

Partial migration in expanding red deer populations at northern latitudes – a role for density dependence?

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Partial migration is common in ungulates living in highly seasonal environments. Typically, at higher latitudes, this involves movement between high elevation summer areas used during breeding and lowland areas with less snow used during winter. Snow depth is regarded the main cause of migration to low elevation, but it is less clear why deer migrate to high elevation in spring. The forage maturation hypothesis explains the upward migration due to plant phenology. We here present also an alternative and non-exclusive hypothesis, that deer migrate uphill in summer to escape competition due to the high density in winter areas (the competition avoidance hypothesis). We also suggest that social fences may play a role at high population density. Based on a unique study of 141 GPS-marked red deer from seven regions covering the main distribution in Norway, we found that the proportion of migrants in the populations varied from 38% to 100%. Migration was more common in areas with a diverse topography, i.e. for areas with access to high elevation. Further, we found evidence that migration was negatively density dependent, and that fall migration was delayed at high density. We suggest that a combination of avoidance of competition in high density winter ranges, social fencing during summer in addition to the forage maturation and predation risk avoidance hypotheses, is needed to explain migration patterns of northern ungulates.

Migration of large mammalian herbivores brings images to mind of huge herds moving over vast distances (Fryxell and Sinclair 1988, Fryxell et al. 1988). Most spectacularly we envisage the Serengeti wildebeest *Connochaetes taurinus* in Africa (McNaughton 1976), while Saiga antelopes *Saiga tatarica* in Asia (Berger et al. 2008), caribou *Rangifer tarandus* (Fancy et al. 1989), mule deer *Odocoileus hemionus* (Nicholson et al. 1997, Sawyer et al. 2009) and elk *Cervus elaphus* in North America (Boyce 1989) are other examples of this fascinating phenomenon. Such large scale migration cycles have received a lot of attention recently due to habitat loss and breaking of migration corridors (Bolger et al. 2008, Berger et al. 2008). Grazing by large herbivores has a major impact on the ecosystems. A good understanding of migration is therefore important to be able to predict also their functional role in the ecosystem.

Most attention has been paid to these long-distance movements of large herd living grazers. Less attention has been paid to the fact that not all individuals migrate in many migratory species or populations. Even in Serengeti wildebeest, some individuals remain stationary (Maddock 1979). Partial migration, where only a part of the population migrates while the other remains in the same area year

round, is a very common feature of many populations of more solitary species in forested areas at higher latitudes. Partial migration has for example been reported for all native forest deer species in Scandinavia, both for a small browser, the roe deer *Capreolus capreolus* (Mysterud 1999), a large browser, the moose *Alces alces* (Ball et al. 2001), as well as for the mixed feeder, the red deer *Cervus elaphus* (Albon and Langvatn 1992). Though this has been reported in many single populations, there have been few studies quantifying variation in partial migration between populations for a given species. Such studies are needed to disentangle causes of variation so as to approach the likely mechanisms causing partial migration.

In the large herbivore literature, it is well documented that snow depth at high altitude forces migration to low elevation in fall (Brazda 1953, LeResche 1974, Mysterud 1999). A currently more interesting question is why migrants return to high elevation areas during summer? The most commonly used hypothesis is the forage maturation hypothesis (Fryxell and Sinclair 1988, Albon and Langvatn 1992, Hebblewhite et al. 2008). The main basis for this hypothesis is that at early phenological stages plants have higher quality as forage than the more matured stages.

Migrating animals benefit by following the snow melt and green-up gradient uphill to feed on plants of higher quality.

Theoretical models of partial migration highlight the central role of density dependence and competition (Kokko and Lundberg 2001). It has been argued that the understanding of migration cycles of large mammalian herbivores can be improved by considering it within a framework of seasonal population limitation (Bolger et al. 2008). No study has so far tested for density dependence in migration of large herbivores, nor developed such a hypothesis in depth conceptually. Migration to high elevation summer ranges can serve as a strategy to avoid intraspecific competition due to high density in winter areas. Nelson (1995) documented that white-tailed deer *Odocoileus virginianus*, known to gather in very high density 'deer yards' during winter, seemed to limit the time spent in the winter range. They initiated migration to the winter range if there was a cold spell, but they returned to the summer range if snow depth remained shallow or melted again after the cold spell. Density may also affect conditions in potential summer ranges. The social fence hypothesis has previously been addressed mainly for dispersal of small mammals and birds (Matthysen 2005). This hypothesis highlights that individuals are not free to use all areas due to presence of other animals. As far as we are aware, this hypothesis has not previously been addressed for migration of large mammals. Many studies report a strong social organization of large mammals especially during the breeding season (Comer et al. 2005), and at high density it may be difficult to find summer ranges without social fences.

In this study, we present the first analysis of a large data set with 141 GPS marked female red deer from seven regions in Norway (Fig. 1). Around the early 1900s the Norwegian

red deer population was confined to five or six genetically separated sub-populations along the south western coast (Haanes et al. 2010). Over the last decades, the red deer has expanded its range considerably, and is now present in most of southern and central Norway spanning a large range of variation in topography and population density (Fig. 1). We aimed to test the following hypotheses (Table 1):

H₁. *The forage maturation hypothesis* (Fryxell and Sinclair 1988, Hebblewhite et al. 2008). We predict an increase in proportion of migrants in areas with access to large variation in altitudes, referred to hereafter as topographic diversity.

H₂. *The competition avoidance hypothesis* (Nelson 1995, this study). We predict increased proportions of migrants with increasing winter range population density.

H₃. *The social fence hypothesis* (Matthysen 2005, this study). If there are social constraints or fences impeding establishment in high density areas during the summer season, we predict a decreasing proportion of migrants as population density increases.

