Research paper

Behavioural response to infrastructure of wildlife adapted to natural disturbances

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HIGHLIGHTS

▶ We tested if infrastructure developments modify wildlife movement over time.
▶ We modelled moose distance and movement rates as a function to infrastructure objects.
▶ Moose-road distances followed a circadian pattern.
▶ Our results suggest temporal adjustments to roads in moose.

ARTICLE INFO

ABSTRACT

Infrastructure is increasingly part of wildlife habitats. However, it is not clear how infrastructure affects habitat quality for wildlife adapted to natural disturbances. While potentially providing suitable habitat such as early-successional forest, infrastructure also enables human access, which may modify animal' movements, especially where hunted species are concerned. To investigated the effect of infrastructure for moose (*Alces alces*, $n = 138$), a heavily harvested species, we modelled circadian distances and movement rates over the year as a function of moose' distance to the nearest road, house and power line in different human-modified landscapes in Sweden (latitude 57–67). Distances between moose and roads followed a circadian pattern. Animals were more likely to be closer to roads between 18:00 in the evening and 6:00 in the morning (i.e., during times when traffic volumes are generally lower). Moose moved relatively faster when 125 m or closer to a road, or alternatively, were closer to roads when more active. We did not find these relationships between moose and houses or power lines. With respect to roads, our results suggest that moose may make a temporal adjustment. During hours when humans are less active, road-near habitats may be sought out. We suggest considering different resolutions to study the impact of different infrastructure types. We recommend future research to investigate animal movement and behaviour in relation to infrastructure to understand the utilization of human-modified habitats over time, and thus providing key information for wildlife management and conservation, particularly for species that are adapted to disturbed landscapes.

1. Introduction

Human activities are increasingly part of wildlife species' environments, and have both direct and indirect impacts on ecosystems and wildlife (Berger, 2007; Bowman, Ray, Magoun, Johnson, & Dawson, 2010; Ingold, 2005). Understanding how human infrastructure influences animal movement and activity patterns will help planners manage resources more sustainably (Coulon et al., 2008; Roever, Boyce, & Stenhouse, 2010).

Infrastructure creates long-lasting ecological footprints of human activity in wildlife habitat, and its effects generally exceed their physical footprint, leading potentially to substantial reductions of effective wildlife habitat (Coulon et al., 2008; Forman & Alexander, 1998; Vistnes & Nellemann, 2008). Of the different types of human expansion into animal habitat, roads have probably the strongest effect because of the habitat fragmentation that results, and because roads are often a precursor for further human activity, e.g., settlement, recreational activity, or hunting (Forman & Alexander, 1998; Hawbaker, Radeloff, Clayton, Hammer, & Gonzalez-Abraham, 2006; Ingold, 2005; Stedman et al., 2004).

However, the prediction of infrastructure impacts and anthropogenic habitat modifications might be more complicated for wildlife species adapted to natural landscape disturbances, such as forest fires or storms that change age and structure of a forest. Human-modified habitats that result in similar disturbances

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may be beneficial for these species (Bergström & Danell, 2009; Bjørneraas et al., 2011; Jiang, Ma, Zhang, & Stott, 2009). For examples, corridors such as roads and power lines may create attractive early-successional habitats due to road-side maintenance (Bowman et al., 2010; Rea, Child, Spata, & MacDonald, 2010; Roever et al., 2010). Intensive forest harvesting also creates more early-successional forests, thus benefitting species such as moose (*Alces alces*) (Lavsund, Nygrén, & Solberg, 2003). Moose is a selective browser and early-successional forage (i.e., young forest), deciduous forest, and coniferous forest are attractive habitats (Bjørneraas et al., 2011; Olsson, Cox, Larkin, Widen, & Olovsson, 2011). In forest-dwelling species, landscape fragmentation, and thus decreased forest connectivity, can affect the movement behaviour of those species (Coulon et al., 2008; Cushman et al., 2011). In human-modified landscapes, moose respond to forest cover by utilizing open habitats preferably during night (Bjørneraas et al., 2011).

If hunting accounts for the major source of mortality, human presence may create a 'landscape of fear', and thereby modify animals' movement behaviour and cause spatiotemporal avoidance of areas that are perceived as more risky (Brown & Kotler,

2007; Coulon et al., 2008; Martin et al., 2010). Human-caused disturbances can provoke anti-predator responses similar to real predation risk, following the same economic principles with hunted populations responding stronger than un-hunted ones (Frid & Dill, 2002; Stankowich, 2008). Moose disturbed by humans leave the area and move faster than before disturbance (Neumann, 2009). For hunted species in human-modified landscapes, habitat use follows circadian patterns, possibly responding to human presence; e.g., Brown bears utilize road-near habitats predominantly at night (Martin et al., 2010).

Animals respond to their environment at different scales in both time and space. To understand thus large-scale patterns in wildlife movement behaviour in human-modified landscapes, analyses at broader spatiotemporal scale that encompass environmental gradients and different seasons are important (Bjørneraas et al., 2011; Bowman et al., 2010; Coulon et al., 2008).

Our goal here was to assess the temporal movement patterns of moose, a heavily hunted species in Sweden, in relation to infrastructure in different environments. Our main objective was to evaluate whether animals change their distribution and movement rates in
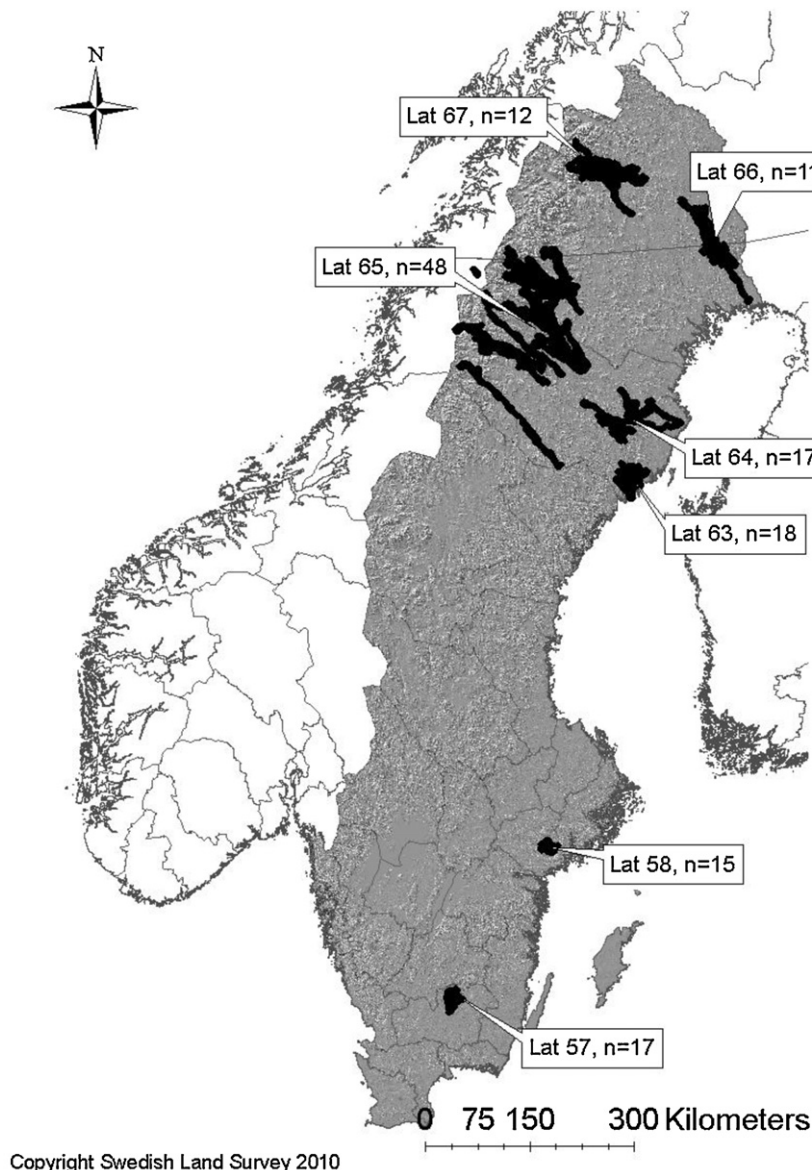
Fig. 1. Map of Fennoscandia. Sweden in grey. Moose GPS-locations in black.

