

Plant phenology, migration and geographical variation in body weight of a large herbivore: the effect of a variable topography

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Summary

1. A central concept in ruminant foraging ecology is that even slight changes in plant quality affect body growth substantially, because ruminants not only gain more protein and energy but also use less time for rumination when eating high-quality forage. Increased access to highly nutritious forage is thus regarded as an important driving force in the evolution of migration in large herbivores, because the temporal and spatial variation in plant quality is huge. Body weight is in turn a major determinant of reproductive performance and survival in ungulates, and therefore important for population dynamics.

2. In the temperate region, the vertical movement of cervids from a low-elevation winter range to a high-elevation summer range is the most common pattern of migration. Migration to high elevations during summer is regarded as a strategy to increase energy intake among northern temperate ungulates.

3. It has been suggested that there is increased forage quality at high elevation. This leads to the prediction that body weights are positively correlated with the proportion of high-altitude habitat. Alternatively, cervids may benefit due to prolonged access to newly emerged forage as they migrate along an altitudinal gradient. If so, it can be predicted that body weights are highest in regions with the highest diversity of different altitudes.

4. The facing of slopes, i.e. the aspect, is also regarded as an important part of the habitat for deer. Access to north-facing slopes is regarded as favourable because plant quality may be higher on north-facing slopes; access to a variety of different aspects is also favourable because this may lead to a variable snow melt and thus a longer time period with access to high-quality forage.

5. In order to test the above predictions (under points 3 and 4), we analysed the spatial variability of body weight of 8452 female and 12 474 male red deer harvested during 1975–98 from 105 municipalities in Norway.

6. Body weight of red deer was positively related to the diversity of altitudes, and negatively related to the proportion of high-altitude habitat *per se*. This demonstrated that the altitudinal migration of cervids is not necessarily due to increased forage quality at high elevation, but rather that migrating cervids gain from prolonged access to newly emerging forage along an altitudinal gradient as they migrate to high elevation during early summer.

7. There was also no support for the hypothesis that access to a high proportion of north-facing slopes was favourable; rather, body weight of red deer was correlated with access to a diversity of aspects. There was thus clear evidence that a variable topography, measured as different altitude levels and aspects, was positively related to body weight of red deer.

8. We discuss the possible causes of why an ideal free distribution is not reached, and conclude that phenological differences in plants related to topography can have a large impact on body weights of cervids, and therefore induce considerable spatial heterogeneity in population dynamics.

Key-words: altitude, demography, foraging, ideal free distribution, plant quality.

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Introduction

Ruminants have a highly specialized physiology that is adapted to extract plant nutrients that often occur in low concentrations and are often protected by structural (e.g. cellulose), mechanical (e.g. spines) or toxic defences (e.g. phenolics) (Van Soest 1994). Concentrations of both nutrients and defences vary considerably both spatially and temporally between, as well as within, plant species (Van Soest 1994). Foraging ruminants in general select those plants, plant parts and/or growth stages that have the highest digestibility and/or nutritive quality (Hanley 1997). Access to a more continuous supply of highly nutritious forage is regarded as an important driving force in the evolution of migration in large herbivores (Fryxell & Sinclair 1988). By selecting forage with high levels of protein and carbohydrates and low levels of secondary metabolites, ruminants not only gain more protein and energy, but they also need less time for rumination (White 1983). This 'multiplier' effect represents a link between foraging ecology and demography of ruminants, because even slight differences in the nutritive quality of forage may thus lead to substantial differences in growth of ruminants (White 1983; Hanley 1997).

In the temperate region, the vertical movement of cervids from a low-elevation winter range to a high-elevation summer range is the most common pattern of migration (Oosenbrug & Theberge 1980; Mysterud 1999). It is widely recognized that food quality may influence direction and timing of seasonal movements of deer (Klein 1965; Morgantini & Hudson 1989). Albon & Langvatn (1992) documented that red deer (*Cervus elaphus* L.) in Norway shot at high elevation were heavier than those that remained at low elevation year round, and the density of red deer in the Scottish highlands was positively correlated with the size of the nearest mountain and with the proportion of ground over 488 m (Clutton-Brock & Albon 1989). However, two different mechanistic explanations, both related to forage quality, have been proposed to explain the altitudinal pattern of migration.