H₄. *The predation risk avoidance hypothesis* (Bergerud et al. 1990, Barten et al. 2001). If migration is to reduce predation on vulnerable offspring, we predict migration even at low density and no clear density dependent relationship.

Material and methods

Study area

Study areas are in Rogaland (termed region S), Hordaland (region SW), Sogn og Fjordane (region W), Møre og Romsdal (region NW) and Sør-Trøndelag (region N) counties

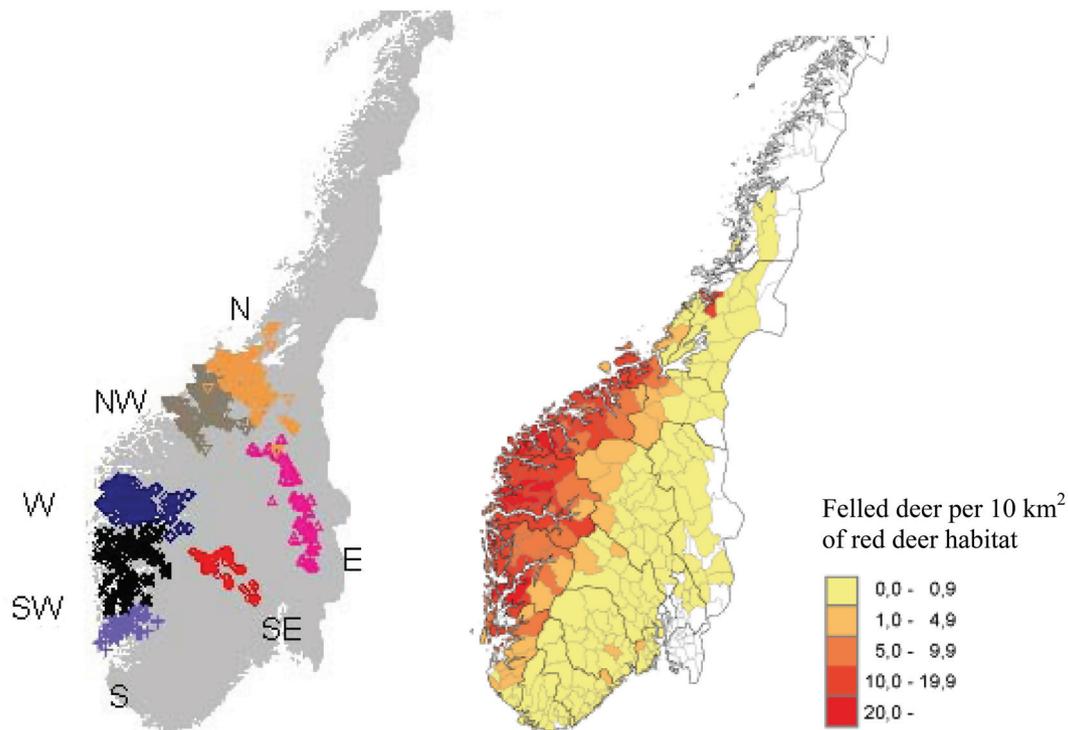


Figure 1. Map showing the location of the seven study areas in southern Norway (left). The location and borders of each area is indicated through plotting GPS-points from marked female red deer. The symbol and colour is unique for each region. The other map (right) gives the number of red deer harvested per 10 km² of red deer habitat in 2009 on a municipality level.

Table 1. An overview of the focal hypotheses tested to explain partial migration in large herbivores. Open cells indicate that there are no clear expectations related to the specified relationships for the given hypothesis. Note that an underlying assumption of all hypotheses is the role of snow in forcing migration to low elevation during fall, and that all hypotheses predict migration to high elevation during summer. Predictions in bold are supported.

Migration trait	Proportion	Distance	Timing	Duration
H ₁ . The forage maturation hypothesis	Migration also at low density	Longer distances if more gentle slopes and high topographical variation	Spring: Linked to speed of green-up	Spring: long duration linked to speed of green-up; longer duration if more gentle slopes and high topographical variation
H ₂ . The competition avoidance hypothesis (winter)	More migration at high density	Longer distances at high density	Early spring migration at high density; delayed fall migration at high density ; long distance migrators leave earlier	Short duration
H ₃ . The social fence hypothesis (summer)	Less migration at high density	Shorter distances at high density	Early spring migration at high density	Short duration
H ₄ . The predation risk avoidance hypothesis	Migration also at low density			Short duration

covering most of the west coast of southern Norway as well as inland localities in Buskerud (region SE) and Hedmark (region E) counties (Fig. 1). Vegetation and climate among these regions reflect a typical coast-inland gradient. In general, temperature and precipitation decline from south to north and from coast to inland, while snow depth increases. The vegetation on the west coast is mainly 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. The inland regions are both in the southern boreal zone. From Rogaland to Møre and Romsdal forests are dominated by deciduous and Scots pine *Pinus sylvestris* forest, but there has been extensive planting of Norway spruce *Picea abies*. Areas in Sør-Trøndelag up to Trondheimsfjorden are dominated by birch *Betula* sp. and pine, whereas spruce forests dominate some areas north of this. The typical habitat type of the inland regions is coniferous forest with Norway spruce and pine as dominating tree species.

Roe deer *Capreolus capreolus* are sympatric to red deer in most regions, apart from most of Sogn og Fjordane. Moose *Alces alces* are abundant in Sør-Trøndelag, Buskerud and Hedmark, but less so in the other regions. Large predators are absent along the west coast, but lynx *Lynx lynx* are common in Buskerud and Hedmark and wolf *Canis lupus* occur in Hedmark.

Red deer data

Red deer females (≥ 1 years of age) were captured and marked with GPS collars during the period 2002–2009 in 64 municipalities in seven regions of Norway (Fig. 1). Animals were darted and immobilized at established winter feeding sites or on cultivated land along roads. All marking procedures were approved by the Norwegian Animal Research Authority.

