

From migration to nomadism: movement variability in a northern ungulate across its latitudinal range

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Abstract. Understanding the causes and consequences of animal movements is of fundamental biological interest because any alteration in movement can have direct and indirect effects on ecosystem structure and function. It is also crucial for assisting spatial wildlife management under variable environmental change scenarios. Recent research has highlighted the need of quantifying individual variability in movement behavior and how it is generated by interactions between individual requirements and environmental conditions, to understand the emergence of population-level patterns. Using a multi-annual movement data set of 213 individual moose (*Alces alces*) across a latitudinal gradient (from 56° to 67° N) that spans over 1100 km of varying environmental conditions, we analyze the differences in individual and population-level movements. We tested the effect of climate, risk, and human presence in the landscape on moose movements. The variation in these factors explained the existence of multiple movements (migration, nomadism, dispersal, sedentary) among individuals and seven populations. Population differences were primarily related to latitudinal variation in snow depth and road density. Individuals showed both fixed and flexible behaviors across years, and were less likely to migrate with age in interaction with snow and roads. For the predominant movement strategy, migration, the distance, timing, and duration at all latitudes varied between years. Males traveled longer distances and began migrating later in spring than females. Our study provides strong quantitative evidence for the dynamics of animal movements in response to changes in environmental conditions along with varying risk from human influence across the landscape. For moose, given its wide distributional range, changes in the distribution and migratory behavior are expected under future warming scenarios.

Key words: age; animal movement; distance; duration; migration; moose; net squared displacement; nomadism; partial migration; snow; timing; ungulates.

INTRODUCTION

Movement is a vital process linking organisms to their ecosystems in space and time; hence changes in movements may have ecosystem-level consequences (Lundberg and Moberg 2003). The movements among animals vary with species, populations, and individuals within a species, which is of long standing interest to ecologists, physiologists, and physicists (Lack 1944, Lundberg 1988, Gilliam and Fraser 2001, Bejan and Marden 2006, Faaborg et al. 2010). A key challenge is to understand the causes and consequences of movement in order to obtain an integrated understanding of animal movements with respect to variable environment conditions and to prepare management strategies accordingly (Nathan 2008, Mandel et al. 2011).

Animal movements range from residence to classic migration with differences in distance, timing and

duration of movements (Börger et al. 2011, Mueller et al. 2011). Along a spatial gradient of resource distribution from coarse to fine, migration and residency are the two extremes, whereas across a temporal gradient of predictability in resources from low to high, nomadism and migration are the extremes (Mueller and Fagan 2008). Many ungulates undertake long distance migrations to escape harsh climate, risk of predation, competition with resident individuals, and for obtaining food to increase survival and reproduction (Fryxell and Sinclair 1988, Hebblewhite and Merrill 2007, Mysterud et al. 2011). Empirical evidence indicates that these factors may vary by species and individuals depending upon the environmental conditions encountered (Barraquand and Benhamou 2008, Brodersen et al. 2008). However, evidence so far is scarce for the variability in movements within a species, especially for large latitudinal gradients and northern seasonal environments (Ball et al. 2001, Cagnacci et al. 2011). Primarily, rainfall and need for water are known to drive animal movements in the arid and semi-arid regions (Holdo et

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al. 2009, Singh et al. 2010), whereas snow has been suggested to be the key factor in the northern latitudes (e.g., Sandegren et al. 1985, Mysterud et al. 2011). At northern latitudes, snow affects broad-scale landscape dynamics, growing season lengths, and temperature, hence producing remarkable but predictable variability, both in animal distributions and behavior, through its effects on food availability and movement costs (Sandegren et al. 1985). These effects weaken as snow cover declines toward south (Hansson and Henttonen 1985). Many studies have focused at identifying population-level movements, but little is known about how variation in snow conditions affects the movement and distribution of multiple populations and individuals of the same species, especially in large ungulates. Understanding variation in population and individual-level movement patterns would be especially important for large ungulates, as they play a key role in ecosystem process and function (Mysterud et al. 2011).

Mueller et al. (2011) predict animals will remain sedentary in static landscapes or landscapes that are dynamic at smaller scales, whereas landscapes that vary across broad scales but are temporally predictable should facilitate migration. In contrast, temporally unpredictable broad-scale landscape dynamics should support nomadism. These predictions can be tested by comparing individuals and populations across a gradient of environmental variations such as snow depth and timing of snow fall and melt. The above predictions also apply at an individual level, whereby an individual may trade off between migrating or remaining sedentary to increase its long-term fitness. For example, survival and reproduction in large herbivores can vary with age and sex of an individual in combination with the environmental conditions (Gaillard et al. 2000, Ericsson and Wallin 2001). Individuals may show a decline in the extent of movement and propensity to move with age due to increasing costs of movement, especially in snow, following age-related changes in physiological condition (Bunnell et al. 1990, Belichon et al. 1996, Ericsson et al. 2001). On the other hand, large herbivore males maximize their long-term fitness by increasing their own survival and mating opportunities, whereas females tend to maximize their offspring survival by selecting safer habitats (Clutton-Brock et al. 1996, Gaillard et al. 2000) and hence there may be sex-specific differences in movement strategies.

Predation risk and risk from humans through hunting, habitat loss, and barrier infrastructure such as roads and fences can also influence movements (Fortin et al. 2005, Neumann et al. 2012). Frair et al. (2005) showed that the scale of movement by elk (*Cervus elaphus*) depends upon the heterogeneity in forage resources and predation risk, whereas Hebblewhite and Merrill (2007) have shown that large-scale migration reduces predation risk for elk. Human hunting and harvest can affect habitat use in elk, white-tailed deer (*Odocoileus virginianus*), and mule deer (*Odocoileus*

hemionus hemionus) (Kufeld et al. 1988, Conner et al. 2001) whereby these species select suboptimal habitats, alter their activity budgets, home range sizes, and fidelity to home ranges. Animals may avoid areas closer to roads and overall avoid areas with high road density at the coarse scale due to risk of collisions with vehicles (e.g., moose [Neumann et al. 2012]). In addition, other associated activities with roads such as human recreation, hunting access, vegetation modification and other infrastructure may disturb animals from adjacent habitats (Rea 2003).

