winters.

2. Compared to Post *et al.* (1999a), we reanalysed sex ratio variation on a greatly extended data set, including four populations of Norwegian red deer, taking into account a finer population substructure.

3. The proportion of male calves shot each autumn declined markedly as density increased in all four populations. The proportion of male calves shot each autumn increased significantly with an increasing NAO index in one of the four populations, but there was no residual effect of the NAO once the effect of snow depth (at low elevation) was controlled for (decreasingly male biased harvest with increasing snow depth).

4. At the west coast of Norway, the NAO is positively correlated with temperature and precipitation. However, since temperatures in this region often are around 0 °C during winter, the relationship between the NAO and snow depth may be difficult to predict.

5. An analysis of variation in snow depth revealed that snow depth was negatively correlated with the NAO at low altitudes (below 400 m), but this relationship was reversed at high altitudes giving a positive correlation between snow depth and the NAO. We therefore suggest that a high NAO index indicates favourable winter conditions for red deer, as red deer winter at low altitude, and since recent studies show that a high index of the NAO is generally positively correlated with body weight in red deer.

6. Female red deer thus reared fewer sons as nutritional stress increased with increasing density and severity of climate in Norway, which is consistent with the birth sex ratios observed on Rum, Scotland.

Key-words: *Cervus elaphus*, density dependence, extrinsic modification hypothesis, North Atlantic Oscillation, ungulates.

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Introduction

Several studies have reported biased offspring sex ratios in mammals (reviews in Williams 1979; Clutton-Brock & Iason 1986; Clutton-Brock 1991; Hewison & Gaillard 1999). Adaptive manipulation of the birth–sex ratio may be expected when costs and/or benefits differ for production of either sex. Trivers & Willard (1973) proposed that in species in which the variance in male reproductive success exceeds that of females, additional parental investment would benefit sons more than daughters, provided that offspring reproductive success is determined by phenotypic quality and that phenotypic quality in turn is determined by the level of maternal care during the juvenile stage (Maynard Smith 1980). Ungulates are regarded as ideal candidates for testing mechanisms regarding adaptive sex ratio variation (Hewison & Gaillard 1999), since most ungulates are sexually dimorphic in body size (Weckerly 1998; Loison *et al.* 1999a), with male breeding success dependent on fighting ability and body size (Clutton-Brock, Guinness & Albon 1982). In addition, ungulates are iteroparous and usually produce only one (or two) young per litter. Ungulates are also generally polygynous, so variance in reproductive success might be greater among males than among females (Hewison & Gaillard 1999).

However, offspring sex ratio variation in ungulates appears notoriously inconsistent among studies (Festa-Bianchet 1996; Hewison & Gaillard 1999; Hewison *et al.* 1999; Kruuk *et al.* 1999). This may be because more than one mechanism affects the sex ratio, and the action of these mechanisms depends on environmental conditions (Kruuk *et al.* 1999). Given the extensive body of evidence for relationships between maternal condition and offspring sex ratios in mammals at the individual level (Clutton-Brock & Iason 1986; Skogland 1986; Cameron *et al.* 1999), it is plausible that all extrinsic factors affecting body condition, such as population density and climate, also may affect offspring sex ratio at a population level (Kruuk *et al.* 1999; Post *et al.* 1999a). Variation in population density and climate is over short time scales. It is therefore likely that selection may not act to change the relationship between body condition and sex ratio which was adaptive for the individual at stable conditions, and hence, it is plausible that the individual response may be evident also at the population scale. Recently, contrasting findings of extrinsic modification of sex ratio by density and climate were reported for red deer (*Cervus elaphus* L.) (Kruuk *et al.* 1999; Post *et al.* 1999a). Kruuk *et al.* (1999) reported that the proportion of males born each year declined with increasing population density and winter rainfall, i.e. as nutritional stress in females increased, whereas Post *et al.* (1999a) reported increasingly male-biased offspring sex ratios at 3–5

months of age with rising numbers of hinds and a high index for the North Atlantic Oscillation (NAO), which they argued indicated increasingly severe winters, i.e. supposedly as nutritional stress in females decreased. Post *et al.* (1999a) suggested that females in poor condition may produce more sons, since poor-quality sons may nevertheless survive better than poor-quality daughters. However, empirical evidence in Norwegian red deer suggests that 'poor sons' have lower survival than 'poor daughters' (Loison *et al.* 1999).

The result of Post *et al.* (1999a) is surprising if we assume that female red deer in poor condition produce fewer sons as is expected in sexually dimorphic ungulates since they meet the assumption of the Trivers & Willard (1973) model. Post *et al.* (1999a) used a pooled set of harvest data on red deer from two large counties in Norway (Rogaland and Hordaland), with significant local variation in red deer density and dynamics, as well as in local weather conditions across the area. The latter is due to the pronounced mountainous topography of the region, whereas the marked increase in total harvest within this region is a result of both increased density and range expansion (Fig. 1). Also, the management practice (i.e. hunting licenses issued) varied in time and space across this area. The choice of spatial scale may be crucially important when studying density dependence (Ray & Hastings 1996; Donalson & Nisbet 1999). It has been demonstrated that local population density was more important than total population density in influencing calf winter survival on the island of Rum, Scotland (Coulson *et al.* 1997), and scale-dependent population dynamics were also demonstrated for Soay sheep (*Ovis aries* L.) on Hirta in the St. Kilda archipelago (Coulson *et al.* 1999). Here we reanalyse sex ratio variation in Norwegian red deer on a greatly extended data set at a finer spatial scale (municipality scale), and assess whether the contrasting conclusions of Post *et al.* (1999a) and Kruuk *et al.* (1999), may be due to Post *et al.* (1999a) performing the analysis with less attention to the possible heterogeneity of subpopulations within the study area.

Material and methods

RED DEER DATA

The study area is the western part of southern Norway, which is the main area inhabited by red deer in Norway (Langvatn *et al.* 1996). Hunting data are recorded by wildlife boards and compiled at the Statistical Bureau of Norway (Statistics Norway 1977–98), from where the actual harvest data were retrieved. Generally, red deer may only be shot between 10 September and 15 November, but between these dates the actual hunting period varies slightly between counties. Red deer hunting in Nor-

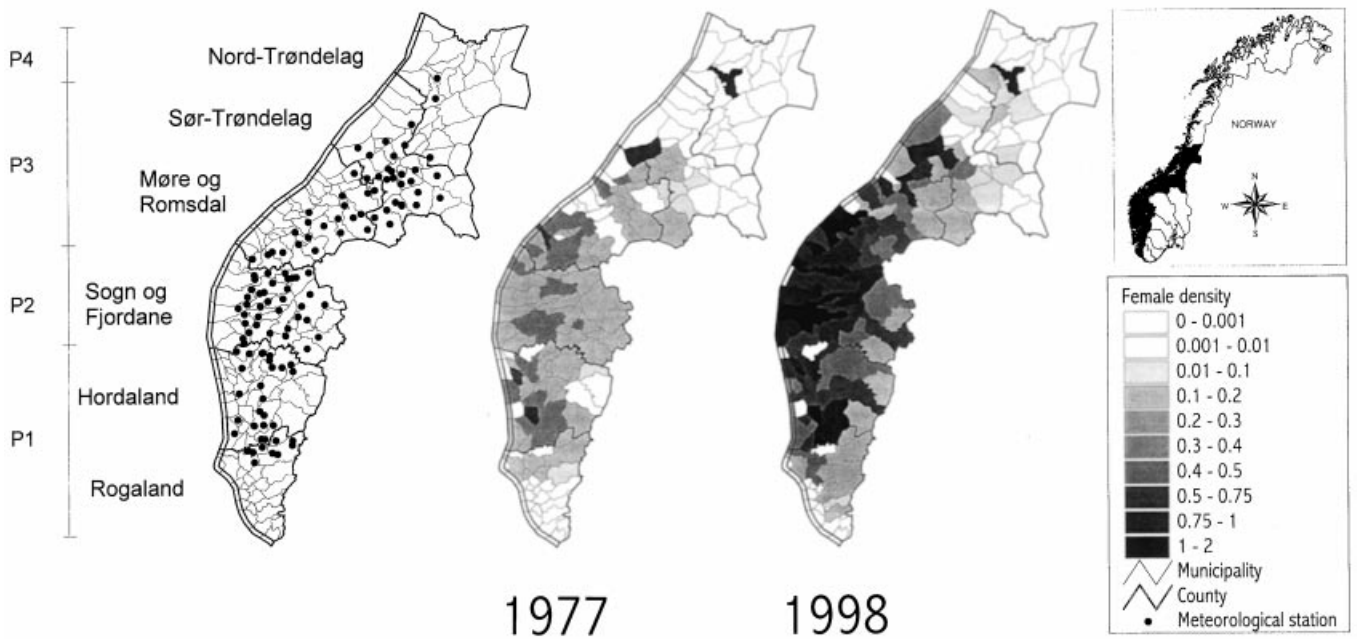


Fig. 1. Geographic location of the study area in Norway, the meteorological stations used, and an index of female density, calculated as number of adult (≥ 1 years) females shot divided by the counting area (see text), in 1977 and 1998. Note that what is referred to as the Hordaland population in Post *et al.* (1999a) is P1.