The most common sampling design was to mark deer in mid-late winter (January–April). With the programmed positioning schedules with one position per hour as a

basis (earliest collars with one position per 1.5 or 2 h), the battery capacity of the GPS-unit most commonly allowed position sampling for a bit longer than one year. The collars were retrieved in late autumn by drop-off or as part of the regular autumn hunt, allowing the same collars to be used on new individuals the next winter. The most common sampling interval for individuals were therefore mid-winter till autumn, or until batteries ran out. In practice this resulted in approximately one year of data per individual. We only included individuals with a sufficient long sampling period that allowed reliably identification of space use patterns. This reduced sample size from a total of 240 marked females down to 141 animals for which the annual pattern of seasonal range use was either migratory or stationary (Table 1). These animals came from 49 municipalities with a mean size of 740 km² (SD = 635).

Covariates

As an index for population density, we used the number of harvested animals per area of red deer habitat as approved by the management authorities in each municipality. Analysis confirm that there is a close correlation between harvest size and other indices of population size, such as the number of seen deer per hunter day and population size estimated with cohort analysis (Mysterud et al. 2007). See also Discussion regarding comparing spatial versus temporal population density.

From earlier work linking body mass of red deer to topography (Mysterud et al. 2001a), we calculated ‘topographic diversity’, as a Shannon-Wiener diversity of altitudes 0–100 m, 100–200 m, 200–300 m, 300–400 m, 400–500 m, 500–600 m and 600–700 m (areas at exactly 0 m and > 700 m were excluded) and proportion of high altitude habitat (segment 250–700 m). Also from earlier demographic work, we retrieved data on distance from the coast and latitude. We also included a variable stating whether data were derived from island or mainland municipalities. All these data were calculated at the scale of municipality, as we have done for demographic data in a series of papers (Mysterud et al. 2001a, Langvatn et al. 2004). The municipalities

represent quite large areas. On average, high topographic diversity would reflect good opportunities for selecting high elevation range within reasonable distance, while a low value would represent that it is quite far to such areas and likely outside normal migration distance. Finally we included 'year' as a factorial variable (2002–2009).

Statistical analyses

Defining migrants and migration distance

We only included annual data from individuals that had continuous relocations (min five relocations in each 16-day period) from at least 1 April 1 until 31 October. These limits were picked because they cover the entire migration period, as well as the full range of the annual vegetation growth (i.e. NDVI > 0, see Fig. 1 in Pettorelli et al. 2005).

We used the Net squared displacement (NSD) pattern to distinguish between migratory and stationary animals (Bunnefeld et al. 2011). NSD combines characteristics from animal movement trajectories (Turchin 1998, Bunnefeld et al. 2011) and is commonly used to estimate the temporal pattern of displacement from a site of origin, such as a marking site (Fryxell et al. 2008). We initially used the approach by Bunnefeld et al. (2011) to aid distinction of different space use strategies, but finalized and corrected designations using visual inspections. This process involved the calculation of NSD using the function `ltraj` in the R library `adehabitar` (Calenge 2006) and the preliminary fitting of five different models representing symmetric seasonal migration, asymmetric seasonal migration, dispersal, nomadic (random walk), and stationary based on the NSD pattern. This was done by fitting the five different models on each NSD time series (Bunnefeld et al. 2011). Each individual was assigned a preliminary space use strategy of the model with the lowest AIC value.

We encountered several problems with the uncritical application of the fully automated process described by Bunnefeld et al. (2011) to our dataset. When plotting the NSD time series and visually inspecting the pattern, it appeared several cases of assignment of incorrect space use strategies (Supplementary material Appendix 1 Table A1). Especially stationary deer were often misclassified, given that we use the most common definition of stationary animals, i.e. those with overlapping winter and summer ranges (LeResche 1974). There were also errors during the estimation of migration parameters for animals designated as migratory, mainly due to functions being fit at incorrect locations in the NSD time series. Because we intended to use only individuals that could be unambiguously designated as either migratory or stationary, we visually inspected all annual NSD and GPS location data for all individuals and made final assignments considering both the automated designations and the observed space use patterns. Although using visual inspection to aid designations introduces a subjective element into the categorization process, the resulting final categorization yielded a set of deer-years with clearly distinguishable space use patterns (Supplementary material Appendix 1 Fig. A1). Ambiguous cases (Supplementary material Appendix 1 Fig. A2) were not resolved by the aid of AICweights, as there was clear evidence in favour of one movement model even when movement pattern was ambiguous or the model-

designated movement pattern differed from the biologically intuitive model (AICweight > 0.95 for best model in 30 out of 32 cases determined to be ambiguous cases). Ultimately, we made assignments to the following categories:

1. Migratory
2. Stationary
3. Stationary with fall excursion
4. Ambiguous or irregular

Only the first three categories were used in the study described here. Individuals designated as stationary with fall excursion exhibited a pattern similar to stationary animals, with the addition of a movement period late in the year, coinciding with the rutting period and/or hunting season. Stationary individuals with fall excursions were considered stationary for the purposes of our analyses, but with the period away from the usual range excluded.

For animals designated as migratory or stationary with fall migration, we fitted separate logistic curves (using the `nls` function in R) to both the movements away from and returning to the winter areas. To ensure that curves were fit to the actual migration period (d = Julian date with decimals), we designated a data range for the fit that included (and extended beyond) migration. The three-parameter logistic function used was of the form:

$$f(d) = \frac{\text{Asym}}{1 + \exp\left(\frac{\text{xmid} - d}{\text{scal}}\right)}$$

The parameters estimated from these fits can be interpreted biologically, with *Asym* (asymptote) representing the average distance between the winter and the summer range (at the time period when migration is occurring), *xmid* (inflection point) the mid-date of migration (i.e. the time when ½ of the total migration distance has been reached, and *scal* (scale parameter) the time needed from the mid-migration date until 75% of the asymptote has been reached (Bunnefeld et al. 2011).