the vicinity of infrastructure such as roads, houses, and power lines over time. Our study included animals in interior southern Sweden, in coastal and interior northern Sweden, in low alpine, and in high alpine areas ranging from latitude 57N to 67N (Fig. 1).

Our main hypothesis was that moose perceive human presence as a risk, because humans account for their main source of mortality, i.e., hunting (see Section 2), and therefore minimize human encounters (Ericsson & Wallin, 2001; Frid & Dill, 2002). Based on our literature review, we formulated the following predictions.

(P1) We predicted that moose would be relatively further away from infrastructure, in particular roads and houses, during times of high human activity (i.e. during daytime).

(P2) We predicted that moose increase their movement rates when closer to these human infrastructures, but we also expected that the different types of infrastructure differ in their impact on moose distribution. More specifically we expect the predicted responses to be more pronounced for road and houses than for power lines, because power line corridors provide abundant forage at early successional stage (Persson, 2003), but generally exhibit little human activity.

The impact of infrastructure cannot be seen without the context of other ecological variables in the surrounding environment. We therefore, formulated two additional predictions, which were closely related to P1 and P2, respectively.

(P3) We predicted that high abundance of attractive habitat for moose (i.e., young forest, deciduous forest, and coniferous forest; Bjørneraas et al., 2011; Jiang, Ma, Zhang, & Stott, 2010; Olsson et al., 2011) would make it more likely that moose are closer to infrastructure objects and move less, reflecting a situation that minimizes perceived risk with possible foraging opportunities.

(P4) We predicted that moose would be relatively further away from infrastructure objects and move faster when in open areas and would avoid those areas during times of higher risk for human encounters. Thus, we expected that areas with lower levels of forest cover, and therefore less concealment, but with higher risk for human disturbances (e.g., open areas, forest corridors, and edge forest) will affect a forest-dwelling species as moose, and thus will increase distances and movement rates.

2. Methods

2.1. Study area

We monitored female moose in seven latitudinal distinct sites in the Swedish provinces of Norrbotten and Västerbotten, hereafter referred to as *regions* (Fig. 1); the high alpine north (Lat67; 67°73′N 19°48′E, WGS84; n = 12 animals), the low alpine (Lat65; 65°94′N 16°93′E, n = 48), the interior region (Lat64; 64°45′N 19°54′E, n = 17), and two coastal regions (Lat66; 66°57′N 22°90′E, n = 11) and (Lat63; 63°70′N 19°74′E, n = 18), plus parts of the provinces of Södermanland (Lat58; 58°97′N 17°10′E, n = 15) and of Kronoberg (Lat57; 57°05′N 14°70′E, n = 17).

The two most northern interior regions, Lat67 and Lat65, were characterized by coniferous and mountainous birch forest with *Salix* ssp., partly above tree line with an average elevation of 1219 m ± 497 SD and 966 m ± 525 SD, respectively (Swedish Land Survey, 2010). Snow cover and the vegetation season lasted 225 days and 100 days, respectively, in Lat67, and 200 days and 120 days, respectively, in Lat65. In both regions, the annual temperature averaged −2 °C (Raab & Vedin, 1995). The northern interior region, Lat64, and two coastal regions, Lat63 and Lat66, were characterized by monocultures of Scots Pine (*Pinus sylvestris*) with patches of deciduous trees and agricultural activity (except Lat66) in flat to gently rolling terrain (Lat64: 249 m ± 144 SD; Lat63: 173 m ± 100 SD; Lat66: 275 m ± 159 SD; Swedish Land Survey, 2010). In Lat64, the annual temperature averaged 1 °C, and the snow cover and the vegetation season lasted 175 days and 140 days, respectively (Raab & Vedin, 1995). In the two northern coastal regions, the average annual temperature was 3 °C and 0 °C in Lat63 and Lat66, respectively (Raab & Vedin, 1995). In Lat63, both snow cover and the vegetation season lasted 150 days, while in Lat66 snow cover lasted 175 and the vegetation season lasted 130 days (Raab & Vedin, 1995). The two study regions in the southern interior, Lat58 and Lat57, were characterized by patches of deciduous and coniferous forest, and agricultural fields in a flat to gently rolled terrain (Lat58: 45 m ± 25 SD; Lat57: 232 m ± 53 SD; Swedish Land Survey, 2010). In both regions, snow cover lasted 75 days and the vegetation season lasted 190 days (Raab & Vedin, 1995). The annual temperatures averaged 5 °C (Lat58) and 6 °C (Lat57), respectively (Raab & Vedin, 1995). In 2005, the major storm "Gudrun" passed through Lat57, which resulted in widespread early-successional forage for moose (Bjorheden, 2007). Among the seven regions the road densities, house densities, and forest connectivity like abundance of interior and peripheral forests, and non-forest areas differed substantially (Table 1). Hunting season for adult moose is long and focuses on the less productive parts of the population (Lavsund et al., 2003). It starts in September for the northern regions, and in October for the southern ones, and lasts until the end of December and January, respectively. Hunting is most intensive during the first weeks of the season.

2.2. Moose data

Between February 2004 and 2009, we immobilized 138 adult female moose from a helicopter using a dart gun to inject a mixture of an anaesthetic and a tranquilizer (ethorphine and xylazine; Kreeger & Arnemo, 2007). We equipped each moose with a Global Positioning System (GPS) collar that sent the calculated locations regularly to a server with help of the Global System for Mobile (GSM; Vectronic Aerospace GmbH, Berlin, Germany). We collected data into the Wireless Remote Animal Monitoring (WRAM) database system for data validation and management (WRAM, 2010). For each moose, we programmed the GPS to calculate a position each hour over the entire year, resulting in an annual data

Table 1

Average road and house densities, and the percentage of different feature classes given by the Morphological Spatial Pattern Analysis (MSPA) to describe forest connectivity in the seven study regions.