H₁: with increasing altitude, there appears to be an increase in the nutritive value of vegetation as herbivores forage (Albon & Langvatn 1992). This improvement may be due to lower temperatures with minimum losses from respiration and slow build up of fibrous tissue of low digestibility (Bliss 1962).

H₂: early phenological stages of plants generally have high nutritional quality in terms of energy and protein

(Van Soest 1994; Van der Wal *et al.* 2000), and time of spring migration usually coincides with the time when the first new vegetation emerges (Klein 1965; Albon & Langvatn 1992; Mysterud 1999). Access to a range of different altitudes may lead to a prolonged period of access to newly emergent high-quality forage.

The facing of slopes (i.e. the aspect) is also regarded as an important part of the habitat for deer.

H₃: access to a high proportion of north-facing slopes is regarded favourable. Later snow melt and lower temperatures on north-facing slopes tend to retard plant development and enhance digestibility (Bennett & Mathias 1984; Hay & Heide 1984). Albon & Langvatn (1992) reported that the protein content of grasses and herbs was higher on north-facing compared with south-facing slopes in May, and found a tendency for red deer hinds inhabiting north-facing slopes in Norway to be heavier. Migratory woodland caribou (*Rangifer tarandus* L.) in the Yukon, Canada, also selected vegetation communities on north-facing slopes (Oosenbrug & Theberge 1980).

H₄: an alternative hypothesis is that access to a diversity of different aspects is favourable to foraging deer, as this may also lead to a variable snow melt and hence a prolonged period with high-quality forage (Stensli 1988).

Body weight is a major determinant of reproductive performance and survival in ungulates (Langvatn *et al.* 1996; Gaillard *et al.* 2000) and therefore important for population dynamics. Even though the temporal variability relative to density-dependent and density-independent factors is well known (reviews in Sæther 1997; Gaillard, Festa-Bianchet & Yoccoz 1998), and some information is available on density distributions between different habitat types (Klein & Strandgaard 1972; Wahlström & Kjellander 1995; Pettorelli *et al.* 2001), remarkably little information exists regarding spatial variability relative to topography (but see Clutton-Brock & Albon 1989). Here we used data from 8452 female and 12 474 male red deer, from 105 municipalities with largely varying topography along the western part of Norway, to test whether the correlation between body mass and altitude is due to (H₁) high-altitude habitat *per se* (i.e. body weight positively relates to proportion of high-altitude habitat) and/or due to (H₂) access to a diversity of altitudes, and whether there is correlation between body weight and (H₃) the proportion of north-facing slopes and/or (H₄) the diversity of aspects. We simultaneously controlled for factors such as age, sex, density (Mysterud *et al.* 2001), cumulative density (A. Mysterud, R. Langvatn, N. Chr. Stenseth & N.G. Yoccoz,

unpublished data) and climate (Post *et al.* 1997), as well as other spatial covariates such as degree of latitude and distance from the coast (Langvatn & Albon 1986).