way are controlled through licenses issued by wildlife boards in each municipality. The number of licences issued is supposed to reflect range quality, areas of suitable habitat, and population status within the municipalities. Consequently, variation in management measures are likely to affect red deer populations at the scale of municipality rather than at the county level. From the hunting statistics we extracted data on number of male and female calves (age 3–5 months) shot each year (total 47762; Appendix) at the scale of municipality in the counties Rogaland, Hordaland, Sogn og Fjordane, Møre og Romsdal, Sør-Trøndelag and Nord-Trøndelag in Norway. To obtain an index for local population density, we divided the number of adult females (≥ 1 years) shot each year by the so-called ‘counting area’ in each municipality (figures for counting area in 1997 was used for all years; Statistics Norway 1977–98; Fig. 1). The ‘counting area’ is the area of suitable red deer habitat within each municipality, constituting the basis for harvest quotas as approved by the management authorities. We hereafter refer to Rogaland and Hordaland as P1 (see Post *et al.* 1999a), Sogn og Fjordane as P2, Møre og Romsdal and Sør-Trøndelag as P3 and Nord-Trøndelag as P4 (Fig. 1) after Forchhammer *et al.* (1998). The justification for this division is partly geographical barriers like fjords and mountain ranges, and partly phytogeographical and climatic characteristics. Separate analyses were conducted for each of these four populations (Table 1, see details below).

Valuable observations with regard to sex ratio variation may come out of the analysis of harvest data (Post *et al.* 1999a), since mortality in red deer during their first summer appears to be sex-biased only in populations exposed to large predators such as bears (Smith & Anderson 1996). No large predator exists at present in the area considered in this paper, and we could therefore assume that mortality is not sex-biased during the first summer (Guinness, Albon & Clutton-Brock 1978). Further, it is unlikely that males have a greater susceptibility of being shot, as licenses for calves are not sex-specific, sexual body-size dimorphism in calves is negligible, and the overall calf sex ratio in harvest data matched exactly the overall foetal sex ratio (Post *et al.* 1999a). However, inter-annual changes in red deer abundance are not necessarily directly reflected in harvest data. In harvested populations, there is usually a time lag between increased or decreased density and increased or decreased harvest quotas (Fryxell, Mercer & Gellately 1988; Fryxell *et al.* 1991; Solberg *et al.* 1999). Thus, changes in harvest figures from one year to the next may imply both increased harvest quotas and/or increased population size (Solberg *et al.* 1999). However, over a time span of 5–10 years, increased harvest certainly reflects increased population size. We therefore use the absolute harvest number when calculating an index for density, and not the year-to-year changes in abundance used when detrending these time series (Post & Stenseth 1999).

Table 1. Descriptive statistics of density variation among municipalities from 1977 to 1998 in four populations (Pop) of red deer in Norway. Total area refers to the total size of land for each defined population. The 'counting area' is the area of suitable red deer habitat at a local scale (within each municipality; Local counting area) or at a population scale (Population counting area), constituting the basis for harvest quotas as approved by the management authorities. Local density was calculated as the number of adult (≥ 1 years) females shot per unit counting area within each municipality. The number of municipalities is the number of municipalities that harvested red deer calves

Pop	Population name	Index of local density: 1977			Index of local density: 1998			Local counting area: 1998 (km ²)			Number of municipalities			Harvest (females)		Population counting area (km ²)		Total area (km ²)
		Min	Mean	Max	Min	Mean	Max	Min	Mean	Max	1977	1998	1977	1998	1977	1998	1977	
P1	Rogaland/Hordaland	0.002	0.095	0.335	0.009	0.206	0.538	18	166	707	28	46	598	1638	8137	24775		
P2	Sogn og Fjordane	0.013	0.080	0.145	0.071	0.390	0.785	100	298	568	24	26	625	2846	7739	18620		
P3	Møre og Romsdal/Sør-Trøndelag	0.006	0.087	0.225	0.003	0.290	1.917	9	259	723	39	52	614	2416	14486	33936		
P4	Nord-Trøndelag	0.433	0.433	0.433	0.002	0.101	0.546	18	369	897	1	5	42	63	4423	22396		

THE NORTH ATLANTIC OSCILLATION

In northern regions on both sides of the Atlantic Ocean, a significant proportion of inter-annual variability in winter precipitation and temperatures is attributable to the dynamics of an atmospheric phenomenon called the North Atlantic Oscillation (NAO; Hurrell 1995). The NAO is a large-scale alternation in atmospheric pressures across the North Atlantic Ocean (Van Loon & Rogers 1978; Lamb & Pepler 1987), and its fluctuations and decadal phases are strongly linked to inter-annual variation as well as long-term changes in temperatures and precipitation in the Northern Hemisphere (Hurrell & Van Loon 1997). The NAO index quantifies the average deviation from the long-term mean sea-level surface pressure difference between Lisbon, Portugal, and Stykkisholmur, Iceland (Hurrell & Van Loon 1997), for the months of December through March. The NAO index may therefore be an index for winter climate. The index can be found at the Climate Indices website: <http://http://www.cdg.ucar.edu:80/cas/climind>. For a further ecologically focused description of this index, see Post, Forchhammer & Stenseth (1999b).

For northern ungulates, severe winters are those with deep snow and low temperatures, which impose extreme energetic costs for foraging, locomotion and thermogenesis (Simpson *et al.* 1978; Parker, Robbins & Hanley 1984; Hobbs 1989). On the west coast of Norway, the NAO is positively correlated with temperature and precipitation. However, since temperatures in this region are often around 0°C during winter, the relationship between the NAO and snow depth may be difficult to predict. Post *et al.* (1999a) found a positive correlation between snow depth and the NAO at two out of four meteorological stations in Hordaland, and thus argued that a high NAO index indicates severe winter conditions. The best correlation between the NAO and winter snow depth was found for Vinter-tun (Geographic location no. 47750), a station located 395 m above sea level (The Norwegian Meteorological Institute, Oslo). Altitude is a strong determining factor for whether precipitation falls as snow or rain. Since red deer mostly stay at low elevation during winter (Albon & Langvatn 1992), this may not be a representative test of whether there is a correlation between winter severity (snow depth) and the NAO for wintering red deer on the west coast of Norway. In this study we therefore use data on snow depth for 123 meteorological stations along the west coast of Norway (Fig. 1).

STATISTICAL ANALYSES

To test for a possible non-linear relationships between the response variables (snow depth and proportion of male calves shot in the subsequent

autumn) and the predictor variables, we fitted generalized additive models (GAM) using smoothing splines (Hastie & Tibshirani 1990; Venables & Ripley 1994; for application of GAM in ecology, see Yee & Mitchell 1991; Lambin *et al.* 1998; Wisser, Peet & White 1998; Bjørnstad *et al.* 1999). Splines are piecewise polynomials that are smooth (twice differentiable) in the spline knots (the control points of the splines) (Bjørnstad *et al.* 1999). The complexity of the curve, i.e. the number of degrees of freedom (d.f._{spline}), associated with the smoothing spline was selected by repeated fitting of the GAM. We fitted the model with varying d.f._{spline} for one variable (1–6), while holding d.f._{spline} of the other variables constant. We then tested the fit of the different models in an ANOVA setting (see Venables & Ripley 1994: pp. 251–252). In no population was there evidence of any non-linearity between response and predictor variables (all $P > 0.10$). Since we found only linear effects, we only present results from parametric models, as these are more desirable if they fit the data adequately (Yee & Mitchell 1991).

We evaluated how snow depth was predicted by the NAO, altitude, degree of latitude and degree of longitude with multiple regression. The average length of the 123 time series was 25 years (range 10–28). The need for transformation of snow depth was assessed using the Box–Cox transformation family, the parameters being estimated using profile log-likelihood (see Venables & Ripley 1994). We therefore transformed snow depth as ‘log (snow depth + 4)’. We explored potential interactions between the continuous predictor variables by considering products. The predictor variables were standardized (mean 0, variance 1) to facilitate the interpretation of the interaction terms (Portier *et al.* 1998). The NAO index is already standardized (it is defined as a normalized pressure difference; Hurrell 1995). When variables are standardized, the coefficient for a variable is the strength of this variable when the other variables are average (because the interaction term is then 0). Separate models were run for December, January, February and March. All models were checked for assumptions of linearity, homoscedasticity, and statistically defined influence values (Cook’s D; Venables & Ripley 1994).