Region	Road density [m km^{-2}]	House density [nr km^{-2}]	Core [%]	Corridor [%]	Perforated [%]	Edge [%]	Non-Forest [%]
Lat67	38	0.2	29	3	1	5	61
Lat66	560	0.5	61	1	6	3	28
Lat65	349	0.4	46	2	4	3	44
Lat64	934	1	72	1	6	1	20
Lat63	1178	2.5	73	1	5	1	20
Lat58	1148	2.6	54	1	2	6	37
Lat57	1822	3.6	57	1	4	3	35

Lat57–Lat67: the studies areas, representing different latitude levels. Core: interior forest area; Corridor: smaller stretches of forest; Perforated: forest edges along openings inside larger forest patches; Edge: part of the forest periphery; Non-Forest: area completely outside the forest.

set of 8594 ± 22 SE locations per individual. We estimated animal movement rates by dividing the Euclidean distance between successive locations by the time elapsed [m h^{-1}], giving animals' speed during the upcoming step/time interval (i.e., the starting location), and thereby calculating animals' response to current conditions, i.e., when "approaching" infrastructure (package *adehabitat* version 1.8.3; Calenge, 2007).

2.3. Environmental data

2.3.1. Land cover data

We summarized Swedish land cover data (25-m resolution) into nine habitat categories based on habitat features important to moose (Ball, Nordengren, & Wallin, 2001; Bjørneraas et al., 2011; Swedish Land Survey, 2010). These were (1) deciduous forest and mixed forest, (2) old coniferous forest, (3) dry coniferous and mixed forest (lichens dominant the ground layer, forest on rock, and other low productive ground), (4) young coniferous forest/clear-cuts, (5) marsh/open pasture, (6) mires, (7) open water, (8) human-modified areas, and (9) non-moose habitat (areas of bare rock, sparsely vegetation, beach, glaciers, perpetual snow, and no data). Habitat variables of the 'non-moose habitat' category were sparsely distributed in the country, and thus made up a negligible portion of all habitats potentially available to moose. 'No data' pixels were outside the study area. In total, the 'non-moose habitat' category captured little of the variance, and thus was not considered for further analysis (Appendix 1). We applied a 250-m resolution grid to calculate the relative abundance in percentage of each of the nine habitat categories within each cell. We used the 250-m resolution to balance high spatial resolution and practical restrictions, and to match average movement rates as documented for moose (Neumann et al., 2012). We used principal component analysis (PCA) to select the habitat variables that captured most of the variance, i.e., variables with high contribution to the two first principal components, and which we used for further analyses (Appendix 1).

2.3.2. Forest connectivity data

Landscape composition and structure influence moose movement over time (Bjørneraas et al., 2011; Leblond, Dussault, & Quellet, 2010). To analyse the influence of forest connectivity on moose movement, we applied the Morphological Spatial Pattern Analysis (MSPA; Vogt et al., 2007), using the Swedish land cover data (25-m resolution; Swedish Land Survey, 2010). We coded the national land cover data as a binary map of forest versus non-forest. Each forest pixel was assigned to one of the resulting MSPA classes. The classes are mutually exclusive and describe the geometry and connectivity of the spatial arrangement of the image objects (Vogt et al., 2007), for example, predicting habitat suitability for forest-dwelling wildlife such as the European bison (*Bison bonasus*; Kuemmerle et al., 2010). For simplicity we summarized *Loop*, *Islet*, *Bridge*, and *Branch* that represent smaller forest stretches and patches into one class hereafter referred to as *Corridor*. We delineated five categories for further analyses (*core forest* (no nonforest neighbours), *corridor forest* (too small to contain core forest), *perforated forest* (forest edges along openings inside larger forest patches), *edge forest* (parts of the forest periphery), and *non-forest* (area completely outside the forest, i.e., pixels with only non-forest neighbours)).

2.3.3. Infrastructure data

To evaluate the impact of infrastructure on moose movement, we calculated the Euclidean distance [m] to the nearest road, house, and power line, respectively at a 25-m resolution. For each moose location, we estimated the respective environmental and infrastructural conditions (i.e., MSPA categories, habitat category, and distances to infrastructure).

We assessed the correlation among the explanatory variables with help of correlation matrices and variance inflation factors, and excluded the explanatory variables that were highly correlated (package *Design* version 2.3-0; Harrell, 2009). Based on our preliminary exploratory analysis, we defined our final set of suitable explanatory variables to build our suite of candidate models that are biologically meaningful and potentially important.

2.4. Data analysis

Movement rates differ for stationary and migratory animals, and change among seasons for migratory animals (Bunnefeld et al., 2011). To control for these difference and for variation among regions, we subdivided the original data set hierarchically into smaller subsets before checking our predictions. We therefore evaluated for each moose the net square displacement [m] as a function of Julian day to distinguish between migratory individuals (1) and individuals lacking a distinct migratory behaviour (0; hereafter referred to as *stationary*; Bunnefeld et al., 2011; Rivrud, Loe, & Mysterud, 2010; Singh, Borger, Dettki, Bunnefeld, & Ericsson, 2012). For migratory moose, we further discriminated different movement phases using breakpoints identified by segmented regression analysis given by movement rates as a function of Julian day (package *segmented* version 0.2-7.2; Muggeo, 2007). If not stated otherwise, all statistical analyses were done separately for stationary moose, and for each of the movement phases for migratory moose.

2.4.1. P1 (inclusive P3 and P4): moose keep larger distances to infrastructure during daytime

To test whether animals maintain relatively larger distances to infrastructure during times of high human activity (i.e., during daytime), we analysed how far moose were located from the nearest road, house, or power line (hereafter referred to as moose-road, moose-house, and moose-power line distance), respectively, as a function of time of the day using a generalized additive mixed model (*gamm*; package *mgcv* version 1.6-2; package *nlme* version 3.1-97; Pinheiro & Bates, 2000; Wood, 2006). The model also included landscape features (i.e., the five MSPA categories and habitat variables (abundance [%] of a given habitat type, indicated by the PCA; Appendix 1)), because environmental features also affect animal movement patterns (Leblond et al., 2010; Martin et al., 2010). Based on our predictions, we formulated six alternative models (Table 2).

2.4.2. P2 (inclusive P3 and P4): moose move faster in proximity to infrastructure

Before analysing moose movement rates, we evaluated the raw data separately for each region, and removed outliers at the high end where the distribution of rates became discontinuous, as these were most likely location errors (Lat67–Lat63 > 5000 m h^{-1}, and Lat58, Lat57 > 3600 m h^{-1}). We tested for differences in movement rates with respect to moose-road, moose-house, and moose-power line distance using a *gamm* (package *mgcv* version 1.6-2, package *nlme* version 3.1-97; Pinheiro & Bates, 2000; Wood, 2006). Moose are differentially active over the day (Neumann et al., 2012), and we therefore included time of the day as a fixed factor. Environmental features shape moose movement patterns over time (Leblond et al., 2010), and we therefore included the landscape features (i.e., MSPA categories and habitat variables (abundance [%] of a given habitat type, indicated by the PCA; Appendix 1)) as before. Based on our predictions, we formulated 13 alternative models (Table 2).