Material and methods

STUDY AREA

The study area was the western part of southern Norway, which is the main area for red deer in Norway (Langvatn *et al.* 1996; Mysterud *et al.* 2000, 2001). Data came from 105 municipalities in the counties Rogaland (6), Hordaland (23), Sogn og Fjordane (22), Møre og Romsdal (30), Sør-Trøndelag (17) and Nord-Trøndelag (7). We refer to Rogaland and Hordaland as population P1, Sogn og Fjordane as population P2, Møre og Romsdal and Sør-Trøndelag as population P3, Nord-Trøndelag as population P4, and the island Hitra as population P5 (Mysterud *et al.* 2001). The vegetation on the west coast of Norway is mostly in the boreonemoral zone. Exceptions to this general pattern are a small area around the Hardangerfjorden in Hordaland, which is in the nemoral zone, and some areas not far from the Trondheimsfjorden, which is in the southern boreal zone. From Rogaland to Møre og Romsdal, forests are dominated by deciduous and Scots pine (*Pinus sylvestris* L.) 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). Areas in Sør-Trøndelag up to Trondheimsfjorden are dominated by birch (*Betula* sp.) and pine, whereas spruce forests dominate some areas north of this. In general, temperature and precipitation decline from south to north and from coast to inland, while snow depth increases (Langvatn *et al.* 1996; Mysterud *et al.* 2000). In summer both the length of the growing season and total degree days decline from south-west to north-east (Langvatn & Albon 1986). Topography is generally steeper inland.

RED DEER DATA

Red deer were sampled during the annual autumn harvest 1965–98 (Langvatn *et al.* 1996; Post *et al.* 1997; Mysterud *et al.* 2001) but in this paper only data from 1975 to 1998 are included as not all covariates could be calculated for the period 1965–74. Hunting is controlled through licenses issued by local wildlife boards in each municipality. Red deer may only be shot between 10 September and 15 November, but between these dates the actual hunting periods vary slightly between counties. In co-operation with local wildlife boards, hunters provided mandibles from all animals shot, together with records of sex, date, locality (municipality) and body weight. Date of shooting was treated as a continuous variable, and quantified as the day on which an animal was recorded as shot, starting with '1' for 1 September and counting consecutively forward

to 31 December, which was numbered as day 122 (Post *et al.* 1997; Mysterud *et al.* 2001). Body weight is dressed weight (i.e. live weight minus head, skin, viscera, bleedable blood and metapodials). Dressed weight in hinds is about 58% of live weight. Age determination in calves and yearlings was based on tooth eruption patterns, whereas older animals were aged using annuli in the cementum of the first incisor (Hamlin *et al.* 2000). Most of these data had been analysed earlier with regard to the temporal variation in body weights (Langvatn *et al.* 1996; Post *et al.* 1997; Mysterud *et al.* 2001), but only data on 469 deer from 1978 and 1983 for geographical variation (distance from the coast and degree of latitude) as well (Langvatn & Albon 1986). The spatial covariates distance from the coast and degree of latitude (Langvatn & Albon 1986) were measured manually on a map in the middle of each municipality (Mysterud *et al.* 2000, 2001).

CARTOGRAPHIC DATA

We obtained all cartographic data about the habitat from the National Mapping Agency of Norway (Statens Kartverk Hønefoss, Norway) in a format that was used directly in a geographic information system (ArcView GIS; ESRI 1996). Data on municipality borders were retrieved as vector data, while data on altitude (in a terrain model) were obtained as raster data with a resolution of 100 × 100 m. By using overlays, we calculated the different spatial covariates of topography for each municipality. We defined the proportion of high-altitude habitat as areas between 250 and 700 m a.s.l. (Albon & Langvatn 1992). Red deer seldom use areas above the treeline, which is at about 700 m a.s.l. on the west coast of Norway (Moen, Lillethun & Odland 1999). The diversity of altitudes was calculated with the Shannon–Wiener information criteria (Hanski 1978), with data on proportion of area within 100-m intervals up to 700 m a.s.l. in each municipality. We calculated the proportion of area facing north and the diversity of aspects (with the Shannon–Wiener information criteria; data: proportion of area facing north, north-east, east, south-east, south, south-west, west and north-west in each municipality). We removed all sea areas by removing altitude below 0.001 m, and we did not include flat areas when calculating aspects. These variables were then entered into the statistical models (see below). There was some correlation between diversity of altitudes, proportion of high-altitude habitat and distance from the coast, but little correlation among the other geographical covariates (Table 1).