We used parametric logistic regression to determine the relationship between the proportion of males shot (each year in each municipality) and the variables female density index (log transformed), the NAO in the year of gestation (same year as calves are shot), the NAO the year prior to harvest (and conception), degree of latitude and distance from the coast. The last two variables were included since it has been demonstrated that body weight increases with latitude and distance from the coast (Langvatn & Albon 1986), and we also used the local (municipality) scale for these variables. We also ran separate models adding a population-specific average of

snow depth in March (from stations below 125 m a.s.l. only) before entering the NAO. The number of male calves shot in a particular year and municipality (S_i , $i = 1, 2, \dots, N$) can be assumed to follow a binomial distribution $\text{Bin}(S_i, p_{(S_i)})$ under the assumption of independence of S_i , where $p_{(S_i)}$ is the proportion of males shot in a particular municipality and year (Hosmer & Lemeshow 1989). Any violation of the assumption of independence will lead to unaccounted heterogeneity (overdispersion), and this was assessed by the statistical significance of the Pearson residual χ^2 of the fitted model (McCullagh & Nelder 1989; Tjur 1998). We also used generalized linear mixed models (GLMM; see Lindsey 1999; Milner *et al.* 1999) to assess if residual heterogeneity between municipalities and years could affect the parameter estimates and their standard errors. Municipalities and years were taken as random effects in the GLMMs, whereas the other factors were kept as fixed factors. We used the statistical package S-Plus when conducting GAM and GLM (Venables & Ripley 1994), whereas GLMM were implemented in the R package (e.g. Lindsey 1999).

Results

THE NAO AS A MEASURE OF WINTER SEVERITY

The correlation between the snow depth and the NAO (Table 2; Jan: $R^2 = 0.370$, $t = -9.616$, $P < 0.001$; Feb: $R^2 = 0.411$, $t = -12.432$, $P < 0.001$; Mar: $R^2 = 0.502$, $t = -9.518$, $P < 0.001$; Dec: $R^2 = 0.412$, $t = 0.215$, $P = 0.830$) along the west coast of Norway from Rogaland to Nord-Trøndelag was dependent on the altitude considered in January, February and March, but not in December when there was no main effect of the NAO (altitude*NAO; Jan: $t = 3.300$, $P = 0.001$; Feb: $t = 3.337$, $P < 0.001$; Mar: $t = 3.424$, $P = 0.001$; Dec: $R^2 = 0.412$, $t = -0.680$, $P = 0.497$). There was negative correlation between the NAO and snow depth at low altitude, whereas above approximately 400 m a.s.l., the correlation was positive (Fig. 2). There was an interaction between the NAO and degree of longitude in January and February only (Jan: $t = 2.106$, $P = 0.035$; Feb: $t = 2.958$, $P = 0.003$; Mar: $t = 1.446$, $P = 0.148$; Dec: $t = 0.269$, $P = 0.788$), i.e. the effect of the NAO on snow depth decreased with longitude, but this disappeared for January when only including significant factors ($t = 1.664$, $P = 0.096$). As expected, snow depth increased with altitude (Jan: $t = 15.187$, $P < 0.001$; Feb: $t = 16.576$, $P < 0.001$; Mar: $t = 19.999$, $P < 0.001$; Dec: $t = 18.823$, $P < 0.001$). However, snow depth increased faster with altitude at the coast than in the inland (longitude*altitude; Jan: $t = -8.426$, $P < 0.001$; Feb: $t = -9.859$, $P < 0.001$; Mar: $t = -12.114$, $P < 0.001$; Dec: $t = -8.307$, $P < 0.001$), and this effect was in turn

Table 2. Parameter estimates (point estimates and 95% confidence limits) for the regression equation $\log(\text{snow depth} + 4) = \alpha + \beta_1(\text{NAO}) + \beta_2(\text{Altitude}) + \beta_3(\text{Latitude}) + \beta_4(\text{Altitude} * \text{Latitude}) + \beta_5(\text{NAO} * \text{Altitude}) + \beta_6(\text{Altitude} * \text{Longitude}) + \beta_7(\text{Altitude} * \text{Longitude}) + \beta_8(\text{Altitude} * \text{Longitude} * \text{Latitude}) + \beta_9(\text{Altitude} * \text{Longitude} * \text{Latitude} * \text{Longitude})$ for data from 123 meteorological stations on the west coast of Norway for an average of 25 years (10–28). Only significant parameters were included when estimating coefficients

	Intercept		NAO		Altitude		Latitude		Altitude* Latitude		NAO*Altitude		NAO* Longitude		Altitude* Longitude		Altitude* Latitude* Longitude	
	95% CL	95% CL	β_1	95% CL	β_2	95% CL	β_3	95% CL	β_4	95% CL	β_5	95% CL	β_6	95% CL	β_7	95% CL	β_8	95% CL
Dec	2.671	[2.644, 2.698]			0.400	[0.361, 0.439]	0.291	[0.265, 0.318]	0.139	[0.078, 0.200]					-0.265	[-0.325, -0.204]	0.169	[0.117, 0.221]
Jan	3.176	[3.140, 3.212]	-0.076	[-0.062, 0.478]	0.428	[0.378, 0.478]	0.257	[0.225, 0.289]	0.160	[0.084, 0.235]	0.039	[0.025, 0.052]			-0.356	[-0.431, -0.281]	0.203	[0.139, 0.267]
Feb	3.340	[3.403, 3.476]	-0.096	[-0.111, -0.082]	0.453	[0.402, 0.504]	0.273	[0.238, 0.308]	0.160	[0.083, 0.237]	0.044	[0.029, 0.058]	0.018	[0.004, 0.032]	-0.415	[-0.492, -0.338]	0.244	[0.178, 0.309]
Mar	3.302	[3.266, 3.339]	-0.081	[-0.095, -0.067]	0.583	[0.532, 0.634]	0.356	[0.323, 0.389]	0.232	[0.155, 0.309]	0.047	[0.033, 0.061]			-0.538	[-0.614, -0.461]	0.290	[0.225, 0.356]

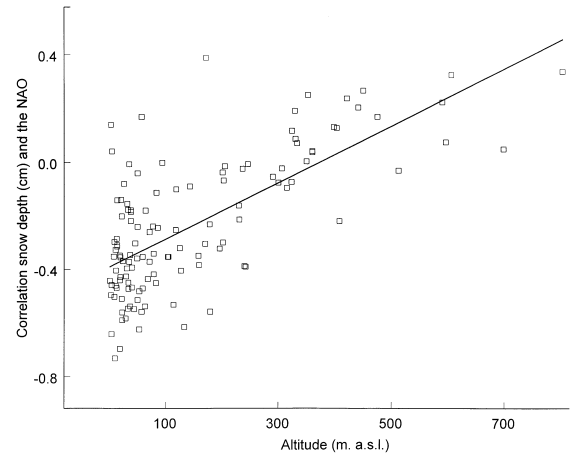


Fig. 2. The correlation between the North Atlantic Oscillation and snow depth in March as a function of altitude in Norway. Each datapoint is a correlation coefficient between the NAO and snow depth for a specific meteorological station. Note that analysis was done directly on snow depth, and that several other factors also affected snow depth (see Table 2).

stronger in the south than in the north (altitude*latitude*longitude; Jan: $t = 5.529$, $P < 0.001$; Feb: $t = 7.089$, $P < 0.001$; Mar: $t = 7.368$, $P < 0.001$; Dec: $t = 6.159$, $P < 0.001$). There was also an interaction between altitude and degree of latitude (Jan: $t = 3.558$, $P < 0.001$; Feb: $t = 3.687$, $P < 0.001$; Mar: $t = 4.981$, $P < 0.001$; Dec: $t = 4.358$, $P < 0.001$), i.e. precipitation tends to fall as snow at lower altitudes further north, probably as an effect of declining temperatures with latitude. There was a main (positive) effect of degree of latitude (Jan: $t = 9.784$, $P < 0.001$; Feb: $t = 10.433$, $P < 0.001$; Mar: $t = 11.893$, $P < 0.001$; Dec: $t = 13.672$, $P < 0.001$), whereas there was no main effect of degree of longitude (Jan: $t = -1.333$, $P = 0.183$; Feb: $t = -1.329$, $P = 0.184$; Mar: $t = 0.102$, $P = 0.919$; Dec: $t = -1.200$, $P = 0.230$). The other interactions were not significant (NAO*altitude*latitude; Jan: $t = 1.220$, $P = 0.223$; Feb: $t = 1.001$, $P = 0.317$; Mar: $t = 1.026$, $P = 0.305$; Dec: $t = 0.136$, $P = 0.892$; NAO*longitude*altitude; Jan: $t = -0.770$, $P = 0.442$; Feb: $t = -1.256$, $P = 0.209$; Mar: $t = -1.670$, $P = 0.095$; Dec: $t = 0.079$, $P = 0.937$; NAO*longitude*altitude*latitude; Jan: $t = -0.159$, $P = 0.874$; Feb: $t = 0.940$, $P = 0.347$; Mar: $t = 1.137$, $P = 0.256$; Dec: $t = -0.592$, $P = 0.554$).