Table 2
The alternative generalized additive mixed models to evaluate moose distance to the nearest infrastructure object (i.e., road, house, or power line) and to evaluate moose movement rates in relation infrastructure and environmental covariates, respectively.

Generalized additive mixed models
Six alternative models to evaluate moose distance to the nearest infrastructure object
Infrastructure ~ region + s(Hour)
Infrastructure ~ region + s(X1) + s(X2) + s(X3)
Infrastructure ~ region + MSPA
Infrastructure ~ region + s(Hour) + s(X1) + s(X2) + s(X3)
Infrastructure ~ region + s(Hour) + MSPA
Infrastructure ~ region + s(Hour) + s(X1) + s(X2) + s(X3) + MSPA
Thirteen alternative models to evaluate moose movement activity
Mhr ~ region + s(Hour) + s(Road)
Mhr ~ region + s(Hour) + s(House)
Mhr ~ region + s(Hour) + s(Power)
Mhr ~ region + s(Hour) + s(Road) + s(House)
Mhr ~ region + s(Hour) + s(Road) + s(X1) + s(X2) + s(X3)
Mhr ~ region + s(Hour) + s(Road) + MSPA
Mhr ~ region + s(Hour) + s(House) + s(X1) + s(X2) + s(X3)
Mhr ~ region + s(Hour) + s(House) + MSPA
Mhr ~ region + s(Hour) + s(Power) + s(X1) + s(X2) + s(X3)
Mhr ~ region + s(Hour) + s(Power) + MSPA
Mhr ~ region + s(Hour) + s(Road) + s(House) + s(X1) + s(X2) + s(X3)
Mhr ~ region + s(Hour) + s(Road) + s(House) + MSPA
Mhr ~ region + s(Hour) + s(Road) + s(House) + s(X1) + s(X2) + s(X3) + MSPA

Region: area where moose ranged; Hour: time of the day; MSPA: features of forest connectivity; $X1$–$X3$: habitat variables; Road: moose distance to the nearest road; House: moose distance to the nearest house; Power: moose distance to the nearest power line; Response variable: log-transformed (road distance, $m\,h^{-1}$) or cube-root transformed (house and power line distance); s( ): indicates a non-parametric smoothed term.

Animals respond in a non-linear way to their environment (Bjørneraas et al., 2011; Neumann et al., 2012). We therefore applied the *gamm* analysis for the analysis of all our predictions in order to account for the hierarchical structure of the data, to correct for autocorrelation, and to fit a non-parametric smoothing curve to the data without needing to specify a non-linear function a priori (Crawly, 2007; Wood, 2006). Thereby, we allowed for a non-linear relationship between the response and explanatory variable. Due to restrictions on data volume that can be handled by *gamm*, we subsampled our original data set. For each individual and day, we randomly selected one location out of the 24-h period, resulting in 360 locations ± 0.7 per moose that were used in the *gamm* analysis. We tested for autocorrelation by computing empirical variograms (package *geoR* version 1.6-32; Ribeiro & Diggle, 2001), and selected the best-supported correlation structure using Akaike's information criterion (AIC; Burnham & Anderson, 2002; Pinheiro & Bates, 2000). Because animal behaviour is often temporally auto-correlated, i.e., animals behave more similar during hours that are closer together, we applied the cyclic spline function for the smoothing of time of the day, which accounts for similarity between end- and start-point in the 24-h period, i.e., a model smoothing function that match one' a clock in the morning with twelve' a clock at night (Wood, 2006). For the other fixed factors, we applied the thin plate regression spline function, which is a low-rank isotropic smoother, providing an optimal smoother irrespective of the dimensionality or rank of the model (Wood, 2006). For the non-parametric parameters, the significant effective degrees of freedom (edf) represent the amount of smoothing, and values >1 indicate a non-linear relationship and higher edf indicate stronger non-linearity (Wood, 2006).

To account for the hierarchical structure of the data (i.e., moose occurred in different regions) and to control for differences among individuals, we considered moose as random effect, nested within region (Pinheiro & Bates, 2000). For each level of analysis (i.e., movement phase or prediction), we selected the models that

fell within the 95% confidence level of models' AIC weights out of our full set of alternative models. We used model averaging based on the information criterion on these models to obtain model-averaged parameter estimates and standard errors, and quantify the influence of each covariate on moose response (using the Akaike information criterion for small sample sizes (AIC$_c$); package *MuMIn* version 1.8.0; Bartón, 2012; Burnham & Anderson, 2002). We used ArcGIS 9.3 for all GIS analyses (ESRI, Redlands, CA, USA). All statistical analyses were carried out in R 2.15.2 for statistical computing (R Development Core Team, 2012). To ensure normality, we log-transformed moose movement rates [$m\,h^{-1}$] and moose-road distance [m], and cube-root transformed moose-house distance [m] and moose-power line distance [m], respectively. For the stationary data set, we removed all no-data values (9% of the original data set) to enable the analysis. If not stated differently, averages are given with standard error, and we used a statistical significance of $p < 0.05$.

3. Results

We classified 92 of the 138 female moose as migratory. All females in the two southern study areas (Lat57 and Lat58, $n = 32$) and 14 (13%) females in the northern study areas were stationary. For migratory moose, we identified four distinct movement phases; winter range, migration to the summer range, summer range, and migration to the winter range.

3.1. P1: moose keep larger distances to infrastructure during daytime

Moose showed a circadian variation in their moose-road distance (Appendix 2). Animals were relatively further away from roads during daytime, and the estimated probability to be closer to a road increased between 18:00 in the evening and 06:00 in the morning (Fig. 2A and B). Stationary animals were on average closer to roads than migratory moose, and migratory moose kept relatively larger distance to the nearest road at their summer range (Fig. 2A). In contrast to moose-road distances, we found no circadian pattern in moose-house distances or moose-power line distances (Appendix 2). In stationary moose, variations in moose-house distances were better explained by abundance of old coniferous forest, deciduous forest, and features of forest connectivity than by time of the day (Appendix 2). Yet, differences among regions accounted for most of the variance in moose-house and moose-power line distances (Fig. 3).

3.2. P2: moose move faster in proximity to infrastructure

Moose were more active when closer to a road (between 0 and 125 m) (Fig. 4). In line with previous finding, moose movement rates followed a circadian pattern (Appendix 3), and movement varied with features of forest connectivity (Appendix 3). Moose-house distances or moose-power line distances had little influence on variations in moose movement rates (Fig. 5).

