

Hierarchical path analysis of deer responses to direct and indirect effects of climate in northern forest

Atle Mysterud^{1,*}, Nigel G. Yoccoz², Rolf Langvatn³, Nathalie Pettorelli^{1,4}
and Nils Chr. Stenseth¹

¹*Centre for Ecological and Evolutionary Synthesis (CEES), Department of Biology, University of Oslo, PO Box 1066, Blindern, 0316 Oslo, Norway*

²*Institute of Biology, University of Tromsø, 9037 Tromsø, Norway*

³*Norwegian Institute for Nature Research, Tungasletta 2, 7085 Trondheim, Norway*

⁴*Institute of Zoology, Zoological Society of London, Regent's Park, London NW1 4RY, UK*

A problem in climate studies has been on how to treat causal chains of explanations and both direct and indirect effects. Mammals in strongly seasonal environments of the boreal forest typically lose condition during winter and gain mass (and reproduce) during the summer season when biomass and plant quality peak. Mass decay of large herbivores during winter is due to direct effects of winter weather, such as increased costs of movement, thermoregulation and reduced access to food when snow is deep. Deer condition during summer is thought to be affected mainly indirectly by weather through plants. High spring temperature speeds up plant development, and deep snow can delay phenology in early summer. Current statistical modelling does not take into account these mechanistic pathways. We used hierarchical Bayes modelling to more mechanistically link global climate, local weather and plant phenology to autumn body mass of red deer in Norway. Red deer were much more affected indirectly through trophic interactions. No solid evidence of direct effects of snow depth was found on autumn body mass. We discuss the implications of our results relative to our ability to predict effects of global change on large mammalian herbivores in the boreal forest.

Keywords: causal chains of explanation; hierarchical Bayes modelling; North Atlantic Oscillation; normalized difference vegetation index; scale of sampling

1. INTRODUCTION

There is increasing consensus among ecologists that climate change is affecting ecosystems (Stenseth *et al.* 2002; Walther *et al.* 2002, 2005; Parmesan 2006). Climate change and variability are not only affecting many species directly, but also through trophic interactions among species (Schmitz *et al.* 2003; Krebs & Bertheaux 2006). There is a huge variety in actual mechanisms by which animals can be affected by climatic variability. Even the same species may be limited by different weather variables depending on year or area. Increased winter mortality in the Soay sheep (*Ovis aries*) population on St Kilda, Scotland was due to years with strong winds, heavy rainfall or extreme cold when the population density was high (Hallett *et al.* 2004). While the red deer (*Cervus elaphus*) population on Rum, Scotland was most strongly affected by heavy winter rainfall (Post & Stenseth 1999), the red deer further north along the west coast of Norway were more strongly influenced by snow depth (Mysterud *et al.* 2000, 2001b; Pettorelli *et al.* 2005a). What unites all of these examples is the fact that they can be related to variation in a single

variable; the state of the North Atlantic Oscillation (NAO) during winter. However, the sign of the correlation of individual performance and the NAO may be opposite for the same species in different regions (Mysterud *et al.* 2003), suggesting local responses are complex.

There is currently somewhat of a gap between detailed studies of behavioural responses to local weather patterns and the literature linking global climate systems such as the NAO to animal performance. It has been argued that if you are mainly interested in good predictions, you should use the NAO and other coarse-scale indices (Stenseth *et al.* 2003). If you are interested in learning about mechanisms, you should use local weather variables (Krebs & Bertheaux 2006). We believe most ecologists are interested in both, and, clearly, to predict well it would be good to understand the mechanism. A well-studied ungulate system is the red deer along the west coast of Norway, having revealed both direct (Loison *et al.* 1999) and indirect (Mysterud *et al.* 2001b; Pettorelli *et al.* 2005a) effects of winter climate and direct effect of spring climate on population ecology and life history (figure 1). During winter, snow depth affects body mass loss (at least of yearlings, Loison & Langvatn (1998)), possibly due to extra energetic costs of movement in snow (Parker *et al.* 1984), thermoregulation (Parker & Robbins 1985) and reduced access to

* Author for correspondence (atle.mysterud@bio.uio.no).

One contribution of 12 to a Theme Issue 'The boreal forest and global change'.

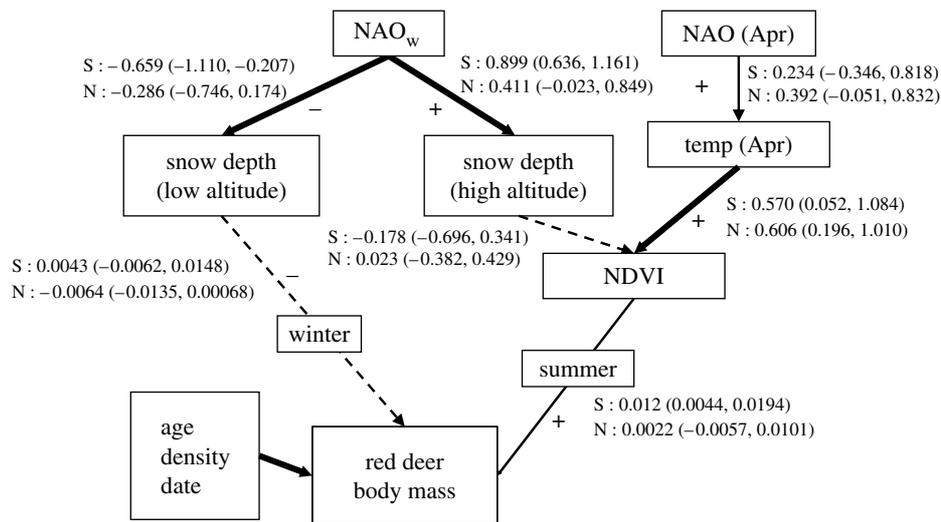


Figure 1. Path analysis diagram for how performance (body mass) of red deer is affected directly and indirectly by climate during summer and winter seasons in northern forests of Norway, 1982–2004. All lines in the diagram represent a specific linear model. Thick solid lines indicate good evidence for an effect (95% credible intervals do not include 0), a thin solid line indicates a weak relationship (credible intervals include 0 marginally) and a thin dotted line indicates no clear relationship. ‘+’, predicted positive effect and ‘-’, predicted negative effect. Regression coefficient estimates are given with their associated 95% credible intervals for the south (S: Kvinnherad) and north (N: Snillfjord/Orkdal) population. NAO_w , North Atlantic Oscillation index during winter months (December to March); $NAO (Apr)$, NAO during April; $NDVI$, Normalized Difference Vegetation Index; temp, temperature.

forage (Mysterud *et al.* 1997). However, since snow accumulation during winter affects early plant growth, plant phenology during spring is delayed at high elevation, leading to a more variable phenology after winters with a high NAO index and thus positively affecting body mass (Pettorelli *et al.* 2005a). Also, a warm April linked to a high phase of the NAO speeds up plant phenology, benefiting deer (Pettorelli *et al.* 2005a). Based on all of these studies, one can build a tentative mechanistic model on how the NAO probably impacts individual performance for this particular system (figure 1).

