TERRESTRIAL VERTEBRATE ECOLOGY - ORIGINAL PAPER

Geographical variation in the influence of density dependence and climate on the recruitment of Norwegian moose

Vidar Grøtan · Bernt-Erik Sæther ·
Magnar Lillegård · Erling J. Solberg ·
Steinar Engen

Abstract The effects of variation in climate on population dynamics are likely to differ within the distributional range of a species, yet the consequences of such regional variation on demography and population dynamics are rarely considered. Here we examine how density dependence and different climate variables affect spatio-temporal variation in recruitment rates of Norwegian moose using data collected over a large geographical area during the hunting season. After accounting for observation error by a Bayesian Markov chain Monte Carlo technique, temporal variation in recruitment rates was relatively independent of fluctuations in local population size. In fact, a positive relationship was as common as a density-dependent decrease in fecundity rates. In general, high recruitment rates were found during autumn 1 year after years with a warm February, and after a warm May or cold June in year $t − 1$ or in year t. Large regional variation was also found in the effects of some of the weather variables, especially during spring. These patterns demonstrate both direct and delayed effects of weather on the recruitment of moose that possibly operate through an effect of body mass on the proportion of the females that sexually mature as 1.5 or 2.5 years old.

Introduction

It has been known since Elton's studies in the beginning of the twentieth century that there may be geographical variation in the population dynamics of vertebrates (Elton 1924). These gradients can be caused by two different mechanisms. Firstly, the strength of density dependence may differ within the species' distributional range. For instance, strength of density dependence was closely related to latitude in several species of North American prairie ducks (Sæther et al. 2008). Secondly, the effects of environmental stochasticity on the population dynamics may also vary regionally. Accordingly, Williams et al. (2003) found in three North American vertebrate species a stronger stochastic effect on the per capita population growth rates in populations located at the periphery of the species' distribution ranges than in populations located towards the centre of the species' distributions. Geographical variation in the effects of environmental stochasticity on population dynamics has also been recorded in Canadian lynx *Lynx canadensis* (Stenseth et al. 1999), roe deer *Capreolus capreolus* (Grøtan et al. 2005), temperate passerines (Sæther et al. 2003a, 2007a) and North American ducks (Sæther et al. 2008).

Geographical patterns in population dynamics must be associated with spatial variation in key demographic traits.

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V. Grøtan · B.-E. Sæther (✉)
Department of Biology, Centre for Conservation Biology,
Norwegian University of Science and Technology,
7491 Trondheim, Norway
e-mail: Bernt-Erik.Sather@bio.ntnu.no

M. Lillegård · S. Engen
Department of Mathematical Sciences, Centre for Conservation
Biology, Norwegian University of Science and Technology,
7491 Trondheim, Norway

E. J. Solberg
Norwegian Institute for Nature Research,
7485 Trondheim, Norway

In ungulates, spatial data on temporal variation in demographic traits are rare (Gaillard et al. 2000). However, in Scandinavian ungulates, regional variation in recruitment rates has been documented for wild reindeer *Rangifer tarandus tarandus* (Skogland 1983, 1985), moose *Alces alces* (Sæther and Haagenrud 1985; Sæther et al. 1996; Solberg et al. 2006a) and red deer *Cervus elaphus* (Langvatn et al. 2004). In many cases these relationships are related to regional differences in body mass or different life history traits such as age at maturity (Sand et al. 1995; Sand 1996). Furthermore, differences in body mass both in space and time are related to climate variation especially during late spring and early summer (Sæther 1985; Solberg and Sæther 1994; Sæther et al. 1996; Solberg et al. 1999; Herfindal et al. 2006a, b). This provides a mechanistic link for how variation in climate may affect the population dynamics of moose. An important effect of such size-dependent variation in demographic variables is that they can induce delayed effects of changes in climate on population dynamics (Solberg et al. 1999).

In this paper we will analyse geographical variation in the recruitment rate, i.e. the number of calves recorded per adult-sized (≥1-year old) female Norwegian moose. During the hunting season moose hunters collect data on the number of individuals observed as well as the structural composition of the population (Solberg et al. 2006a). We will use these data to relate changes in number of calves per female to variation in climatic variables and density.

Materials and methods

Moose observation data

Recruitment rate was calculated based on observation data collected annually as part of the moose observation monitoring program in Norway (Solberg et al. 2006a). Data were collected from most of the forested part of Norway (approximately 80,000 km^2), except from the counties on the west coast and from Finnmark in the very north (see below). In the latter areas moose densities are still low, moose harvesting irregular (<4% of the annual harvest) and only few hunter observations of moose are reported each year (Solberg et al. 2006a). Most of the study area is found in the boreal vegetation zone except for the very southern part, which extends into the nemoral vegetation zone (Moen 1999). For more details about the study area, see Solberg et al. (2002) and references therein.

The observation monitoring is a systematic reporting (on standardised forms) of sex and age (calf or adult) of moose observed by moose hunters during the hunting season (4–5 weeks in late September and October), from which several indices of population structure and density are

calculated. Most important are the 'moose seen per hunter-day' as an index of population density, and 'calves per female' and 'females per male' as indices of recruitment rate and adult sex ratio, respectively. The moose observation monitoring was gradually introduced in Norwegian municipalities from the mid 1960s, and since the mid 1980s it has been the main system for monitoring moose population density and structure in almost all (>85%) municipalities with moose hunting in Norway (Lavsund et al. 2003; Solberg et al. 2006a). Currently, the national data base (www.hjortevilt.no) includes close to 4.5 million observations obtained through 9 million hunter-days (i.e. number of hunters × days hunting), and each year roughly 250,000 new observations collected by close to 60,000 moose hunters (450,000 hunter-days) are added to the data base (Solberg et al. 2006a).