To reduce spatial autocorrelation and issues potentially arising from differences in variances due to varying frequency of GPS relocations, for most analyses we reduced the data for each individual to the first location in each four-hour period (i.e. a maximum of six relocations per individual per day). However, migrations often occurred over a very short time (e.g. less than a day), resulting in an insufficient number of data points during migration to fit a logistic curve to the data. We therefore used hourly NSD data to fit the logistic functions and to estimate migration parameters. Despite using hourly data, model fitting still failed for several return migrations (summer range to winter range). We added evenly spaced dummy NSD data points between consecutive hourly NSD values using linear interpolation before model fitting to resolve this problem.

For comparisons of summer and winter ranges described in the next sections, we excluded the time period of migration (away from and returning to the winter range), which we defined as starting at $\text{xmid} - 2 \text{scal}$ and ending at $\text{xmid} + 2 \text{scal}$.

In five cases (excluding the fourth space use category), individuals were monitored for two consecutive years that

fit the above criteria. In all cases the individuals repeated the same strategy (all migratory) in the second year. For each of these individuals, we only used the first year of monitoring, as their number was too low to warrant the increase in model complexity by considering random effects (i.e. individual id).

Testing hypotheses of partial migration

We analysed partial migration with a generalized linear mixed model (GLMM) fitted with the function `lmer` in the library `lme4` (Bates and Maechler 2009) in R (R Development Core Team 2008). We used migration status (seasonally migratory = 1, stationary = 0) as response variable. The model was fitted with a logit link and errors were assumed to be binomially distributed. We were mainly interested in the effect of topographic diversity and population density. However, we also used model selection (using AIC and BIC) to see whether latitude, distance from the coast, year (as factor) and whether data derived from an island or not improved model fit. There was no correlation between population density and topographic diversity ($r = 0.004$). We used `GAMplot` to explore potential nonlinearities (library `mgcv`; Wood 2006). We then chose adequate transformations or higher order terms for the GLMM based on the `GAMplot`. As the data were not balanced with respect to year and municipalities, we were unable to look for interactions with the year effect. We used 'municipality' ($n = 49$) as a random term.

Analysis of migration traits (migration distance, time and duration of migration and altitude of winter and summer range) was restricted to migrating individuals. We used LME with Gaussian distribution and the same model structure as above, with population density and topographic diversity as fixed terms and municipality as random term (unless otherwise stated). Based on plotting of distributions, we log-transformed the response variables before analyses.

Results

The proportion of migrating individuals varied largely between regions, from 0.38 in region SW to 1.00 in region E (Table 2, Fig. 2). Proportion of migrants was best explained by a positive effect of topographic variation and a negative effect of population density (Table 3). This was consistent with the forage maturation and social fence hypotheses (Table 1). Neither latitude, distance from the coast, proportion of high altitude habitat, whether the municipality was an island or not, nor year (as a factor) entered the best model (Supplementary material Appendix 1 Table A2). `GAMplotting` showed that the effect of topographic variation peaked at a value around 1.5, and then was slightly lower up to the highest values at 1.934. When using this information for the GLMM, we found that a 2nd order term for topographic diversity yielded a better model (AIC = 117.9 vs 120.0), but this did not impact the negative effect of density notably (estimate = -1.089 , SE = 0.475 , $z = -2.293$, $p = 0.022$).

Migrants typically had winter range at a lower elevation than the summer range (Fig. 3). Altitude of winter range was at a lower elevation at high population density (Table 4). This was contrary to the prediction of increased use of higher elevation at high density from the competition avoidance

Table 2. An overview of sample sizes of GPS-marked female red deer from Norway. Two stationary deer in the SW region had fall excursion.

Region	S	SW	W	NW	N	SE	E	Sum
Number marked	20	45	48	56	25	21	25	240
Number with full annual cycle	14	21	34	32	15	13	12	141
Number migrating	10	6	17	16	7	10	9	75
Stationary	3	10	7	7	6	1		34
Irregular space use	1	5	10	9	2	2	3	32
Prop. migrating	0.77	0.38	0.71	0.70	0.54	0.91	1.00	

hypothesis (Table 1). Migration distance decreased markedly with increasing population density, but there was no effect of topographic diversity (Table 4). Fall migration was later at high density (Table 4), as predicted by the avoidance of competition hypothesis (Table 1). However, timing of fall migration was not related to migration distance (model with only density: AIC = -110.8 ; model adding migration distance: AIC = -86.8) when this term was added to a model including population density as the other predictor variable. There was no effect of neither density nor topographic diversity on either duration of spring or fall migration or timing of spring migration (Table 4).