From our review of published findings, it remains unclear how environmental variation, and risk from humans and predators may interact to affect the probability of migration in ungulates at northern latitudes. Moreover, competition can also affect the probability to migrate at high densities (Mysterud et al. 2011). We hereby test the following predictions to explain variation in movements of individuals and multiple populations of a single species across a latitudinal gradient of environmental variation:

- P1) At the population level, annual “migration” should be more prominent in the north where broad-scale but predictable variation occurs in the landscape; i.e., large but predictable variation in snow depth among clearly separated high resource seasonal ranges. “Nomadism” and “sedentary” movements will be more prominent in the south, with large but random variation in different seasonal ranges where individuals will seek resources whose availability is not dependable. In addition, the average snow depth across spatial scales will determine the distance, timing, and duration of migration at population levels: larger migratory distances and durations at larger spatial scales of higher mean snow depths and delayed migration at increasing snow depths.
- P2) Hence, the populations in the north will be characterized by larger migratory distances, longer duration of migration, and will begin their spring migration later than the populations in the south. These expectations will be reversed for autumn migrations.
- P3) At the individual level, the propensity to migrate will decrease with age due to increasing costs of migration, especially at northern latitudes where thermoregulation and movement within snow incurs great costs.
- P4) Males will begin their migration earlier in spring to benefit from the high quality food and for maximizing intake. Females may delay the spring migrations to time movements with the availability of food and safety for the offspring. Conversely, there will be no differences in the timing of autumn migrations between the sexes, with the timing of snow in autumn driving return migrations of all individuals.

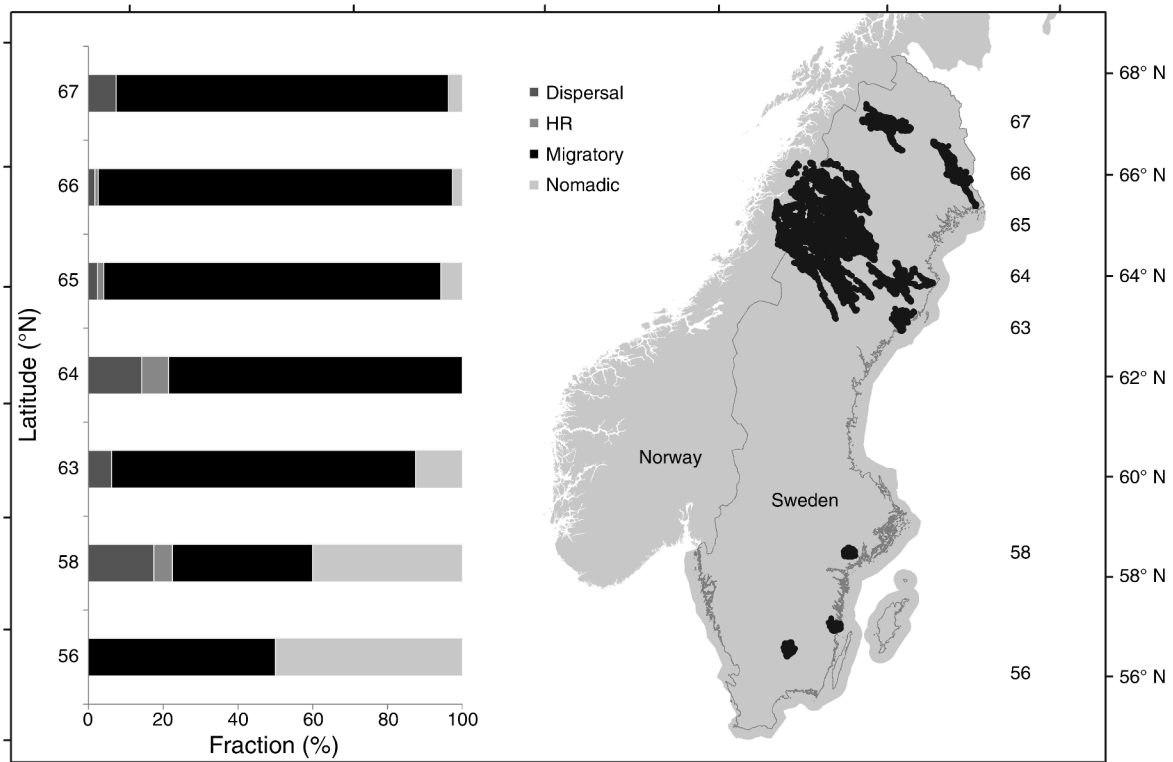


FIG. 1. Study area in Sweden and marked populations. The black dots on the map of Sweden are animal locations, and the numbers on the right of the map are the latitudes/study sites. The plot shows the fraction of different movements (migration, nomadic, residence, dispersal) in moose populations across a latitudinal gradient in Sweden.

P5) If the risk factors (predation risk, hunting pressure, and road density) override the influence of environment, then they will explain more variation in inter-population movements than only snow depth or other factors such as the length of the growing season and temperature.

P6) However, if competition drives movements, then density will explain variation in the propensity to migrate.

Using a multiannual movement-tracking GPS (global positioning system) data set of individually marked moose (*Alces alces*; see Plate 1) from seven populations in Sweden spanning across a large environmental gradient, we test the above predictions (P1–P6). The populations are characterized by the geographically distinct areas where the individuals were marked. We identify and quantify individual and population-level movement modes; quantify the effect of latitude in the prevalence of different movement modes, and then identify which environmental or risk factors explain the differences observed between populations at a latitudinal scale. We then focus on the migratory individuals and compare the distance, timing and duration of migration across populations and identify individual-level differences based on their sex and age. Insights from this study highlight the importance of

comparing populations and individuals across large climatic gradients to identify drivers of movement and species responses toward climate and anthropogenic factors.

STUDY AREA AND METHODS

The study area spans across Sweden, where individuals have been marked at seven different latitudes spanning from 56° to 67° N (Fig. 1). The north of Sweden is characterized by mountains in the west and the Baltic coast in the east is dominated by boreal forests, with mostly subarctic climate and long and snowy winters. The elevation in the north ranges from 1930 m to sea level, decreasing toward the east coast; whereas the south is characterized by generally very low elevations mostly at sea level (Appendix: Fig. A1). The median length of the vegetation-growing season ranges from about 100 days in the north to 211 days in the south (data available online).⁶ The maximum snow depth varies from about 261 cm in the mountains to a minimum of 40 cm in the south (Table 1). Moose is the dominant large herbivore across Sweden. It occurs along with sparse numbers of roe deer (*Capreolus capreolus*) in the north, with roe deer and wild boar

⁶ <http://www.smhi.se/kunskapsbanken/klimat/vegetationsperiod-1.6270>

TABLE 1. Characteristics (mean \pm SE) of the seven study sites for different covariates.