3.3. P3: the abundance of attractive habitat modifies moose response to infrastructure

Animals were relatively closer to roads where abundances of young and old coniferous forest were higher, while the relationship was the opposite for deciduous forest and in stationary moose for mixed forest on low-productive ground (Appendix 2). With respect to houses, moose that migrated to their summer range were often closer were the abundance of deciduous forest was higher (Appendix 2). Stationary moose were further away from houses where deciduous forest, mixed forest on low productive ground
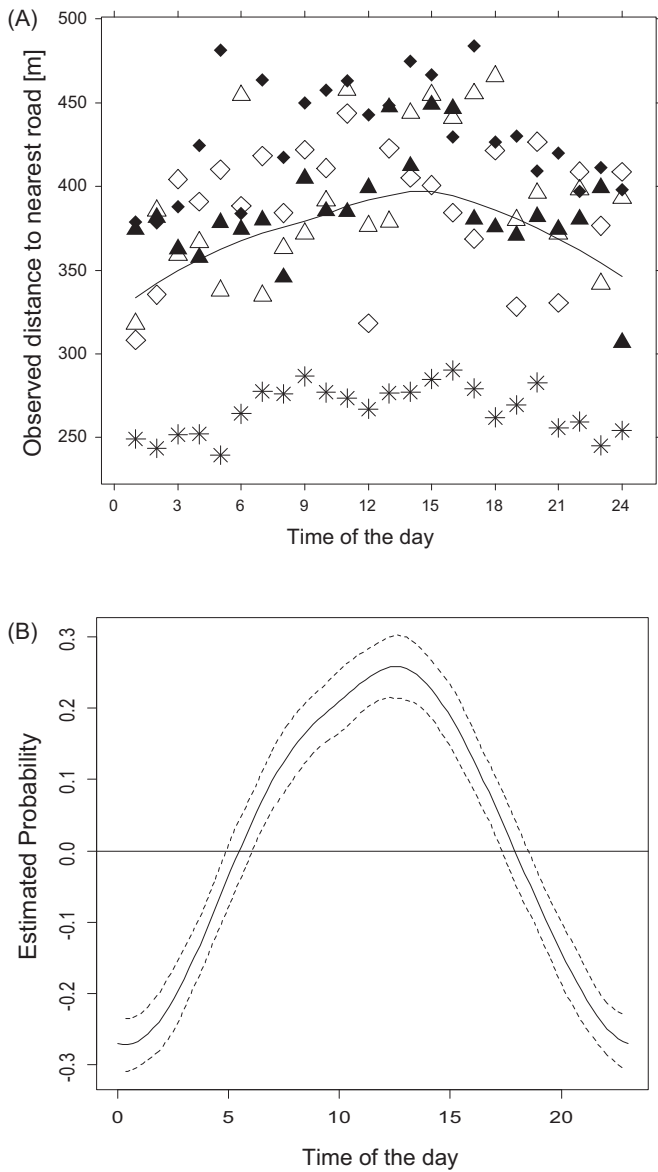
(A)

(B)

Fig. 2. Average moose-road distance [m] at different times of the day. Only regions where moose were on average within 1 km to the nearest road were included. (A) Observed distances, *filled triangle*: winter range; *filled diamond*: summer range; *open triangle*: migration to winter range; *open diamond*: migration to summer range; *star*: stationary moose. (B) Estimated shape of moose distance to the nearest road ± SE given by the generalized additive mixed model (response variable cube-root transformed).

and old coniferous forest occurred in higher abundances (Appendix 2). Variation in moose distances to the nearest power line did not show any relation to the abundance of attractive habitat (Appendix 2). In contrast to stationary moose, the abundance of attractive habitat had no influence on variations in movement rates for migratory moose (Fig. 5). In stationary moose, the abundance of old coniferous and deciduous forest was positive related to movement (Appendix 3).

3.4. P4: forest connectivity modifies moose response to infrastructure

Features of forest connectivity affected moose-road distances in migratory animals at the winter range and in stationary animals (Table 3). Moose that ranged in corridor forest, or non-forest area kept larger distances to the nearest road compared to moose that
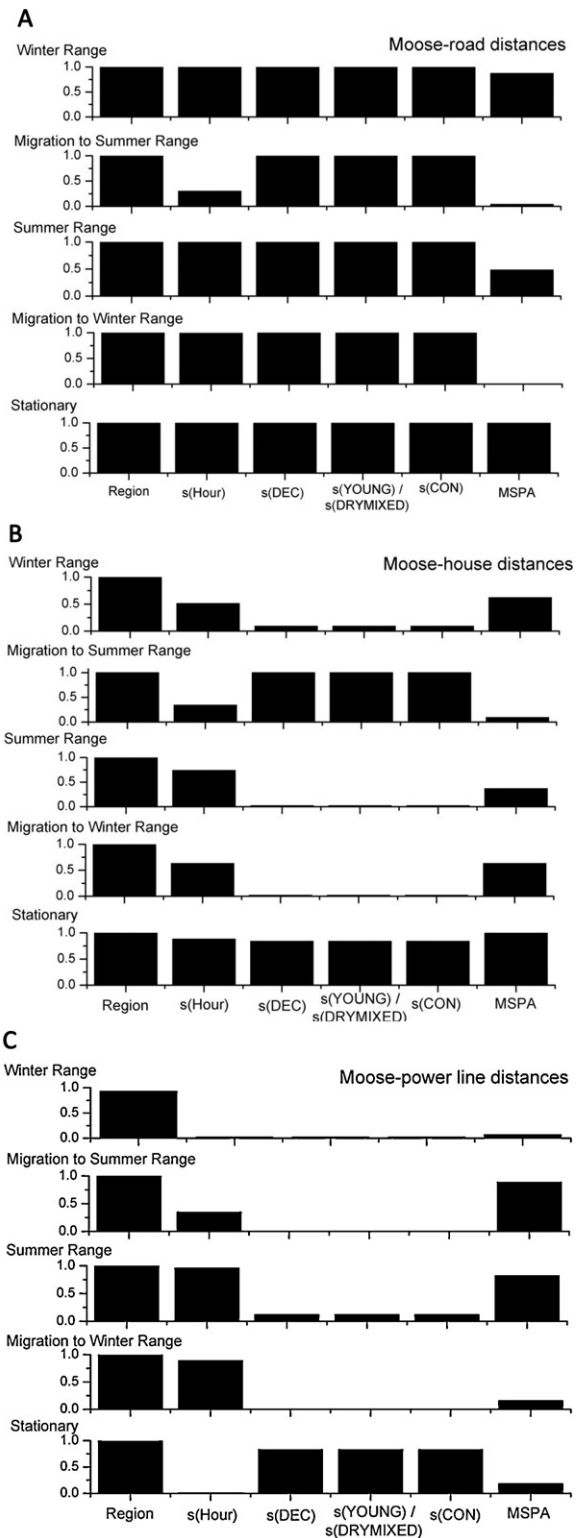

Fig. 3. Relative importance of environmental covariates in explaining (A) *moose-road distances*, (B) *moose-power line distances*, and (C) *moose-power line distances* across Sweden for stationary moose and for migratory moose during four distinct movement phases. Importance is based on the Akaike information criterion for small sample sizes (AIC$_c$) over all models that fell into the 95% confidence level of AIC weights.