Discussion

Partial migration is regarded as particularly useful to understand the mechanisms for why migration evolves. We found extensive geographical variation in partial migration for female red deer in Norway. The proportion of migrants varied from 38% in region SW to 100% in region E (Fig. 2). Our study is the first to report empirical evidence of (negative) density dependence in likelihood of migration in deer,

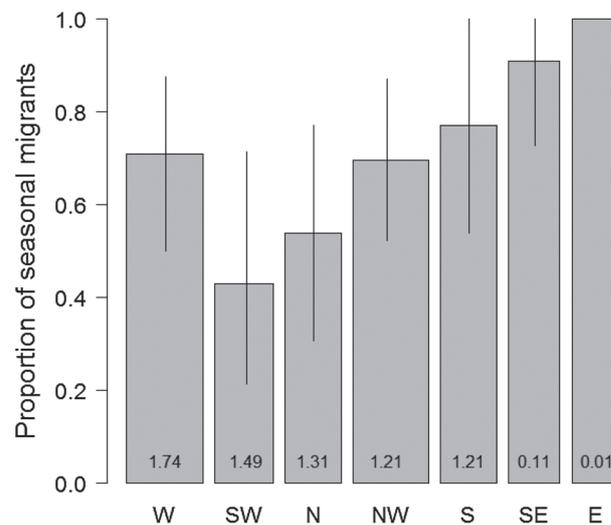


Figure 2. Barplot showing the proportion of seasonally migrating female red deer in each region of Norway only taking into account the individuals showing a clear migratory or stationary strategy. The width of each bar is proportional to the square root of the sample size (number of deer) per area. The error bars are the 95% bootstrap confidence limits. The mean deer density (shot per km²) in the years of observation is presented as text in each bar.

Table 3. Parameter estimates and test statistics from the most parsimonious model (Table A1), a mixed effect logistic regression model with “municipality” as random terms, predicting probability of migration of red deer in Norway. Lower/upper limit = lower/upper 95% confidence limit. Confidence limits giving a 95% confidence interval not overlapping 0 are bolded.

	Estimate	SE	Lower limit	Upper limit
Intercept	-0.989	1.174	-3.337	1.359
Density	-1.246	0.449	-2.145	-0.347
Topographic diversity	2.082	0.720	0.642	3.522

which is the main finding of our study. The mechanistic basis of this density dependence is less clear. The reduced proportion of migrants at high density supported the social fence hypothesis, while the later fall migration at high density supported the competition avoidance hypothesis.

Spring migration – plant phenology or escaping competition at high density?

Migration is more common at northern latitudes and at high altitudes, and an obvious explanation is linked to stronger spatial variation in seasonal limitations. The main factor causing migration to low elevation in fall is snow. It is well documented that large herbivore migration can be driven by rainfall cycles linked to plant development in Africa (McNaughton 1976) and snow melt cycles affecting plant maturation at northern latitudes (Albon and Langvatn 1992, Hebblewhite et al. 2008). The forage maturation hypothesis is the most well developed hypothesis to explain migration uphill in spring (Fryxell and Sinclair 1988, Albon and Langvatn 1992). It was recently thoroughly tested for elk in North America (Hebblewhite et al. 2008), and a now classic study has shown this for VHF collared red deer in region N in Norway (Albon and Langvatn 1992). It was therefore not surprising that topographic diversity, likely reflecting variation in plant phenology (Pettorelli et al. 2005), positively affected the probability of migration. However, the argument of

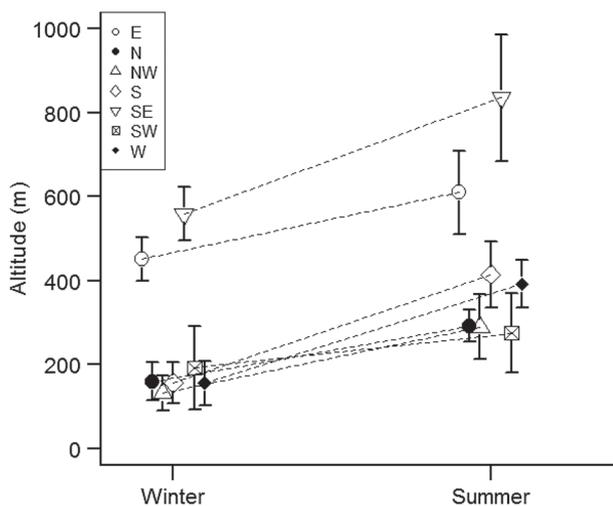


Figure 3. Pattern of seasonal migration along altitudinal gradients for 7 regions of Norway. Point estimates are the mean across individual females conforming to the seasonal migration strategy. Error bars are 95% confidence limits.

following the spring wave of plant phenology mainly applies to grasses. Much of the browse are situated above snow cover and its phenology is not likely as tightly linked to snow melt, though good documentation for this is lacking. If so, we would not expect similar strong altitudinal migration in browsers. However, it is well documented that browsers like roe deer (Mysterud 1999), white-tailed deer (Nelson 1995) and moose (Ball et al. 2001) follow the same main altitudinal migration. We do not suggest that the forage maturation hypothesis is wrong, it is certainly well supported and likely applies in our case (Albon and Langvatn 1992, Mysterud et al. 2001a). However, the same main altitudinal pattern of migration may be a result of avoidance of competition due to high density in the winter range. For red deer in Norway, both processes would work in the same main direction.

The avoidance of competition hypothesis

We highlight that the avoidance of competition hypothesis yields some novel predictions regarding details in the migration pattern, while the main altitudinal migration can fit all hypotheses (Table 1). Some patterns predicted are consistent with what is already reported in the literature. The best evidence comes from white-tailed deer, where migrating deer seemed to spend minimal time in the winter areas, likely due to high competition in those areas (Nelson 1995). We would predict long distance migrants to arrive earlier in the winter ranges, due to a higher chance of being caught in snow, but found no support for this. For roe deer, some migrants waited until snow depth forced them to the winter range (Mysterud 1999). Speed of migration is also an issue. Red deer (Albon and Langvatn 1992) and elk (Dalke et al. 1965) moved gradually to their summer range, as would be predicted by the forage maturation hypothesis. The avoidance of competition hypothesis predicts a rapid escape as soon as conditions allow. This leads also to some clear predictions when it comes to climatic effects during autumn and winter (Table 1). If the animals try to restrict time in winter range to a minimum, the migration pattern could reflect opportunistic responses to periods of reduced snow depth during winter, i.e. potentially resulting in several migration events of the same individual (Nelson 1995). Also, we would expect facultative migration, which has been observed in mule deer (Nicholson et al. 1997).