Variable	Study site						
	56	58	63	64	65	66	67
Elevation (m)	187 \pm 4.5	146 \pm 13.4	42 \pm 5.5	240 \pm 10.3	484 \pm 19.3	373 \pm 13.0	502 \pm 11.4
Vegetation period (days)	198 \pm 1.6	194 \pm 0.8	160 \pm 0.0	150 \pm 0.0	133 \pm 1.3	135 \pm 0.5	114 \pm 1.0
Temperature Sum ($^{\circ}$ C)	1426 \pm 4.8	1461 \pm 9.2	899 \pm 82.5	948 \pm 3.45	619 \pm 20.6	735 \pm 13.1	392 \pm 15.9
Road density (roads/km ²)	1.5 \pm 0.0	1.5 \pm 0.0	0.5 \pm 0.0	0.5 \pm 0.0	0.5 \pm 0.01	0.4 \pm 0.0	0.3 \pm 0.0
Mean snow depth (cm)	80 \pm 0.0	87.2 \pm 1.5	140 \pm 0.0	140 \pm 1.6	164 \pm 5.7	141 \pm 0.9	143 \pm 1.2
Harvest (moose shot/1000 ha)	0.076 \pm 0.0	0.079 \pm 0.0	0.032 \pm 0.0	0.035 \pm 0.0	0.035 \pm 0.0	0.03 \pm 0.0	0.026 \pm 0.0
Bear density (bears/km ²)	0	0	0.002 \pm 0.0	0.1 \pm 0.0	0.4 \pm 0.0	0.5 \pm 0.0	0.6 \pm 0.0
Moose density (moose/1000 ha)	0.5 \pm 0.0	0.5 \pm 0.0	0.2 \pm 0.01	0.3 \pm 0.0	0.3 \pm 0.0	0.21 \pm 0.0	0.1 \pm 0.0

(*Sus scrofa*) in central Sweden, and with red deer (*Cervus elaphus*), roe deer, fallow deer (*Dama dama*), and wild boar in the south of Sweden. Brown bears (*Ursus arctos*) are present mostly in the north, lynx (*Lynx lynx*) are spread throughout Sweden, and wolves (*Canis lupus*) are restricted to central and western Sweden. In the areas where we have marked animals, only bears are present at 63° and further north and thus are expected to kill moose. Hence we only included bears as predators.

Movement data

The data set comprises 408 moose (64 males and 334 females) marked with GPS collars and tracked across Sweden. The time period of tracking ranges from 2003 to 2011, with individual moose tracked for up to five years with one location per day. Animals were darted, sedated, and equipped with a GPS/GSM neck collar (Vectronic Aerospace GmbH, Berlin, Germany) during winter. The data was entered into the wireless remote animal monitoring (WRAM) database system for data validation and management (*available online*).⁷ For the analyses, all location data sets were converted into moose years of tracking, our temporal unit of analysis, with the year starting on 21 March, when all the individuals are still in their winter ranges. Given our interest in yearly movements, we excluded all individuals sampled for less than 330 days. This resulted in 213 individuals and 317 moose years. We included both sexes in the analyses (32 males and 285 females) and animals were categorized based on the latitude of the areas where they were marked. Seven different latitudinal zones were identified based on the capture area of the marked animals: zones 56 ($n = 6$ moose), 58 ($n = 40$), 63 ($n = 16$), 64 ($n = 14$), 65 ($n = 61$), 66 ($n = 103$), and 67 ($n = 27$). These groups of animals live in areas characterized by different environmental conditions (see *Covariates of environmental variation and risk*) and

are henceforth addressed as seven populations (see Fig. 1 and Fig. A1 [in the Appendix]). The birth year of the animals was estimated while collaring, age was then calculated for the analyses and was verified as estimated through tooth sectioning after the retrieval of any dead animals (Ericsson and Wallin 2001). This method has been developed during several decades of radio tracking of individuals and validating through the tooth sectioning from the jaws obtained. In our study, about 15% of the individuals could be validated from tooth sectioning after the jaws were obtained from hunters.

Covariates of environmental variation and risk

To relate individual differences in movement to potential drivers, we collected spatial data across Sweden on different environmental covariates: vegetation growing season length, mean snow depth (cm), temperature sum ($^{\circ}$ C), index of moose density (number of moose harvested/1000 ha), harvest pressure (number of moose observed $\cdot 1000 \text{ ha}^{-1} \cdot [\text{hour of observation}]^{-1}$), bear density (number of bears/1000 ha), and area under roads per county (%) as a measure of road density. The spatial data on median vegetation growing season length, temperature sum (daytime), and mean snow depths across Sweden were obtained from the Swedish Meteorological and Hydrological Institute (*data available online*).⁸ Temperature sum is the sum of the positive differences between diurnal mean temperatures and 5° C. It is used in ecological studies, especially in the Scandinavian region, to relate with the growth of forest in the boreal region (Solantie 2004). The index of moose density across Sweden was estimated using the annual hunting area statistics obtained from the Swedish Association for Hunting and Wildlife Management (SAHWM) at the county level (*data available online*).⁹ SAHWM is assigned by the Swedish govern-

⁷ <http://www.slu.se/WRAM/>

⁸ <http://www.smhi.se/klimatdata/meteorologi/sno>

⁹ <http://www.jagareforbundet.se/Viltet/Viltovervakningen/Algavskjutning/>

ment to run the moose monitoring. The number of moose hunted per 1000 ha was estimated using the ratio of number of licenses distributed and fulfilled to the number of moose hunted. Harvest pressure for each county was estimated using the hunter observation system data sets from SAHWM. The hunter observation system is a method used to record number of moose seen per hunter per hour of observation during the hunting season (Ericsson and Wallin 1999, Solberg and Sæther 1999). The map of bear density was obtained from the annual reports of the Scandinavian bear project (*available online*).¹⁰ Bear density was estimated based on the number of bears encountered per hour during the annual hunting seasons and reported by hunters (Kindberg et al. 2011). We included the mean observations from 1998–2011. Wolves were not considered here because we did not have marked animals in the areas with wolves. Due to the known effect of road density on moose behavior and movement (Neumann et al. 2012), we recorded the road density within each county using data from the Statistical Bureau of Sweden (*data available online*).¹¹ This is regarded in our study as an index of the level of disturbance likely experienced by moose due to traffic infrastructure and related activities.

DATA ANALYSES

Movement characteristics and modes

We used the net squared displacement (NSD) modeling approach combined with nonlinear mixed effects models to separate migratory moose from resident, dispersing, or nomadic individuals and estimate the distance, timing, and duration of migration for the subset of migratory individuals (P1–P3; Börger and Fryxell, *in press*). The NSD is the square of the distance to the first location for each location of a movement path of an animal (Turchin 1998). The estimates are then fitted to functions (Fig. 2). The NSD model for migration is based on a double sigmoid function with five parameters to estimate the distance (δ), timing (spring θ_s and autumn θ_a) and duration of spring (ϕ_s) and autumn (ϕ_a) migrations for each marked individual and a given year (Bunnefeld et al. 2011):

$$NSD = \frac{\delta}{1 + \exp\left(\frac{\theta_s - t}{\phi_s}\right)} + \frac{-\delta}{1 + \exp\left(\frac{\theta_a - t}{\phi_a}\right)} \quad (1)$$

where δ is the asymptotic height, θ is the time at which migration reaches half of its asymptotic height, ϕ is the time elapsed between reaching one-half and three-quarters of the migration distance, and t is the number of days since start (here, 21 March). The model assumes an exact return to the departure area. To