ranged in core forest, except for stationary animals that behaved the opposite (Table 3). Stationary moose occurred relatively closer to houses in all other types of forest and non-forest areas compared to core forest (Table 3). Moose at their summer range occurred closer
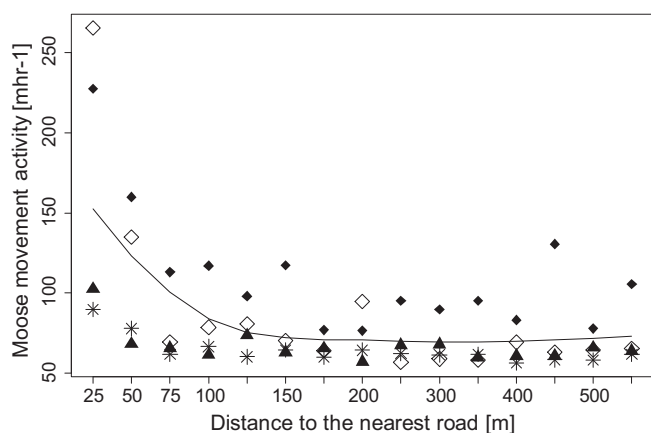
Fig. 4. Average moose movement rates [m h^{-1}] at different distances to the nearest road for stationary moose and migratory moose during different movement phases. Only movement phases with significant model-averaged coefficients are included (Appendix 3). *Filled triangle*: winter range; *filled diamond*: summer range; *open diamond*: migration to summer range; *star*: stationary moose. For visual reasons, we averaged distance into categories.
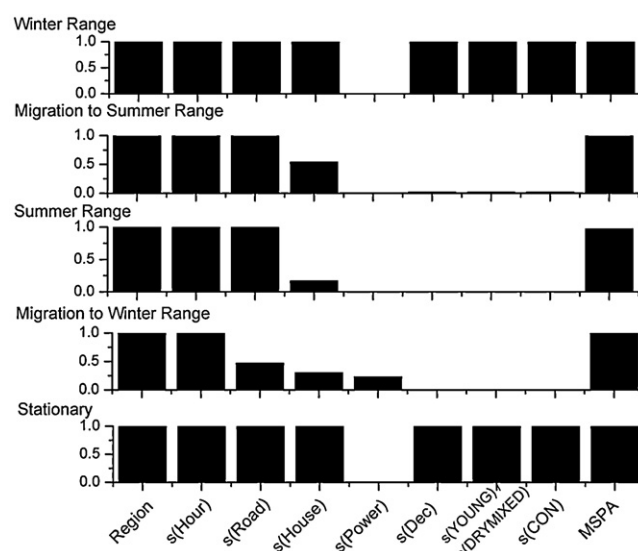

Fig. 5. Relative importance of environmental covariates in explaining moose movement rates across Sweden for stationary moose and for migratory moose during four distinct movement phases. Importance is based on the Akaike information criterion for small sample sizes (AIC$_c$) over all models that fell into the 95% confidence level of AIC weights.

to power lines when in edge forest or non-forest areas compared to core forest (Table 3). Animals in non-forest areas moved relatively faster than in core forest areas (Table 3). Moreover, stationary moose and moose that migrated to their winter ranges were more active in corridor and perforated forest compared to core forest (Table 3).

4. Discussion

Our goal was to evaluate the influence of infrastructure (i.e., roads, houses, and power lines) on moose movement over time in

different human-modified environments. Here, we modelled circadian distances and movement rates over a year as a function of moose-road, moose-house, and moose-power line distances, respectively. With respect to roads in more densely settled areas, our results supported our prediction that wildlife adjusted their distance to infrastructure depending on the time of day, most likely due to variations in human activity as moose kept relatively larger distances to roads during daytime. We also found support for

Table 3
Differences in moose distances to the nearest road, house, and power lines [m] ± SE and differences in moose movement rates [mhr-1] ± SE, respectively, with respect to features of forest connectivity as given by the model-averaged coefficients in Appendices 2 and 3, respectively. Significant different distances compared to the intercept (core forest) in bold, $p < 0.05$.

Phase	Core (intercept)	Corridor	Perforated	Edge	Non-Forest
Moose-road distance [m] ± SE					
WRange	217 ± 29	**246 ± 15**	232 ± 7	235 ± 10	**237 ± 8**
MigrSummer	201 ± 18	214 ± 5	204 ± 5	208 ± 7	**212 ± 6[a]**
SRange	254 ± 59	264 ± 5	246 ± 6	258 ± 7	255 ± 5
MigrWinter	271 ± 58	279 ± 16	283 ± 11	292 ± 12	262 ± 9
Stationary	147 ± 12	**131 ± 5**	143 ± 3	**138 ± 3**	**131 ± 3**
Moose-house distance [m] ± SE					
WRange	900 ± 61	906 ± 4	900 ± 2	**907 ± 3**	904 ± 2
MigrSummer	870 ± 57	866 ± 4	869 ± 2	875 ± 3	870 ± 2
SRange	701 ± 82	698 ± 2	699 ± 1	700 ± 2	**698 ± 1[b]**
MigrWinter	649 ± 98	651 ± 6	654 ± 4	650 ± 4	644 ± 3
Stationary	340 ± 27	**331 ± 2**	**336 ± 2**	**333 ± 1**	**331 ± 1**
Moose-power line distance [m] ± SE					
WRange	2328 ± 83	2331 ± 12	2331 ± 6	2331 ± 8	2331 ± 7
MigrSummer	2214 ± 628	2208 ± 9	2221 ± 5	2209 ± 7	**2202 ± 5**
SRange	2524 ± 683	2505 ± 11	2519 ± 6	**2504 ± 8**	**2508 ± 6**
MigrWinter	2441 ± 1028	2459 ± 20	2432 ± 14	2453 ± 14	2450 ± 12
Stationary	3520 ± 827	3519 ± 9	3517 ± 6	3519 ± 5	3513 ± 5
Moose movement rates [m h^{-1}] ± SE					
WRange	20 ± 1	24 ± 3	22 ± 1	23 ± 2	**28 ± 2**
MigrSummer	29 ± 2	30 ± 5	29 ± 3	31 ± 4	**47 ± 4**
SRange	39 ± 2	38 ± 4	35 ± 2	36 ± 3	**43 ± 2**
MigrWinter	31 ± 3	**52 ± 10**	**44 ± 6**	35 ± 5	**43 ± 4**
Stationary	24 ± 1	**34 ± 3**	**29 ± 2**	26 ± 1	**33 ± 1**

WRange: winter range; MigrSummer: migration to summer range; SRange; summer range; MigrWinter: migration to winter range; Stationary: stationary moose; Core: interior forest area; Corridor: smaller stretches of forest; Perforated: forest edges along openings inside larger forest patches; Edge: part of the forest periphery; Non-Forest: area completely outside the forest.

