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Large herbivore migration plasticity along environmental gradients in Europe: life-history traits modulate forage effects

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The most common framework under which ungulate migration is studied predicts that it is driven by spatio–temporal variation in plant phenology, yet other hypotheses may explain differences within and between species. To disentangle more complex patterns than those based on single species/ single populations, we quantified migration variability using two sympatric ungulate species differing in their foraging strategy, mating system and physiological constraints due to body size. We related observed variation to a set of hypotheses. We used GPS-collar data from 537 individuals in 10 roe *Capreolus capreolus* and 12 red deer *Cervus elaphus* populations spanning environmental gradients across Europe to assess variation in migration propensity, distance and timing. Using time-to-event models, we explored how the probability of migration varied in relation to sex, landscape (e.g. topography, forest cover) and temporally-varying environmental factors (e.g. plant green-up, snow cover). Migration propensity varied across study areas. Red deer were, on average, three times more migratory than roe deer (56% versus 18%). This relationship was mainly driven by red deer males which were twice as migratory as females (82% versus 38%). The probability of roe deer migration was similar between sexes. Roe deer (both sexes) migrated earliest in spring. While

territorial male roe deer migrated last in autumn, male and female red deer migrated around the same time in autumn, likely due to their polygynous mating system. Plant productivity determined the onset of spring migration in both species, but if plant productivity on winter ranges was sufficiently high, roe deer were less likely to leave. In autumn, migration coincided with reduced plant productivity for both species. This relationship was stronger for red deer. Our results confirm that ungulate migration is influenced by plant phenology, but in a novel way, that these effects appear to be modulated by species-specific traits, especially mating strategies.

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Introduction

Partial migration, when only part of the population migrates, is widespread in many taxa and provides an ideal context to explore the underlying drivers of migratory behavior. In ungulates partial migration is common, depending on both extrinsic (e.g. forage, weather) and intrinsic factors (e.g. sex or age; Cagnacci et al. 2011, Mysterud et al. 2011). However, only a few studies to date have tested for differing determinants of migration in sympatric ungulate species (Mysterud et al. 2012, Hopcraft et al. 2014). Thus, comparing migration behavior between species with contrasting life histories that share the same wide range of ecological conditions presents a powerful approach to identify potential drivers of migration in relation to variation in benefits and constraints.

In temperate environments, the proportion of migrants in ungulate populations is expected to increase with latitude and elevation due to greater and more predictable seasonality (i.e. across-year predictability in plant green-up), decreasing forage availability and increasing snow depth (Mueller et al. 2011). Most frequently, ungulates at northern latitudes migrate from lower elevation winter ranges to high elevation summer ranges (Albon and Langvatn 1992). The forage maturation hypothesis (FMH) predicts that uphill migration in spring is driven by progressive plant green-up as the snowmelt advances, allowing migrants access to higher quality forage during summer as compared to individuals that remain as residents in summer (Albon and Langvatn 1992, Hebblewhite et al. 2008). While this hypothesis was proposed for herbivores that feed mainly on graminoids, the phenology of browse species differs (Hebblewhite et al. 2008) and is often more spatially and temporally heterogeneous than that of graminoids (Golluscio et al. 2005). Indeed, we know little about if, and how, migration behavior of ungulates varies among species in relation to the browser–grazer continuum (Mysterud et al. 2012). Also, in contrast to spring migration, the drivers of autumn migration are commonly attributed to plant senescence and increasing snow depths that restrict locomotion at high elevation (Sabine et al. 2002, Brinkman et al. 2005, Monteith et al. 2011). Knowledge on species- and sex-specific migration variation can aid ungulate management planning which requires matching biological and administrative scales (Meisingset et al. 2018), and will be important if management actions or anthropogenic impacts disproportionately affect animals with different migration tactics (Found and St. Clair 2016, Sawyer et al. 2016).

Variation in migration behavior among species is expected due to differences in biology, morphology and life history. It has been shown that the costs of migration are higher for smaller bodied species due to limited energy storage capacity and the resulting allometric energetic constraints (body size constraint hypothesis; Hein et al. 2012). Similarly, the benefits and constraints of migration may differ between sexes. Differences in costs, and hence migration behavior, between males and females are expected to be particularly acute for sexually dimorphic species (Bowyer 2004), but may also vary with different reproductive schedules such as mating and parturition.

Herein, we contrast migration behavior of two of the most widely distributed sympatric ungulates in Europe, roe deer *Capreolus capreolus* and red deer *Cervus elaphus*. Roe and red deer differ in their feeding behavior, body size, and mating system, but range across the same latitudinal and environmental gradients from southern France to central Norway (Fig. 1). Red deer are classified as mixed feeders, with a diet of graminoids, forbs and roughage (Hofmann 1989), whereas roe deer are browsing concentrate selectors with a diet rich in soluble plant cell contents of mainly forbs and shrubs (Verheyden et al. 2011). Roe deer are particularly selective for highly nutritious plant parts across diverse plant species, and are limited by plant quality rather than biomass (Storms et al. 2006). Red deer are larger (average weight in kg: males 160, females 108), sexually dimorphic, capital breeders that produce a single offspring, and follow a polygynous mating system with strong female philopatry and males that defend harems during the rut in September–October (Moyes et al. 2006). The much smaller and almost monomorphic roe deer (average weight in kg: males 28, females 27) are income breeders that produce multiple offspring and have a weakly polygynous, male-territorial mating system with the rut occurring in July and August followed by a period of delayed implantation until mid-winter (Vanpe et al. 2009).