Indices based on hunter moose observations have been validated against independent estimates from cohort analyses (Gangsei 1999; Solberg and Sæther 1999; Solberg et al. 2002, 2006a), aerial surveys (Ericsson and Wallin 1999; Sylvén 2000) and field observations (Rolandsen et al. 2003). Annual variation in the indices seems to provide a fair estimate of the variation in population density and structure given that the number of hunter-days is reasonably high [>500–1,000 hunter-days (Ericsson and Wallin 1994; Sylvén 2000; Solberg et al. 2006b)]. The moose is probably well suited for such a census method as it is solitary living and mainly lives in forests, reducing the variance caused by chance observations of larger groups. Moreover, although the numbers of large carnivores are increasing, densities are still low in Norway (e.g. <50 wolves *Canis lupus* and <150 brown bears *Ursus arctos*; Wabakken et al. 2001; Swenson et al. 1995; http://www.rovviltportalen.no). Hence, varying predation pressure is unlikely to have a strong impact on the variation in observed recruitment rates.

In the present study, we used data collected in 1986–2004. During this period data were available from a large number of municipalities. All municipalities included in the analyses had at least 14 years of data with an average number of observations larger than 200 individuals. We used the number of observed calves per adult female as an estimate of recruitment rate. We also considered using the proportion calves of all moose observed as an estimate of recruitment rate, but this index was degraded due to the large variation in adult sex ratio during the study period following sex-biased harvesting (Solberg et al. 2002; Sæther et al. 2003b). Similarly, the twinning rate (e.g. number of calves per calf-rearing female) has been found to be a precise index of variation in recruitment rate and population performance (Franzmann and Schwartz 1985), but this index is typically less variable than calves per female, probably because it does not include annual

variation in the proportion of young females (2 and 3 year olds) that start to reproduce. Moreover, Solberg et al. (2006a) found a positive correlation between the annual variation in calving rate (observed proportion of adult females with calf/calves) and twinning rate (which, when multiplied, constitutes the recruitment rate) in Norwegian municipalities over 24 years (mean correlation coefficient = 0.41), indicating that the observed calves per female reflects variation in both twinning rates and calving rates over years. We used the total number of moose recorded per hunter-day as an estimate of population density.

Weather data

Weather data were obtained from the Norwegian Meteorological Institute. We included only monthly averages of temperature and precipitation from January to July and monthly averages of snow cover from January to April. Previous studies have shown that weather during this period influences many phenotypic characteristics (Sæther 1985; Solberg and Sæther 1994; Sand 1996; Sæther et al. 1996; Post and Stenseth 1999; Herfindal et al. 2006b) and demographic variables (Solberg et al. 1999) of moose. In cases were there were no weather data available for a municipality we used data from the closest weather station in a nearby municipality. The mean distance between weather stations was 41.0 km.

Model

The observed recruitment rates is affected by observation error as the individuals seen during hunting will just be a sample of the individuals present. To estimate parameters of interest we therefore use a state–space approach (Buckland et al. 2004; Clark and Bjørnstad 2004; Clark 2007) with separate models for the state (the unobserved process) and the observations.

We modelled the recruitment rate R at location i at time t as a simple linear regression

$$R_{it} = \alpha_i + \beta_i Z_{it} + \gamma_i N_{it} + \sigma_i \varepsilon_{it}, \tag{1}$$

where α is the intercept, β is the effect of a covariate Z varying with time t, γ is the effect of density N and σ is the SD of the residual environmental variation not explained by other components in the model for each locality i. Interaction effects between density and weather variables were estimated by estimating coefficients for the product of density and weather variables after subtracting the mean values for density and weather variables in each municipality. However, the interactions were small and generally not significant and were excluded from the final models.

To account for spatial autocorrelation in the environmental noise (Engen et al. 2005; Grøtan et al. 2005) we let ε_{it} follow a standard multinormal distribution and a time-independent correlation matrix (Σ) with elements depending on the distance among localities (h) and scale of spatial autocorrelation (r) modelled as $\rho(h) = e^{-h/r}$.

The relationship between observed recruitment rates (Y_{it}) and process recruitment rates (R_{it}) was modelled as

$$Y_{it} \sim N\big(R_{it}, \sigma_Y / \sqrt{F_{it}}\big), \tag{2}$$

where σ_Y is the SD of observation error for recruitment rates and F_{it} is the number of females observed.

To allow for possible observation error in our density variable, the relationship between observed moose per hunter day (M_{it}) and the actual number of moose present per hunter day was modelled as

$$M_{it} \sim N\big(N_{it}, \sigma_N / \sqrt{H_{it}}\big), \tag{3}$$

where σ_N is the SD of observation error for the number of moose seen per hunter day and H_{it} is the number of hunter days in municipality i at time t. Thus, for both the recruitment rate and the observed moose per hunter day we model the observation error as a nonlinearly decreasing quantity with increasing number of females and number of hunter days, respectively.