SEX RATIOS IN RED DEER

In all four populations, the proportion of male calves shot each autumn declined markedly as density increased (Fig. 3; Table 3; P1: d.f. = 1, $\chi^2 = 11.604$, $P < 0.001$; P2: d.f. = 1, $\chi^2 = 58.823$, $P < 0.001$; P3: d.f. = 1, $\chi^2 = 23.344$, $P < 0.001$; P4: d.f. = 1, $\chi^2 = 4.085$, $P = 0.043$). This includes the popula-

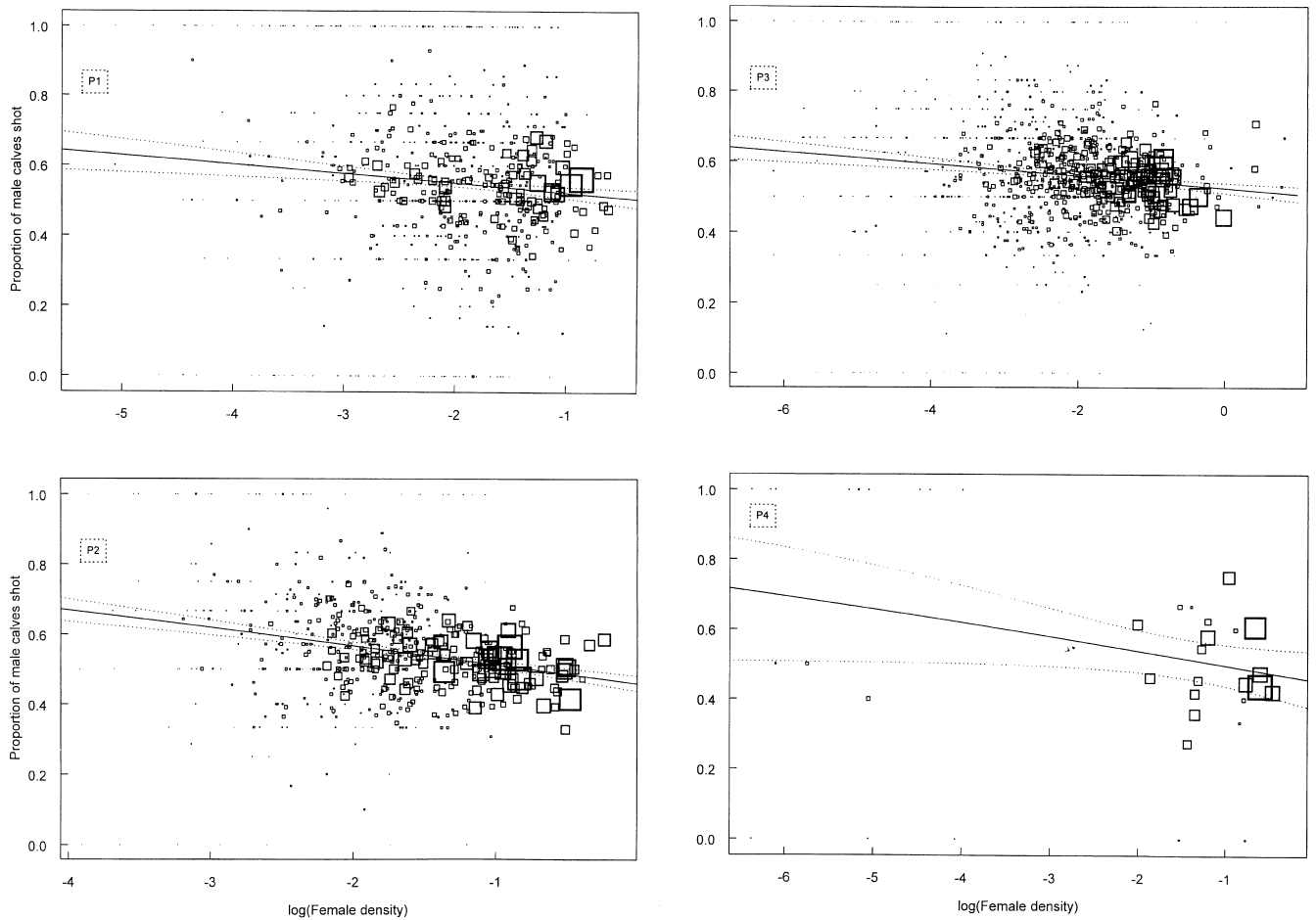


Fig. 3. Proportion of male calves shot each autumn as a function of density in four populations of Norwegian red deer; (a) P1; (b) P2; (c) P3; (d) P4. Each square represents data from one municipality one year. The size of the square is directly proportional to the sample size.

tion (P1) used in Post *et al.* (1999a). The effect of density, as estimated from the regression coefficient, was stronger in P2 compared to P1 and P3 (Table 3). This comparison was justified as we use $\log(\text{density})$, and the regression coefficient therefore represents the impact of a relative increase in density, not an absolute one (i.e. they represent the impact of the same relative increase in density). Our analysis confirmed that the proportion of male calves shot each autumn increased with increasing NAO in P1 independent of density (Fig. 4; $\chi^2 = 5.234$, $P = 0.022$), but there was no evidence for an effect of the NAO on offspring sex ratios in the other populations (P2: $\chi^2 = 0.136$, $P = 0.712$; P3: $\chi^2 = 2.503$, $P = 0.114$; P4: $\chi^2 = 0.185$, $P = 0.667$). There was no effect of the NAO one year before gestation (P1: $\chi^2 = 0.011$, $P = 0.916$; P2: $\chi^2 = 0.521$, $P = 0.471$; P3: $\chi^2 = 1.311$, $P = 0.252$; P4: $\chi^2 = 3.226$, $P = 0.080$). In the model with snow depth entered before the NAO, there was clear evidence that the proportion of male calves shot each autumn decreased with increasing snow depth in March, but this was significant only in P1 (P1: χ^2

$= 4.129$, $P = 0.042$; P2: $\chi^2 = 2.005$, $P = 0.157$; P3: $\chi^2 = 0.634$, $P = 0.426$; P4: $\chi^2 < 0.001$, $P = 0.979$). There was no residual effect of the NAO after snow depth was accounted for (P1: $\chi^2 = 2.449$, $P = 0.118$). The proportion of male calves shot each autumn further declined with degree of latitude in P1 only (P1: $\chi^2 = 9.228$, $P = 0.002$; P2: $\chi^2 = 0.064$, $P = 0.800$; P3: $\chi^2 = 0.537$, $P = 0.464$; P4: $\chi^2 = 0.880$, $P = 0.348$). In P2, the proportion of male calves shot each autumn increased with increasing distance from the coast ($\chi^2 = 7.556$; $P = 0.006$), but not in the other populations (P1: $\chi^2 = 0.066$, $P = 0.798$; P3: $\chi^2 = 2.477$, $P = 0.116$; P4: $\chi^2 = 0.047$, $P = 0.829$). There was no evidence of overdispersion in the models when including only significant factors (P1: d.f. = 793, $\chi^2 = 794.597$, $P = 0.477$; P2: d.f. = 564, $\chi^2 = 558.358$, $P = 0.559$; P3: d.f. = 1018, $\chi^2 = 971.859$, $P = 0.847$; P4: d.f. = 42, $\chi^2 = 34.087$, $P = 0.802$). This indicates that the amount of residual heterogeneity between municipalities and years was small, and that including years and municipalities as random factors would not affect the results significantly. Indeed, regression

Table 3. Parameter estimates (point estimates and 95% confidence limits) for the logistic regression equation $\text{logit}(\text{proportion of males}) = \alpha + \beta_1(\ln(\text{density of females})) + \beta_2(\text{NAO}) + \beta_3(\text{Latitude}) + \beta_4(\text{Distance to coast})$ for red deer harvest data on calves (age 3–5 months) from four populations (Pop) in Norway. Only significant parameters were included when estimating coefficients in bold, whereas non-significant coefficients are from the full model

Pop	Intercept		Log(female density)		The NAO		Latitude		Distance to coast	
	α	95% CL	β_1	95% CL	β_2	95% CL	β_3	95% CL	β_4	95% CL
P1	0.276	[0.043, 0.509]	-0.096	[-0.160, -0.032]	0.022	[0.003, 0.041]	-0.060	[-0.099, -0.020]	0.011	[-0.075, 0.097]
P2	-0.293	[-0.705, 0.118]	-0.192	[-0.252, -0.133]	0.003	[-0.011, 0.017]	0.009	[-0.039, 0.057]	0.068	[0.019, 0.118]
P3	0.094	[0.037, 0.151]	-0.071	[-0.099, -0.042]	-0.009	[-0.021, 0.003]	0.023	[-0.009, 0.055]	0.054	[-0.014, 0.122]
P4	-0.182	[-0.490, 0.127]	-0.168	[-0.323, -0.012]	0.008	[-0.096, 0.112]	0.268	[-1.468, 2.004]	-0.310	[-3.174, 2.554]

coefficients and their standard errors were very similar (e.g. for population P1, the regression coefficient for density was estimated to be -0.101 , $SE = 0.035$ when including municipality as a random factor, and -0.092 , $SE = 0.035$ when including year as a random factor; the GLM estimate was -0.092 , $SE = 0.035$; all models including NAO, degree of latitude and distance from the coast as covariates). The estimates of the random factor standard deviation were always small (e.g. for population P1: municipalities: 0.048 , $SE = 0.021$; years: 0.0009 , $SE = 0.021$).