We first quantified variation in migration propensity (the proportion of migratory animals in the studied sample), distance, and timing in spring and autumn between species, populations and sexes using data from multiple populations covering wide ecological gradients in Europe. Next, we evaluated the relative contributions of abiotic and biotic factors as determinants of spatio–temporal variation in migration probability between species and sexes. We tested several hypotheses that have been proposed to explain variation in migration behavior, taking advantage of the expected
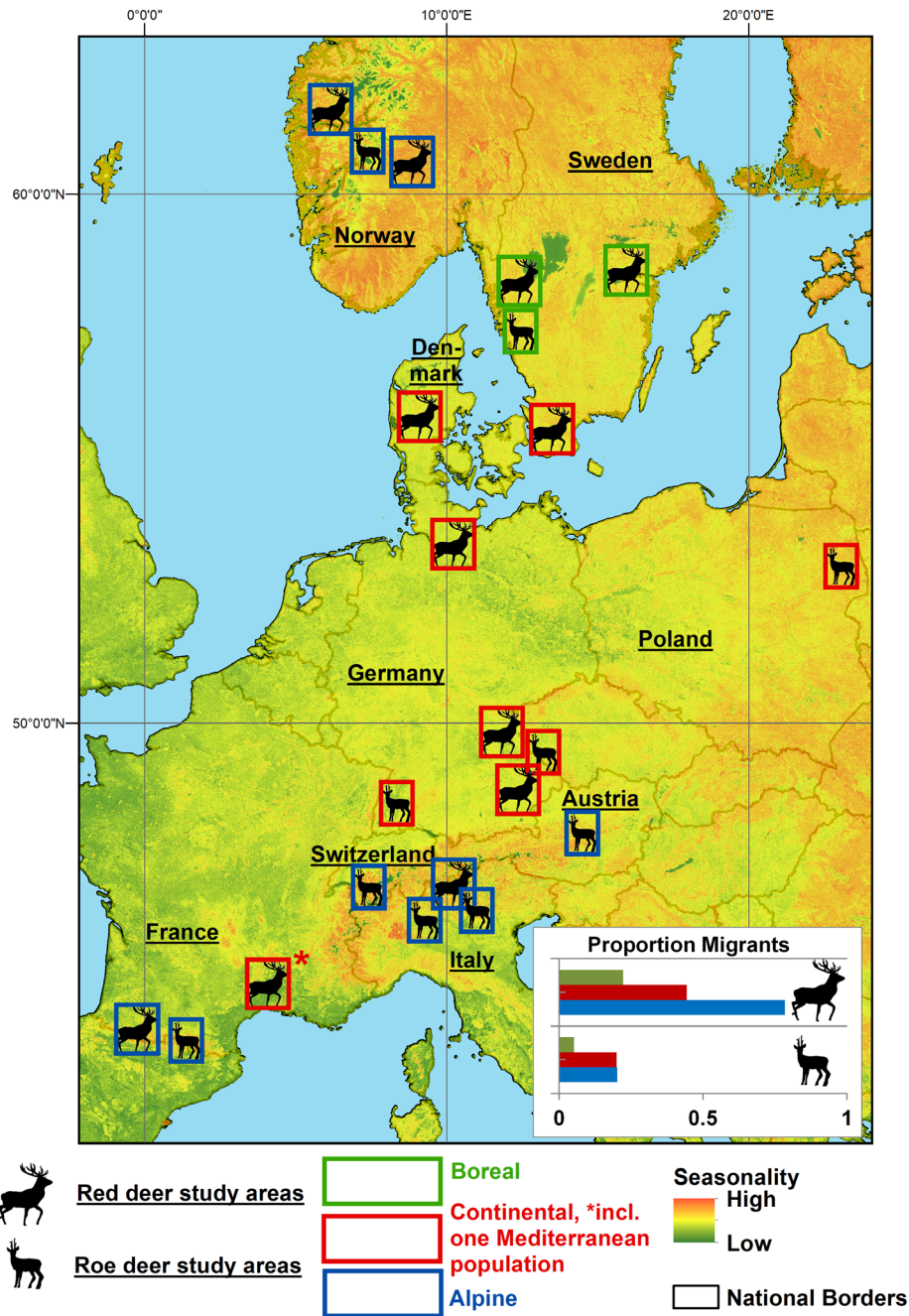
Figure 1. Roe and red deer ($n_{roe} = 273$, 10 populations; $n_{red} = 264$, 12 populations) study area locations. Each population is associated with a biogeographic region. The spatial contingency (seasonality) layer is in the background, where red shades indicate high seasonality and green shades indicate low seasonality. The proportion of migrants by species in each biogeographic region is shown in the bar graph. GPS collar data were collected between 1999 and 2014.

differences between species. While forage maturation should affect energetic intake rates in all ruminants, the magnitude of the effects may affected by ruminant physiology (Owen-Smith and Novellie 1982, Fryxell 1991, Mysterud et al. 2012, Merkle et al. 2016). Under the FMH migration of roe and red deer should be more common in more seasonal land-scapes, characterized by higher topographic complexity and predictable variation in forage (FMH) (Albon and Langvatn 1992; P_1, Table 1). However, because the smaller roe deer are highly selective browsers, ingesting relatively small amounts of high quality forage to meet their energy requirements (Hofmann 1989), we expected the magnitude of these effects to be stronger for red deer, which are bulk feeders, than for roe deer (Fryxell 1991, Mysterud et al. 2012). Consequently, we predicted that the proportion of migratory red deer should be higher than roe deer within a given setting (P_2).

Table 1. Predicted differences between partially migratory roe and red deer (n_{roe} = 273, 10 populations; n_{red} = 264, 12 populations) for the overall frequency (i.e. probability), distance, and timing of migration. Study areas of both species ranged across similar latitudinal gradients in Europe and animal location data were collected between 1999 and 2014.

	Between population	Between species	Between sexes
Frequency	P_1: Higher proportion of migrants with increasing topographic complexity and latitude, winter severity, predictability of forage (*FMH*). Results: Confirmed (contingency, constancy and measures of topographic diversity were significant predictors of migration probability).	P_2: Under the *FMH*, higher proportion of migrants in red deer populations than in roe deer populations. Results: Confirmed (56% of all red and 18% of all roe deer were migratory), although this was mainly driven by a higher probability of migration in red deer males.	P_7: Red deer males are the most migratory and no differences in migration frequency between roe deer males and females due to low sexual dimorphism (*Body size constraint hypothesis*). Results: Confirmed (migratory probability was not significantly different between male and female roe deer, but it was significantly different between male and female red deer).
Distance	NA	P_4: Red deer migrate further than roe deer because of larger body size (*Body size constraint hypothesis*). Results: Confirmed (red deer migrated almost twice as far as roe deer).	P_8: Red deer males migrate further than females because of body size dimorphism, fewer differences in roe deer (*Body size constraint hypothesis*). Results: Confirmed (significant differences between the sexes for red deer, but not for roe deer).
Timing	P_3: Spring migration correlates with forage green-up and autumn migration correlates with onset of winter (*FMH*). Results: Partially confirmed (spring migration correlated with plant phenology for both species, but snow cover was not significant in autumn for either species, but plant senescence was).	$P_{3.1}$: Roe deer autumn migration is more driven by snow and red deer autumn migration by plant senescence. (*Body size constraint hypothesis*) Results: Partially confirmed (both red and roe deer migrations were driven by plant senescence as one would predict under the FMH). Snow was not significant for either species. $P_{3.2}$: Red deer migration more affected by plant green-up and senescence than roe deer (later in spring, earlier in autumn; *FMH*). Results: Partially confirmed (especially red deer males migrated later in spring and earlier in autumn).	P_5: Female roe- and red deer migration more synchronized due to parturition. Results: Confirmed (spring migrations in females had lower standard deviations). P_6: Roe deer males migrate first in spring and last in autumn (compared to roe deer females and red deer of both sexes) to establish and maintain territories for maximum duration. (*Competition avoidance hypothesis*) Results: Partially confirmed. Roe deer migrated slightly before red deer in spring (only significant at the 0.1 level) and later in autumn, but no sex-specific differences were found for spring migration. In autumn roe deer males were the last to migrate.