Estimation of parameters

Expressions for the log likelihood in state–space models often become complicated (e.g. De Valpine and Hastings 2002). Here we choose to use a Bayesian approach in combination with Markov chain Monte Carlo (MCMC) techniques (Clark and Bjørnstad 2004; Clark 2007; Sæther et al. 2007b) to obtain posterior distributions of parameters in the model. To simplify notation in the following, we write the vector $\mathbf{Y}_t = (Y_{1t}, Y_{2t},…, Y_{nt})'$ for all observed recruitment rates at time t across all n localities. Similar notation will be used for the residual component ($\boldsymbol{\varepsilon}_t$), number of females observed ($\mathbf{F}_t$), observed moose seen per hunter day ($\mathbf{M}_t$), the process (state) observed moose seen per hunter day ($\mathbf{NF}_t$) and the number of hunter days ($\mathbf{H}_t$) at time t. Similarly, the vector $\boldsymbol{\theta} = (\theta_1, \theta_2,…, \theta_n)'$ is the n values for a parameter θ at n locations. The Bayesian approach requires that we define full probability distributions for unobservable ($\boldsymbol{\varepsilon}_t$, $\mathbf{N}_t$) and observed ($\mathbf{Y}_t$, $\mathbf{M}_t$) quantities as well as prior distributions for parameters that are not directly conditioned on other parameters or data. In this case we need to define prior distributions for $\boldsymbol{\alpha}$, $\boldsymbol{\beta}$, $\boldsymbol{\sigma}$, $\boldsymbol{\gamma}$, σ_y, σ_N and r. As we have little prior information on the parameters we chose independent and uninformative priors

$$\boldsymbol{\alpha}, \boldsymbol{\beta}, \boldsymbol{\gamma} \sim N(0, 10^6)$$
$$\boldsymbol{\sigma}^2, \sigma_y^2, \sigma_N^2 \sim \text{IG}(0.001, 0.001)$$
$$r \sim U(30, 600)$$

denoted in the following as $\pi(\boldsymbol{\alpha})$, $\pi(\boldsymbol{\beta})$, $\pi(\boldsymbol{\sigma})$, $\pi(\boldsymbol{\gamma})$, $\pi(\sigma_y)$, $\pi(\sigma_N)$ and $\pi(r)$ for $\boldsymbol{\alpha}$, $\boldsymbol{\beta}$, $\boldsymbol{\sigma}$, $\boldsymbol{\gamma}$, σ_y, σ_N and r, respectively. IG and U represent the inverse gamma and uniform distribution, respectively. The prior for r is given in kilometres. Using Bayes' theorem, the joint posterior distribution of unknown quantities conditioned on the data, $\pi(\boldsymbol{\alpha}, \boldsymbol{\beta}, \boldsymbol{\sigma}, \sigma_y, \sigma_N, \boldsymbol{\varepsilon}_1, \ldots, \boldsymbol{\varepsilon}_T, \mathbf{N}_1, \ldots \mathbf{N}_T | \mathbf{Y}_1, \ldots, \mathbf{Y}_T, \mathbf{F}_1, \ldots, \mathbf{F}_T, \mathbf{M}_1, \ldots, \mathbf{M}_T, \mathbf{H}_1, \ldots, \mathbf{H}_T, \mathbf{Z}_1, \ldots, \mathbf{Z}_T)$ is proportional to

$$\pi(\boldsymbol{\alpha})\pi(\boldsymbol{\beta})\pi(\boldsymbol{\gamma})\pi(\boldsymbol{\sigma})\pi(\sigma_y)\pi(\sigma_N)\pi(r) \prod_{t=1}^{T}$$

$$\left(\mathbf{Y}_t | \sigma_y, \boldsymbol{\alpha}, \boldsymbol{\beta}, \boldsymbol{\gamma}, \boldsymbol{\varepsilon}_t, \mathbf{Z}_t, \mathbf{N}_t\right) \prod_{t=1}^{T} (\boldsymbol{\varepsilon}_t | r, \boldsymbol{\sigma}) \prod_{t=1}^{T} (\mathbf{N}_t | \mathbf{M}_t, \sigma_N). \quad (4)$$

The posterior distribution was estimated by MCMC techniques using the program WinBUGS (Spiegelhalter et al. 2003) and the add-on module GeoBUGS (Thomas et al. 2004).

Results

The observation error was $\sigma_Y = 1.26$ (95% confidence interval 1.20–1.31). This represents the SD in the estimates of the recruitment rate when only one female is recorded. When we included population size or different climate variables as covariates, there was little variation in the estimates of σ_Y (range of variation in the median values of $\hat{\sigma}_Y$ for 36 covariates: 1.20–1.26). The precision in the observations will rapidly increase with the number of females recorded (Eq. 2), so for 100 observations of females $\sigma_Y/\sqrt{F} = 0.126$ (Fig. 1). Furthermore, the annual records of the number of adult female moose in the different municipalities were usually so large (Fig. 1) that $\sigma_Y/\sqrt{F}$ was small. For instance, the mean number of observations per year was 431 adult females, giving $\sigma_Y/\sqrt{F} = 0.061$ (Fig. 1).

There was large variation in recruitment rates among the different parts of Norway (Fig. 2). Comparing the different counties the mean recruitment rate ranged from 0.58 calves per female in the county of Vestfold to 0.86 calves per female in the county of Østfold in southeastern Norway (Fig. 2).

Significant density dependence in the recruitment rate was found in 14.8% of the municipalities. Thus, significant direct negative feedback of population size on the recruitment rate of local Norwegian moose populations did not occur more often than expected by chance. In fact, 10.4% the density regulation was positive, i.e. the recruitment rate increased with local population size.