Discussion

Recent studies have demonstrated that extrinsic factors affecting body condition of ungulates, such as density and climate, may also affect offspring sex ratios (Kruuk *et al.* 1999; Post *et al.* 1999a). The surprising result of Post *et al.* (1999a), that female red deer in Norway produced increasingly male-biased offspring sex ratios as density increased, was not supported by our analysis of an expanded data set and with a higher spatial resolution, taking into account local density reflecting population heterogeneity. Sex ratios among calves shot in autumn became less male-biased as density increased in all four populations of Norwegian red deer, as earlier reported by Kruuk *et al.* (1999) for red deer on Rum, Scotland. Our contrasting result was not due to any mistakes in the analysis performed by Post *et al.* (1999a); their conclusion was right at the coarse (population) scale. Rather, during the time span of their study (1977–93), the number of municipalities harvesting red deer calves increased from 28 to 40 in P1 (referred to in Post *et al.* (1999a) as the Hordaland population). The decreasing proportion of male calves harvested with increasing local density within the original 28 municipalities was counteracted at the coarse (population) scale by an increased number of male calves harvested in the 12 new municipalities (range expansion) with a low population density. Surprisingly therefore local (municipality) and coarse (population) scale sex ratio were negatively correlated for this period in P1. The strong effect of local density on population sex ratio was paralleled by decreased adult body weights (A. Mysterud, N.G. Yoccoz, N.C. Stenseth & R. Langvatn, unpublished results). Body weight of Norwegian red deer also decreases with increasing distance from the coast (Langvatn & Albon 1986), but distance from the coast was a poor predictor of sex ratio variation, as it only affected the proportion of males born in Sogn og Fjordane (P2).

An increase in the NAO resulted in increasingly male-biased sex ratios in P1, as previously reported by Post *et al.* (1999a), but not in the other three populations. Post *et al.* (1999a) suggested that the NAO index was positively correlated with snow depth and thus high index values indicated severe

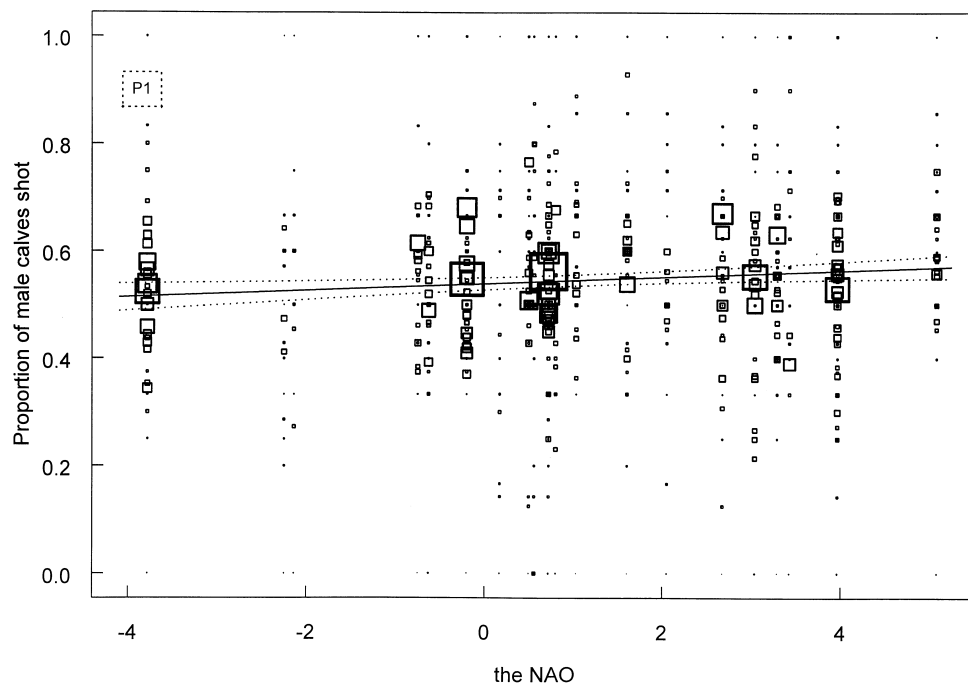


Fig. 4. Proportion of male calves shot each autumn as a function of climate (NAO) in Rogaland and Hordaland (P1) in Norway. Each square represents data from one municipality one year. The size of the square is directly proportional to the sample size.

winters for red deer. In addition, Post *et al.* (1997) and Post & Stenseth (1999) reported that body weights of Norwegian red deer were negatively correlated with the NAO. That females in poor condition (i.e. high NAO index) produce more sons (Post *et al.* 1999a) may thus seem inconsistent with Kruuk *et al.* (1999), who reported that the proportion of red deer males born on Rum each year declined with winter rainfall which was associated with nutritional stress during pregnancy. However, we challenge the view that high NAO values indicate severe winters for red deer in Norway, as both the reported positive correlation between the NAO and snow depth (Post *et al.* 1999a) and the negative correlation between the NAO and red deer body weight (Post *et al.* 1997; Post & Stenseth 1999) were not supported. First, red deer in Norway winter at low elevations (Albon & Langvatn 1992). Although a high NAO index was indicative of higher precipitation, the warmer temperatures at higher NAO (Hurrell 1995; Post *et al.* 1997) result in a negative correlation between snow depth and the NAO at low elevation (Fig. 2). Forage in the field layer is thus probably more easily available to red deer in these coastal and lowland areas during winters with a high NAO index (Loison, Langvatn & Solberg 1999b), and the higher temperatures also represent less cold stress to the animals (Simpson *et al.* 1978). Loison *et al.* (1999b) reported that body weight of Norwegian red deer in their study population

(Snillfjord in Sør-Trøndelag) was positively correlated with the NAO. Recently, we have found that body weights of red deer in Norway in general were positively correlated with the NAO when taking population substructure into account and using an index for local density, although this relationship was reversed at very low NAO values (A. Mysterud, N.G. Yoccoz, N.C. Stenseth & R. Langvatn, unpublished results). Further work is needed to determine how the NAO describes local weather at different altitudes and latitudes in different geographical regions before any firm conclusion can be drawn regarding global climate effects on demography and population dynamics of northern ungulates in general (e.g. Post *et al.* 1997, 1999a,b; Forchhammer *et al.* 1998; Post & Stenseth 1998, 1999).

The evolutionary origin of sex ratio variation in relation to body condition may be adaptive and apply on a relative basis between individuals (Trivers & Willard 1973). However, the extrinsic modification of ungulate sex ratios by population density and climate occurs at a population scale and may not be adaptive (Kruuk *et al.* 1999; Post *et al.* 1999a). The physiological mechanism by which sex ratio is determined in red deer remains unknown, which indeed has been a major problem with studies of sex ratio variation in large herbivores in general (Hewison & Gaillard 1999). Possible mechanisms include a higher *in utero* mortality of males under harsh conditions, and modification of the sex ratio

at conception and/or implantation. The effect of density on harvest sex ratio can be through both these mechanisms, and our reanalyses revealed that the NAO was a less important predictor of sex ratio than population density also in P1, as measured by the regression coefficients (Table 3). The proportion of stillbirths in the polytocous roe deer (*Capreolus capreolus* L.) increased with increasing density (Andersen & Linnell 1998). The magnitude of foetal mortality among prime age female red deer is probably low because the proportion of prime age females that ovulated approached 100% by 15 November in Norwegian red deer, and because close to 100% of these females showed signs of parturition and were lactating when shot during the following autumn (Langvatn *et al.* 1996). However, we cannot rule out foetal mortality as a mechanism among yearling and primiparous hinds, which also have a more variable ovulation rate (Langvatn *et al.* 1996). Indeed, it is difficult to explain the effect of the NAO in population P1 otherwise, since the NAO is measured from December through March (Hurrell 1995), i.e. during gestation. It is assumed that also body condition at the time of conception affects the sex ratio (Trivers & Willard 1973; Hewison & Gaillard 1999). Consequently, sex ratio variation may be dependent on summer food resources and involving both density-dependent and density-independent mechanisms. Furthermore, it is well documented that the period from spring through early autumn is the prime period for growth and build-up of body condition, a natural consequence both from a resource perspective (Wood, Cowan & Nordan 1962; Klein 1964; Anderson, Medin & Bowden 1974; Mitchell, McCowan & Nicholson 1976; Langvatn 1994), and in terms of physiological (Moen 1978; Kay 1985; Parker *et al.* 1993) and hormonal status of animals (Bahnak *et al.* 1981; Ryg & Langvatn 1982; Ryg 1982). Although the NAO is an index of severity of winter climate, it may also be correlated with summer foraging conditions because increased snow depth may lead to a prolonged period of snow melt and hence access to newly emergent and high quality forage (Albon & Langvatn 1992; Langvatn 1994; Post & Stenseth 1999). However, the NAO of the year prior to gestation did not affect sex ratios, and hence there was no evidence of any indirect effect of the NAO on the summer ranges that could influence condition of individual red deer hinds sufficiently at time of conception to affect harvest sex ratios the next autumn.

On the basis of this study, our conclusions are as follows.

1. There is evidence that with increasing density and severity of winter climate (low NAO), females may produce decreasingly male-biased offspring sex ratios. There was thus support for the extrinsic modification hypothesis (Kruuk *et al.* 1999; Post *et al.* 1999a).

2. There was no evidence that abiotic factors can be more influential than density-dependent resource limitation in altering sex ratios (Post *et al.* 1999a), as density was about twice as important as winter climate measured with the NAO index.

3. These patterns imply that there is, at present, no empirical evidence for the hypothesis that females in poor condition produce more sons as poor sons may nevertheless survive better than poor daughters (Post *et al.* 1999a), or that the contradiction may be explained by considering interactions between the timing of sex-specific foetal growth spurts and environmental stress on maternal condition (Forchhammer 2000).