The main approach to investigate direct versus indirect effects is based on path analysis (Shipley 2002). Such methods are similar to linear models in the sense that they assume linear relationships among predictor and response variables, but they differ in the sense that they can assume that specific relationships do not exist: for example, one can assume that the NAO has an effect on red deer body mass only through its effect on snow depth and plant phenology. In our case, classical path models cannot be used because we have two levels of variability in the data: individual red deer body mass which depends on individual characteristics such as age or date of harvesting, as well as repetitive variables such as plant phenology, red deer density and climatic variables that are measured only on an annual basis. Our situation could therefore be seen as an example of hierarchical models (Draper 1995), but with specific restrictions concerning linear relationships among the variables. Such approaches are now implemented within the framework of hierarchical Bayes modelling (e.g. Clark & Gelfand 2006). Since data are recorded at two scales, these approaches are therefore suitable to more mechanistically link global climate (NAO), local weather (temperature and snow depth) and plant phenology (Normalized Difference

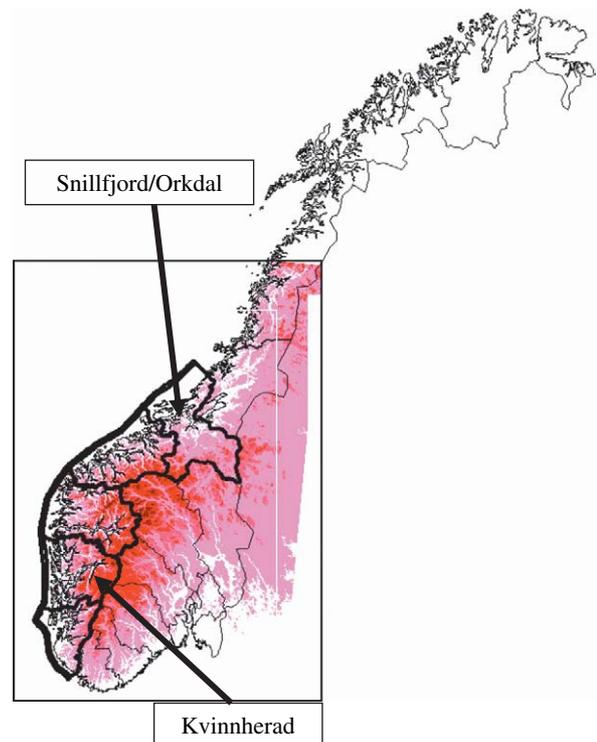


Figure 2. The location of the northern (Snillfjord/Orkdal) and southern (Kvinnherad) study sites of red deer along the southwest coast of Norway on a topographic map.

Vegetation Index, $NDVI$) to autumn body mass of red deer (*C. elaphus*) along the west coast of Norway.

2. MATERIAL AND METHODS

(a) Study area

Red deer are at their northern limit in Norway, mainly living in the hemiboreal (or boreonemoral) region (Abrahamsen *et al.* 1977). Exceptions are a small area around the Hardangerfjorden, Hordaland county, which is in the

nemoral zone, and some areas not far from the Trondheimsfjorden which is in the southern boreal zone. In Kvinnherad municipality (figure 2), Hordaland county, forests are dominated by deciduous and pine forest. However, there has been a large-scale programme for planting Norway spruce (*Picea abies* L.), which is an important winter habitat for red deer (Ahlén 1965). Snillfjord and Orkdal municipalities (figure 2), Sør-Trøndelag county, are dominated by birch (*Betula* spp. L.) and pine (*Pinus sylvestris* L.).

(b) Red deer data

The data derive from municipalities Kvinnherad, Hordaland county in the south and the adjacent municipalities Snillfjord and Orkdal, Sør-Trøndelag county in the north of the red deer distribution range along the southwest coast of Norway. The data used are a subset of the much larger dataset from the whole of the southwest coast (e.g. Mysterud *et al.* 2001b; Pettorelli *et al.* 2005a). The reason for selecting these areas is that data from most years between 1982 and 2004 are available (when data on NDVI have been gathered, see below), and as long a time frame as possible is important for considering climate effects.

Data on red deer derive from hunted animals. The hunting period lasts from 10 September to 15 November. Hunting is controlled through licenses issued by local wildlife boards in each municipality. For each deer, the sex, date, location (municipality) and dressed body mass, together with the mandibles, were provided by the hunters. Recorded body mass is dressed mass (i.e. live mass minus head, skin, viscera, bleedable blood and metapodials). Dressed mass in hinds is approximately 58% of live mass (Langvatn 1977) and highly correlated ($r=0.994$) with total mass in Cervids (Wallin *et al.* 1996). From the mandibles, we could age calves and yearlings based on tooth eruption patterns (Loe *et al.* 2004), whereas older animals were aged using annuli in the cementum of the first incisor (Hamlin *et al.* 2000).

It is well known that harvesting data may give bias in some cases (e.g. Martínez *et al.* 2005; Mysterud *et al.* 2006). However, for this time period in Norway, it is unlikely that harvesting bias is strong. Certainly, quotas (given as calf, yearling and adults of each sex) ensure that harvesting is not random. However, within these categories, and based on our detailed experience with the system, there is not likely to be strong selection for phenotypic traits such as body mass. Part of this is due to the hunting tradition, which is for meat and not for trophies (Milner *et al.* 2006). Part of this is also due to the large quotas and limited time for hunting, which for moose (*Alces alces*) populations have been shown to reduce selectivity (Solberg *et al.* 2000). It is simply a high cost in terms of lost chances to be selective in the forested habitat along the west coast of Norway, where group size of red deer is small (average of 1.5 female per male in mixed groups; Bonenfant *et al.* 2004). The only probable bias we may have (though not documented) is that females with offspring are less likely to be shot than females without (as reported for Norwegian moose populations; Nilsen & Solberg 2006). However, since most females from 3 to 13 years of age ovulate and are likely to calve (Langvatn *et al.* 2004), this is probably not an important factor. Further, any small bias this may yield has probably been constant over the time period, so that it is unlikely to interfere with the main factor of interest here, i.e. the climate effects.

(c) NDVI data

As a proxy for vegetative phenology (greenness), we used the NDVI which has been used extensively as a proxy of vegetation

dynamics (review in Pettorelli *et al.* 2005b). Data are collected by the National Oceanic and Atmospheric Administration satellites (<http://eosdata.gsfc.nasa.gov/>). From these, NDVI values (ranging from -1 to 1) have been produced from visible and near-infrared reflectance measurements ($\text{NDVI} = (\text{NIR} - \text{RED}) / (\text{NIR} + \text{RED})$, where NIR is the near infrared light reflected by the vegetation and RED is the red visible light reflected by the vegetation). The spatial scale of resolution (pixel size) is 64 km^2 and an NDVI value is available on a 10-day basis, from 13 July 1981 to present. Based on an earlier study (Pettorelli *et al.* 2005a), we chose to use NDVI on 1 May as a measure of the greenness in spring, which is the average date of vegetation start in the study area along the west coast of Norway. There are 25 pixels for Kvinnherad, 11 pixels for Orkdal and 10 pixels for Snillfjord.