Next, because spring migration is hypothesized to be influenced by plant green-up (Bischof et al. 2012, Lendrum et al. 2013, Merkle et al. 2016, Aikens et al. 2017), while the onset of winter snowfall is the main trigger for autumn migration (Sabine et al. 2002, Fieberg et al. 2008, Monteith et al. 2011), we predicted that migration timing would correlate with green-up in spring and snowfall in autumn, respectively, for both species (P_3). However, we predicted that roe deer migration would be more tightly linked to snow accumulation due to their much smaller body size and associated locomotive constraints ($P_{3.1}$; Cagnacci et al. 2011). Given the species-specific differences in diet, we predicted that spring migration would be later for red than for roe deer due to the delayed and more homogenous green-up of graminoids compared to forbs and shrubs ($P_{3.1}$; Hebblewhite et al. 2008). Similarly, graminoids commonly senesce before forbs and shrubs in autumn (Hebblewhite et al. 2008), hence, we predicted that red deer should initiate autumn migration earlier than roe deer ($P_{3.2}$). In addition, under the body size constraint hypothesis (Hein et al. 2012), we predicted that red deer would migrate farther than roe deer (P_4).

In terms of sex-specific constraints, we predicted that migration would be more synchronized (i.e. less variable) in females of both species compared to males, because the growing season coincides with parturition and is therefore especially important for females (P_5, Parker et al. 2009). For a species with a territorial mating system such as roe deer, the competition avoidance hypothesis suggests that males should establish their mating territories as early as possible on their summer ranges (Mysterud 1999). Furthermore, there is a 'home advantage' in territorial disputes conveyed by prior residence (Hoem et al. 2007). Consequently, we predicted that roe deer males would initiate spring migration earlier compared to roe deer females and both sexes of the non-territorial red deer (P_6). Similarly, we expected male roe deer to postpone autumn migration as long as possible with a view to potentially remaining on their territory over winter to gain a mating advantage for the following year. In contrast, females should migrate earlier to minimize the risk of being trapped by unfavorable snow conditions with their offspring of the current year. We expected no difference between sexes in autumn migration timing in red deer due to the autumn breeding season that may even require synchronized migration, especially because red deer are polyestrous and sticking with females for the remainder of autumn may be advantageous for red deer males (P_6). Due to the higher

sexual dimorphism in red compared to roe deer, we expected red deer males to be more migratory (P_7) and migrate longer distances (P_8) compared to red deer females and roe deer of both sexes (Bowyer 2004).

Methods

Animal location data

We used GPS collar data collected between 1999 and 2014 on a total of 537 subadult (12–24 months) or adult (> 24 months) individuals ($n_{red} = 264$, $n_{subadults} = 31$, $n_{adults} = 184$, $n_{unclassified} = 49$ (≥ subadult); $n_{roe} = 273$, $n_{subadults} = 26$, $n_{adults} = 247$). The data covered 10 roe and 12 red deer populations, spanning similar latitudinal gradients, with the northernmost populations in south-central Norway and the southernmost populations in southern France (Fig. 1, see Supplementary material Appendix 1 Table A1 and A2 for site characteristics and sample sizes). Roe deer were captured using box traps or drive nets, and red deer were darted from the ground under approved animal care protocols from the respective regions and countries. GPS collars were programmed to obtain fixes every 15 min to 12 h. GPS data were screened for errors using a standard procedure based on animal movement theory (Bjorneraas et al. 2010). Average fix success was high, i.e. 0.94 (SD = 0.09) for roe and 0.96 (SD = 0.12) for red deer, obviating the need for concern about GPS acquisition bias (Frair et al. 2010).

Describing migration behavior

First, to classify animals as residents or migrants and to test for differences in migration parameters between populations, species and sexes (P_1, P_2, P_4, P_5, P_6, P_7, P_8 in Table 1) we used data between 1 January of the first year of monitoring and 15 February of the following year. Due to variable fix rates and to reduce the influence of outliers (e.g. due to exploratory movements), we reduced GPS data to one average location per day (Gurarie et al. 2017). If animals were monitored for multiple years, we evaluated migration in each of the years. We used a combination of methods, including the net-squared displacement (NSD; Bunnefeld et al. 2011) and a supervised spatial clustering method (Cagnacci et al. 2011). The NSD method assesses the cumulative squared displacement from the initial location. We fit five movement models that included resident, migrant, mixed-migrant (migrants that do not return to the exact same winter range), nomad and disperser to these trajectories using non-linear models (Bunnefeld et al. 2011). We selected the best model for each individual-year using AIC (Burnham and Anderson 2002). Because we were primarily interested in contrasting migration events with resident behavior, we excluded nomads (five animals) and pooled mixed-migrants with migrants. No individuals fit a dispersal strategy. We compared the NSD classification with the results from a supervised spatial clustering algorithm that classifies animals as either resident or migratory (Cagnacci et al. 2011).

If the two methods gave contradictory results for a given individual-year, we visualized trajectories and assigned a movement type by eye (Bischof et al. 2012). Both red (Jarnemo 2008) and roe deer (Debeffe et al. 2014) may move to separate breeding areas in late summer, which are only used for short periods. Therefore, we excluded late migration events that implied departure from the winter after 15 July. We extracted the timing of spring and autumn migration events and the migration distance using NSD (Bunnefeld et al. 2011). To test for differences in migration propensity between species and sexes (nested variable within species), we used generalized linear mixed models (GLMM) with a logit link function and binomial error structure. We used linear mixed models (LMM) to test for differences in migration distance and timing (Julian date) in spring and autumn between species and sexes. We tested for non-linear relationships and transformed response variables where appropriate. The factor 'study area' was included as a random intercept in all models. We also tested for 'year' as a random intercept, but do not report results below due to non-significance.