STATISTICAL ANALYSIS

We used a combination of general linear models (GLM) and generalized additive models (GAM; Venables & Ripley 1994) to analyse variation in body weight. A logarithmic transformation [$\ln(\text{weight})$] of

Table 1. Correlations between different geographical covariates from the 105 municipalities on the west coast of Norway for which red deer data were available. Correlation values above 0.5 are in bold

	Degree of latitude	Distance from the coast	Diversity of altitudes	Proportion of high-altitude habitat	Diversity of aspects
Distance from the coast	0.008				
Diversity of altitudes	0.138	0.517			
Proportion of high-altitude habitat	0.159	0.764	0.762		
Diversity of aspects	-0.078	0.213	0.012	0.156	
Proportion of north-facing slopes	0.511	-0.157	0.183	0.051	-0.087

Table 2. Parameter estimates [obtained from the general linear model, i.e. least-squares (LS) estimates, and from 1000 parametric bootstrap replicates] with bootstrapped standard errors and confidence intervals (CI). The reference level for the factor population is 'P1'. Other parameters are given as differences between levels

Parameter	LS estimate	Bootstrap estimate	Bootstrap SE	95% CI
Females				
Intercept	2.86	2.84	0.322	2.21, 3.50
Age 1–2 years	0.129	0.129	0.002048	0.125, 0.133
Age 3–5 years	0.0258	0.0257	0.002029	0.0218, 0.0299
Age 6–20 years	0.00273	0.00272	0.000715	0.00130, 0.00416
Age ≥ 21 years	-0.0348	-0.0346	0.008074	-0.0510, -0.0186
Density	-0.0532	-0.0529	0.010191	-0.0736, -0.0328
Cumulative density	-0.00210	-0.00217	0.001711	-0.00552, 0.00132
Date of culling	-0.0000225	-0.0000210	0.0000624	-0.000150, 0.000102
Diversity of altitude habitats	0.0300	0.0301	0.009399	0.0112, 0.0488
Proportion of high-altitude habitat	-0.0378	-0.0365	0.017818	-0.0734, -0.00215
Diversity of aspects	1.56	1.57	0.153919	1.25, 1.87
Proportion of north-facing slopes	-0.578	-0.579	0.09743	-0.773, -0.383
NAO	0.00270	0.00270	0.000616	0.00147, 0.00393
Distance from the coast	0.0379	0.0376	0.004913	0.0281, 0.0477
Degree of latitude	-0.00160	-0.00156	0.002686	-0.00697, 0.00377
Population (P2–P1)	0.0236	0.0234	0.006142	0.0113, 0.0359
Population (P3–P1)	0.0298	0.0297	0.005159	0.0195, 0.0402
Population (P4–P1)	0.0125	0.0127	0.006077	0.000381, 0.0247
Population (P5–P1)	-0.0160	-0.0160	0.002877	-0.0218, -0.0103
Males				
Intercept	2.22	2.24	0.347	1.52, 2.91
Age 1–2 years	0.293	0.293	0.00276	0.287, 0.298
Age 3–4 years	0.133	0.133	0.00267	0.128, 0.139
Age 5–7 years	0.0104	0.0104	0.00401	0.00236, 0.0184
Age ≥ 8 years	-0.0164	-0.0164	0.00338	-0.0231, -0.00959
Density	-0.0932	-0.0931	0.00975	-0.113, -0.0738
Cumulative density	0.00198	0.00194	0.00162	-0.00126, 0.00522
Date of culling	-0.000920	-0.000930	0.0000609	-0.00105, -0.000800
Diversity of altitude habitats	0.0590	0.0595	0.00814	0.0428, 0.0753
Proportion of high-altitude habitat	-0.136	-0.136	0.0172	-0.171, -0.102
Diversity of aspects	1.87	1.855	0.165	1.54, 2.20
Proportion of north-facing slopes	-0.776	-0.777	0.0919	-0.959, -0.592
NAO	0.00363	0.00365	0.000565	0.00250, 0.00476
Distance from the coast	0.0641	0.0641	0.00515	0.0538, 0.0744
Degree of latitude	-0.00203	-0.00218	0.00279	-0.00761, 0.00355
Population (P2–P1)	0.0262	0.0265	0.00638	0.0134, 0.0389
Population (P3–P1)	0.0340	0.0342	0.00559	0.0228, 0.0451
Population (P4–P1)	0.00915	0.00926	0.00592	-0.00270, 0.0210
Population (P5–P1)	-0.0233	-0.0230	0.00273	-0.0288, -0.0178