The NDVI data can be processed in different ways to remove errors (review in Pettorelli *et al.* 2005b). In a previous analysis (Pettorelli *et al.* 2005a), we used the so-called PAL data that are no longer updated, while we here use the GIMMS data which are considered the best time series of the NDVI currently available. At the scale of each specific municipality, the mean and standard deviation of NDVI-GIMMS on 1 May (per year for all pixels) are highly correlated (Kvinnherad: $r=0.806$ [$r=0.939$]; Orkdal: $r=0.813$ [$r=0.901$]; Snillfjord: $r=-0.093$ [$r=0.686$])—values in brackets are correlations obtained after removing the extreme outlying value for 1987). As this is not the case with the PAL data (figure 3), it is probable that this is related to the different error processing. It is likely, but remains to be determined, whether this is related to the use of a spatial smoother (krieging). We therefore only use the mean of NDVI in further modelling.

(d) Global climate and local weather data

We used the principal component analysis (PCA)-based winter (December–March; hereafter termed NAO_w) and April index of the NAO (Hurrell 1995; Hurrell *et al.* 2003) as our global-scale climate index. The NAO_w has a strong impact on the population ecology of red deer along the southwest coast of Norway (Post *et al.* 1997; Mysterud *et al.* 2000, 2001b, 2005; Pettorelli *et al.* 2005a). In previous studies we have shown that there is an interaction between global climate (NAO_w) and topography that determines local weather conditions (Mysterud *et al.* 2000; Pettorelli *et al.* 2005a). We therefore know that a high NAO_w index is correlated with less snow at low elevation, which corresponds to the main wintering areas of red deer (Albon & Langvatn 1992). We therefore use snow depth at low elevation when it comes to the possible direct effect of winter weather on red deer body mass. In contrast, a high NAO_w index is correlated with more snow at high elevation, which extends into the summer ranges of red deer (some deer do remain at low elevation during summer as well). We therefore used data deriving from high elevation to measure any indirect effect of snow depth working through plant phenological development. The NAO in April is positively correlated with temperature and an early start of the growing season (Pettorelli *et al.* 2005a).

There are a large number of meteorological stations along the west coast of Norway, but not all municipalities have weather stations and not all of them cover the years 1982–2004. A further problem is that few of them measure temperature, while many measure precipitation owing to the importance of hydropower in Norway. It is also experienced that temperature is more spatially correlated than precipitation (including snow depth). We therefore searched for stations within or as close to the municipality of interest as

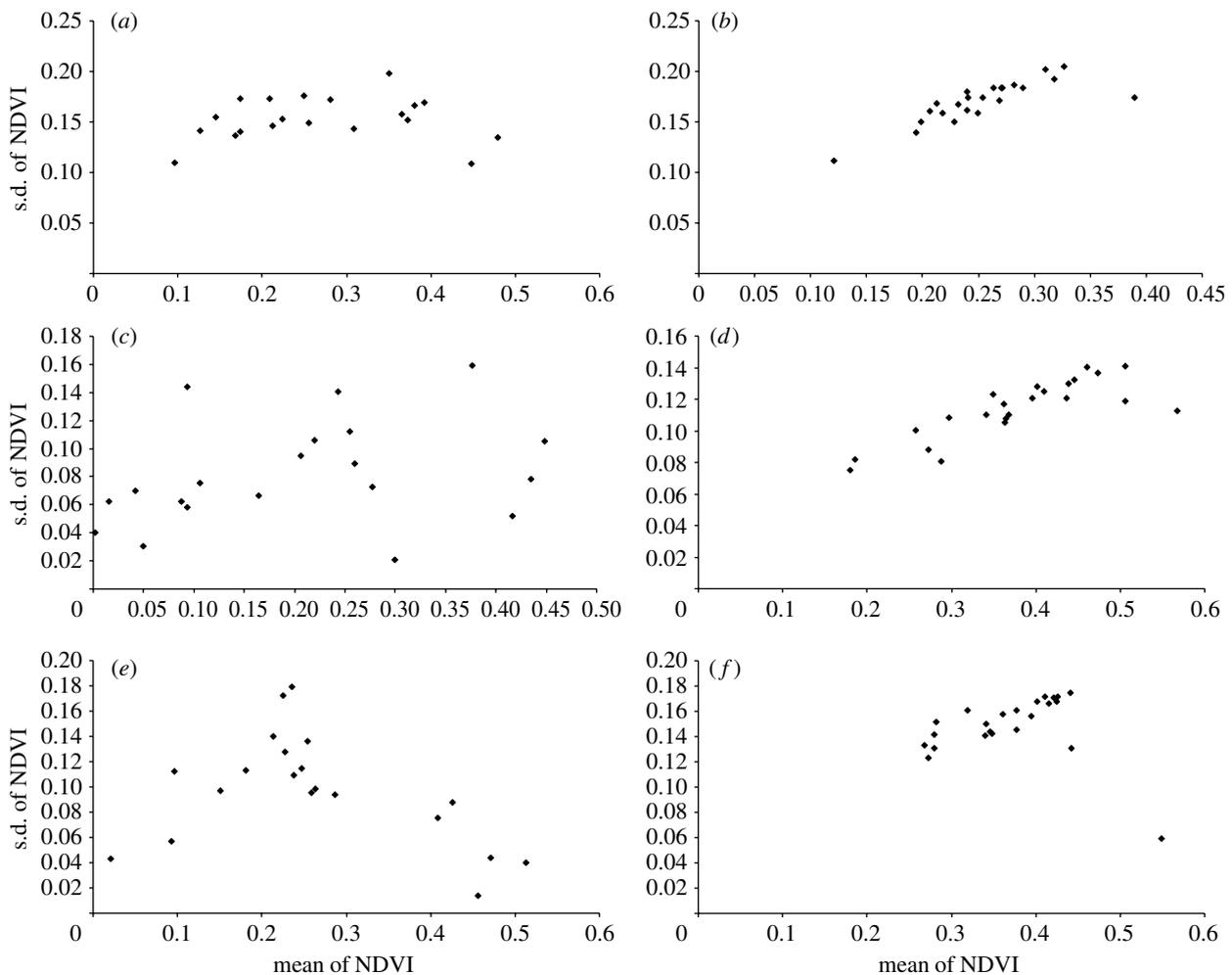


Figure 3. The relationship between mean and standard deviation of NDVI on 1 May each year in municipalities Kvinnherad (south) and Orkdal and Snillfjord (north). (*a,c,e*) The old PAL series (1982–2001); (*a*) Kvinnherad-NDVI, (*c*) Orkdal-NDVI and (*e*) Snillfjord-NDVI, while (*b,d,f*) are the new GIMMS series (1982–2004), (*b*) Kvinnherad-NDVI, (*d*) Orkdal-NDVI and (*f*) Snillfjord-NDVI).

possible. However, we also paid particular attention to the elevation and distance from the coast, so as to find as representative weather stations as possible for both high and low elevation for each municipality.