As stated above, the prediction for the interspecific pattern is that also browsers may migrate altitudinally, and that quality of high elevation summer ranges is not necessarily higher than that of low elevation ranges used for wintering. In roe deer (Mysterud 1999) and black-tailed deer *Odocoileus hemionus columbianus* (Loft et al. 1984), that are browsers (or concentrate feeders), summer home ranges were considerably larger at high elevation, suggesting high elevation areas provided lower forage quality, but we cannot exclude the possibility of simply more dispersed forage. Also for moose, it was documented that calves from females remaining in winter ranges at low elevation had better growth than migrants (Sæther and Heim 1993). These patterns are consistent with what would be expected by the competition avoidance hypothesis.

A prediction of the avoidance of competition hypothesis is that deer in winter may stay at somewhat higher elevation

Table 4. Parameter estimates and test statistics of mixed effect models with “municipality” as random terms, predicting distance, duration and timing of migration of red deer in Norway. All response variables were log-transformed. Lower/upper limit = lower/upper 95% confidence limit. Confidence limits giving a 95% confidence interval not overlapping 0 are bolded.

	Estimate	SE	Lower limit	Upper limit
A. Distance				
Intercept	10.504	0.705	9.094	11.915
Density	-0.416	0.170	- 0.756	- 0.075
Topographic diversity	-0.143	0.451	-1.045	0.758
B. Duration - spring				
Intercept	13.257	1.526	10.206	16.308
Density	-0.096	0.368	-0.832	0.640
Topographic diversity	-1.564	0.975	-3.513	0.385
C. Duration - fall				
Intercept	10.531	1.391	7.749	13.314
Density	-0.245	0.339	-0.924	0.433
Topographic diversity	-0.016	0.896	-1.809	1.776
D. Timing - spring				
Intercept	4.692	0.228	4.236	5.147
Density	-0.045	0.054	-0.152	0.062
Topographic diversity	0.138	0.143	-0.148	0.425
E. Timing - fall				
Intercept	5.404	0.132	5.140	5.669
Density	-0.064	0.031	- 0.126	- 0.002
Topographic diversity	0.129	0.083	-0.037	0.295
F. Altitude winter range				
Intercept	5.614	0.846	3.921	7.306
Density	-0.455	0.190	- 0.836	- 0.075
Topographic diversity	-0.019	0.529	-1.077	1.039

at high density. If so, we might get a reversal of predictions, i.e. a lower proportion of migrants and shorter migration distances at high density (Table 1). We found no evidence for deer wintering at higher elevation at high density. Either the hypothesis is wrong, or it may in our case be due to the extensive use of agricultural pastures and to some extent winter feeding sites that are mainly at low elevation (Godvik et al. 2009). The cost of wintering at higher elevation may therefore be severe. In contrast, we found that the elevation of the winter range decreased with density. We cannot fully explain this, but it may be related to that we compare spatial density variation. The areas with lowest population density are the inland regions with on average higher elevations (Fig. 3).

Social fences on summer range?

Deer species typically show high fidelity to both their summer and winter ranges (Tierson et al. 1985, Sweanor and Sandegren 1989, Van Deelen et al. 1998, Igota et al. 2004). Older females usually have more exclusive summer ranges than younger animals (Aycrigg and Porter 1997). At the time when offspring separate from their mothers, the older animals in the population are likely already in their summer range. A deer trying to find a summer range may try to avoid areas with non-kin. In white-tailed deer (Tierson et al. 1985, Aycrigg and Porter 1997) and roe deer (Wahlström and Liberg 1995), females therefore often establish close to their mothers. In white-tailed deer, all fawns returned as yearlings to their mother's summer range, but among 2–3 year olds, only 67–80% did so (Nelson 1998). Indeed, 20% of the

offspring of non-migratory deer became migrants (Nelson 1998). From the avoidance of competition hypothesis, we predicted an increasing proportion of migrants at high density, but we found the reverse. It might be that deer trying to establish as migrants at higher density have more trouble finding areas without ‘social fences’. For red deer in region N, 20 years of capture–mark–recapture data showed that the proportion of young males dispersing was negatively related to density (Loe et al. 2009). During the period of the study, population density increased considerably both within the municipality hosting the catching locations, and in neighbouring municipalities. Although the number of dispersing young males decreased as population density rose, the distance they dispersed increased. This could likely be because it took a longer distance to reach low density areas. This was based on males. In addition, although being related dispersal and migration are different processes. Still, the results from this study suggest further exploration of social fences in range use establishment.

Spatial versus temporal density dependence

A weakness of our study is that we only contrast areas of varying population density, while we have no good measure of variation in habitat quality which is important for the level of competition. Along the west coast (regions S, SW, W, NW and N), we have good data on body mass. Earlier studies that used number of shot deer as a density index found expected patterns of density dependence in other life history traits (body weights: Mysterud et al. 2001b; sex ratio of calves: Mysterud et al. 2000; female reproduction: Langvatn et al. 2004). There was a consistent negative relationship between body weight and density across municipalities (Loe et al. 2009). Though intercepts differ slightly, this suggests that in our case density was mainly a measure of resource availability and that high density did not reflect high habitat quality. We therefore find it likely that density dependence in the proportion of migrants represents a robust test of the competition avoidance and social fence hypotheses.