body weight was used in order to get residuals with constant variance when using GLM. We used GAM to assess the robustness of the results with regard to misspecification of the systematic part of the model. As the GAM analyses showed that all the topographic variables gave a monotonic response that was linear or close to linear, we only give results obtained using GLM

models, mainly because coefficients of linear models are easily comparable between studies and interactions can easily be tested for. However, we used GAM to describe graphically the relationship between body weight and the topographic covariates. All statistical analyses were performed in the statistical package S-Plus (Venables & Ripley 1994).

The body weight of red deer follows the typical three-stage Caughley-like pattern of mammals (Caughley 1966; Gaillard *et al.* 1998; Mysterud *et al.* 2001). However, as body weight in the first stage is not linearly related to age, we used a four-stage model for age with thresholds at 2.5, 4.5 and 7.5 years of age for males, and 2.5, 5.5 and 20.5 years of age for females. Thresholds were estimated by minimizing the residual sum of squares, but analyses were robust when using other thresholds or a three-stage model. As these thresholds were different in males and females (Mysterud *et al.* 2001), separate GLM models were used for each sex. Calves were excluded from both models. Other covariates, such as the North Atlantic oscillation index (NAO; Post *et al.* 1997), density (Mysterud *et al.* 2001), cumulative density of the last 10 years prior to harvest (A. Mysterud, R. Langvatn, N. Chr. Stenseth & N.G. Yoccoz, unpublished data), date of culling (Post *et al.*

1997), distance from the coast and degree of latitude (Langvatn & Albon 1986), were included in the model in order to correct for bias due to the imbalance in the study design. Fitting a too complex model would result in estimates with lower bias but lower precision, and bias is a more important issue in observational studies (Cochran & Rubin 1973). We therefore used a model including terms that may not be significant but that could influence the estimates for the coefficients of interest. Parametric bootstrapping (Efron & Tibshirani 1993) was used to calculate confidence intervals for parameter estimates. A total of 1000 bootstrap samples was used.

Results

The body weights of both female and male red deer clearly increased with an increasing diversity of altitudes within municipalities (H_2 ; Table 2 and Fig. 1; N_{females}