For Kvinnherad, we used the weather station at Eidfjord-Bu (no. 49580) at 165 m a.s.l. for temperature in April, Sauda (no. 46610) at 5 m a.s.l. for snow depth (average of max) at low elevation during December–March, while we used the station at Liset (no. 49750; Eidfjord) at 748 m a.s.l. for snow depth at high elevation. For Snillfjord and Orkdal, we used stations at Tingvoll-Hanem (no. 64550; Møre og Romsdal) at 69 m a.s.l. for temperature in April, Sandstad (no. 65450 Hitra; Sør-Trøndelag) at 20 m a.s.l. for snow depth at low elevation and Hafsås, Sunndal and Møre og Romsdal (no. 63530) at 698 m a.s.l. for snow depth at high elevation.

(e) Other covariates

As data for each analysis below derive from a single or two adjacent municipalities, we did not need to enter the spatial covariates we frequently use to control for imbalance in the sampling design (e.g. Mysterud *et al.* 2001a). For Snillfjord and Orkdal, we entered municipality as a factor. We also entered an index for population size, which has affected body mass more than climate over this time period (Mysterud *et al.* 2001c). When analysing data from a single municipality, we only entered the harvest size. When analysing the two adjacent municipalities Snillfjord and Orkdal, we used

instead the harvest size relative to the amount of red deer habitat (as in previous analysis; Mysterud *et al.* 2001c). Over the study period, the number of harvested red deer increased from 314 in 1982 to 805 in 2004 in Kvinnherad, from 57 to 280 in Orkdal and from 100 in 1982 to 323 in 2004 in Snillfjord. Based on reconstruction of cohorts, it is safe to assume that the annual harvest is fairly well correlated with the actual population size (Mysterud *et al.* 2007). We also entered date of harvest to control for possible growth or decay during the hunting season.

(f) Statistical analyses

We used hierarchical Bayes modelling with sampling-based methods for fitting and analysis (see Clark & Gelfand (2006) for an introduction). Models included a specification of relationships among environmental variables (climate and NDVI) on one hand (with years as units) and individual body mass and other covariates (date of harvest and density index) on the other (with deer as units). Linear models were used throughout (except splines for modelling nonlinear relationship between body mass and age; see below). These linear models were therefore defined at two levels of variability: years for phenology and climatic variables, and individual deer for body mass. Yearly values for variables such as phenology that are used to predict body mass are assumed to be functions of other climatic variables such as spring temperature or snow depth, but uncertainties in the

relationships is taken into account in such models (something one cannot do using, for example, residuals, such as body mass standardized by age and shooting date). Graphical models with two levels of variation can be fitted in a Bayesian framework. Bayesian methods assume prior distributions for model parameters (regression coefficients and residual variances) and use Bayes' theorem to derive the posterior distributions of parameters. Numerical methods based on Markov Chain Monte Carlo simulations are used to derive posterior distributions. Model fitting and model diagnostics (in particular, the convergence of numerical simulations) were done using the library BRugs and coda in the R environment (R Development Core Team 2006; Thomas *et al.* 2006), using R v. 2.4.0. Prior distributions are usually chosen so as to be uninformative, for example, a normal distribution with mean 0 and a very large variance for a regression coefficient. The following prior distributions were used: normal for regression intercepts and slopes with a mean of 0 and a variance of 10^6 , and Gamma for the inverse of residual variances with shape and scale parameters 0.001 and 0.001, respectively. An initial burn-in of 20 000 iterations was used, and posterior distributions of parameters were based on 20 000 more iterations. We used three chains to check for the stability of posterior distribution estimates (as recommended, for example, in Clark & Gelfand (2006)), and assessed convergence and autocorrelation using the diagnostics tools available in BRugs and coda (e.g. convergence test based on Gelman & Rubin (1992)). We fitted different models with varying levels of complexity regarding the relationships among climatic variables and phenology. Model selection was partly based on our *a priori* expectations regarding direct and indirect effects, credible intervals and the deviance information criterion (DIC), which trades off the fit of the model as measured by the posterior expected deviance (\bar{D}) and the complexity of the model as measured by the effective number of parameters (P_D). DIC is a criterion similar to AIC, in the sense of finding a compromise between model fit and model complexity ($DIC = \bar{D} + P_D$). As sample size is hard to define in models with two levels of variability (e.g. Vaida & Blanchard 2005), DIC is based on an estimate of effective sample size directly based on data and model used.

We only present the final results, focusing on the median of posterior distributions and 95% credible intervals (i.e. intervals that cover 95% of the posterior distribution) to interpret effect sizes and their associated uncertainty. More complex models gave similar estimates for regression coefficients, but did always include parameter estimates with credible intervals including 0.

Linearity and residuals were assessed initially using additive models (AM; Hastie & Tibshirani 1990; Wood 2006). Based on previous work on the system, we have a good idea on what to expect. We focused on females only, as males lose much body mass during the rutting season, making it much more complex to model annual mass (Yoccoz *et al.* 2002). As age explains most of body mass variation, it is important to model this correctly (Mysterud *et al.* 2001c; Yoccoz & Gaillard 2006). We ended up pooling all individuals above 12 years of age (few individuals are older than 12 years of age and estimates were therefore not reliable). Based on the AM plotting, we then fitted a third-order polynomial from 0 to 3 years of age, and thereafter a linear segment. This is thus a kind of threshold model for age but using the same first-order derivative for 3 years of age as for a regular spline. At the scale of municipality, the mean and standard deviation of the NDVI was highly positively correlated (see above and figure 3), and we therefore retained

the mean of NDVI for further modelling. All variables except age were standardized (mean = 0, s.d. = 1) to make estimates more stable and easier to compare.

3. RESULTS

(a) Relationship among environmental variables
An overview of predicted relations as well as estimated effects is presented in figure 1 (all parameters in table 1). The behaviour of numerical chains was found to be satisfactory (e.g. all scale reduction factors were estimated as 1; Gelman & Rubin 1992) and the sample size corrected for autocorrelation used to calculate posterior distributions and credible intervals was at least 15 000 for all parameters. All posterior distributions were approximately normal (figure 4). As expected from previous work (Mysterud *et al.* 2000), the NAO during winter had a negative effect on snow depth at low elevation (winter range), while the effect is opposite at high elevation (summer range; figure 1; table 1). This effect was slightly more marked in the south (Kvinnherad) than in the north (Snillfjord/Orkdal), probably due to the fact that with increasing latitude the overall winter temperature is colder, making the difference in snow fall due to elevation smaller (snowing further down for a given NAO_w value). Also as expected, the NAO in April has a positive effect on temperature in April (Pettorelli *et al.* 2005a); however, the 95% credible intervals included 0 and the evidence was therefore not strong. Temperature in April in turn strongly influenced the NDVI on 1 May. The effect of snow depth on the NDVI on 1 May (associated with increased variability in NDVI) was weakly negative, but the evidence for the effect was weak. There was no evidence for a direct effect of the NAO_w on NDVI, after controlling for the weak effect of snow depth on NDVI.