The highest proportion of significant effects of a climate covariate was found for temperature during February in year $t-1$, i.e. in 13.2% of the municipalities the recruitment rate was significantly positively correlated with higher February temperature the preceding year (Fig. 3). In total such a positive effect of temperature during this month was found in 82.1% of the municipalities (Fig. 3; probability of a binomial probability of 0.5 is $P < 0.00001$). Similarly, recruitment was poor after high precipitation in this month (negative coefficients in 66% of the municipalities, $P < 0.00001$). High recruitment rates were also found after a warm May in year $t-1$ (68% of municipalities, $P < 0.00001$) and in year t (65% of municipalities, $P < 0.00001$), and after cold June

Fig. 1 The relationship between the estimated observation error ($\sigma_Y/\sqrt{F}$ in the recruitment rate and the number of observations of adult female moose (*solid line*). The *bars* show the actual distribution (frequency) of the number of moose recorded in each municipality over all years. The *dashed line* indicates the mean number of observed females
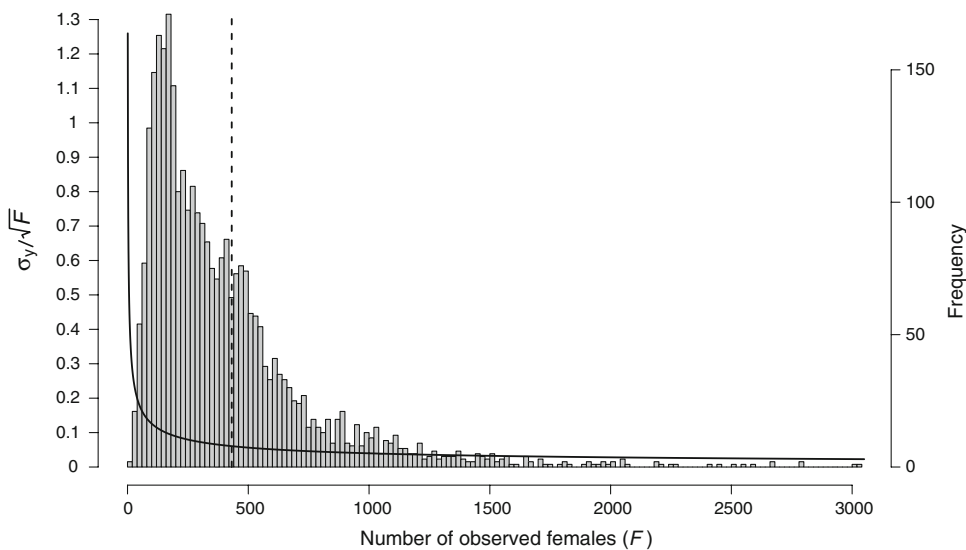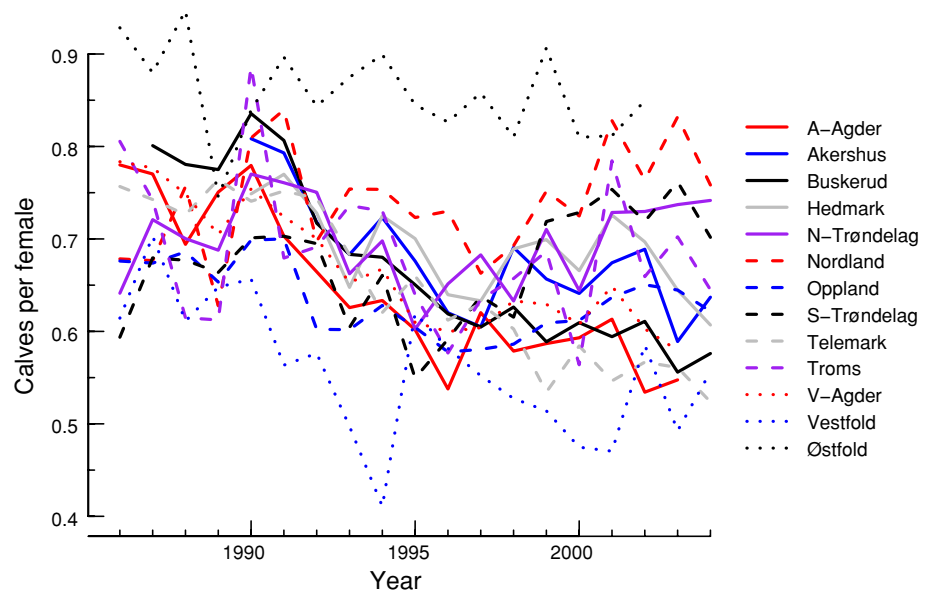
Fig. 2 Annual variation in the observed recruitment rate (calf per cow) in different counties of Norway

[negative coefficients in 63% ($P < 0.000001$) and 57% ($P = 0.064$) of the municipalities in year t and $t-1$, respectively].

For some climate variables there were regional differences in their effects on moose recruitment (Figs. 3, 4). In southern Norway recruitment was negatively correlated with temperature during April in 65% of the municipalities (probability of a binomial probability of 0.5 is $P = 0.001$), whereas a positive effect of temperature during this month was found in most municipalities in northern Norway (72%, $P < 0.00001$). Positive effects of May temperature in year t and year $t-1$ as well as a negative effect of June temperature in year t were found in both parts of Norway. However, in northern Norway there was also a positive effect on recruitment of temperatures during March and April as well as of snow depths during the period January–March in year $t-1$, which were not found in southern Norway. Finally, the effects of temperature during June in year $t-1$ were opposite in the two parts of Norway (Fig. 4). In the south there was a lagged negative effect of June temperature in 75% of the municipalities, whereas a positive effect was found in 72% of the municipalities in northern Norway.