[a] $p = 0.046$.
[b] $p = 0.049$.

our prediction that wildlife' movement rates increase with proximity to roads as moose moved faster when within 125 m of a road.

Relatively larger distances to roads during daytime and faster movement near roads suggest that moose did not perceive roads as neutral objects. Yet, roads may have a complex behavioural influence, and alter animal movement behaviour at different times due to different reasons. Roads can act as source of disturbance (Coulon et al., 2008; Eldegard, Lyngved, & Hjeljord, 2012; Jiang et al., 2009), can be a shield against predation (Berger, 2007), and can provide attractive resources for wildlife adapted to disturbed landscapes (Bowman et al., 2010; Rea et al., 2010). Faster movement in the vicinity of a road may reflect an impact of the road itself (Roever et al., 2010). Elk (Cervus elaphus) on the other hand move faster with distance to roads (Forester et al., 2007). Active moose spend most time feeding (Van Ballenberghe & Miquelle, 1990). Thus, instead of a disturbance effect, alternatively, higher movement rates by moose in road proximity may reflect moose foraging in road-near habitats that provide attractive forage (Rea et al., 2010). However, increased rates of movement near roads may also indicate a transition between habitats as moose that cross roads move faster (Dussault et al., 2007). Unfortunately, animal movement data have limited ability to give detailed information about animal behaviour. Technological improvements that merge information given by location and activity sensor data provide promising outlooks for future studies of animal behaviour (Lottker et al., 2009), and thereby may help to improve our understanding about wildlife's utilization of different habitats over time beyond what we were able to accomplish here.

Moose can respond positively to anthropogenic landscape disturbances (Bjørneraas et al., 2011; Lavsund et al., 2003; Schneider & Wasel, 2000). Road corridors often not only provide early-successional roadside forage (Bowman et al., 2010; Rea et al., 2010), but may also generate trade-off situations, balancing perceived risk with foraging opportunities (Eldegard et al., 2012). In moose, selection of road-near habitat might therefore be scale-dependent with road avoidance at a coarse scale and a selection of road corridors at finer scales as part of a strategy to increase access to preferred forage (Laurian et al., 2008). Game species such as Brown bears (Ursus arctos) and moose utilize road-near or open habitats more during night, suggesting a response by wildlife to human activity during daytime (Bjørneraas et al., 2011; Martin et al., 2010). We found a circadian pattern of moose-road distance, indicating a behavioural adjustment of moose to avoid road-related disturbance by humans. Such circadian pattern was not evident when distance to houses or power line was evaluated, suggesting that moose perceived those structures differently than roads.

The lack of a circadian pattern in moose distances to houses indicates either that moose do not associate houses with disturbance or predation risk, or that they consider that risk to be temporally constant. In spite of the fact that housing distribution is closely related to road distribution (Hawbaker et al., 2006), stationary objects like houses may be less disturbing than roads where human activities may be less predictable. Yet, Norwegian moose moved further away from houses during daytime (Lykkja et al., 2009). Moose management is very similar between Sweden and Norway (Lavsund et al., 2003), and therefore we would expect similar moose response towards humans in both countries. The spatiotemporal resolution of the analysis can affect to which extent impacts by infrastructure developments on wildlife are possible to detect (Vistnes & Nellemann, 2008). Patterns that take place on larger scale might be difficult to detect with data of too high resolution, and vice versus. The lack of a circadian pattern for moose-house distances in our study in contrast to Lykkja et al. (2009) suggests that the higher spatial resolution (moose-house distances calculated on 25-m pixel used in our study may have retained too much variation in moose-house distances over the day to detect a circadian pattern compared to the lower spatial resolution (100-m pixel) used by Lykkja et al. (2009).

Like roads, power lines are man-made corridors creating early-successional forest because of regular clearance measures. Compared to roads, power lines generally are used less by humans, which may explain differences in moose distances to power lines versus roads. Furthermore, both the relative location, and the density of roads and power lines may also differ considerably, and thereby affect wildlife differently. Generally, roads follow topography closely (Forman & Alexander, 1998), and in that way may coincide with wildlife travel routes (Bruggeman, Garrott, White, Watson, & Wallen, 2007). In contrast, power lines track topography less closely, but follow the shortest way possibly, and also occur typically in much lower densities. Nevertheless, some species such as reindeer (Rangifer tarandus) utilize areas close to power lines less (Vistnes & Nellemann, 2008). Species differ in their disturbance threshold with respect to infrastructure and may be driven by different trade-offs (Bowman et al., 2010). For moose, power lines may act as attractants because the juxtaposition of early seral growth and mature forest cover. This is also true of roads where access to forage and edge must be balanced with disturbance from traffic.

Forest connectivity was correlated to moose-road distances and we found that migratory moose maintained larger distances to roads when in smaller forest patches or non-forest areas, but the opposite for stationary moose. Roads may be perceived more risky, and hence avoided, when animals are in smaller forest patches and open landscape compared to larger continuous forest areas that provide close refuge. Alternatively, larger continuous forest areas have fewer roads, and thus have possibly lower disturbance levels. In terms of moose-house distances, we found stationary moose closer to houses when not in core forest, while migratory moose did not show any strong pattern relative to houses. Higher proximity to houses in non-forest areas by stationary moose is the opposite pattern from what has been observed for roe deer (Capreolus capreolus), which avoid buildings in particular when in open landscapes (Coulon et al., 2008). Similarly, roe deer respond more negatively to roads that were closer to houses, which suggest a cumulative disturbance effects in roe deer by human activity. In our study, forest connectivity also influenced moose movement activity as animals in non-forest areas (i.e. open areas), moved faster than in core forest areas. For forest-dwelling species, forest cover can shape movement patterns (Cushman et al., 2011; Godvik et al., 2009). Being a forest-dwelling species, moose selected habitat that provide concealment and moose in urbanized landscapes avoid open areas such as agricultural land and open water (Jiang et al., 2009; Olsson et al., 2011). Faster movement of moose in non-forest areas relatively to core forest areas may also reflect transition between habitats. In addition, non-forest areas may provide higher levels of human disturbances, and thus may be perceived as more risky, resulting in higher movement rates (Forester et al., 2007; Roever et al., 2010).

In Sweden, hunting accounts for the major source of mortality in adult moose, and moose disturbed by hunting activity move faster (for about 3 h following disturbance) and shift area (Ericsson & Wallin, 2001; Neumann, 2009), which potentially may affect our analyses. However, disturbance impacts are short-termed and are difficult to detect when the exact position and timing of the disturbance is unknown (Neumann, Ericsson, & Dettki, 2009). We found no indication of hunting disturbance, but given the level of our analyses (movement rates during movement phases or for stationary moose) we did not expect to do so. Rather we assumed moose movement patterns on larger scales such as daily and seasonal variations

to overlay possible momentary changes caused by hunting disturbances.