(b) Effect of environmental variables on body mass

There was a fairly strong effect of the NDVI on body mass, especially in the south (the evidence for such an effect being weaker in the north), while we found no clear evidence of a direct effect of winter snow depth on red deer (figure 1). Mass decay of deer during winter in these coastal areas was thus much less important for autumn mass than the increase in deer condition during summer which is mainly affected indirectly by climate through plants (i.e. trophic interactions). As known, the effects of age and population density on body mass of red deer were marked (figure 4).

4. DISCUSSION

Boreal forests are situated at northern latitudes and there is naturally a strong seasonality in the way climate affects deer populations. Our analysis suggests that summer fattening linked to plant phenology development during summer is a more important climatic factor for body condition in autumn than winter decay related to snow depth. Though body mass development of yearlings during winter is linked to winter harshness (snow and temperature pooled in PCA; Loison & Langvatn 1998), it is evident from our analysis that the magnitude of these effects are much smaller, being

Table 1. Results from the hierarchical path analysis of how climate affects red deer autumn body mass from Norway, years 1982–2004. (All variables except age and municipality are standardized. Effect of age assumes a threshold at 3 years of age, with a third-order cubic term for younger individuals and a linear effect only for older individuals.)

parameter	estimate	95% credible intervals	
		lower limit	upper limit
<i>southern: Kvinnherad</i>			
effect on body mass			
intercept	4.005	3.995	4.014
NAO _w	0.004681	−0.00388	0.01324
NDVIm	0.01193	0.004433	0.01944
age (linear effect)	0.01223	0.009796	0.01467
age (cubic term, for age ≤ 3)	0.03052	0.02969	0.03135
density index	−0.01938	−0.02781	−0.0109
date of harvesting	0.008463	0.002031	0.01491
snow—low altitude	0.004305	−0.00618	0.0148
indirect effects—operating on other environmental variables			
snow (high altitude) → NDVIm	−0.1779	−0.6962	0.3414
tmp (Apr) → NDVIm	0.5701	0.05162	1.084
NAO _w → snow (high altitude)	0.8988	0.6355	1.161
NAO _w → snow (low altitude)	−0.6591	−1.11	−0.2066
NAO (Apr) → tmp (Apr)	0.2338	−0.3459	0.8177
<i>northern: Snillfjord and Orkdal</i>			
effect on body mass			
intercept	4.092	4.081	4.103
NAO _w	−0.00385	−0.01238	0.004664
NDVIm	0.00220	−0.00569	0.01008
age (linear effect)	0.01667	0.01409	0.01926
age (cubic term, for age ≤ 3)	0.02801	0.02722	0.02880
density index	−0.02792	−0.03623	−0.01956
date of harvesting	0.01769	0.01045	0.02493
municipality	−0.00838	−0.02452	0.00770
snow (low altitude)	−0.00644	−0.01353	0.00067
indirect effects—operating on other environmental variables			
snow (high altitude) → NDVIm	0.02327	−0.3855	0.4303
tmp (Apr) → NDVIm	0.6056	0.1973	1.015
NAO _w → snow (high altitude)	0.4126	−0.0238	0.8495
NAO _w → snow (low altitude)	−0.2863	−0.7458	0.1745
NAO (Apr) → tmp (Apr)	0.3916	−0.0498	0.8324

overshadowed by the indirect effect operating through plants. The winter NAO markedly affects pattern of snow accumulation (Mysterud *et al.* 2000) and thus increases variation in plant phenology as measured by the NDVI at broad population scales (Pettorelli *et al.* 2005a). It has been shown that the NAO operates through increased soil moisture, which affects plant growth during summer (Kettlewell *et al.* 2006). Our study lends some further support to such indirect effects, but evidence pointed mainly to an effect of spring climatic conditions on plant phenology (see also Stewart *et al.* 2005). This does not necessarily imply that summer is more important than winter for population dynamics. The ‘Klein hypothesis’ (1965) states that while summer season determines the quality of the animals (body mass), winter is the more critical period for limiting deer population sizes. Summer foraging conditions are decisive for condition during rut and thus most important for breeding (Langvatn *et al.* 2004). Body mass in autumn also has an effect on winter survival of calves (Loison & Langvatn 1998).

Current work on climate effects on mammals has been criticized: ‘correlations abound but mechanistic

understanding is limited owing to long causal chains and indirect effects’ (Krebs & Berteaux 2006). Path analysis is intuitively appealing to biologists, as it offers a good solution to issues related to causal chains of explanations. It is indeed very common that there are clear mechanistic hypotheses for how the environmental factors of interest are related to each other (in our case reviewed in figure 1). There are a number of reported mechanistic ways by which weather is known to affect different deer populations in northern areas in general (e.g. Weladji *et al.* 2002), and explicitly being able to quantify the relative role of each of these factors for a specific population is exciting. However, a limitation with ordinary path analysis is that it requires data on a similar scale. Data on seasonal climate indices typically have one value per year, while data on animals are typically numerous. Using a yearly average is problematic because other covariates such as age vary among individuals and years. Moreover, this will greatly decrease the precision of estimated effects. While it is clearly important to have long time series in order to estimate precisely temporal changes, methods that explicitly take into account different levels of variation