The presence of regional variation in the climate impact on the recruitment rate of moose was also assessed by selecting the monthly climate variable that explained the highest proportion of the temporal variation in the number of calves per female in the municipalities. Again a clear pattern appeared (Fig. 5). Over larger areas in southern and central Norway temperatures during April or May in either year t or $t-1$ were generally the best predictors of recruitment rates. In addition, in some areas, especially in the lowlands of the southern and south-eastern parts of

Norway, temperatures during June were also the most important environmental covariates (Fig. 5). Finally, in the northern parts of the county of Nord-Trøndelag in central Norway, temperature during February was the variable which explained the largest proportion of the variance in the recruitment rate.

Discussion

This study indicates that recruitment of Norwegian moose is influenced by variation in different climate variables and that large regional variation exists in the effects of climate (Figs. 3, 4). A specific climatic variable may even have opposite effects on recruitment rate dependent on where in Norway the population is located (Figs. 3–5). Recruitment rate was only to a small degree influenced by negative density-dependent effects (Figs. 3a, 4a).

This study is based on data collected by a large number of hunters over large parts of Norway. It is based on the number of animals recorded during the hunting season. Obviously, this figure will be influenced by several sources of error (Rolandsen et al. 2003), e.g. observation conditions, sex- and age-specific differences in moose behaviour and ability of the hunters to correctly identify the different age and sex categories. Thus, estimates derived from these data represent only indices of the population density and structure. However, several studies indicate that these indices provide reliable estimates of changes in size and structural composition of single populations over time (Ericsson and Wallin 1999; Solberg and Sæther 1999). Some studies have suggested that the relationship between moose observations by

Fig. 3 The distribution of the effects (β_j) in different municipalities j of **a** density in year t, temperatures during **b** February, **c** April, **d** May and **e** June in year $t-1$ and temperatures during **f–h** April–June in year t on moose recruitment rates (calves per female) in southern (*grey bars*) and northern (*black bars*) parts of Norway. For location of the two parts of Norway, see *solid lines* on the maps in Fig. 4
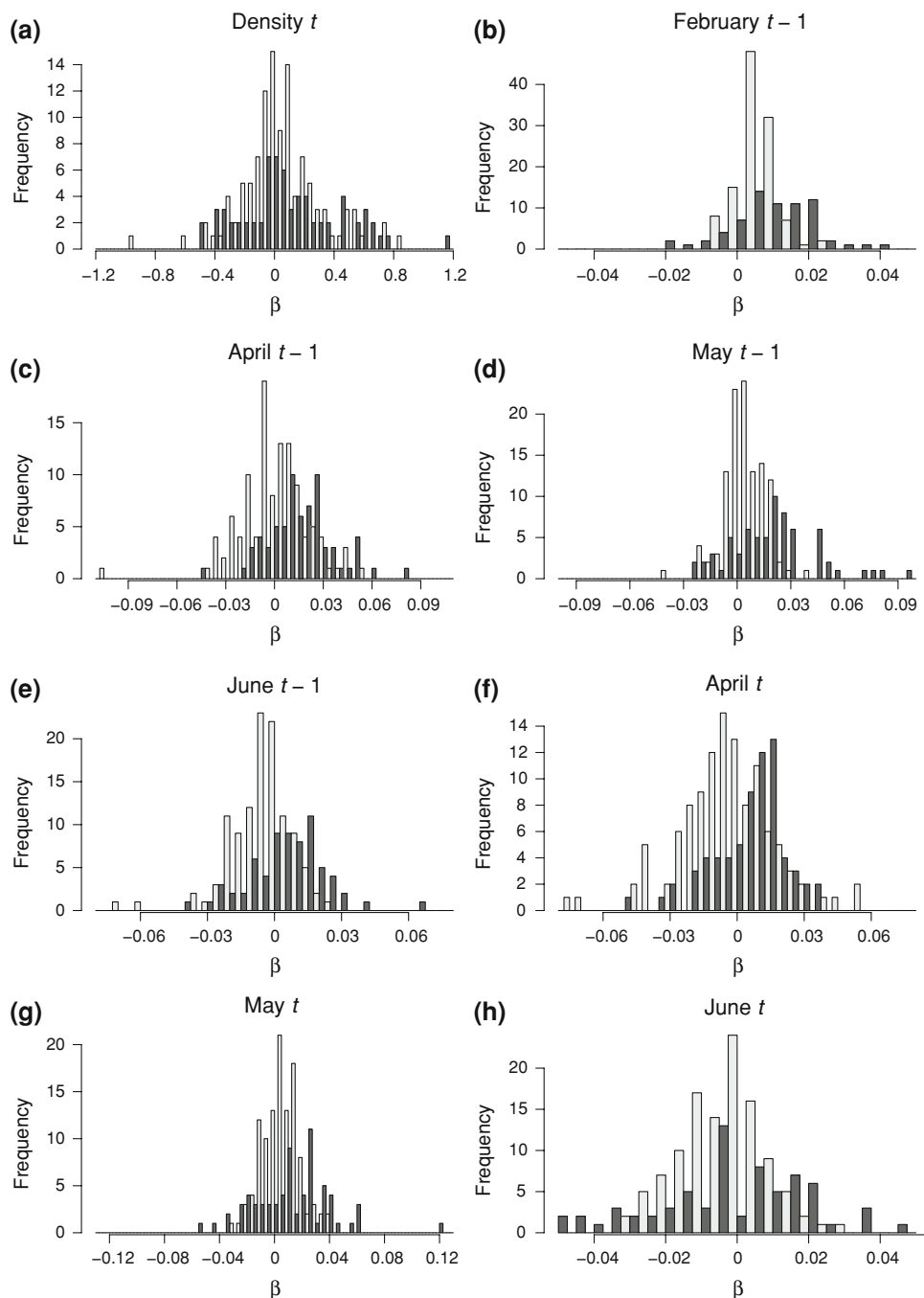

hunters and independent estimates of population size obtained through other methods is monotonically positive (Fryxell et al. 1988; Ericsson and Wallin 1999; Solberg and Sæther 1999), but that the index obtained from hunter observations does not always increase proportionately with density at high population densities (Ericsson and Wallin 1999). Such a relationship can reduce our ability to reveal density-dependent effects on the recruitment rate (Fig. 3a). Our analyses also showed (Fig. 1) that the

annual number of records in the different municipalities were so large that the precision in the estimates was quite high.