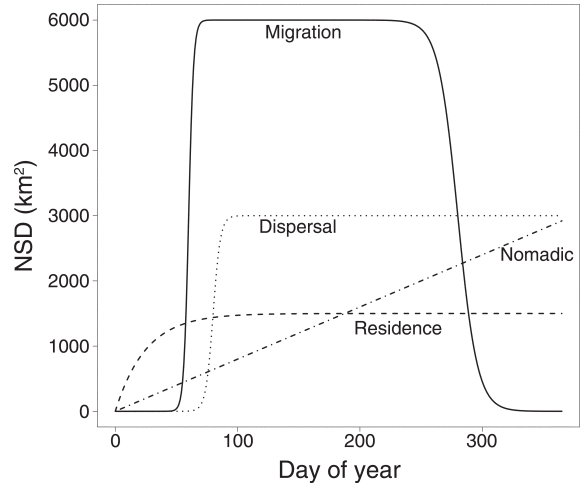


FIG. 2. Expected net squared displacement (NSD) plots for different movements.

model dispersal a three-parameter logistic model is used (Börger and Fryxell, *in press*):

$$NSD = \frac{\delta}{1 + \exp\left(\frac{\theta - t}{\phi}\right)} \quad (2)$$

where δ is the asymptotic height, θ is the time at which migration reaches half δ , ϕ is the time between reaching one-half and three-quarters of migration, and t is the number of days since 21 March of the year. Residency (home range) is modeled using a two-parameter asymptotic regression model through the origin,

$$NSD = \phi_1 [1 - \exp(-\phi_2 t)] \quad (3)$$

where ϕ_1 is the asymptote at the steady-state equilibrium and ϕ_2 is the logarithm of the rate constant, and nomadic movements using a single-parameter linear regression model through the origin,

$$NSD = 4Dt \quad (4)$$

where D is the diffusion constant (multiplied by 4 for two-dimensional movements) and t denotes the time since start (Börger and Fryxell, *in press*).

The models were fitted to all data using nonlinear mixed models, which allow for including variation between individuals for all model parameters. We used the nlme package (Pinheiro and Bates 2000) within the R environment for statistical computing, after having estimated the NSD values using the AdehabitatLT library in R (Calenge et al. 2009). As we were interested in finding the best movement model for each moose and year, we used a unique moose-year identifier as random grouping term.

Model fit for each individual and year (moose-year) was evaluated using the concordance criterion

¹⁰ <http://www.bearproject.info/>

¹¹ <http://www.scb.se>

$$CC_i = 1 - \frac{\sum_{j=1}^{n_i} (y_{ij} - \hat{y}_{ij})^2}{\sum_{j=1}^{n_i} (y_{ij} - \bar{y})^2 + \sum_{j=1}^{n_i} (\hat{y}_{ij} - \bar{\hat{y}})^2 + n_i(\bar{y} - \bar{\hat{y}})^2} \quad (-1 \leq CC \leq 1). \quad (5)$$

Here \bar{y} and $\bar{\hat{y}}$ are the means of the observed (y_{ij}) and predicted (\hat{y}_{ij}) values for individual i and n_i is the subject-specific number of locations. The concordance criterion is especially suited for nonlinear models; it measures the level of agreement between the observed and predicted values and is a combined measure of the degree of accuracy and precision of pairs of values of y_i and \hat{y}_i on the identity line (the 45° line through the origin) and any $CC \leq 0$ indicates lack of fit (Huang et al. 2009). The movements were then classified into migratory, dispersal, stationary, and nomadic, depending on the highest CC value obtained for each individual and year (Börger and Fryxell, *in press*).

Proportion of movement categories

We estimated the proportion of individuals within each movement category at each latitudinal location and proportion of different movement behaviors among the sexes to test (P1–P2). We then selected all the migrant individuals from the data set and performed further analyses on these. We estimated the mean (\pm SE) migration distance (δ), the start of spring and autumn migrations (estimated as $\theta \pm 3\phi$; see Börger and Fryxell, *in press*), and the duration of spring and autumn migration at each latitude and for both sexes.

Effect of age, sex, and latitude on migration patterns

For the migratory movement sets we extracted the estimated movement parameters (δ , θ_s , θ_a , ϕ_s , and ϕ_a) along with their latitude, sex, age (range 2 to 17 years), and year of observation (P3–P4). Generalized linear mixed effects models (GLMM) were then used to estimate the relationship between migration behavior and age, sex, and latitude (R package *available online*).¹² Model selection was conducted using Akaike's information criterion (AIC). Final models were selected based on $\Delta AIC < 4$ and model-averaging techniques were used to estimate variable importance (Anderson 2008).

P propensity to migrate and environmental drivers

To test for the tendency of an individual to migrate (or not) throughout the considered latitudinal gradient, and identify the predictor variables (P5 and P6), we again used GLMMs, with binomial family and logit link and individual animal identity as a random effect. A further analysis on the subset of nonmigratory move-

ments was beyond the scope of the paper and requires a larger number of nonmigratory movement paths.

Specifically, we evaluated which of the environmental conditions experienced by an individual in the winter range (before migration) are related to the decision to migrate or not in a given year (see Fig. A1 for covariates). To do so, we calculated the mean of the environmental covariates (listed in *Covariates of environmental variation and risk*) for the first week of each moose-year location data set (i.e., the week of 21–28 March). We excluded all moose-year sets that started in Norway due to lack of data on environmental covariates from Norway and were left with 189 individual animals and 267 moose years. We quantified the collinearity among the environmental covariates using Pearson's rho and did not include within the same model strongly correlated covariates ($\rho \geq 0.75$). To deal with the correlated covariates we used multi-model averaging procedures (Anderson 2008). To do so, based on the seven environmental covariates, we set up five different combinations of not strongly correlated covariates; in each we also included age, to correct for variation in migration propensity independent of the environmental conditions, and all interactions. The five combinations were vegetation period + mean snow depth, temperature + mean snow depth, road density + mean snow depth + elevation, moose density + mean snow depth + elevation and mean snow depth + elevation + bear density + harvest pressure. For each model, we selected the most parsimonious simplified model using the Akaike information criterion for small sample sizes (AIC_c) within the MuMIn library in R and then used model averaging procedures (using AIC_c [Burnham and Anderson 2002]) to evaluate the relative support for each of the five different model groups, obtain model-averaged parameter estimates and unconditional standard errors, and quantify the influence of each covariate on individual propensity to migrate.