Factors affecting migration probability

We used time-to-event models to explore the link between the probability of migration in red and roe deer across European environmental gradients in spring and autumn (P_1, P_3, Fieberg et al. 2008). We applied Cox proportional hazards (PH) models to estimate the effect of categorical (e.g. sex) and continuous variables on the conditional daily migration probability (or hazard) of individual i migrating at time t, given the set of individuals under observation and at risk of migration (i.e. the risk set; Cox 1972). The Cox PH model: $h_i(t|X) = h_0(t)\exp(\beta X_i)$, estimates the hazard of migration (h_i) for individual i at time t as a function of the baseline hazard (h_0) experienced by all individuals at time t multiplied by the exponential expression of risk coefficients (β) and predictors (X_i) for individual i. Assuming independent fates among individuals, the full maximum likelihood estimates of the β's can be constructed by multiplying the partial likelihood estimates at each ordered failure time t, which are then used to derive a hazard ratio (HR) for each risk coefficient (Hosmer et al. 2008). Because the estimation of the HR is independent of the baseline hazard (i.e. h_0 cancels out), the Cox PH model makes no assumptions about the distribution of migration times and is thus considered semi-parametric (Hosmer et al. 2008). We used the Andersen–Gill formulation of the Cox PH model to accommodate time-dependent covariates and staggered entry (Andersen and Gill 1982). All individual risk sets started either on 15 February or 1 June for spring and autumn periods, respectively, or at least one day before the first migration event if data were not available sooner. Resident animals were censored one day after the last migration event occurred. We used Martingale residuals to detect model outliers and tested for non-proportionality of hazards using the scaled Schoenfeld residuals (Hosmer et al. 2008). We also included a shared frailty term (or random effect) for study area to account for non-independence in

migration propensity among individuals within a given study area (Cleves et al. 2002).

To explain variation in migration timing, we considered time-dependent covariates as well as averaged variables across the seasonal ranges of each individual. We also included sex as a categorical factor. We standardized all continuous covariates so that effect sizes were comparable to factors. We either transformed coefficients or used quadratic terms to model non-linear relationships with predictor variables. All covariates were screened for collinearity using the Pearson's correlation coefficient threshold of $|r| > 0.6$ for variable removal. We retained the variables with the lowest p-value combinations. From this starting point, we built a small subset of biologically plausible candidate models and selected the most informative models using a manual stepwise process (Hosmer and Lemeshow 2000) based on the Akaike information criterion for small sample sizes (AIC_c; Burnham and Anderson 2002). When two of the highest ranked models differed by less than two AIC_c units (ΔAIC_c), we chose the most parsimonious model to avoid inclusion of uninformative parameters (Arnold 2010). These analyses were conducted using the R package 'survival' (Therneau 2015).

Environmental covariates
To assess the importance of time-independent environmental covariates for migratory behavior, we averaged covariates within seasonal ranges (winter: January–March; summer: June–August) using equal-sized areas. We centered the radius of the average resident home range around the centroid of summer and winter GPS locations for each individual using the intercept coefficient of the resident NSD model (Nielsen et al. 2014; $r = 0.79$ km [$SD = 0.51$; 1.96 km^2] for roe and $r = 1.12$ km [$SD = 0.84$; 3.94 km^2] for red deer), and then sampled 1000 random locations within each seasonal range. We considered topography, seasonality of vegetation, and land cover as time-independent predictors. Specifically, we derived elevation and slope from the NASA Shuttle Radar Topography Mission (SRTM) digital elevation model (DEM; Jarvis et al. 2008) for latitudes < 60°N and from the NASA/METI Advanced Spaceborne Thermal Emission and Reflection Radiometer (ASTER) DEM (Hirano et al. 2003) for latitudes > 60°N. To test for the effects of seasonality and inter-annual variability of vegetation, we derived contingency (high values imply strong seasonality) and constancy (high values imply low inter-annual variability) described by Colwell (1974) from normalized difference vegetation index (NDVI) time-series derived from the NASA Moderate Resolution Imaging Spectroradiometer (MODIS, resolution: 250 m). For details on the estimation of contingency and constancy indices see Peters et al. (2017). Forest cover has been shown to have important benefits to deer for concealment and thermoregulation (Dussault et al. 2004), and Cagnacci et al. (2011) demonstrated that migration probability was a function of forest cover in roe deer. We used MOD44B percent tree cover (resolution: 250 m) in each deer range (DiMiceli et al. 2011). To subsume populations by

their time-independent landscape attributes and for visualization purposes, we grouped them by biogeographical regions: boreal ($n_{red} = 2$, $n_{roe} = 1$), continental ($n_{red} = 6$, includes one Mediterranean population; $n_{roe} = 3$), alpine ($n_{red} = 4$, $n_{roe} = 6$, Fig. 1; EEA 2015).

To index time-varying conditions, we derived daily averaged, time-dependent environmental covariates for each individual deer. We matched animal locations with daily interpolated NDVI values (based on 8-day composites). For the time-to-event analysis, we excluded five animals for which GPS data were collected before availability of NDVI MODIS satellite data. Because we expected deer to respond to cumulative changes in plant phenology, we also calculated a metric of change in NDVI by taking the difference in NDVI at time t and the NDVI the week prior to t (ΔNDVI). We characterized winter conditions with presence/absence data of snow cover with MOD10A2 using 8-day composite maximum snow extent data and calculated the percentage of daily GPS locations that were covered by snow for each deer. Spatial data management was conducted using a PostgreSQL 9.3 PostGIS 2.1 database.

Data accessibility

Animal location data as well as remote sensing data for this paper are subject to third-party data sharing agreements, but they are stored permanently in the EURODEER spatial database <www.eurodeer.org>, which is an open project and access to the data can be granted upon contacting the responsible contacts listed on the website. Eurodeer is based on a public server and thus, a stable database.