The relative balance of high versus low elevation areas for a given region may be important in yielding the pattern of seasonal migration and overall density dependence, as it affects the extent of seasonal resource limitation. Differing proportion of high versus low elevation areas will affect the total density dependence exhibited by the whole population, as the proportion of low elevation areas will likely limit the overall population size. In areas with a high proportion of low elevation areas, a higher overall population density can likely be sustained, with resulting higher density dependence and thus smaller deer (as in many coastal areas). In contrast, inland areas with a higher proportion of high elevation areas can overall sustain fewer animals, but since they spread out during summer, density dependence during the important growing season is reduced also for stationary animals resulting in larger individuals. This will be a mechanism adding to the benefit of following the plant phenological development in such areas (Mysterud et al. 2001a).

Differing landscape features between regions also make it more uncertain to compare spatial variation in migration traits such as altitude of winter range and timing of migration. The two inland areas are located at a higher

elevation (Fig. 3). This might explain the increased altitudes used at low density, which does not support the competition avoidance hypothesis, but it may also provide an alternative explanation of the supporting result of later fall migration at high elevation. Further, snow depth is the main factor for wintering at low elevation, and habitat may play an important role for snow cover patterns. It is clear that coniferous forest habitat may provide areas of shallow snow depth similar to low elevation, as shown for sika deer migration patterns with some upward migration to coniferous forest habitat (Igota et al. 2004). The inland regions have much more extensive coniferous forests. Assessing temporal variation in density rather than spatially as in our case would likely be needed to validate this (Table 1). However, such datasets are not available today. Clearly, more long-term studies in a given area would also allow an assessment of climate-density interaction related predictions (Table 1).

Can we ignore predators when they are not present?

Predation may play an important role for migration (Hebblewhite and Merrill 2007). Neonates and calves are more prone to predation (Linnell et al. 1995), and migration may therefore serve as a strategy to avoid areas with high predation risk (Edwards 1983, Festa-Bianchet 1988, Hebblewhite and Merrill 2007). The predation risk avoidance hypothesis can also be applied to seasonal spacing behaviour: while it may be advantageous for a large herbivore to join high local densities or herds in order to decrease individual predation risk, it may be more advantageous to live solitary and secretive during calving season (Bergerud et al. 1990, Barten et al. 2001). The main altitudinal migration upwards in spring may therefore also be predicted based on predation, and it may apply to both grazers and browsers. Predators are absent in most of our study areas (except some documented cases in region SE and E), but many aspects of ungulate behaviour have been shaped by predation to such a degree in the past (Byers 1997, Bowyer 2004), that this cannot be ignored. Direct observations suggests that red deer males in Norway (region 'N') are more frequently grazing in the alpine zone in late summer than females (Bonenfant et al. 2004), which may reflect choice for forest areas as an anti-predator strategy of females with offspring, at the expense of higher quality forage in the alpine zone in late summer.

Conclusion

We highlight that several hypotheses can predict the same main pattern of altitudinal migration, and that more detailed predictions are needed. We found strong evidence for density dependence in migration. The decreasing proportion of migrants at high density did not support the avoidance of competition hypothesis, but suggests a role of social fences. Insight into these processes can have marked implications for population dynamics and therefore also for management and conservation of large herbivores.

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References

- Albon, S. D. and Langvatn, R. 1992. Plant phenology and the benefits of migration in a temperate ungulate. – *Oikos* 65: 502–513.
- Aycrigg, J. L. and Porter, W. F. 1997. Sociospatial dynamics of white-tailed deer in the central Adirondacks mountains, New York. – *J. Mammal* 78: 468–482.
- Ball, J. P. et al. 2001. Partial migration by large ungulates: characteristics of seasonal moose *Alces alces* ranges in northern Sweden. – *Wildlife Biol.* 7: 39–47.
- Barten, N. L. et al. 2001. Habitat use by female caribou: tradeoffs associated with parturition. – *J. Wildlife Manage.* 65: 77–92.
- Bates, D. and Maechler, M. 2009. lme4: linear mixed-effects models using Eigen and S4 classes. – R package ver. 0.999375-32. <<http://CRAN.R-project.org/package=lme4>>.
- Berger, J. et al. 2008. Protecting migration corridors: challenges and optimism for Mongolian saiga. – *Plos Biol.* 6: 1365–1367.
- Bergerud, A. T. et al. 1990. Spring migration and dispersion of woodland caribou at calving. – *Anim. Behav.* 39: 360–368.
- Bolger, D. T. et al. 2008. The need for integrative approaches to understand and conserve migratory ungulates. – *Ecol. Lett.* 11: 63–77.
- Bonenfant, C. et al. 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.
- Bowyer, R. T. 2004. Sexual segregation in ruminants: definitions, hypotheses, and implications for conservation and management. – *J. Mammal* 85: 1039–1052.
- Boyce, M. S. 1989. The Jackson elk herd. Intensive wildlife management in North America. – Cambridge Univ. Press.
- Brazda, A. R. 1953. Elk migration patterns, and some of the factors affecting movements in the Gallatin river drainage, Montana. – *J. Wildlife Manage.* 17: 9–23.
- Bunnefeld, N. et al. 2011. A model-driven approach to quantify migration patterns: individual, regional and yearly differences. – *J. Anim. Ecol.* 80: 466–476.
- Byers, J. A. 1997. American pronghorn. Social adaptations and the ghost of predators past. – Univ. of Chicago Press.
- Calenge, C. 2006. The package "adehabitat" for the R software: a tool for the analysis of space and habitat use by animals. – *Ecol. Model.* 197: 516–519.
- Comer, C. E. et al. 2005. Fine-scale genetic structure and social organization in female white-tailed deer. – *J. Wildlife Manage.* 69: 332–344.
- Dalke, P. D. et al. 1965. Seasonal movements of elk in the selway river drainage, Idaho. – *J. Wildlife Manage.* 17: 333–338.
- Edwards, J. 1983. Diet shifts in moose due to predator avoidance. – *Oecologia* 60: 185–189.
- Fancy, S. G. et al. 1989. Seasonal movements of caribou in Arctic Alaska as determined by satellite. – *Can. J. Zool.* 67: 644–650.
- Festa-Bianchet, M. 1988. Seasonal range selection in bighorn sheep: conflicts between forage quality, forage quantity, and predator avoidance. – *Oecologia* 75: 580–586.
- Fryxell, J. M. and Sinclair, A. R. E. 1988. Causes and consequences of migration by large herbivores. – *Trends Ecol. Evol.* 3: 237–241.
- Fryxell, J. M. et al. 1988. Why are migratory ungulates so abundant? – *Am. Nat.* 131: 781–798.