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References

- Albon, S.D. & Langvatn, R. (1992) Plant phenology and the benefits of migration in a temperate ungulate. *Oikos*, **65**, 502–513.
- Andersen, R. & Linnell, J.D.C. (1998) Ecological correlates of mortality of roe deer fawns in a predator-free environment. *Canadian Journal of Zoology*, **76**, 1217–1225.
- Anderson, A.E., Medin, D.E. & Bowden, D.C. (1974) Growth and morphometry of the carcass, selected bones, organs, and glands of mule deer. *Wildlife Monographs*, **39**, 1–122.
- Bahnak, B.R., Holland, J.C., Verme, L.J. & Ozoga, J.J. (1981) Seasonal and nutritional influences on growth hormone and thyroid activity in white-tailed deer. *Journal of Wildlife Management*, **45**, 140–147.
- Bjørnstad, O.N., Fromentin, J.-M., Stenseth, N.C. & Gjøsæter, J. (1999) A new test for density-dependent survival: the case of the coastal cod populations. *Ecology*, **80**, 1278–1288.
- Cameron, E.Z., Linklater, W.L., Stafford, K.J. & Veltman, C.J. (1999) Birth sex ratios relate to mare condition at conception in Kaimanawa horses. *Behavioral Ecology*, **10**, 472–475.
- Clutton-Brock, T.H. (1991). *The Evolution of Parental Care*. Princeton University Press Princeton, NJ.
- Clutton-Brock, T.H., Guinness, F.E. & Albon, S.D. (1982). *Red Deer. Behaviour and Ecology of Two Sexes*. Edinburgh University Press, Edinburgh.
- Clutton-Brock, T.H. & Iason, G.R. (1986) Sex ratio variation in mammals. *Quarterly Review of Biology*, **61**, 339–374.
- Coulson, T.N., Albon, S.D., Guinness, F.E., Pemberton, J.M. & Clutton-Brock, T.H. (1997) Population substructure, local density, and calf winter survival in red deer (*Cervus elaphus*). *Ecology*, **78**, 852–863.

- Coulson, T., Albon, S., Pilkington, J. & Clutton-Brock, T. (1999) Small-scale spatial dynamics in a fluctuating ungulate population. *Journal of Animal Ecology*, **68**, 658–671.
- Donalson, D.D. & Nisbet, R.M. (1999) Population dynamics and spatial scale: effects of system size on population persistence. *Ecology*, **80**, 2492–2507.
- Festa-Bianchet, M. (1996) Offspring sex ratio studies of mammals: does publication depend upon the quality of the research or the direction of the results? *Ecoscience*, **3**, 42–44.
- Forchhammer, M.C. (2000) Timing of foetal growth spurts can explain sex ratio variation in polygynous mammals. *Ecology Letters*, **3**, 1–4.
- Forchhammer, M.C., Stenseth, N.C., Post, E.S. & Langvatn, R. (1998) Population dynamics of Norwegian red deer: density-dependence and climatic variation. *Proceedings of the Royal Society London Series B*, **265**, 341–350.
- Fryxell, J.M., Hussell, D.J.T., Lambert, A.B. & Smith, P.C. (1991) Time lags and population fluctuations in white-tailed deer. *Journal of Wildlife Management*, **55**, 377–385.
- Fryxell, J.M., Mercer, W.E. & Gellately, R.B. (1988) Population dynamics of Newfoundland moose using cohort analysis. *Journal of Wildlife Management*, **5**, 14–21.
- Guinness, F.E., Albon, S.D. & Clutton-Brock, T.H. (1978) Factors affecting reproduction in red deer (*Cervus elaphus*) hinds on Rhum. *Journal of Reproduction and Fertility*, **54**, 325–334.
- Hastie, T. & Tibshirani, R. (1990) *Generalised Additive Models*. Chapman & Hall, London.
- Hewison, A.J.M., Andersen, R., Gaillard, J.-M., Linnell, J.D.C. & Delorme, D. (1999) Contradictory findings in studies of sex ratio variation in roe deer (*Capreolus capreolus*). *Behavioral Ecology and Sociobiology*, **45**, 339–348.
- Hewison, A.J.M. & Gaillard, J.-M. (1999) Successful sons or advantaged daughters? The Trivers–Willard model and sex-biased maternal investment in ungulates. *Trends in Ecology and Evolution*, **14**, 229–234.
- Hobbs, N.T. (1989) Linking energy balance to survival in mule deer: development and test of a simulation model. *Wildlife Monographs*, **101**, 1–39.
- Hosmer, D.W. & Lemeshow, S. (1989) *Applied Logistic Regression*. Wiley, New York.
- Hurrell, J.W. (1995) Decadal trends in the North Atlantic Oscillation: regional temperatures and precipitation. *Science*, **269**, 676–679.
- Hurrell, J.W. & Van Loon, H. (1997) Decadal variations in climate associated with the North Atlantic Oscillation. *Climatic Change*, **36**, 310–326.
- Kay, R.N.B. (1985) Seasonal variation of appetite in ruminants. *Recent Advances in Animal Nutrition* (ed. W. Haresign), pp. 199–210. Butterworths, London.
- Klein, D.R. (1964) Range-related differences in growth of deer reflected in skeletal ratios. *Journal of Mammalogy*, **45**, 226–235.
- Kruuk, L.E.B., Clutton-Brock, T.H., Albon, S.D., Pemberton, J.M. & Guinness, F.E. (1999) Population density affects sex ratio variation in red deer. *Nature*, **399**, 459–461.
- Lamb, P.J. & Pepler, R.A. (1987) North Atlantic Oscillation: concept and an application. *American Meteorological Society*, **68**, 1218–1225.
- Lambin, X., Elston, D.A., Petty, S.J. & MacKinnon, J.L. (1998) Spatial asynchrony and periodic travelling waves in cyclic populations of field voles. *Proceedings of the Royal Society London Series B*, **265**, 1491–1496.
- Langvatn, R. (1994) Climate associated variation in the resource base for red deer (*Cervus elaphus*) – relationships to body size and reproductive performance within and between cohorts. PhD Thesis, University of Oslo.
- Langvatn, R. & Albon, S.D. (1986) Geographic clines in body weight of Norwegian red deer: a novel explanation of Bergmann's rule? *Holarctic Ecology*, **9**, 285–293.
- Langvatn, R., Albon, S.D., Burkey, T. & Clutton-Brock, T.H. (1996) Climate, plant phenology and variation in age at first reproduction in a temperate herbivore. *Journal of Animal Ecology*, **65**, 653–670.
- Lindsey, J.K. (1999) *Models for Repeated Measurements*. Oxford University Press, Oxford.
- Loison, A., Gaillard, J.-M., Pelabon, C. & Yoccoz, N.G. (1999a) What factors shape sexual size dimorphism in ungulates? *Evolutionary Ecology Research*, **1**, 611–633.
- Loison, A., Langvatn, R. & Solberg, E.J. (1999b) Body mass and winter mortality in red deer calves: Disentangling sex and climate effects. *Ecography*, **22**, 20–30.
- Maynard Smith, J. (1980) A new theory of sexual investment. *Behavioral Ecology and Sociobiology*, **7**, 247–251.
- McCullagh, P. & Nelder, J.A. (1989) *Generalized Linear Models*. Chapman & Hall, London.
- Milner, J.M., Elston, D.A. & Albon, S.D. (1999) Estimating the contributions of population density and climatic fluctuations to interannual variation in survival of Soay sheep. *Journal of Animal Ecology*, **68**, 1235–1247.
- Mitchell, B., McCowan, D. & Nicholson, I.A. (1976) Annual cycles of body weight and condition in Scottish red deer, *Cervus elaphus*. *Journal of Zoology*, **180**, 107–127.
- Moen, A.N. (1978) Seasonal changes in heart rates, activity, metabolism, and forage intake of white-tailed deer. *Journal of Wildlife Management*, **42**, 715–738.
- Parker, K.L., Gillingham, M.P., Hanley, T.A. & Robbins, C.T. (1993) Seasonal patterns in body mass, body composition, and water transfer rates of free-ranging and captive black-tailed deer (*Odocoileus hemionus sitkensis*). *Canadian Journal of Zoology*, **71**, 1397–1404.
- Parker, K.L., Robbins, C.T. & Hanley, T.A. (1984) Energy expenditure for locomotion by mule deer and elk. *Journal of Wildlife Management*, **48**, 474–488.
- Portier, C., Festa-Bianchet, M., Gaillard, J.-M., Jorgenson, J.T. & Yoccoz, N.G. (1998) Effects of density and weather on survival of bighorn sheep lambs (*Ovis canadensis*). *Journal of Zoology*, **245**, 271–278.
- Post, E., Forchhammer, M.C. & Stenseth, N.C. (1999b) Population ecology and the North Atlantic Oscillation (NAO). *Ecological Bulletins*, **47**, 117–125.
- Post, E., Forchhammer, M.C., Stenseth, N.C. & Langvatn, R. (1999a) Extrinsic modification of vertebrate sex ratios by climatic change. *American Naturalist*, **154**, 194–204.
- Post, E. & Stenseth, N.C. (1998) Large-scale climatic fluctuations and population dynamics of moose and white-tailed deer. *Journal of Animal Ecology*, **67**, 537–543.
- Post, E. & Stenseth, N.C. (1999) Climatic variability, plant phenology, and northern ungulates. *Ecology*, **80**, 1322–1339.
- Post, E., Stenseth, N.C., Langvatn, R. & Fromentin, J.-M. (1997) Global climate change and phenotypic variation among red deer cohorts. *Proceedings of the Royal Society London Series B*, **264**, 1317–1324.
- Ray, C. & Hastings, A. (1996) Density dependence: are we searching at the wrong spatial scale? *Journal of Animal Ecology*, **65**, 556–566.