Results

Describing migration behavior

Migratory propensity differed between species, populations and biogeographical regions (Fig. 1, 2, Supplementary material Appendix 1 Fig. A1, Fig. A3, Fig. A4; P_1 in Table 1). Red deer were, on average, over three times more likely to migrate (141 migrants out of 264 individuals: 56%) than roe deer (51 migrants out of 273 individuals: 18%; Fig. 1, 2, Supplementary material Appendix 1 Fig. A1; P_2 in Table 1). This result was unaffected when we considered only a single monitoring year per individual (migrants: 19% roe and 60% red deer). These between-species differences were strongly driven by the higher migration propensity of male red deer ($\beta_{red} = 0.801$, SE = 0.737, p-value = 0.274; $\beta_{red-m} = 2.084$, SE = 0.408, p-value < 0.001; Table 2, Supplementary material Appendix 1 Fig. A2; P_7 in Table 1). Based on animals that were monitored for more than one year, we observed facultative migration in both species: in roe deer, 8% of females and 9% of males switched between migration and residency in successive years, while the equivalent figures for red deer were < 1% for females and 23% for males. We also found statistically significant differences in migration distance
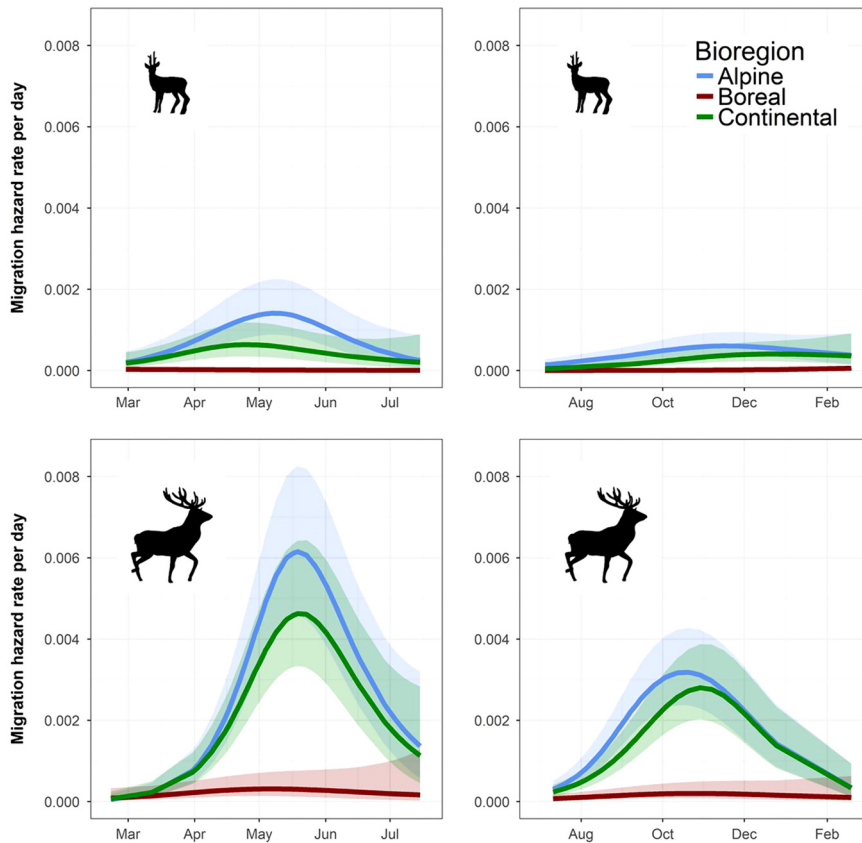
Figure 2. The cumulative spring (left panels) and autumn (right panels) migration hazard over time with 95% confidence intervals for roe deer in 10 populations (top row) and red deer (bottom row) in 12 populations across Europe grouped by biogeographic regions. GPS collar data were collected between 1999 and 2014.

Table 2. Coefficients, standard errors (SE) and p-values for the generalized mixed effects model (GLMM) to test for differences in migration propensity and linear mixed models (LMM) to test for differences in migration distance and timing (spring and autumn) between red deer and roe deer (main effect) and between the sexes of each species (nested effect). Study area was included as a random intercept in all models.

	Coefficient	SE	p-value
Migration propensity			
Intercept	−1.655	0.507	0.001
spp (red deer)	0.806	0.737	0.274
spp (roe deer) : sex (male)	0.237	0.359	0.510
spp (red deer) : sex (male)	2.084	0.408	<0.001
Migration distance (m, log-transformed)			
Intercept	7.903	0.242	<0.001
spp (red deer)	0.953	0.333	0.004
spp (roe deer) : sex (male)	0.228	0.219	0.297
spp (red deer) : sex (male)	0.298	0.149	0.046
Spring migration timing (Julian date, log-transformed)			
Intercept	4.778	0.050	<0.001
spp (red deer)	0.117	0.062	0.058
spp (roe deer) : sex (male)	−0.016	0.074	0.825
spp (red deer) : sex (male)	0.148	0.048	0.002
Autumn migration timing (Julian date)			
Intercept	289.916	10.264	<0.001
spp (red deer)	−13.933	13.788	0.312
spp (roe deer) : sex (male)	22.567	11.041	0.041
spp (red deer) : sex (male)	0.046	7.488	0.995

between roe and red deer ($\bar{x}_{roe} = 6\,107$ m, SD $= 7\,614$ m; $\bar{x}_{red} = 12\,434$ m, SD $= 12\,124$ m; $\beta_{red} = 0.953$ (log(m)), SE $= 0.333$, p-value $= 0.004$; Table 2, Fig. 3; P_4 in Table 1). In addition, LMMs indicated that red deer males migrated further than females ($\beta_{red-m} = 0.298$ (log(m)), SE $= 0.149$, p-value $= 0.046$, but no between-sex difference for roe deer ($\beta_{roe-m} = 0.228$ (log(m), SE $= 0.219$, p-value $= 0.297$); P_8 in Table 1).

Regarding the timing of migration, we found differences between species in the start of spring migration such that roe deer migrated, on average, two weeks earlier than red deer ($\bar{x}_{roe} = 9$ May, SD $= 53.8$; $\bar{x}_{red} = 23$ May, SD $= 40.5$; Fig. 2, Supplementary material Appendix 1 Fig. A2). Also, female roe deer initiated spring migration 10 days earlier than males on average, but variation was much higher among males ($\bar{x}_{roe-f} = 5$ May, SD $= 35.60$; $\bar{x}_m = 15$ May, SD $= 72.90$; Fig. 2, Supplementary material Appendix 1 Fig. A2; P_6 in Table 1). Red deer females migrated in spring almost a month earlier than males on average, but again, variation was much lower among females than among males ($\bar{x}_{red-f} = 13$ May, SD $= 29.69$; $\bar{x}_{red-m} = 11$ June, SD $= 51.78$, Supplementary material Appendix 1 Fig. A2; P_5 in Table 1). Indeed, the observed between-species differences in the timing of spring migration were strongly driven by the late departure of red deer males ($\beta_{red} = 0.117$, SE $= 0.062$, p-value $= 0.058$; $\beta_{red-m} = 0.148$, SE $= 0.018$, p-value $= 0.002$, Table 2; $P_{3.1}$, P_6 in Table 1). In autumn, roe deer migrated later than red deer ($\bar{x}_{roe} = 4$ November, SD $= 50.0$; $\bar{x}_{red} = 4$ October, SD $= 38.1$; Fig. 2, Supplementary material Appendix 1 Fig. A2), but this difference was not statistically significant. However, we found that roe deer females initiated autumn migration about 24 days earlier on average than males ($\bar{x}_f = 17$ October, SD $= 48.07$; $\bar{x}_m = 10$ November, SD $= 51.01$; P_6 in Table 1). Roe deer males were the last to depart from their summer ranges ($\beta_{roe-m} = 22.567$, SE $= 11.041$, p-value $= 0.041$; Table 2, Supplementary material Appendix 1 Fig. A2; $P_{3.1}$ in Table 1). In contrast to the timing of migration in spring, red deer males and females migrated in autumn at around the same time ($\bar{x}_f = 2$ October, SD $= 34.66$; $\bar{x}_m = 7$ October, SD $= 44.42$).