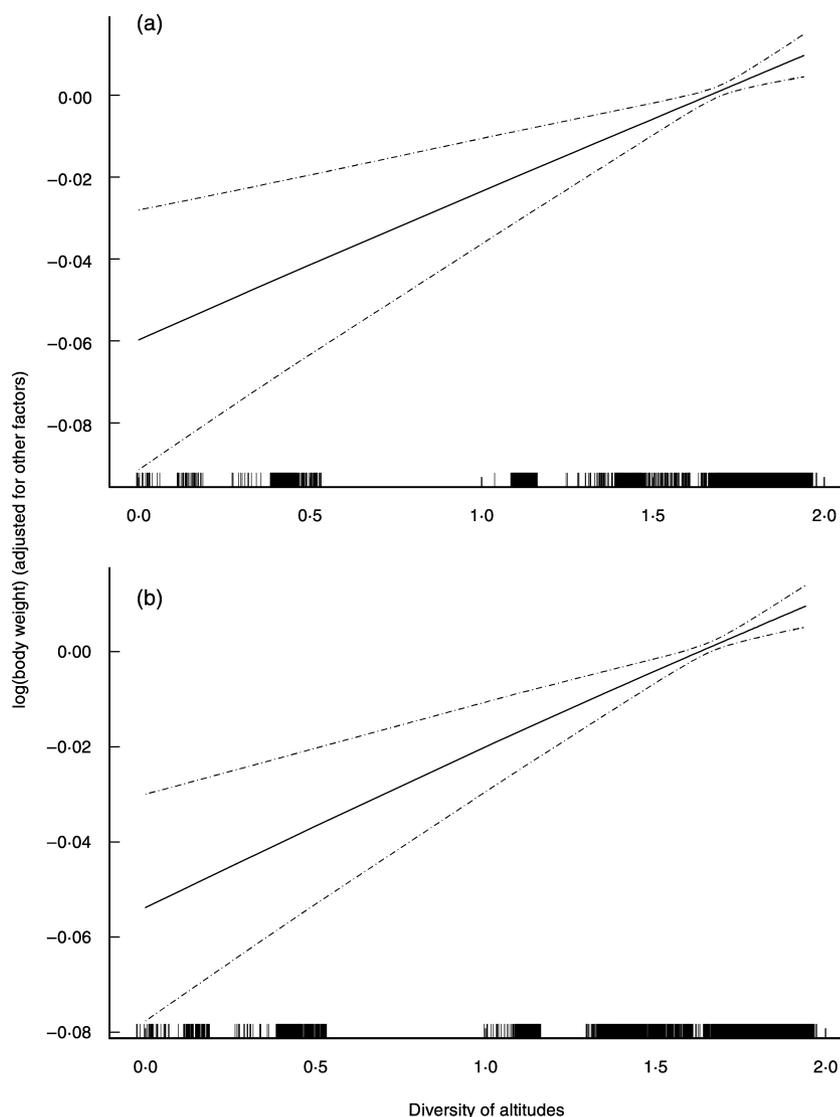


Fig. 1. The relationship between body weight of (a) female and (b) male red deer and diversity of altitudes within 105 municipalities along the west coast of Norway, presented as a result of fitting an additive model to the red deer data on body weights with smooth functions on a continuous predictor (with $d.f._{\text{splines}} = 1$ for diversity of altitudes). The dashed lines are 95% pointwise confidence intervals. The tick marks show the locations of the observations on that variable (Venables & Ripley 1994).