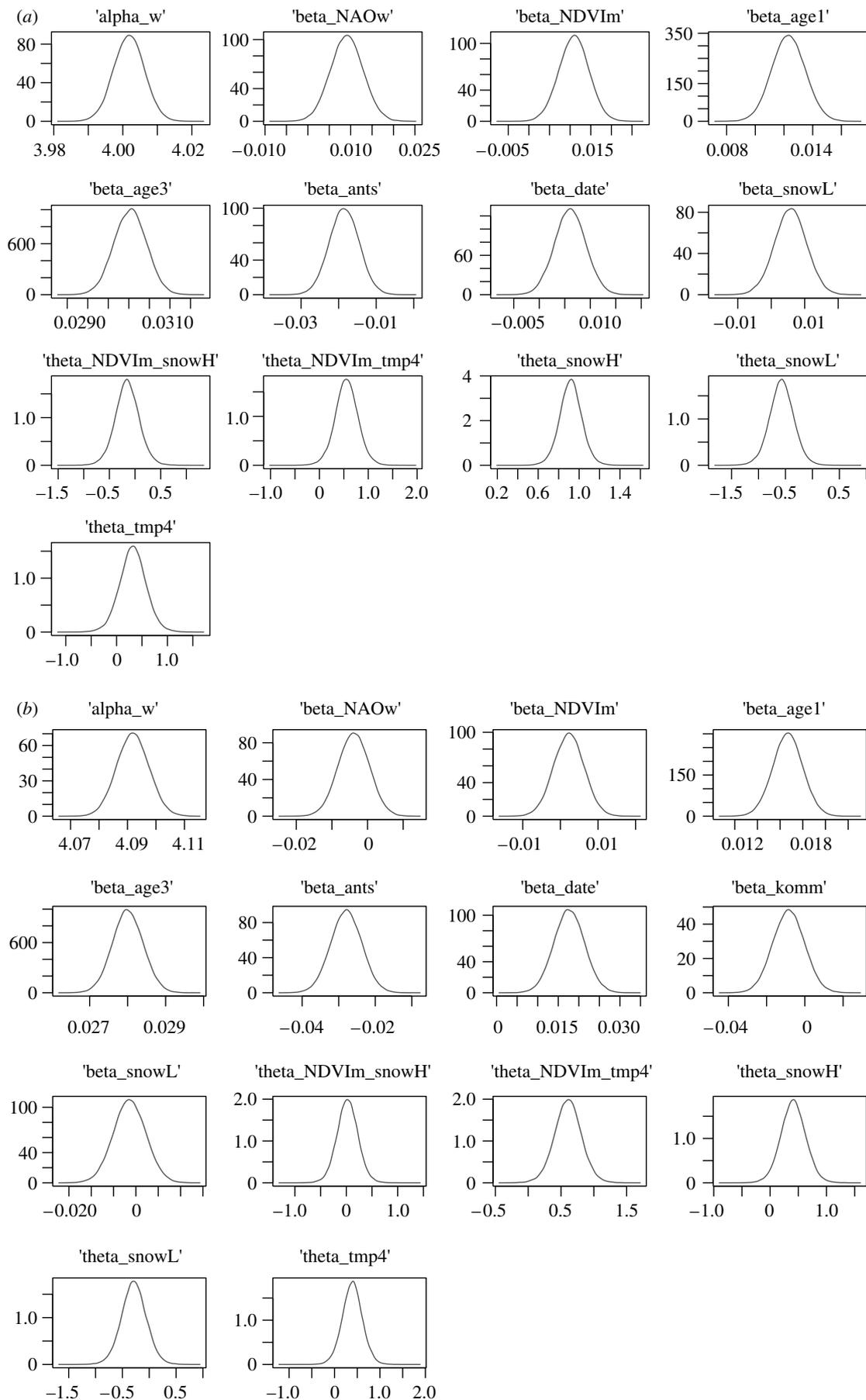


Figure 4. The distributions of the estimated parameters (estimates along x -axis) were approximately normal for both populations. (a) Kvinnherad municipality (south) and (b) Snillfjord/Orkdal municipality (north) ('alpha', intercept; 'beta', effects on body mass of red deer and 'theta', effects among climate variables (figure 1). NAO_w, North Atlantic Oscillation index during winter months; NDVI_m, mean of the NDVI on 1 May; 'age 1' and 'age 3', age effects (see §2); 'ants', density index; 'date', date of harvest; 'snowL', snow depth at low elevation; 'snowH', snow depth at high elevation and 'tmp4', temperature in April).

as well as direct and indirect effects represent an important development (Clark & Gelfand 2006). Our use of hierarchical Bayes modelling is novel in this respect, enabling us to fully use the potential of the data at a subpopulation scale.

Some of the relationships we have reported in previous analyses at broader scales (Mysterud *et al.* 2000, 2001*b*; Pettorelli *et al.* 2005*a*) are nevertheless not significant or weaker here (figure 1). The relationships are much stronger in the southern (Kvinnherad) compared with the northern area (Orkdal/Snillfjord); this result was expected due to the stronger impact of the NAO further south (figure 1). The relationship between the NAO and temperature in April was as predicted, though not significant, probably due to inclusion of data from only a single weather station. A more complicated issue is the one between the NAO_w, snow depth and NDVI. More snow is predicted to delay the NDVI, but since increases in the NAO_w give more snow at high elevation and less snow at low elevation, we expect mainly increased variance in NDVI with increasing NAO_w. However, mean and variance of the NDVI were highly correlated and not possible to separate. It remains to be determined with certainty whether this is related to the spatial smoothing of the NDVI-GIMMS data; in any case, it limits the value of this part of the analysis. Also, the scale of the NDVI is 8 × 8 km; thus, the NDVI is measured over many elevations, making it difficult to capture year-related variation in phenology at the relevant scale within a municipality. In the previous analysis (Pettorelli *et al.* 2005*a*) we found that the effect of the NAO_w interacted with the proportion of high-elevation habitat within a municipality (i.e. a very coarse scale), thus increasing variance in NDVI at high NAO. Clearly, more fine-scale data on the NDVI would be rewarding to determine with more precision how plant phenology is linked to snow accumulation at the scale of deer movements. Newer satellites such as MODIS might provide insights in that respect.

Forecasting and predicting effects of global climate change on mammal populations are challenging (Berteaux *et al.* 2006). To progress, we need statistical tools to link the various datasets in better ways so as to solve frequent problems of data that are measured at different scales. Hierarchical path analysis as outlined here solves some of these issues. We can now link the NAO to environmental variables in the same model as the deer data, even though datasets are not replicated at the same scale. Whether such approaches will enable better predictions remains to be seen. Integrating possible interactions with age and/or density is also important in future studies (Coulson *et al.* 2001). There is somewhat of a limitation that the correlation between the NAO and local weather variables may change between periods (Mysterud *et al.* 2003). Indeed, the strength of correlation between the NAO and performance of animals and birds therefore similarly varies over time (Durant *et al.* 2004), and a stronger focus on regime shifts in ecology linked to climate may be necessary (Hörnfeldt 2004; Hörnfeldt *et al.* 2005; Smith *et al.* 2006).