Factors affecting migration probability

Our analyses on the factors influencing the daily cumulative probability of migration across European environmental gradients suggested that, based on the most parsimonious model, spring migration in roe deer was affected by time-varying NDVI, time-varying ΔNDVI, average slope and proportion of forest cover on the winter range (Table 3, Supplementary material Appendix 1 Table A3; P_1, P_3 in Table 1). The rate of change in plant green-up initiated migration rather than the absolute value of NDVI (Table 3, P_3 in Table 1), because the daily probability of migration from the winter range decreased with increasing time-varying NDVI values (HR $= 0.27$), whereas it increased with increasingly positive values of time-varying ΔNDVI (HR $= 2.31$). In addition, the daily probability of migration increased with increasing slope (HR $= 2.28$) and forest cover (HR $= 2.63$; P_1 in Table 1).

In autumn, the daily probability of roe deer migration back to the winter range decreased with increasing time-varying values of NDVI (HR $= 0.28$). Furthermore, the daily probability of autumn migration increased with increasing levels of seasonality in the summer range (i.e. contingency; HR $= 1.82$; P_1 in Table 1). We found no statistical difference in the daily probability of roe deer migration between males and females (P_7 in Table 1). In contrast to our expectation that autumn migration should coincide with the onset of winter, especially in roe deer, we found no statistical support for an effect of snow (P_3 and $P_{3.1}$ in Table 1). Lastly, the propensity to migrate did not significantly vary among study areas for either season (p-value frailty term > 0.1) in roe deer.

From the most parsimonious model, the daily probability of spring migration in red deer increased with increasingly positive values of time-varying ΔNDVI (HR $= 1.25$) and decreasing snow cover (HR $= 0.63$; Table 3, Supplementary material Appendix 1 Table A3; P_1, P_3 in Table 1). In addition,

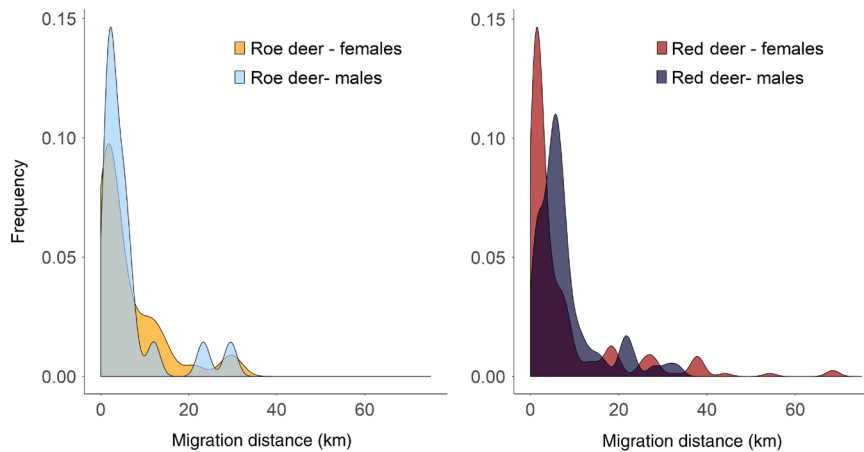Figure 3. Frequency plot of migration distance for roe and red deer ($n_{roe} = 51$, $n_{red} = 165$) by sex across Europe between 1999 and 2014.

Table 3. Hazard ratios (HR), p-values and 95% CI of the most parsimonious models describing the daily probability of migration (spring and autumn) for a) roe and b) red deer $n_{roe}=273$, $n_{red}=264$) across Europe between 2000 and 2014. All variables are standardized.

	Roe deer			Red deer		
	HR	p	95% CI	HR	p	95% CI
Spring						
NDVI*	0.27	0.004	(0.12–0.66)	/	/	/
Δ NDVI*	2.31	0.008	(1.25–4.27)	1.25	0.056	(0.47–1.03)
Snow modis %*	/	/	/	0.632	0.100	(0.03–1.20)
Forest cover	2.63	0.005	(1.33–5.17)	/	/	/
Slope	2.28	<0.001	(1.46–3.55)	/	/	/
Contingency	/	/	/	1.806	0.002	(1.24–2.61)
Sex - male	/	/	/	1.520	0.051	(0.98–2.36)
Frailty (study ID)		0.95			<0.001	
Autumn						
NDVI*	0.28	0.004	(0.12–0.66)	0.401	<0.001	(0.27–0.60)
Contingency	1.82	0.076	(0.94–3.51)	/	/	/
Constancy	/	/	/	0.85	0.054	(0.53–1.36)
Sex - male	/	/	/	2.37	<0.001	(1.57–3.57)
Frailty (study ID)		0.95			<0.001	

*Time-varying covariates.

the daily probability of migration in spring increased with increasing seasonality (i.e. contingency; HR = 1.81; P_1 in Table 1). Males had a higher daily probability of migrating than females (HR = 1.52; P_7 in Table 1).

In autumn, the daily probability of red deer migration was lower when absolute values of NDVI on the summer range were still high (HR = 0.40) and when inter-annual variability in plant productivity decreased (i.e. constancy; HR = 0.85; P_1 in Table 1). In addition, similarly to spring, the daily probability of migrating back to the winter range was higher in males than females (HR = 2.37). Finally, for red deer, the probability of migration differed between study areas (p-value frailty term < 0.01).

Discussion

Even in sympatric populations migration behavior can vary markedly, suggesting different constraints on migration (Mysterud et al. 2012, Hopcraft et al. 2014). In our broad-scale analysis of partial migration in two widespread, but ecologically contrasting ungulates, migration behavior between species, populations and sexes was plastic. As predicted, we found that migration propensity was linked to variation in environmental conditions across populations, and specifically, increased with heterogeneity and predictability of plant phenology and topographic complexity (P_1). The tradeoff between costs and benefits of migration appears to be a function of the level of variation in heterogeneous environmental conditions (Mueller et al. 2011, Shaw and Couzin 2013), and whether shifting ranges at a certain cost will yield a shift in ecological niches with a certain benefit (Peters et al. 2017). Migration in environments that are homogeneous across vast spatial extents, as for the boreal population in our analyses, is not expected to be beneficial. Similarly, the decision to migrate is commonly based on cues of temporal changes or

seasonality, linked to favorable or unfavorable conditions in the destination and departure ranges, respectively (Dingle and Drake 2007). Indeed, in our analysis, variability of plant productivity, more than productivity alone per se, led to initiation of spring and autumn migrations (P_3). Consistently, proxies related to predictability of seasonal conditions, such as seasonality (contingency) and inter-annual variability (constancy), were also predictors of migration (Mueller et al. 2011).