- Ryg, M. (1982) Seasonal changes in weight gain, growth hormone, and thyroid hormones in intact and castrated male moose (*Alces alces alces*). *Canadian Journal of Zoology*, **60**, 2941–2946.
- Ryg, M. & Langvatn, R. (1982) Seasonal changes in weight gain, growth hormone, and thyroid hormones in male red deer (*Cervus elaphus atlanticus*). *Canadian Journal of Zoology*, **60**, 2577–2581.
- Simpson, A.M., Webster, A.J.F., Smith, J.S. & Simpson, C.A. (1978) Energy and nitrogen metabolism of red deer (*Cervus elaphus*) in cold environments; a comparison with cattle and sheep. *Journal of Comparative Biochemistry and Physiology*, **60**, 251–256.
- Skogland, T. (1986) Sex ratio variation in relation to maternal condition and parental investment in wild reindeer *Rangifer t. tarandus*. *Oikos*, **46**, 417–419.
- Smith, B.L. & Anderson, S.H. (1996) Patterns of neonatal mortality of elk in northwest Wyoming. *Canadian Journal of Zoology*, **74**, 1229–1237.
- Solberg, E.J., Sæther, B.-E., Strand, O. & Loison, A. (1999) Dynamics of a harvested moose population in a variable environment. *Journal of Animal Ecology*, **68**, 186–204.
- Statistics Norway (1977–98) *Official Hunting Statistics of Norway*. Statistics Norway, Oslo and Kongsvinger.
- Tjur, T. (1998) Nonlinear regression, quasi likelihood, and overdispersion in generalized linear models. *American Statistician*, **52**, 222–227.
- Trivers, R.L. & Willard, D.E. (1973) Natural selection of parental ability to vary the sex ratio of offspring. *Science*, **179**, 90–92.
- Van Loon, H. & Rogers, J.C. (1978) The seesaw in winter temperatures between Greenland and northern Europe. I. General description. *Monthly Weather Review*, **106**, 296–310.
- Venables, W.N. & Ripley, B.D. (1994) *Modern Applied Statistics with S-Plus*. Springer Verlag, New York.
- Weckerly, F.W. (1998) Sexual-size dimorphism: influence of mass and mating system in the most dimorphic mammals. *Journal of Mammalogy*, **79**, 33–52.
- Williams, G.C. (1979) The question of adaptive sex ratio in outcrossed vertebrates. *Proceedings of the Royal Society London Series B*, **205**, 567–580.
- Wiser, S.K., Peet, R.K. & White, P.S. (1998) Prediction of rare-plant occurrence: a southern Appalachian example. *Ecological Applications*, **8**, 909–920.
- Wood, A.J., McT., Cowan, I. & Nordan, H.C. (1962) Periodicity of growth in ungulates as shown by deer of the genus *Odocoileus*. *Canadian Journal of Zoology*, **40**, 593–603.
- Yee, T.W. & Mitchell, N.D. (1991) Generalized additive models in plant ecology. *Journal of Vegetation Science*, **2**, 587–602.

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Municipality	Pop	Year/																													Total		
		1977	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998										
Samnanger	P1	2		3	2	1		3	7	10	8	2	2	9	9	3	3	2	6	5	6	6	6	6	6	6	6	6	6	6	6	16	102
Os	P1	2	5	7	12	11	9	5	11	8	7	6	6	5	5	5	6	5	3	14	8	17	8	17	8	17	8	17	8	17	13	175	
Austevoll	P1	1	2	2	1			2	1	3	2	1	3	1	3	1	1	8			5	1										4	45
Sund	P1	2	2	2	3	4	1	2	3	1		1		1	1	2	2	1	1	1	6	4	6	4	5	7	5	7	6	6	31	31	
Fjell	P1	2	1	3	2			2	3	2	2	1	1	4	2	2	2	1	2	6	6	4	6	4	6	4	5	7	5	7	59	59	
Askøy	P1	8	4	6		1		2	3	4	2	1	2	2	2	2	1	1	4	1	1	1	1	1	1	1	6	8	8	8	58	58	
Vaksdal	P1	4	6	5	5	11	9	8	12	8	7	9	11	14	8	11	19	18	15	19	25	19	25	19	25	19	25	21	27	27	272	272	
Modalen	P1	1	4	2	2	1	2	3	5	2	4	4	3	5	3	1	5	5	3	3	5	8	8	5	8	4	4	9	9	81	81		
Osterøy	P1	1	3	6	2	2	2	6	7	19	19	16	17	5	3	7	6	6	9	22	24	27	27	27	27	27	27	27	28	28	258	258	
Meland	P1	1		1	4	1	3	3	12	7	7	7	7	7	6	3	4	4	7	12	13	12	12	12	12	12	15	15	33	33	164	164	
Øygarden	P1								2																						13	13	
Radøy	P1	1							8	10	6	9	13	11	11	11	6	12	13	19	25	24	24	24	24	27	27	33	33	228	228		
Lindås	P1	4	10	2	7	7	6	7	23	25	32	24	48	34	21	10	18	18	25	40	42	42	42	42	42	42	42	51	73	526	526		
Austrheim	P1								1	2	1	1	2	1	1	2	2	2	1	4	2	2	2	2	2	2	6	7	30	30	30	30	
Masfjorden	P1	8	9	7	11	6	13	7	20	28	21	19	21	12	10	12	15	21	29	37	25	32	25	32	25	32	32	36	36	399	399		
Flora	P2	11	23	21	22	49	51	55	42	46	70	63	59	59	62	59	70	86	84	112	116	116	116	116	116	116	158	146	1464	1464	1464	1464	
Gulen	P2	10	22	9	13	15	10	11	10	17	23	25	19	19	20	16	16	16	28	30	36	36	36	36	36	36	45	62	492	492	492	492	
Solund	P2			1		5	5	10	13	10	15	10	5	7	9	13	28	25	31	30	30	30	30	30	30	30	35	30	312	312	312	312	
Høylandet	P2	3	3	13	14	17	13	17	23	23	24	13	10	21	15	15	48	45	56	64	64	64	64	64	64	64	64	82	769	769	769	769	
Høyanger	P2	6	16	14	14	19	15	19	13	21	32	40	39	30	30	26	45	45	74	45	61	64	64	64	64	64	82	82	82	82	82	82	
Vik	P2	3	4	6	3	15	10	3	2	4	10	2	5	2	1	6	14	14	19	16	11	16	11	16	11	16	15	22	189	189	189	189	
Balestrand	P2	5	10	12	13	9	6	5	10	11	16	12	23	22	18	16	17	20	31	35	42	42	42	42	42	43	51	427	427	427	427	427	
Leikanger	P2	4	8	1	3	2	3	2	2	5	6	2	6	4	4	3	2	1	4	7	7	7	7	7	7	8	8	92	92	92	92	92	
Sogndal	P2	3	12	13	10	7	12	15	19	8	19	16	11	15	18	16	12	12	18	17	19	19	19	19	19	32	33	337	337	337	337	337	
Aurland	P2	1	2	2	1	3	3	6	3	5	6	3	2	1	3	4	2	5	9	9	11	18	16	16	16	16	19	125	125	125	125	125	
Lærdal	P2	6	14	20	13	15	13	10	16	16	12	15	18	14	17	16	25	12	21	50	33	33	33	33	33	34	46	436	436	436	436	436	
Årdal	P2	3	2	2	4	2	5	2	3	6	4	3	4	5	7	6	6	4	7	10	14	14	14	14	14	10	9	118	118	118	118	118	
Luster	P2	4	14	12	17	10	16	14	13	16	25	20	19	21	22	35	26	37	33	29	26	26	26	26	26	36	26	471	471	471	471	471	
Askvoll	P2	2	12	23	16	23	12	20	21	26	14	20	18	11	6	8	14	25	28	42	44	44	44	44	44	56	62	503	503	503	503	503	
Fjaler	P2	11	8	8	9	18	10	21	12	15	12	16	21	17	12	21	18	24	33	38	35	35	35	35	49	51	459	459	459	459	459	459	
Gaular	P2	13	14	20	27	14	18	21	25	28	26	24	34	21	34	38	58	63	96	74	72	72	72	72	72	115	145	980	980	980	980	980	
Jølster	P2	4	12	6	4	2	6	9	6	11	14	10	18	7	12	19	18	23	34	38	36	36	36	36	56	61	406	406	406	406	406	406	
Førde	P2	3	10	8	10	13	7	14	19	13	9	9	15	14	15	12	18	17	23	27	42	42	42	42	43	59	400	400	400	400	400	400	
Nausdalen	P2	4	6	16	14	12	16	19	21	23	22	20	23	28	27	24	33	40	55	53	52	52	52	52	58	72	638	638	638	638	638	638	
Bremanger	P2	24	27	50	47	60	58	56	65	68	60	71	78	77	92	93	89	142	110	97	101	101	101	101	107	107	113	1685	1685	1685	1685	1685	
Vågsøy	P2	2	2	1	9	15	8	8	1	5		3	1	1	7	1	3	17	23	26	26	26	26	26	31	42	232	232	232	232	232	232	
Selje	P2	8	12	6	16	15	11	11	8	10	6	9	10	10	12	10	9	13	26	19	41	41	41	41	42	42	38	352	352	352	352	352	352
Eid	P2	7	21	15	24	24	30	26	17	20	26	24	35	44	44	39	54	84	76	86	95	95	95	95	112	105	1008	1008	1008	1008	1008	1008	