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REFERENCES

- Abrahamsen, J., Jacobsen, N. K., Kalliola, R., Dahl, E., Wilborg, L. & Pahlsson, L. 1977 Naturgeografisk regioninndeling av Norden. *Nord. Utredn. Ser. B* **34**, 1–135.
- Ahlén, I. 1965 Studies on the red deer, *Cervus elaphus* L., in Scandinavia. *Swed. Wildl. Res.* **3**, 177–376.
- Albon, S. D. & Langvatn, R. 1992 Plant phenology and the benefits of migration in a temperate ungulate. *Oikos* **65**, 502–513. (doi:10.2307/3545568)
- Berteaux, D. *et al.* 2006 Constraints to projecting the effects of climate change on mammals. *Clim. Res.* **32**, 151–158. (doi:10.3354/cr032151)
- Bonenfant, C., Loe, L. E., Mysterud, A., Langvatn, R., Stenseth, N. C., Gaillard, J.-M. & Klein, F. 2004 Multiple causes of sexual segregation in European red deer: enlightenments from varying breeding phenology at high and low latitude. *Proc. R. Soc. B* **271**, 883–892. (doi:10.1098/rspb.2003.2661)
- Clark, J. S. & Gelfand, A. E. 2006 *Hierarchical modelling for the environmental sciences*. Oxford, UK: Oxford University Press.
- Coulson, T., Catchpole, E. A., Albon, S. D., Morgan, B. J. T., Pemberton, J. M., Clutton-Brock, T. H., Crawley, M. J. & Grenfell, B. T. 2001 Age, sex, density, winter weather, and population crashes in Soay sheep. *Science* **292**, 1528–1531. (doi:10.1126/science.292.5521.1528)
- Draper, D. 1995 Inference and hierarchical modeling in the social sciences. *J. Edu. Behav. Stat.* **20**, 115–147. (doi:10.2307/1165353)
- Durant, J. M., Anker-Nilssen, T., Hjermann, D. Ø. & Stenseth, N. C. 2004 Regime shifts in the breeding of an Atlantic puffin population. *Ecol. Lett.* **7**, 388–394. (doi:10.1111/j.1461-0248.2004.00588.x)
- Gelman, A. & Rubin, D. B. 1992 Inference from iterative simulation using multiple sequences. *Stat. Sci.* **7**, 457–511.
- Hallett, T. B., Coulson, T., Pilkington, J. G., Clutton-Brock, T. H., Pemberton, J. M. & Grenfell, B. 2004 Why large-scale climate indices seem to predict ecological processes better than local weather. *Nature* **430**, 71–75. (doi:10.1038/nature02708)
- Hamlin, K. L., Pac, D. F., Sime, C. A., DeSimone, R. M. & Dusek, G. L. 2000 Evaluating the accuracy of ages obtained by two methods for Montana ungulates. *J. Wildl. Manage.* **64**, 441–449. (doi:10.2307/3803242)
- Hastie, T. & Tibshirani, R. 1990 *Generalized additive models*. London, UK: Chapman and Hall.
- Hörnfeldt, B. 2004 Long-term decline in numbers of cyclic voles in boreal Sweden: analysis and presentation of hypotheses. *Oikos* **107**, 376–392. (doi:10.1111/j.0030-1299.2004.13348.x)
- Hörnfeldt, B., Hipkiss, T. & Eklund, U. 2005 Fading out of vole and predator cycles? *Proc. R. Soc. B* **272**, 2045–2049. (doi:10.1098/rspb.2005.3141)
- Hurrell, J. W. 1995 Decadal trends in the North Atlantic Oscillation: regional temperatures and precipitation. *Science* **269**, 676–679. (doi:10.1126/science.269.5224.676)
- Hurrell, J. W., Kushnir, Y., Ottersen, G. & Visbeck, M. 2003 *The North Atlantic Oscillation. Climatic significance and environmental impact*. Washington, DC: American Geophysical Union.
- Kettlewell, P. S., Easey, J., Stephenson, D. B. & Poulton, P. R. 2006 Soil moisture mediates association between the