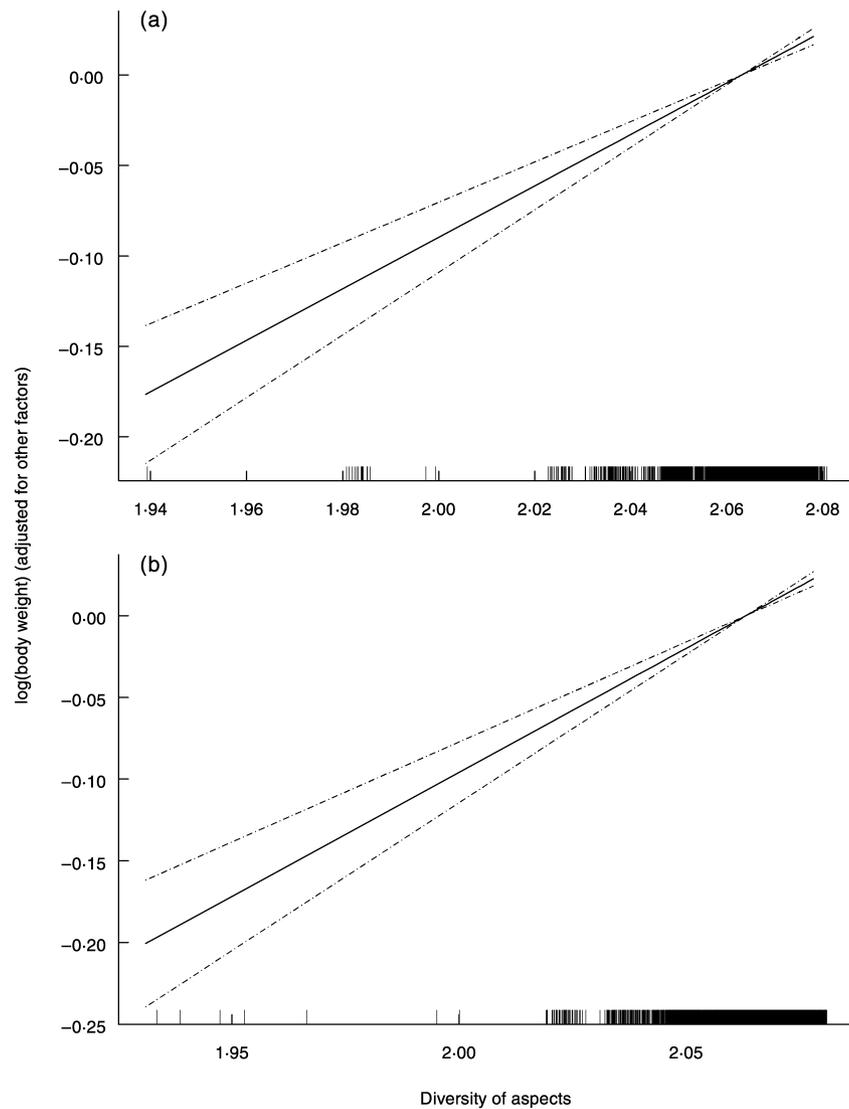


Fig. 2. The relationship between body weight of (a) female and (b) male red deer and diversity of aspects within 105 municipalities along the west coast of Norway, presented as a result of fitting an additive model to the red deer data on body weights with smooth functions on a continuous predictor (with $d.f._{splines} = 1$ for diversity of aspects). The dashed lines are 95% pointwise confidence intervals. The tick marks show the locations of the observations on that variable (Venables & Ripley 1994).

= 8452, $R^2_{females}$ (full model) = 0.589, $N_{males} = 12474$, R^2_{males} (full model) = 0.747). Body weight was not positively related to the proportion of high-altitude habitat (H_1), in fact the slope estimate was negative (Table 2). The slope estimates were also negative for the correlation between body weight and proportion of north-facing slopes, and hence there was no support for H_3 . Rather, there was a positive relationship between body weight and diversity of aspects (H_4 ; Fig. 2 and Table 2). There was thus clear evidence that a variable topography, measured both as different altitude levels and slopes, was positively related to body mass of red deer. We simultaneously controlled for the positive effect of distance from the coast, degree of latitude and the NAO, the negative effect of density, as well as the effect of age, population, cumulative density and date of culling (Table 2). The factor 'population' was organized along a gradient from south to north (except P5).

Exclusion of population made the effect of degree of latitude highly significant [females: bootstrap estimate = 0.100, bootstrap SE = 0.00068, 95% CI = (0.0087, 0.0114); males: bootstrap estimate = 0.0095, bootstrap SE = 0.00063, 95% CI = (0.0082, 0.0108)].

Discussion

The period spring through early autumn is the prime period for growth and build-up of body condition for temperate ungulates (Klein 1964; Mitchell, McCowan & Nicholson 1976). Spatial variation in body weight is likely to reflect spatial differences in plant quality and/or the duration of access to plants in young phenological stages (Langvatn & Albon 1986; Van der Wal *et al.* 2000), in addition to spatial variation in density (Mysterud *et al.* 2001) and density in the previous year (A. Mysterud, R. Langvatn & N. Chr. Stenseth & N.G.

Yoccoz, unpublished data). Our study provides evidence for the first time that body mass of temperate cervids does not increase with proportion of high-altitude habitat *per se* (H_1) but that a diversity of different altitudes gives the highest body weights (H_2). The evidence suggests that migrating cervids gain from a prolonged period with access to newly emergent forage, which is associated with peak protein levels (Van Soest 1994), as they migrate over a range of altitudes. The distribution of favourable vegetation types may also be an important factor for cervids in an altitudinal gradient (Clutton-Brock & Albon 1989). However, diversity of plants is stable to about 700 m a.s.l. and vegetation is fairly similar up to about 700 m a.s.l. on the west coast of Norway (Odland & Birks 1999), making this an unlikely explanation of the observed pattern.