Geographical variation in population density is likely to explain the large differences in recruitment rate (Fig. 2) and in body mass (Hjeljord and Histøl 1999; Hjeljord et al. 2000) between the counties of Østfold and Vestfold. These two counties are located in southeastern Norway at opposite sides of the Oslofjord with a similar climate and

Fig. 4 Regional differences in the effects of population size in **a** year t and the effects of temperature during **b** February, **c** April, **d** May, and **e** June in year $t-1$, and temperature in **f** April, **g** May and **h** June in year t on the recruitment rate (calves per female) of Norwegian moose. *Blue* denotes municipalities in which there are negative effects of the covariate, whereas *red* represents regression coefficients larger than 0. The *solid line* shows the border between southern and northern parts of Norway

(a) Density t

(b) February $t-1$

(c) April $t-1$

(d) May $t-1$
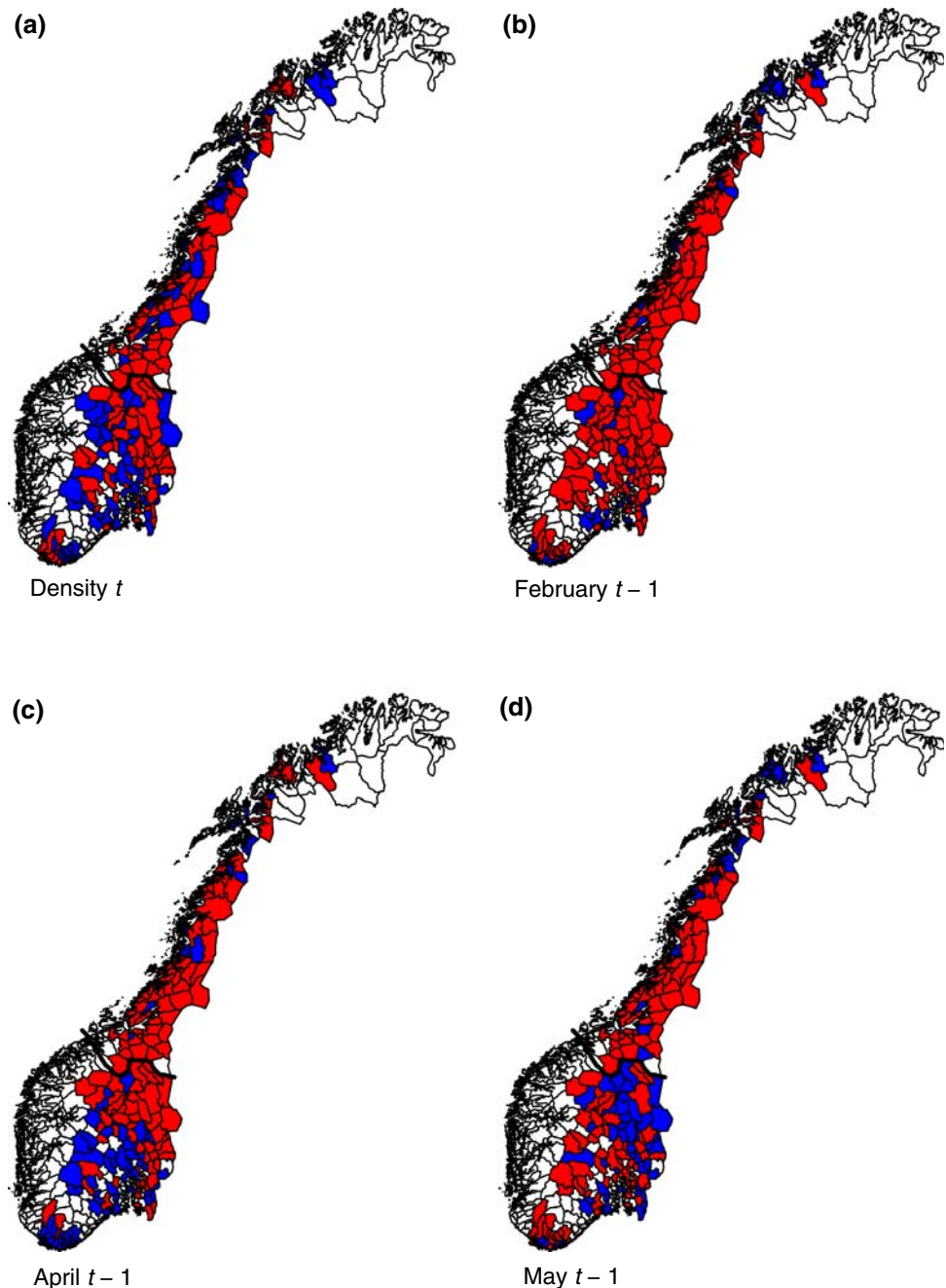
topography, but with much higher densities of moose in Vestfold than in Østfold. However, within a municipality there were only small effects of density dependence on recruitment rate. This is in accordance with previous results (Sæther et al. 1996), indicating that density-dependent reduction in fecundity of moose only appears at extremely high densities. This also seems to be a general pattern in the population dynamics of large herbivores (Fowler 1981, 1987). In fact, in most cases the effects of density were positive. Two mechanisms can explain such a relationship:

1. Fluctuations in the age structure, e.g. caused by changes in the harvest rates (Solberg et al. 1999), may induce autocorrelations in the population fluctuations (Lande et al. 2006; Engen et al. 2007). As a consequence, an increase in the proportion of high reproductive age-classes may appear at high population sizes (Sæther and Haagenrud 1983), which will give a high reproductive rate, resulting in a positive relationship between the recruitment rate and population size.