- Fryxell, J. M. et al. 2008. Multiple movement modes of large herbivores at multiple spatiotemporal scales. – *Proc. Natl Acad. Sci. USA* 105: 19114–19119.
- Godvik, I. M. R. et al. 2009. Temporal scales, tradeoffs and functional responses in habitat selection of red deer. – *Ecology* 90: 699–710.
- Haanes, H. et al. 2010. Genetic structure in an expanding cervid population after population reduction. – *Conserv. Genet.* 11: 11–20.
- Hebblewhite, M. and Merrill, E. H. 2007. Multiscale wolf predation risk for elk: does migration reduce risk? – *Oecologia* 152: 377–387.
- Hebblewhite, M. et al. 2008. A multi-scale test of the forage maturation hypothesis in a partially migratory ungulate population. – *Ecol. Monogr.* 78: 141–166.
- Igota, H. et al. 2004. Seasonal migration patterns of female sika deer in eastern Hokkaido, Japan. – *Ecol. Res.* 19: 169–178.
- Kokko, H. and Lundberg, P. 2001. Dispersal, migration, and offspring retention in saturated habitats. – *Am. Nat.* 157: 188–202.
- Langvatn, R. et al. 2004. Timing and synchrony of ovulation in red deer constrained by short northern summers. – *Am. Nat.* 163: 763–772.
- LeResche, R. E. 1974. Moose migrations in North America. – *Nat. Can.* 101: 393–415.
- Linnell, J. D. C. et al. 1995. Who killed Bambi? The role of predation in the neonatal mortality of temperate ungulates. – *Wildlife Biol.* 1: 209–223.
- Loe, L. E. et al. 2009. Negative density-dependent emigration of males in an increasing red deer population. – *Proc. R. Soc. B* 276: 2581–2587.
- Loft, E. R. et al. 1984. Seasonal movements and summer habitats of female black-tailed deer. – *J. Wildlife Manage.* 48: 1317–1325.
- Maddock, L. 1979. The “migration” and grazing succession. – In: Sinclair, A. R. E. and Norton-Griffiths, M. (eds), *Serengeti. Dynamics of an ecosystem*. Univ. of Chicago Press, pp. 104–129.
- Matthysen, E. 2005. Density-dependent dispersal in birds and mammals. – *Ecography* 28: 403–416.
- McNaughton, S. J. 1976. Serengeti migratory wildebeest: facilitation of energy flow by grazing. – *Science* 191: 92–94.
- Mysterud, A. 1999. Seasonal migration pattern and home range of roe deer (*Capreolus capreolus*) in an altitudinal gradient in southern Norway. – *J. Zool.* 247: 479–486.
- Mysterud, A. et al. 2000. Relationships between sex ratio, climate and density in red deer: the importance of spatial scale. – *J. Anim. Ecol.* 69: 959–974.
- Mysterud, A. et al. 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.
- Mysterud, A. et al. 2001b. 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.
- Mysterud, A. et al. 2007. Monitoring population size of red deer: an evaluation of two types of census data from Norway. – *Wildlife Biol.* 13: 285–298.
- Nelson, M. E. 1995. Winter range arrival and departure of white-tailed deer in northeastern Minnesota. – *Can. J. Zool.* 73: 1069–1076.
- Nelson, M. E. 1998. Development of migratory behavior in northern white-tailed deer. – *Can. J. Zool.* 76: 426–432.
- Nicholson, M. C. et al. 1997. Habitat selection and survival of mule deer: tradeoffs associated with migration. – *J. Mammal* 78: 483–504.
- Pettorelli, N. et al. 2005. Importance of climatological downscaling and plant phenology for red deer in heterogeneous landscapes. – *Proc. R. Soc. B* 272: 2357–2364.
- Sæther, B.-E. and Heim, M. 1993. Ecological correlates of individual variation in age at maturity in female moose (*Alces alces*): the effects of environmental variability. – *J. Anim. Ecol.* 62: 482–489.
- Sawyer, H. et al. 2009. Identifying and prioritizing ungulate migration routes for landscape-level conservation. – *Ecol. Appl.* 19: 2016–2025.
- Sweaner, P. Y. and Sandegren, F. 1989. Winter-range philopatry of seasonally migratory moose. – *J. Appl. Ecol.* 26: 25–33.
- Tierson, W. C. et al. 1985. Seasonal movements and home ranges of white-tailed deer in the Adirondacks. – *J. Wildlife Manage.* 49: 760–769.
- Turchin, P. 1998. Quantitative analysis of movement. Measuring and modeling population redistribution in animals and plants. – Sinauer.
- Van Deelen, T. R. et al. 1998. Migration and seasonal range dynamics of deer using adjacent deeryards in northern Michigan. – *J. Wildlife Manage.* 62: 205–213.
- Wahlström, L. K. and Liberg, O. 1995. Patterns of dispersal and seasonal migration in roe deer (*Capreolus capreolus*). – *J. Zool.* 235: 455–467.
- Wood, S. 2006. Generalized additive models: an introduction with R. – Chapman and Hall.

Supplementary material (available online as Appendix O19439 at www.oikosoffice.lu.se/appendix). Appendix 1