- winter North Atlantic Oscillation and summer growth in the Park Grass experiment. *Proc. R. Soc. B* **273**, 1149–1154. (doi:10.1098/rspb.2005.3428)
- Klein, D. R. 1965 Ecology of deer range in Alaska. *Ecol. Monogr.* **35**, 259–284. (doi:10.2307/1942139)
- Krebs, C. J. & Berteaux, D. 2006 Problems and pitfalls in relating climate variability to population dynamics. *Clim. Res.* **32**, 143–149. (doi:10.3354/cr032143)
- Langvatn, R. 1977 *Criteria of physical condition, growth and development in Cervidae—suitable for routine studies*. Stockholm, Sweden: Nordic Council for Wildlife Research.
- Langvatn, R., Mysterud, A., Stenseth, N. C. & Yoccoz, N. G. 2004 Timing and synchrony of ovulation in red deer constrained by short northern summers. *Am. Nat.* **163**, 763–772. (doi:10.1086/383594)
- Loe, L. E., Meisingset, E. L., Mysterud, A., Langvatn, R. & Stenseth, N. C. 2004 Phenotypic and environmental correlates of tooth eruption in red deer (*Cervus elaphus*). *J. Zool. Lond.* **262**, 83–89. (doi:10.1017/S0952836903004436)
- Loison, A. & Langvatn, R. 1998 Short- and long-term effects of winter and spring weather on growth and survival of red deer in Norway. *Oecologia* **116**, 489–500. (doi:10.1007/s004420050614)
- Loison, A., Langvatn, R. & Solberg, E. J. 1999 Body mass and winter mortality in red deer calves: disentangling sex and climate effects. *Ecography* **22**, 20–30. (doi:10.1111/j.1600-0587.1999.tb00451.x)
- Martínez, M., Rodríguez, V., Jones, O. R., Coulson, T. & San Miguel, A. 2005 Different hunting strategies select for different weights in red deer. *Biol. Lett.* **1**, 353–356. (doi:10.1098/rsbl.2005.0330)
- Milner, J. M., Bonenfant, C., Mysterud, A., Gaillard, J.-M., Csányi, S. & Stenseth, N. C. 2006 Temporal and spatial development of red deer harvesting in Europe—biological and cultural factors. *J. Appl. Ecol.* **43**, 721–734. (doi:10.1111/j.1365-2664.2006.01183.x)
- Mysterud, A., Bjørnsen, B. H. & Østbye, E. 1997 Effects of snow depth on food and habitat selection by roe deer *Capreolus capreolus* along an altitudinal gradient in south-central Norway. *Wildl. Biol.* **3**, 27–33.
- Mysterud, A., Yoccoz, N. G., Stenseth, N. C. & Langvatn, R. 2000 Relationships between sex ratio, climate and density in red deer: the importance of spatial scale. *J. Anim. Ecol.* **69**, 959–974. (doi:10.1046/j.1365-2656.2000.00454.x)
- Mysterud, A., Langvatn, R., Yoccoz, N. G. & Stenseth, N. C. 2001a Plant phenology, migration and geographic variation in body weight of a large herbivore: the effect of a variable topography. *J. Anim. Ecol.* **70**, 915–923. (doi:10.1046/j.0021-8790.2001.00559.x)
- Mysterud, A., Stenseth, N. C., Yoccoz, N. G., Langvatn, R. & Steinheim, G. 2001b Nonlinear effects of large-scale climatic variability on wild and domestic herbivores. *Nature* **410**, 1096–1099. (doi:10.1038/35074099)
- Mysterud, A., Yoccoz, N. G., Stenseth, N. C. & Langvatn, R. 2001c The effects of age, sex and density on body weight of Norwegian red deer: evidence of density-dependent senescence. *Proc. R. Soc. B* **268**, 911–919. (doi:10.1098/rspb.2001.1585)
- Mysterud, A., Stenseth, N. C., Yoccoz, N. G., Ottersen, G. & Langvatn, R. 2003 The response of the terrestrial ecosystems to climate variability associated with the North Atlantic Oscillation. In *The North Atlantic Oscillation* (eds J. W. Hurrell, Y. Kushnir, G. Ottersen & M. Visbeck), pp. 235–262. Washington, DC: American Geophysical Union.
- Mysterud, A., Meisingset, E. L., Langvatn, R., Yoccoz, N. G. & Stenseth, N. C. 2005 Climate-dependent allocation of resources to secondary sexual traits in red deer. *Oikos* **111**, 245–252. (doi:10.1111/j.0030-1299.2005.14197.x)
- Mysterud, A., Tryjanowski, P. & Panek, M. 2006 Selectivity of harvesting differs between local and foreign roe deer hunters: trophy stalkers have the first shot at the right place. *Biol. Lett.* **2**, 632–635. (doi:10.1098/rsbl.2006.0533)
- Mysterud, A., Meisingset, E. L., Veiberg, V., Langvatn, R., Solberg, E. J., Loe, L. E. & Stenseth, N. C. 2007 Monitoring population size of red deer: an evaluation of two types of census data from Norway. *Wildl. Biol.* **13**, 285–298. (doi:10.2981/0909-6396(2007)13[285:MPSO RD]2.0.CO;2)
- Nilsen, E. B. & Solberg, E. J. 2006 Patterns of hunting mortality in Norwegian moose (*Alces alces*) populations. *Eur. J. Wildl. Res.* **52**, 153–163. (doi:10.1007/s10344-005-0023-1)
- Parker, K. L. & Robbins, C. T. 1985 Thermoregulation in ungulates. In *Bioenergetics of wild herbivores* (eds R. J. Hudson & R. G. White), pp. 161–182. Boca Raton, FL: CRC Press, Inc.
- Parker, K. L., Robbins, C. T. & Hanley, T. A. 1984 Energy expenditure for locomotion by mule deer and elk. *J. Wildl. Manage.* **48**, 474–488. (doi:10.2307/3801180)
- Parmesan, C. 2006 Ecological and evolutionary responses to recent climate change. *Annu. Rev. Ecol. Evol. Syst.* **37**, 637–669. (doi:10.1146/annurev.ecolsys.37.091305.110100)
- Pettorelli, N., Mysterud, A., Yoccoz, N. G., Langvatn, R. & Stenseth, N. C. 2005a Importance of climatological downscaling and plant phenology for red deer in heterogeneous landscapes. *Proc. R. Soc. B* **272**, 2357–2364. (doi:10.1098/rspb.2005.3218)
- Pettorelli, N., Vik, J. O., Mysterud, A., Gaillard, J.-M., Tucker, C. & Stenseth, N. C. 2005b Using the satellite-derived normalized difference vegetation index (NDVI) to assess ecological responses to environmental change. *Trends Ecol. Evol.* **20**, 503–510. (doi:10.1016/j.tree.2005.05.011)
- 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. *Proc. R. Soc. B* **264**, 1317–1324. (doi:10.1098/rspb.1997.0182)
- R Development Core Team 2006 *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Schmitz, O. J., Post, E., Burns, C. E. & Johnstone, K. M. 2003 Ecosystem responses to global climate change: moving beyond color mapping. *BioScience* **53**, 1199–1205. (doi:10.1641/0006-3568(2003)053[1199:ERTGCC]2.0.CO;2)
- Shipley, B. 2002 *Cause and correlation in biology: a user's guide to path analysis, structural equations and causal inference*. Cambridge, UK: Cambridge University Press.
- Smith, M. J., White, A., Lambin, X., Sherratt, J. A. & Begon, M. 2006 Delayed density-dependent season length alone can lead to rodent population cycles. *Am. Nat.* **167**, 695–704. (doi:10.1086/503119)
- Solberg, E. J., Loison, A., Sæther, B.-E. & Strand, O. 2000 Age-specific harvest mortality in a Norwegian moose *Alces alces* population. *Wildl. Biol.* **6**, 41–52.
- Stenseth, N. C., Mysterud, A., Ottersen, G., Hurrell, J. W., Chan, K.-S. & Lima, M. 2002 Ecological effects of climate fluctuations. *Science* **297**, 1292–1296. (doi:10.1126/science.1071281)

- Stenseth, N. C., Ottersen, G., Hurrell, J. W., Mysterud, A., Lima, M., Chan, K.-S., Yoccoz, N. G. & Ådlandsvik, B. 2003 Studying climate effects on ecology through the use of climate indices: the North Atlantic Oscillation, El Niño Southern Oscillation and beyond. *Proc. R. Soc. B* **270**, 2087–2096. (doi:10.1098/rspb.2003.2415)
- Stewart, K. M., Bowyer, R. T., Dick, B. L., Johnson, B. K. & Kie, J. G. 2005 Density-dependent effects on physical condition and reproduction in North American elk: an experimental test. *Oecologia* **143**, 85–93. (doi:10.1007/s00442-004-1785-y)
- Thomas, A., O'Hara, R. B., Ligges, U. & Sturtz, S. 2006 Making BUGS open. *R News* **6**, 12–17.
- Vaida, F. & Blanchard, S. 2005 Conditional Akaike information for mixed-effects models. *Biometrika* **92**, 351–370. (doi:10.1093/biomet/92.2.351)
- Wallin, K., Cederlund, G. & Pehrson, Å. 1996 Predicting body mass from chest circumference in moose *Alces alces*. *Wildl. Biol.* **2**, 53–58.
- Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T. J. C., Fromentin, J.-M., Hoegh-Guldberg, O. & Bairlein, F. 2002 Ecological responses to recent climate change. *Nature* **416**, 389–395. (doi:10.1038/416389a)
- Walther, G.-R., Hughes, L., Vitousek, P. & Stenseth, N. C. 2005 Consensus on climate change. *Trends Ecol. Evol.* **20**, 648–649. (doi:10.1016/j.tree.2005.10.008)
- Weladji, R. B., Klein, D. R., Holand, Ø. & Mysterud, A. 2002 Comparative response of *Rangifer tarandus* and other northern ungulates to climatic variability. *Rangifer* **22**, 33–50.
- Wood, S. 2006 *Generalized additive models: an introduction with R*. Boca Raton, FL: Chapman and Hall.
- Yoccoz, N. G. & Gaillard, J.-M. 2006 Age structure matters for Alpine ibex population dynamics: comment on Lima & Berryman (2006). *Clim. Res.* **32**, 139–141. (doi:10.3354/cr032139)
- Yoccoz, N. G., Mysterud, A., Langvatn, R. & Stenseth, N. C. 2002 Age- and density-dependent reproductive effort in male red deer. *Proc. R. Soc. B* **269**, 1523–1529. (doi:10.1098/rspb.2002.2047)