2. Most Norwegian moose populations have increased in size during the last three decades (Solberg et al.

Fig. 4 continued

(e)

June $t-1$

(f)

April t

(g)

May t

(h)

June t
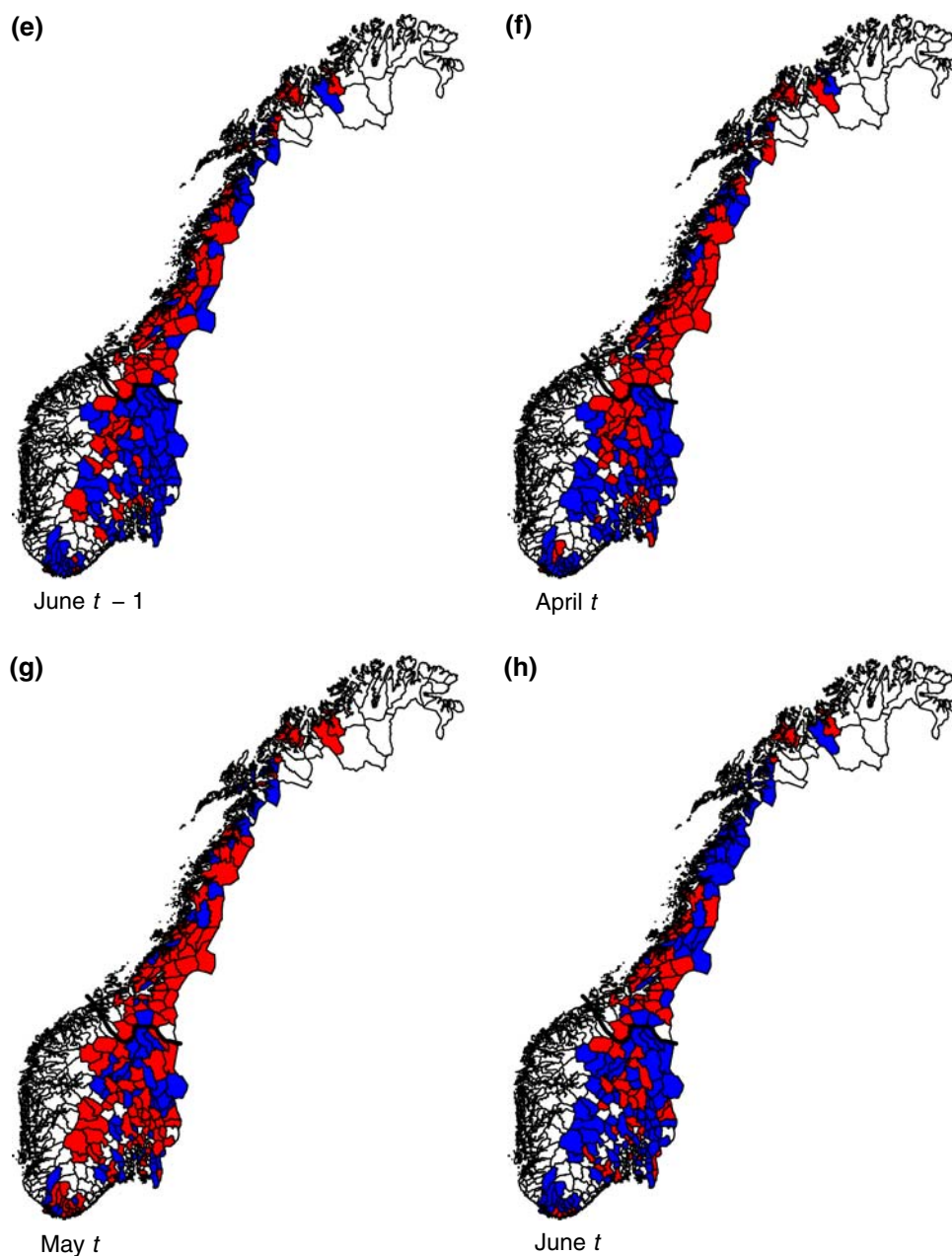
2006a). This population increase has resulted in heavy browsing pressure in many wintering areas (Sæther and Andersen 1990), which may have affected the productivity of preferred plant species and induced long-term changes in the composition of the vegetation (Bergström and Danell 1995; Côté et al. 2004). Moreover, during the last two decades there has been a gradual decrease in forestry activity, reducing the number of clear cuts and increasing the average age of the forest (Lavsund et al. 2003; Solberg et al. 2006b). Such changes in vegetation composition may require many years, resulting in long time delays between changes in moose density and variation in the resource

supply. For a period this may lead to a positive relationship between density and recruitment rate.