Mysterud et al. (2012) previously compared the proportion of migrants within sympatric red and roe deer females inhabiting the same region in Norway and, similar to our results, found a much higher migration tendency by red deer (94%) compared to roe deer (27%). Since environmental conditions were similar and both populations occurred at low density, they concluded that multiple causes affected migration in these two species. As a key novelty, our large-scale analyses especially highlighted species- and sex-specific differences in migration behavior and subsequently, we reason that individuals appear to be affected by environmental conditions in relation to their life histories. Specifically, as predicted under the FMH we also found red deer to be almost three times more migratory than the selective browser, roe deer (P_2), but this difference was especially pronounced in males. Similarly, red deer migrated twice as far as roe deer and, again, red deer males migrated furthest. These observations support our predictions under the body size constraint hypothesis, i.e. that migratory propensity should be male-biased for red deer only (P_7), that red deer migrate further than roe deer due to their larger body size (P_4), and that red deer males migrate further than females with no such differences between the sexes in roe deer (P_8) (Hein et al. 2012). Finally, differences in the timing of migration, with red deer males migrating last in spring and roe deer males last in autumn, may be linked to the respective mating strategies of the two species. Indeed, this supports our prediction that

roe deer males should remain on their territories as long as possible (P_6).

The FMH provides the most common framework under which ungulate migrations are studied (Hebblewhite et al. 2008, Holdo et al. 2011, Sawyer and Kauffman 2011, Bischof et al. 2012, Merkle et al. 2016, Aikens et al. 2017). Considering phenological variation at broader temporal scales (e.g. between years and seasons), our study supports the notion that migration should be more prevalent when predictability of seasonal forage resources is high (P_1; Mueller et al. 2011). More precisely, our results suggest that seasonality and inter-annual variability affected the propensity to migrate for both red deer (in spring and autumn) and roe deer (in autumn only). Our grouping of populations into broad biogeographic regions coincides with this concept. Spatial and temporal variation is highest in alpine habitats due to diverse topography and strong seasonal variability. In contrast, the spatial heterogeneity is especially lowest in boreal habitats. Due to such low spatiotemporal landscape heterogeneity, the cost of the geographic distance a migrant has to travel to achieve an ecological displacement may overcome the benefits of migration (Shaw and Couzin 2013). Thus, phenological variability may affect the propensity to migrate as well as the pattern of migration within populations.

At a finer scale, when looking at daily or seasonal variation in plant phenology, recent research has suggested that spatial gradients in plant green-up also influence the timing and speed of herbivore migration. For elk *Cervus canadensis* (Hebblewhite et al. 2008) and mule deer *Odocoileus hemionus* (Monteith et al. 2011, Aikens et al. 2017) in North America, the initiation of migration coincided with plant green-up and was affected by overall productivity. We found that the daily migration probability of both roe and red deer increased when the rate of change in plant productivity was high, confirming the general predictions under the FMH (P_3, $P_{3.1}$, $P_{3.2}$). But, roe deer were more likely to remain resident on their winter ranges in spring if absolute plant productivity was high. These small bodied browsers, which selectively feed on small quantities of a wide range of high quality browse, may not benefit as much from migrating to closely track forage green-up compared to ungulates which rely on graminoids or mixed forage such as red deer (Fryxell 1991, Hebblewhite et al. 2008). Thus, due to their digestive physiology roe deer may be able to fulfill their energy requirements at smaller foraging patches within their annual resident ranges, reducing the forage benefits of migration. Merkle et al. (2016) compared the movements of five ruminant species in North America in relation to green-up and found variation in how closely species tracked plant phenology, also pointing towards mechanisms such as ruminant physiology that may affect migration patterns between species. Surprisingly, our results indicated that the timing of spring migration was linked to snow melt in red deer, while we found no such relationship for roe deer, even though roe deer migrated, on average, two weeks earlier than red deer. This is somewhat unexpected and partially rejects $P_{3.1}$, that roe deer migration should be affected more

by snow than red deer migration. One reason may be that, as long as snow is below the threshold that constrains locomotion, much browse is accessible even when there is snow cover compared to graminoids which are at ground level. Hence, browsers may therefore not be as sensitive to snow melt as grazers from a forage point of view (Mysterud et al. 2011). Interestingly, research on mule deer, another browser species, suggested that migration in spring was affected by snow depth rather than by snow disappearance (Monteith et al. 2011). Here, we used coarse-grained (500 m resolution) satellite data of snow presence and we expect that absolute snow depth data would potentially give different results. Future research should use fine-scale empirical environmental data to assess whether species-specific migration schedules are best explained by the time lapse between distribution and depth of snow and green-up of graminoids compared to forbs and shrubs (Hebblewhite et al. 2008).

There is no consensus on differences in the probability of migration between sexes in ungulates, in part, because few studies have focused on the drivers of male migration. For example, all male mule deer migrated in a study by Nicholson et al. (1997), but only 50% of females migrated, while Ferguson and Elkie (2004) found no sex-differences in migration propensity of caribou *Rangifer tarandus caribou*. In our study the probability of migration was higher for male red deer, while we found no sex differences in the probability of migration for roe deer as predicted under the body size constraint hypothesis (P_7). This is in contrast to Mysterud (1999) who found that 70% of female roe deer, but only 38% of the males were migratory in a low-density population in southeastern Norway. Our results of the overall low migratory probability and sex-related differences in roe deer could also be a function of density in this small territorial cervid (e.g. the competition avoidance hypothesis, Mysterud et al. 2011). For example, Eggeman et al. (2016) suggested that elk switch in a facultative manner between resident and migratory behavior as a function of density, forage and predation risk. Also, Mysterud et al. (2012) found that migration propensity as well as timing were effected by red deer densities in Norway, where the probability to migrate was higher and the initiation of migration in autumn were delayed at high density. Unfortunately, we were unable to estimate densities and thus, address its effects on the overall probability of migration and sex-related migratory differences. This could be a profitable avenue for future research.

Migration is energetically costly, especially for smaller territorial species, and body size has been suggested to constrain migration distances and propensity (Hein et al. 2012), which may also modulate the effects of FMH on migration behavior across species and between sexes. For example, underlining the impact of body size on migration behavior, we found that red deer migrated almost twice as far as roe deer, as predicted by their larger body size (P_4). Migration distance was similar for both sexes in roe deer, as expected due to their low sexual size dimorphism (P_8; Cagnacci et al. 2011). Notably, the effect sizes of the between sex differences in migration

distance were similar for both species, but roe deer showed more variation. Even though red deer males are about 1.5 larger than females, we did not expect such large differences based on adult sexual body size dimorphism alone. Rather, males and females in polygynous mating species are often driven by different constraints related to reproduction and social organization (Bowyer 2004). Segregation between male and female red deer has been shown to be highest during parturition, possibly to avoid risk (Bonenfant et al. 2004), emphasizing once more the importance of considering life histories in migration studies.