RESULTS

Proportion of movement categories

Out of a total of 213 individuals and 317 movement paths (Fig. 3), 84% of individuals were identified as migratory, 10% as nomadic, 5% as dispersers, and 2% as resident. This trend was also true for the sexes, where the migratory strategy dominated among the individuals of both sexes (males were 88% migrants, 8% nomadic, and 4% dispersers; females were 83% migrants, 10% nomadic, 5% dispersers, and 2% resident) followed by nomadism, dispersal, and residency. Across the latitudinal gradient, the proportion of migrants vs. other movements was variable, with a higher occurrence of mixed movements (nomadic, residency, and dispersal) in the southern latitudes as compared to the prevalence of the migratory strategy in the north supporting prediction 1; i.e., migration should be more prominent in areas with high seasonality but predictability (P1; Figs. 1 and

¹² <http://CRAN.R-project.org/package=lme4>

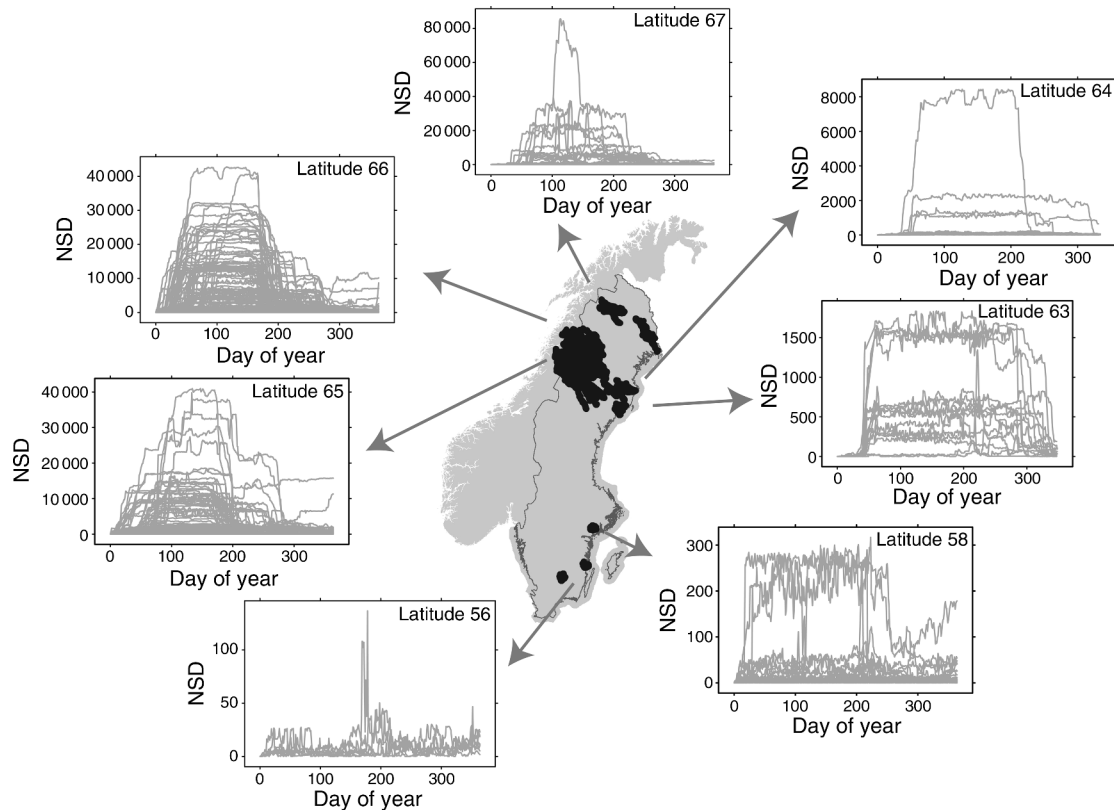


FIG. 3. Net squared displacement patterns (km^2) for each individual moose at each study area in Sweden.

3). The number of migrants increased from about 39% in the south to 95% in the north for 66° latitude, whereas the number of nomadic individuals decreased from 50% in the southernmost population to about 3% in the northernmost population.

Migration distance

There was a notable trend of decreasing migration distance from north to south supporting P2, that populations further north will have larger migratory distances (Fig. 4a). This decreasing trend consistently continued till 66° . The population at 67° in the mountainous region was an exception as it mainly undertakes a short altitudinal migration, hence resulting in short horizontal distances measured (mean = 30.0 km, range 3–80 km). The population with the largest mean migratory distance was the one at 66° (103.1 km) and the smallest was at 56° (5.1 km). Nevertheless, within each population there was large individual variability in migration distances (e.g., 4.4–5.7 km in population 56 or 5.4–217.0 km in population at 66° ; see Fig. 4a). Males and younger animals travelled larger distances and migratory distances varied among different years supporting P3 and P4 that the propensity to migrate should decline with age (Table 2).

Timing of migration

The timing of migration was variable between years. The individuals in southern populations began their spring migration earlier (~ 5 –10 May) than those in the north (~ 15 –24 May) with an average difference of a week and delayed their autumn migration (north, 15–30 October; south, ~ 5 –30 November; Fig. 4b) by the same period as compared to those in the north supporting P3, that animals in the north will have longer duration of migration. Males began their migration later than females for both spring and autumn (Table 2). Age had an effect on the timing of migration; in general, younger individuals began spring migration earlier ($P = 0.06$) and delayed their autumn migration compared to older individuals ($P = 0.04$, Table 2).

Duration of migration

Where the individuals in the south migrated only a few kilometers, they took <1 day to complete their seasonal movement, however, individuals in the north took about 1–2 weeks on average to complete a one way trip, supporting P1. The duration of both spring and autumn migration also varied between the sexes, as males consistently took longer than females for both ways (4.7 ± 2.2 days longer than females; Fig. 4c, Table