A problem with analyses of climate influences on population dynamics is that a relationship may appear just by chance because of the large number of environmental covariates that often are included. Studies of ungulate populations have shown that weather conditions that occur during short periods of the year can cause large demographic effects. For instance, in Soay sheep *Ovis aries*, bad weather that coincides with periods of high mortality strongly influences changes in population size especially during February–April (Hallett et al. 2004). Identifying
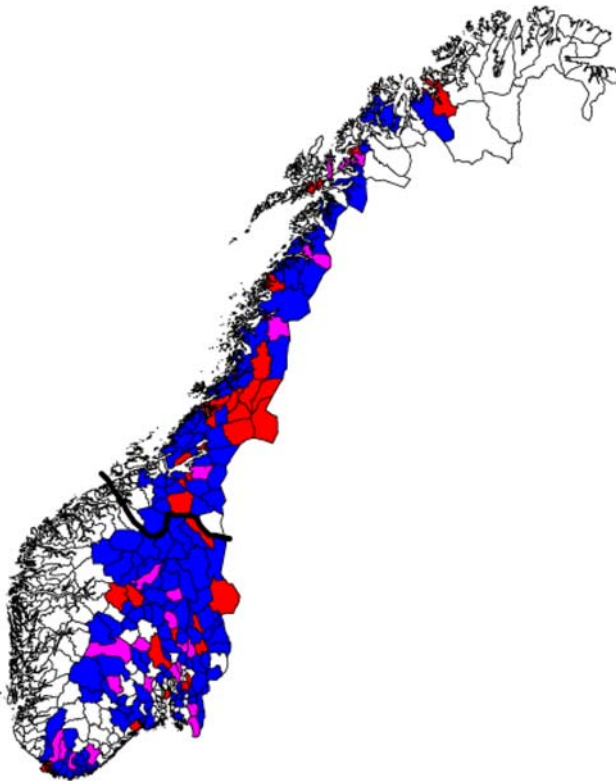
Fig. 5 Regional variation in environmental variables that explain the largest proportion of the variance in the recruitment rate (calves per female) of moose. *Red* represents municipalities in which temperature during February in year $t-1$ is the best covariate. Municipalities in which the highest proportion of variance was explained by temperature during April and May or the temperature in June in either year t or $t-1$ are denoted by *blue* and *pink*, respectively. The most influential covariate for each municipality was found by standardizing the covariates (mean = 0, SD = 1) and thereafter ranking the absolute values of the regression coefficients. The *solid line* shows the border between southern and northern parts of Norway

such critical periods will be difficult in extensive studies such as ours, which may open the results to influences of spurious correlations without any functional significance (Grosbois et al. 2008). However, the patterns that emerged from the present analyses correspond well to previous analyses of weather influences on key demographic variables of the moose. For instance, they showed that climate during winter as well as during spring and early summer most strongly affected the recruitment rate of moose (Figs. 3–5). Furthermore, the 1-year lagged effects of climate were in general stronger than the climate influences during the same year (Figs. 3, 4). In particular, high temperatures during late spring, but a cold June, had a positive effect on the recruitment rate (Figs. 3–5). Previously we have demonstrated that early onset of reproduction is associated with large yearling body mass (Sæther and Haagenrud 1983, 1985), which in turn is associated with the weather during the first two summers of the female's

life (Sæther 1985; Solberg and Sæther 1994; Solberg et al. 1999; Herfindal et al. 2006b). Thus, the delayed influence of weather during late spring and early summer on the recruitment rate may be a size-dependent effect of the proportion of the females that sexually mature at 1.5 or 2.5 years old. Similarly, the effects of winter weather may operate on the female body mass. Reduced snow cover during winter can have a dramatic, positive effect on size (Sæther et al. 1996) and body condition (Sæther and Gravem 1988) of moose calves, probably because of easier access to food in the field layer during winter (Sæther et al. 1996). There are also some indications that moose yearlings grow bigger after cold winters (Herfindal et al. 2006b). In contrast, we found a mild February with high precipitation to be associated with high recruitment rates the following year. Because these effects were mainly found in the more continental areas and at higher altitudes (Fig. 5), it is likely that the winter temperature was still quite low and that most of the precipitation came as snow. A possible explanation for the observed relationship may thus be that high accumulation of snow during winter affects body growth and in turn fecundity. This can occur if snow-rich winters lead to extended periods of snowmelt, which in turn increase the period with emerging food plants of high quality in spring (Mysterud et al. 2001; Solberg et al. 2004). This will lead to a rapid increase in the body mass of young individuals, increasing the probability of sexual maturity and the twinning rate among females especially in the youngest age-classes (Sæther and Haagenrud 1983, 1985; Sand et al. 1995; Sæther et al. 1996; Garel et al. 2009). The direct effects of climate (Figs. 3, 4) also suggest that weather during spring or early summer influences the rate of fetus loss and/or the proportion of calves surviving to the autumn. Given the very high survival rates of moose calves previously reported from Norway (Stubsjøen et al. 2000; Sæther et al. 2007c), we believe that this effect is mainly operating as fetus loss and/or calf mortality just after birth.

Whatever the mechanisms, the results of this study provide another demonstration that the influence of the same climate variable can show large regional variation in the effects on the local dynamics of vertebrate populations (see Sæther 1985, 1997; Mysterud et al. 2000; Aanes et al. 2003; Sæther et al. 2003a, 2004, 2006, 2007a; Grøtan et al. 2005, 2008). This implies the need for a management practices that account for regional climate-induced differences in population dynamics. Furthermore, these results suggest that the effects of the expected changes in climate on moose population dynamics will show a large regional variation across Norway and probably also in the whole of Fennoscandia. This means that future management decisions about the size and structure of the quotas must be made over relatively small spatial scales.

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