Municipality	Pop	Year/												Total										
		1977	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988		1989	1990	1991	1992	1993	1994	1995	1996	1997	1998
Hornindal	P2		1	3	1	4	1	6	7	3	21	7	8	10	3	8	5	19	19	17	11	30	25	209
Gloppen	P2	11	14	15	16	22	21	28	24	40	40	30	33	24	32	31	49	54	83	103	89	106	110	975
Stryn	P2	7	9	2	7	11	11	17	13	15	17	24	29	25	37	37	23	72	62	98	95	154	163	928
Molde	P3	2	6	6	8	10	13	19	14	8	14	13	4	5	10	10	8	11	17	18	20	22	28	260
Ålesund	P3	6	12	4	18	18	19	18	27	19	18	15	14	8	6	13	14	16	14	22	24	26	32	363
Vanylven	P3	5	14	13	11	10	13	9	14	23	11	12	19	13	21	30	28	29	40	53	50	80	76	574
Sande	P3	5	20	3	6	11	14	13	11	13	8	6	14	15	10	11	16	23	20	22	19	51	46	357
Herøy	P3	2	6	7	11	6	11	7	10	4	6	8	12	10	14	16	12	19	21	20	19	21	22	264
Ullstein	P3	12	7	10	8	11	8	11	11	11	10	4	9	5	8	7	16	18	20	20	20	27	23	276
Hareid	P3	7	4	10	8	8	9	16	28	33	26	15	22	21	19	11	25	25	41	47	32	50	58	515
Volda	P3	3	14	10	25	21	24	26	20	39	44	36	42	52	41	43	52	62	65	92	98	108	95	1012
Ørsta	P3	26	42	39	48	43	47	57	69	84	39	53	76	60	67	87	94	127	101	123	138	166	205	1791
Ørskog	P3	5	3	4	3	3	2	5	3	13	9	9	10	9	7	11	12	11	14	22	10	34	15	214
Norddal	P3	3	1	7	8	6	2	13	10	11	10	9	18	11	14	16	21	22	36	29	35	40	44	366
Stranda	P3	4	8	7	8	16	10	15	20	19	12	7	24	22	33	39	53	72	67	72	51	78	76	713
Stordal	P3	6	4	8	5	5	5	8	11	5	5	7	8	5	8	3	12	26	32	44	30	52	35	324
Sykkylven	P3	5	16	15	17	23	10	24	25	32	16	23	30	26	24	36	39	56	42	47	57	65	46	674
Skodje	P3	6	4	11	11	11	14	17	19	21	14	15	24	14	18	19	15	30	40	42	48	54	35	482
Sula	P3					5	4	3	4	6	4	4	3	3		2	4	4	10	16	12	10	15	109
Giske	P3	2	2		1	2	2	3	1	1	3	5	3	2	1	7	7	11	19	12	17	15	12	117
Haram	P3	3	5	2	2	2	1	6	18	24	26	21	31	24	28	33	35	67	97	129	74	136	99	863
Vestnes	P3	14	22	18	18	20	21	18	25	28	12	12	26	22	27	34	37	67	86	131	80	154	81	953
Rauma	P3	13	12	15	13	16	10	22	31	38	26	22	38	22	25	36	52	72	112	117	95	135	124	1046
Nesset	P3		12	7	19	18	15	17	7	10	9	13	12	11	14	24	16	28	35	27	29	35	32	390
Midsund	P3	5	8	7	5	9	10	13	7	15	12	12	13	11	14	14	21	22	22	33	30	36	28	347
Aukra	P3											1	4	5	4	5	3	2	1	1	3	1	1	30
Fræna	P3	6	10	18	12	18	17	15	22	14	12	12	12	11	11	15	19	27	36	34	34	44	42	441
Eide	P3	3	3	9	11	9	8	12	8	8	6	5	2	4	5	6	12	12	16	18	21	28	26	162
Averøy	P3										5	11	4	12	10	18	16	21	40	39	40	46	41	374
Frei	P3	1	1					1	1	6	6	5	1	1								1	1	25
Gjennes	P3	4	12	16	24	19	17	22	34	24	15	10	30	17	18	25	27	35	33	49	47	63	65	606
Tingvoll	P3	9	14	31	35	34	36	38	55	96	84	73	79	57	57	42	42	74	103	86	83	125	114	1367
Sunnal	P3	1	1	4	8	7	6	12	53	78	35	28	39	34	26	31	43	34	54	59	69	82	80	784
Surnadal	P3	11	19	25	39	30	27	47	43	60	33	32	30	32	34	28	39	31	38	47	44	56	52	797
Rindal	P3	2	6	2	3	5	7	9	4	16	6	3	4	4	2	4	9	9	7	4	6	9	11	132
Aure	P3	34	29	61	46	67	57	64	51	64	53	47	60	47	58	63	64	61	82	111	116	120	96	1451
Halsa	P3	4	7	12	12	8	12	9	12	15	16	28	20	16	16	20	33	48	29	35	29	29	29	439
Tustna	P3	1	1	7	9	14	8	12	16	15	21	19	20	20	22	24	22	28	31	29	30	33	27	409
Smøla	P3								1		2	7	7	9	7	5	1		1	1	6	7	15	69

Municipality	Pop	Year/																													Total
		1977	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998								
Hemne	P3	10	12	20	28	20	27	30	28	30	26	32	29	23	15	17	25	30	31	35	32	48	26	574							
Snillfjord	P3	17	24	22	17	16	29	36	39	55	52	42	44	41	43	40	44	42	46	55	77	97	100	978							
Hitra	P3	6	85	34	32	58	53	76	80	59	58	61	58	46	46	58	65	93	71	72	89	79	90	1369							
Frøya	P3								1	1		4	4	7	2	4	4		5	1	6	3	5	43							
Ørland	P3										1						1					1	1	3							
Agdenes	P3	3	3	3	7	2	12	9	15	11	13	14	4	6	9	12	12	14	22	12	12	29	12	236							
Rissa	P3																1	2						3							
Bjugn	P3			1		1	3	4	4	6	9	6	5	4	4	5	10	12	9	5	6	3	3	100							
Alfjord	P3	1			1				1	1		1		1			1	2	2	1	2	2	5	19							
Oppdal	P3	2	3	6	2	3	3	8	5	9	5	4	3	1	5	2	4	5	8	7	10	3	8	103							
Rennebu	P3	2	3	4	6	2	4	5	3	4	6	4	3	3	2	6	1	1	5	4	3	6	4	78							
Meldal	P3	5	5	8	12	8	14	16	17	21	18	23	19	20	22	27	22	21	22	20	25	30	27	402							
Orkdal	P3	1	7	8	13	8	16	15	16	21	15	23	22	20	17	23	23	30	34	27	38	37	34	448							
Holtålen	P3				1		1			1														3							
Midtre	P3	1	1	1	1	1	1	2	6	3	4	3	6	3	4	10	10	12	10	8	8	4	6	104							
Gauldal																															
Melhus	P3	1	1	2	6	1		4	2	2	2	5	5	2	4	8	7	2	1	2	5	9	1	71							
Skaun	P3	1	3	6	14	6	12	13	7	10	10	8	11	10	8	6	8	13	20	13	20	25	19	243							
Klebu	P3																														
Malvik	P3																1	1	1	2	1	1	1	5							
Selbu	P3			1					2		1	1	1	1	1	1	1	1	3	1	3	4	3	23							
Steinkjer	P4																		1	2	2	2	2	6							
Namsos	P4	3	2	3	5	5	2	6	11	14	8	16	12	19	11	11	13	13	18	19	19	28	32	270							
Meråker	P4						1	1					3	1	1									7							
Sjørdal	P4											1			1		2	2	1	1	5	4	1	18							
Verdal	P4						1	1	1	1	1	1	1	1	1	1	1	1			1	1	1	11							
Verran	P4																1	1			1	1	1	5							
Namdalseid	P4						2	1	1		1			1					1			2	1	10							
Snåsa	P4					1	1												1	1				3							
Grong	P4																		1	1				5							
Høylandet	P4																	1	1					3							
Total		511	874	969	1097	1220	1199	1451	1724	1952	1789	1651	1916	1677	1766	1877	2304	2948	3401	3773	3880	4853	4930	47762							