Social organization may modulate migration behavior. In particular, sex-specific differences in timing of migration are expected to arise due to the timing of breeding and parturition (P_5 and P_6, Mysterud 1999, Jarnemo 2008, Cagnacci et al. 2011). In spring, nutritional demands of females are highest due to the last part of gestation and lactation (Robbins and Robbins 1979), and forage conditions during this period drive variation in offspring survival in ungulates (Cook et al. 2013). The timing of spring migration may have important implications for juvenile birth weight and probability of survival (Lomas and Bender 2007). Thus, females may be constrained to synchronize migration date with birth and peak protein levels of emergent vegetation (Loe et al. 2005), which is consistent with our prediction (P_5) and observations of higher synchronization in spring migration in females of both roe and red deer compared to males (smaller SDs in migration dates; Fig. 3). Similar relationships have been found in moose *Alces alces*, where females migrated earlier to synchronize parturition with forage availability (Singh et al. 2012). Interestingly, roe deer males migrated at around the same time as females of both roe and red deer, likely because males need to establish their mating territory as early as possible in the same areas as female roe deer select to give birth and raise their fawns as predicted under the competition avoidance hypotheses (P_6; Wahlström 2013). Similarly, the breeding system of red deer may also be the main reason for sex-specific differences in migration behavior in that species. For example, while female red deer experience the same constraints as roe deer females linked to parturition (P_5), male red deer are not constrained by the requirements of territoriality. Due to strong female philopatry, apart from during the rut, red deer males spend most of the year in areas irrespective of the distribution of females, possibly also avoiding density-dependent and inter-sexual competition in this way (Jarnemo 2008).

In autumn, both species prolonged residency on their summer ranges in those areas where plant productivity was highest. This is consistent with the fact that higher elevations often experience a second phase of late summer green-up so that plant senescence is generally delayed ($P_{3.2}$; Albon and Langvatn 1992). Similarly, mule deer (Nicholson et al. 1997, Monteith et al. 2011) and white-tailed deer *Odocoileus virginianus* (Nelson 1995) delayed their autumn migration in a mountainous area, likely also to take advantage of higher forage quality on their summer ranges and to avoid high

competition on winter range. Even small improvements in body condition during late autumn or early winter may substantially reduce winter mortality in harsh winter environments (Holand and Staaland 1992). Interestingly, red deer of both sexes and roe deer females, which should also benefit from delayed forage productivity, migrated earlier than roe deer males in autumn. Unlike red deer, roe deer are only very weakly dimorphic in body size and thus, both sexes are similarly limited by energetic constraints. The earlier migration by roe deer females than males in autumn is therefore unlikely to be explained by prolonged plant quality. In accordance with our prediction under the competition avoidance hypothesis (P_6), this suggests that social processes (here, territoriality) may also modulate initiation of return migrations. Male roe deer are territorial only during the summer when the rut takes place, but a given male may run the risk of losing his territory the following year if he migrates to a winter range, as site occupancy is likely a strong determinant of success in territorial defense (Linnell and Andersen 1998, Hoem et al. 2007). Hence, facultative migratory individuals may attempt to overwinter on their summer ranges in order to gain an earlier start on territorial establishment the following year (Wahlström 2013). Furthermore, roe deer males may not need to synchronize autumn migration with females because their mating season is already concluded. In contrast, red deer often rut on their winter ranges or migrate to separate rutting grounds (Jarnemo 2008), which may explain the more synchronized migration with red deer females in autumn. Interestingly, we found no effect of snow on autumn migration dates for either species, rejecting in part $P_{3.1}$. Again, this could be an artifact of the coarse-grained snow data presence data we used. However, Rivrud et al. (2016) also found that most red deer had already left summer ranges before the first snow fall in Norway.

Indirect and direct anthropogenic factors can alter the cost–benefit balance of seasonal migration for partially migratory ungulate populations (Middleton et al. 2013). For example, supplementary feeding in winter is widely practiced across Europe (Ossi et al. 2017) and has been shown to alter behavior of elk in terms of distance migrated, the timing of arrival to, duration on, and departure from summer ranges (Jones et al. 2014). Furthermore, besides the benefits of access to higher quality forage, migration may also result in demographic benefits due to the avoidance of mortality risk (Fryxell et al. 1988, Eggeman et al. 2016). For example, Hopcraft et al. (2014) showed that two sympatric large herbivores, wildebeest *Connochaetes taurinus* and zebra *Equus burchelli*, responded to different environmental cues in the same landscape. Wildebeest tended to move in response to forage quality more or less regardless of predation risk, while zebra traded off predation risk and access to high-quality forage. For the populations we studied, hunting is the biggest source of mortality and interestingly, Rivrud et al. (2016) showed that the onset of hunting triggered the initiation of migration in autumn in red deer more than forage deterioration or onset of winter in Norway. Here we were not able

to evaluate these factors, but depending on data availability further research should focus on understanding how hunting regimes and artificial feeding may affect migration behavior in sympatric species across wide latitudinal gradients.

In conclusion, we have shown that migration behavior differs between two sympatric ungulate species across a large latitudinal and environmental gradient and our results on variability in propensity, distance and timing of migration support the idea that migration behavior is multi-causal, modulated by species-specific traits and life-history in general. Importantly, previous studies often treated ungulate migration as a fixed and discrete phenomenon of clear migrant versus resident behavior. It is becoming more evident though that ungulate migration is very flexible and most ungulates display behavioral plasticity in migration propensity in response to environmental conditions or stochastic events (Cagnacci et al. 2011, Eggeman et al. 2016). This behavioral plasticity is exemplified by partial migration (Dingle and Drake 2007), but also by variation in other migration parameters, such as distance and timing (Sawyer et al. 2016). The drivers of plasticity in partially migratory populations may be species-specific, and migratory plasticity is likely best explained as a complex adaptive behavioral gradient in response to spatio–temporal variation in abiotic and biotic factors that comprise the ecological niche of a species, population or individual. Analyses on other sympatric ungulate species elsewhere are likely to further our understanding of how species-specific traits affect migration.

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Supplementary material (availabel online as Appendix oik-05588 at <www.oikosjournal.org/appendix/oik-05588>). Appendix 1.