Later snow melt and lower temperatures on north-facing slopes tend to retard plant development and enhance digestibility (Bennett & Mathias 1984; Hay & Heide 1984), but we found no evidence that body mass increased with increasing proportion of north-facing slopes. On the contrary, slope estimates for the proportion of north-facing slopes were negative (Table 2). However, studies of foraging behaviour have shown that ungulates select different aspects as the seasons progress (Stensli 1988). Any factor leading to a delayed snow melt may extend the period of access to newly emergent, high-quality forage. Indeed we found a positive correlation between red deer body weight during autumn harvest and (H_3) the variability of aspects. Further, our analysis, with a much larger data set and a more detailed spatial resolution, also confirmed that body weights of red deer in Norway increased with distance from the coast and degree of latitude, as reported by Langvatn & Albon (1986) for a sample of 469 red deer from six main regions in Norway. The residual effect of distance from the coast, after the effect of access to a diversity of altitudes is controlled for, is probably due to microclimatic differences between coastal and inland areas. The analysis also provided further evidence that cervids typically follow Bergmann's rule, with larger individuals at northern latitudes (Sæther & Haagenrud 1985; Andersen, Duncan & Linnell 1998). The mechanistic basis of both these gradients is probably related to differences in plant quality rather than thermal capacity (Langvatn & Albon 1986). Our results provide corroborative evidence for the hypothesis that differences in plant quality as they relate to phenology is a main determinant of spatial variation in body weight of temperate herbivores. Further, due to the different evolutionary trajectories of the sexes (Clutton-Brock, Guinness & Albon 1982), we would have expected males to be more sensitive to the factors structuring the spatial heterogeneity. Indeed, based on the parameter estimates (Table 2), stags were about twice as sensitive to variation in diversity of altitudes as were hinds.

The large differences in body mass associated with

geographical covariates reflect different habitat availabilities at the scale of municipalities of western Norway. The size of the 105 municipalities included in this study was on average 601 km² (range 48–2702 km²). Albon & Langvatn (1992) reported an average migration distance of 34 km (range 3–68 km) for 12 adult red deer hinds in the northern part of our study area (deer marked in Snillfjord municipality). Body weight is closely correlated with important fitness measures in both male and female ungulates (Clutton-Brock *et al.* 1982; Langvatn *et al.* 1996; Gaillard *et al.* 2000). One may ask why more individuals do not migrate to municipalities offering a more variable topography (altitude and aspect), until an ideal-free distribution is reached (*sensu* Fretwell & Lucas 1970). Red deer on Rum, Scotland, showed higher calf survival in poor habitats with low local density (Coulson *et al.* 1997), and lifetime reproductive success of red deer hinds was highest on the poorest habitat that also had the lowest hind density (Conradt, Clutton-Brock & Guinness 1999). Migration routes of moose (*Alces alces* L.) have also been reported to be highly traditional and resistant to habitat changes (Sweaner & Sandegren 1988, 1989; Andersen 1991). Furthermore, two out of three studies on roe deer (*Capreolus capreolus* L.) report violation of the ideal free distribution as judged from body mass (Klein & Strandgaard 1972; Wahlström & Kjellander 1995; Pettorelli *et al.* 2001), even though this species is well known for its high proportion of long-distance dispersers (Wahlström & Liberg 1995). Evidently, deer are usually not able to distribute themselves across landscapes so that an ideal free distribution is reached. This is in accordance with recent modelling work predicting that the ideal free distribution is not necessarily a good predictor of animal distributions at a large scale, and that the extent of the area over which an ideal free distribution should be used is similar to the maximum daily movement of the animals under study (Tyler & Hargrove 1997).

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