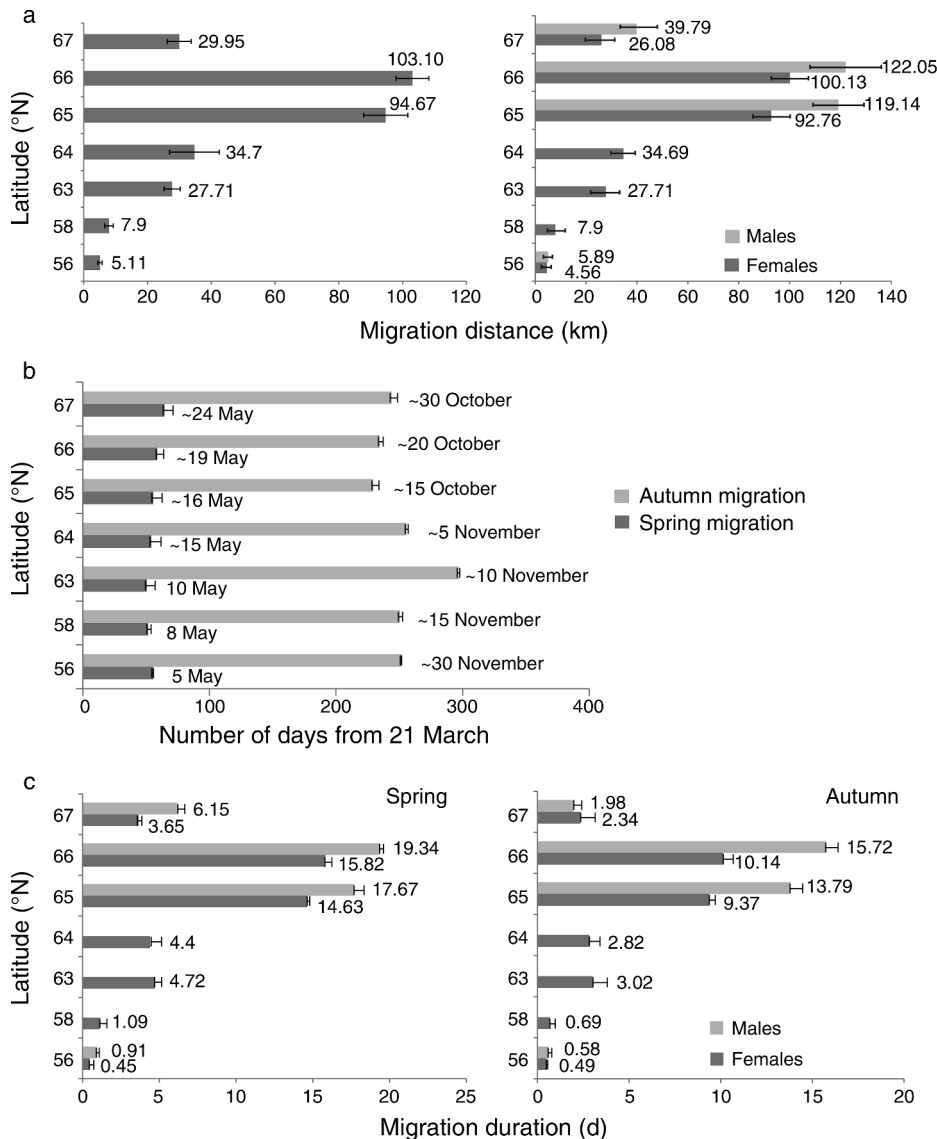


FIG. 4. Migratory characteristics of all moose populations and both sexes across a latitudinal gradient in Sweden. (a) Distance traveled by all individuals (left-hand side) and by sexes (right-hand side). (b) Timing of spring and autumn migration of sexes (number of days since 21 March). (c) Duration of spring and autumn migration (number of days; mean number is shown next to each bar). Error bars show SE.

2). Their duration of spring and autumn migration did not differ significantly (Table 2).

Propensity of individuals to migrate and the role of environmental drivers

The data on individuals tracked over multiple years ($n = 51$ moose) showed evidence for a propensity to migrate every year, but also of a marked variability among and within individuals. This was also observed in the variation in the distance, timing, and duration of migration explained by the random effect individual moose (Table 2): 35 moose always migrated, 7 never, and 6 migrated half of the period tracked. Using all data

($n = 213$ individuals and 317 moose-years) we found strong evidence for a spatial variation in the propensity to migrate among study areas with increasing propensity to migrate going north ($P < 0.001$). Accounting for age, this latitudinal gradient in the propensity to migrate was strongly related to environmental conditions before departure and models with the environmental covariates were strongly favored ($\Delta AIC > 10$) compared to models with only the study-area as a factor or latitude as a numeric covariate.

Most of the variation observed among the populations was due to differences in snow depth and road density, with an additional contribution of temperature,

TABLE 2. Results of the generalized linear mixed effects models (GLMM) for the effects of age, sex, year, and latitude on the migratory characteristics of marked moose in Sweden.

Variable	Distance		Spring timing		Autumn timing		Spring duration		Autumn duration	
	Metric	Error	Metric	Error	Metric	Error	Metric	Error	Metric	Error
Fixed effects										
Intercept	-381.0	83.9	-76.5	50.7	350.6	49.8	-91.0	26.7	-58.1	17.1
Age	-0.8	1.1	0.1	0.4	1.9	0.6	-0.0	0.2	-0.0	0.1
Year 2006	15.8	13.3	4.1	7.7	-28.8	7.5	3.3	4.1	2.1	2.6
Year 2007	33.4	13.6	6.2	8.3	-57.9	8.2	12.7	4.3	8.1	2.7
Year 2008	26.5	13.8	8.5	8.8	-28.9	9.0	9.3	4.4	6.0	2.8
Year 2009	19.6	13.0	8.1	7.6	-41.7	7.4	6.2	4.1	3.9	2.6
Year 2010	19.7	13.2	-2.0	7.8	-38.7	7.6	6.8	4.1	4.3	2.6
Year 2011	24.5	13.6	0.0	8.1	-46.0	8.0	8.6	4.2	5.5	2.7
Latitude	6.5	1.3	2.1	0.8	-1.0	0.7	1.4	0.4	0.9	0.2
Sex (males)	15.4	11.3	8.7	6.3	-0.4	6.1	7.3	3.4	4.7	2.2
Random effects										
Animal identity	1704.2	41.2	451.5	21.2	307.7	17.5	158.8	12.6	65.2	8.0
Residual	227.1	15.0	189.3	13.7	274.5	16.5	31.6	5.6	12.9	3.6

Notes: For fixed effects, the metric is the coefficient, and error is SE; for random effects, the metric is variance, and error is SD. Age and latitude are continuous variables; sex (total females = 241, total males = 26; females at latitude $56^\circ = 4$, $58^\circ = 40$, $63^\circ = 16$, $64^\circ = 14$, $65^\circ = 58$, $66^\circ = 88$, $67^\circ = 21$; males at latitude $56^\circ = 2$, $65^\circ = 3$, $66^\circ = 15$, $67^\circ = 6$) and year are categorical. Positive coefficients for latitude show increasing trend with latitude, and coefficients for sex are the relative estimates of males with respect to females. All variables were included in each final model after model selection and averaging using the Akaike information criterion (AIC).

harvest pressure, and moose density, and a small influence of the length of the vegetation period/growing season supporting P1, P5, and P6, but with no support for an effect of bear density (Fig. 5). The propensity to migrate also varied within individuals according to age, generally decreasing with age, although depending upon the environmental conditions encountered, in line with P6. Among the migrants, younger moose always migrated, independent of snow depth (similarly, individuals from areas with low snow depth always

migrated, independent of age), whereas older individuals were less likely to migrate, especially if they were in areas characterized by high snow depth (Table 3, Fig. 6a). Only older individuals' movement was negatively related to high road density (reduced probability to migrate; Fig. 6b). The negative effect of deep snow cover existed only in areas with low road density (Table 3). Additionally, the higher propensity to migrate from areas with high hunting pressure was related to interactions with age (a reduced propensity of older

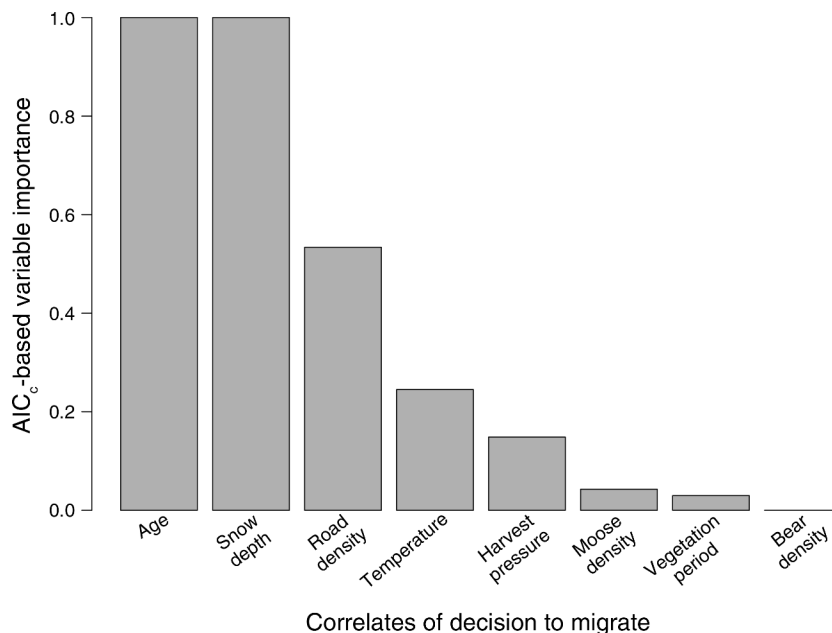


FIG. 5. Relative influence of environmental and human-associated covariates in explaining the latitudinal gradient in moose migration propensity across Sweden. Importance is based on the Akaike information criterion for small sample sizes (AIC_c).

TABLE 3. Model-averaged parameter estimates of the correlates of migration propensity (GLMM with binomial family and logit link, with individual moose-year as random effect).

Covariate name	Estimate	SE	z	P
Intercept	7.5	1.5	4.9	0.00
Age	0.3	1.8	0.2	0.84
Harvest pressure	0.2	3.7	0.3	0.71
Snow depth	-5.5	3.1	1.7	0.08
Moose density	-0.1	2.6	1.0	0.31
Road density	-1.0	3.9	0.4	0.64
Temperature	-0.7	2.9	1.0	0.32
Age \times harvest pressure	-1.2	4.2	1.9	0.05
Age \times snow depth	-12.1	5.5	2.2	0.03
Age \times moose density	-0.2	3.8	1.6	0.11
Age \times road density	-5.0	4.8	1.9	0.06
Age \times temperature	-2.5	5.4	1.8	0.06
Harvest pressure \times snow depth	3.2	7.1	2.9	0.00
Snow depth \times moose density	0.9	6.4	3.4	0.00
Snow depth \times road density	9.0	6.4	2.5	0.01
Snow depth \times temperature	3.2	3.1	3.9	0.00

Notes: All numerical covariates were mean-centered and standardized by dividing by 2SD. Model-averaged estimates and unconditional standard errors (among five competing models [see the Appendix]) were obtained based on the Akaike information criterion for small sample sizes (AIC_c) statistic following Burnham and Anderson (2002) model averaging procedures, using the MuMIn library in the R software for statistical computing.

moose to migrate from high hunting areas) and snow depth (increased migration propensity in areas with high snow depth and high harvest pressure; Table 3).

DISCUSSION

Our unique multiannual data set along the latitudinal gradient of Sweden shows remarkable variation in the proportion of migrants vs. other movements within and across populations and individual life history (sex and age) (P1–P6). The key findings from our study are: the population-level movements may show a clear pattern along a gradient of environment variation, individuals within a population may exhibit multiple movements variable in time, the propensity of an individual to migrate declines with age affected by snow conditions and road density, and sex-specific demands may lead to variation in movements of sexes. Although we categorized four different movements from the data, migration was the dominant. Hence most of the results are discussed in the context of migration.

Population: latitudinal gradient and environmental variation

Given the variation in the environmental conditions, we build evidence that each population within species has their own suite of response to variation and heterogeneity. Recently, this has been demonstrated for migrating birds (Turkey Vulture *Cathartes aura*) in North America (Mandel et al. 2011), for fish (roach *Rutilus rutilus* [Brodersen et al. 2008], sockeye salmon *Oncorhynchus nerka* [Eliason et al. 2011]), and for mammals (Saiga antelope *Saiga tatarica* [Singh et al.

2010]). Overall, these empirical evidences support the theoretical prediction that the more unpredictable the landscape is at broad scales, as in the south in our case, the more variation in movement should be observed within a species' range. Furthermore, our data also suggests that partial migration, whereby a fraction of population migrates, may be a part of the solution for how to handle landscape heterogeneity and seasonality (Kaitala et al. 1993).

Evidence from other large herbivores suggests that environmental variation drives migration, although data rarely comes from a large-scale gradient and multiple populations (Fryxell and Sinclair 1988, Cagnacci et al. 2011, Mysterud et al. 2011). Single species and local site-specific studies often suggest precipitation and productivity to be key environmental variables to explain why migration occurs. In our 1100-km latitudinal gradient study, snow was the dominant environmental factor in explaining population-level differences in movement behavior. Snow depth was negatively correlated with

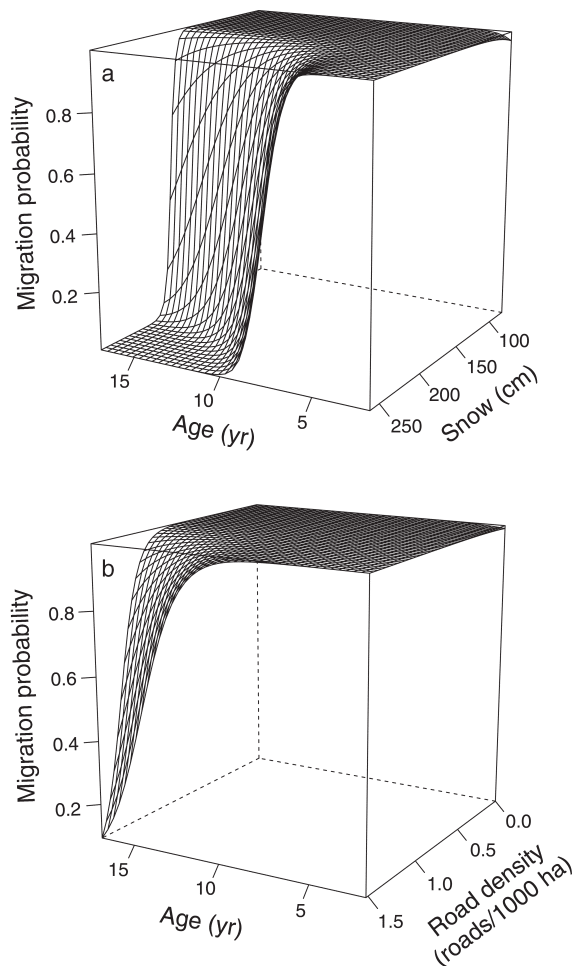


FIG. 6. Three-dimensional plots showing the interactions between age of the moose and (a) snow depths and (b) road density.

the length of the vegetation period/growing season ($r^2 = -0.73$). The length of the growing season in the north ranges between 90 and 125 days, whereas in the south, it varies between 140 and 180 days (Fig. S1). Populations also responded to these differences by altering their distance, timing and duration of migration. This is visible in our results with the observation that migration distances were short in the south (where the absolute scale of change was small, <10 km) in contrast to about 100 km in the north. Our results concurred with Mueller et al.'s (2011) predictions that milder conditions for a longer period of time may promote a higher probability of other movements (nomadism and residency).

Our study also suggests that the differences in snow depth between the areas result in differences in the timing of snowmelt in spring and arrival of snow in autumn, which determine the timing and duration of migration among the populations at different latitudes. These results are in line with Ball et al.'s (2001) suggestions for a single site. The significant effect of year on distance, timing, and duration of migration clearly points toward this evidence, where these movement characteristics may vary with conditions encountered in a particular year.

Risk

Between predation risk and human-associated risk, only the latter explained a major part of the variation in population-level patterns. Road density (i.e., a proxy for human presence in the landscape) was related to the observed differences in the movements among the populations throughout the gradient. Migration of older moose was negatively related to road density, but snow depth also interacted with roads. Increased road density was related to more nonmigratory movement modes in the south indicating an interesting interaction, which seeks further investigation of cause and effect. One likely explanation could be that the road safety activities to reduce collisions such as vegetation clearing and modifications that change the habitat profiles promoting certain species than the others or using forage repellents, unpalatable species, or diversionary feeding, have an effect (Rea 2003). Harvest pressure was positively related to migration but also interacted with age, showing that older individuals may migrate less under high hunting pressure. This could likely be due to the fact that the rutting season coincides with the harvest season in Sweden (which is also variable across the latitudes, see Garel et al. [2009]). Nonetheless, since harvest pressure is variable in space and time, its effect on movement could be more complex under dynamic conditions. Predators had been few or absent from Scandinavia for long periods of time but are making a strong comeback (Sand et al. 2006). Bear density did not emerge out as an important covariate, since our southern marked populations are not exposed to bears (Kindberg et al. 2011) and it may not have a strong influence in the north during the winter, since the bears hibernate. Nevertheless, Swenson et al.

(2007) report that brown bears killed about 26% of the moose calves in south-central counties of Sweden. Lack of data on moose movement from those areas prevented us to make any further analyses.

Individuals: effect of age and sex

We show that the tendency of an individual to migrate declined with age interacting with variation in environmental conditions (Table 3 and Fig. 3). This confirms our prediction that costs of migration in older individuals especially in snow may be higher than benefits and hence age may affect the probability of migration and migratory distance. However, this could also be due to learning whereby an individual may identify the most optimal migration route or movement behavior and hence migratory distances may decline in time (van Moorter et al. 2009). Younger individuals on average traveled longer distances and migrated earlier than older individuals in spring and delayed autumn migration (Table 2). A likely explanation could be to avoid competition for food (in spring) and mates (in autumn) with older and dominant individuals (Yoccoz et al. 2002). This would require estimates for densities, food availability, age structure and rutting behavior, which was beyond the scope of this study, but should receive immediate attention.

The sex of an individual also had a significant effect on movement behavior, where males travelled longer distances, migrated later, and took longer time for migration at all latitudes. This is likely a result of higher energy demands in males especially after the rut and long winter, and the need to build up the lost body mass to prepare for the following rut (McCullough 1999). They may hence migrate later. Unlike the females that need to synchronize the timing of migration with food availability and select suitable calving locations to increase reproductive success, "the need to breed," males are probably more driven by the "need to feed" and hence also venture over a larger area to look for better forage (McCullough 1999). Expectedly, they may then undertake longer migrations as compared to females.

Overall, we suggest that a combination of environmental and human induced factors is responsible for generating variable movements observed among different moose populations across the latitudinal gradient. These factors may not be mutually exclusive and interact in interesting patterns. Harsher conditions in the north prevent larger human settlements and higher densities, which then require fewer infrastructures to sustain smaller populations. The climate change scenarios from Sweden predict milder snow conditions in the northern latitudes and reductions in summer precipitation in the south (Swedish Meteorological and Hydrological Institute [SWECLIM]; scenarios available online).¹³ Under these scenarios when north-

¹³ <http://www.smhi.se/klimatdata/klimatscenarioer/scenariokartor>



PLATE 1. A GPS collared female adult moose (*Alces alces*) in Sweden. Photo credit: N. J. Singh.

ern regions may become warmer and milder conditions become more common, animals may have access to high quality food resources much earlier in season and for a longer period, which may involve shorter movements. These may also result in changes in the species' impact on the structure and components of its ecosystem (Lundberg and Moberg 2003). In contrast, at the individual levels and smaller temporal scales across sites, the life histories interacted with the local environment to produce variable movements. How robust the individual-level movements are to the future large-scale changes in the environment and human use of the landscape remains to be tested. More high-resolution data on these variables at the within-population level will help to answer these questions.

The estimation of population-level movement patterns will assist managers and conservationists in preparing strategies to tackle climate change as well as ecological networks for migratory species to link populations (Singh and Milner-Gulland 2011). Feasibility of ecological networks in protecting migratory species is currently a hot topic of discussion among the policy makers at the United Nations Convention on Migratory Species (UNEP-CMS 2011). Our results also have important implications for general wildlife management, since spatially explicit hunting strategies are practiced in many countries and variability in hunting pressure across space and time can significantly affect

animal movement at multiple scales. In many countries, hunting licenses for large animals are issued based on population estimates obtained from surveys conducted during different times of the year in the management areas. The encounter rates of animals during such surveys will depend upon the movement strategy of individuals and populations during that period. For example, if most animals from a population in a particular region are migratory, the surveys conducted in the wrong season may not give accurate estimates for effective management. Moose hunting in Scandinavia is focused around the rut, but what impacts hunting may have on long-term movements is a question for future research. We advocate more in-depth studies on the impact of hunting and infrastructure on individual and population-level movements as well as studies addressing likely effects of climatic changes.

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SUPPLEMENTAL MATERIAL

Appendix

A figure showing covariates and a correlation matrix for the covariates used to explain the latitudinal gradient in moose population movement patterns across Sweden (*Ecological Archives* A022-108-A1).