We found that migratory moose were often relatively closer to roads during their summer and winter migration compared to distances at their summer range. These findings suggest first that roads may coincide with moose migration routes as suggested for bison (*Bison bison*; Bruggeman et al., 2007), and secondly that animals kept larger distances to roads during calving season. In winter, moose use forest stands created by silviculture (Ball et al., 2001), which are permeated by smaller forest roads. Thus, winter browsing may help explaining the lower moose-road distances during this period. Such variation in response to infrastructure suggests that the local environment (e.g., the habitat matrix) modifies wildlife's response to infrastructure (Coulon et al., 2008).

5. Conclusions

We found circadian patterns in moose response to roads in more densely settled areas, suggesting that roads affect moose spatiotemporal movement patterns in human-modified landscapes. Human activity on roads and road-near attractive habitat may lead to complex decisions for wildlife species that are hunted. In moose, we suggest temporal adjustments: animals range close to roads during times of less human activity. With respect to houses, lower spatial resolution may improve the ability to determine their impact on wildlife movement patterns. We recommend future research to focus on animal movement patterns and behaviour in relation to infrastructure over time to improve our understanding about wildlife's temporal utilization of human-modified habitats.

Better knowledge can help to target wildlife management measures more efficiently in terms of traffic safety, forest damage, and conservation, particularly for species adapted to disturbed landscapes.

Appendix 1.

Variable loadings given by the principal component analysis (PCA; R function princomp). For our future analyses, we selected the habitat variables that captured most of the variance, i.e., variables with high contribution to the two first principal components. The variables selected for future analyses are marked in bold.

	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9
Winter range									
SD	42.0	32.9	25.9	18.7	11.5	9.7	2.9	1.2	0
Prop Var	0.43	0.26	0.16	0.09	0.03	0.02	0	0	0
CON	−0.26	**0.76**	−0.27	0.31	0.21		0.13	−0.11	−0.33
DEC	−0.45	**−0.62**	−0.45	0.13	0.22		0.13	−0.11	−0.33
DRYMIXED		0.11		−0.86	0.31		0.14	−0.11	−0.33
HUMAN							−0.93	−0.14	−0.33
MASH					−0.50	0.78	0.15	−0.12	−0.33
MIRE		−0.13	0.81	0.32	0.26		0.13	−0.12	−0.33
NON-HABITAT								0.94	−0.33
WATER					−0.68	−0.63	0.15	−0.12	−0.33
YOUNG	**0.85**	−0.11	−0.23	0.18	0.20		0.13	−0.11	−0.33
Migration to the summer range									
SD	41.6	29.5	23.6	20.6	9.9	7.5	1.8	1.1	0
Prop Var	0.46	0.23	0.15	0.11	0.03	0.01	0	0	0
CON	**0.65**	0.59	0.19		0.20	0.11	0.14	−0.11	−0.33
DEC		**−0.58**	0.60	0.31	0.23	0.19	0.14	−0.11	−0.33
DRYMIXED			−0.72	0.52	0.23	0.11	0.14	−0.11	−0.33
HUMAN							−0.92	−0.19	−0.33
MASH					−0.22	−0.90	0.16	−0.11	−0.33
MIRE		−0.32	−0.24	−0.80	0.23	0.10	0.14	−0.11	−0.33
NON-HABITAT								0.94	−0.33
WATER					−0.85	0.37	0.15	−0.11	−0.33
YOUNG	**−0.76**	0.45	0.19		0.19	0.11	0.14	−0.11	−0.33
Summer range									
SD	43.1	29.5	27.1	17.9	12.1	8.5	1.6	1.1	0
Prop Var	0.46	0.22	0.18	0.08	0.04	0.02	0	0	0
CON	0.40	**0.73**	−0.17	0.29	0.17	0.12	−0.31	0.21	
DEC	**−0.85**	0.11	−0.24	0.13	0.17	0.12	−0.31	0.21	
DRYMIXED	0.10			−0.86	0.29	0.16	−0.31	0.21	
HUMAN							0.58	0.82	
MASH					−0.88	0.29	−0.31	0.22	
MIRE		−0.20	0.82	0.31	0.20	0.13	−0.31	0.21	
NON-HABITAT									−0.99
WATER					−0.13	−0.91	−0.32	0.22	
YOUNG	0.32	**−0.64**	−0.49	0.24	0.19	0.11	−0.31	0.21	

	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9
Migration to the winter range									
SD	45.5	29.9	24.3	16.3	14.1	9.7	1.0	0.6	0.1
Prop Var	0.50	0.22	0.14	0.06	0.05	0.02	0	0	0
CON	0.56	**0.67**		0.27		0.12	−0.14	0.11	−0.33
DEC	**−0.80**	0.34	−0.21	0.18		0.12	−0.14	0.11	−0.33
DRYMIXED				−0.74	−0.51	0.21	−0.14	0.12	−0.33
HUMAN							0.92	0.19	−0.34
MASH				−0.32	0.84	0.22	−0.15	0.11	−0.33
MIRE		−0.30	0.78	0.35		0.15	−0.14	0.12	−0.33
NON-HABITAT								−0.93	−0.35
WATER						−0.92	−0.15	0.11	−0.33
YOUNG	0.19	**−0.58**	−0.58	0.34	−0.11	0.11	−0.14	0.11	−0.33
Stationary									
SD	34.6	25.9	23.1	21.5	18.7	14.3	2.6	0.7	0
Prop Var	0.35	0.20	0.16	0.13	0.10	0.06	0	0	0
CON	**0.89**	0.24				0.10	0.13	−0.12	−0.33
DEC	−0.39	**0.70**		0.36	−0.27		0.14	−0.12	−0.33
DRYMIXED		**−0.56**	−0.64	0.24	−0.23	0.15	0.14	−0.12	−0.33
HUMAN							−0.93	−0.13	−0.33
MASH	−0.15			−0.85	−0.24	0.23	0.14	−0.12	−0.33
MIRE	−0.16				0.88	0.23	0.13	−0.12	−0.33
NON-HABITAT								0.94	−0.33
WATER						−0.92	0.14	−0.12	−0.33
YOUNG		−0.37	0.76	0.29	−0.18	0.11	0.13	−0.12	−0.33

SD: standard deviation of the principal components; Prop Var: proportional variance of the principal components; CON: old coniferous forest; DEC: deciduous forest; DRYMIXED: mixed forest on low productive ground; HUMAN: human-modified areas; MASH: marsh/open pasture; MIRE: mires; NON-HABITAT: non-moose habitat; WATER: open water; YOUNG: young coniferous forest.

Appendix 2.

Model-averaged coefficients for alternative models within the 95% confidence level of the AICc weights. Covariates were found to be correlated to moose distances to the nearest infrastructure objects (roads, houses, power lines) using a generalized additive mixed model. Moose-road, moose-house, moose-power line distance [m] as a function of time-of-day and environmental characteristics for stationary moose, and in the four movement phases of migratory moose. Moose were applied as random effect, nested in region. Non-parametric smoothed terms are indicated by s( ). Region: area where moose ranged; Hour: time of the day; DEC: deciduous forest; YOUNG: young coniferous forest; CON: old coniferous forest; DRYMIXED: mixed forest on low productive ground; MSPA: features of forest connectivity. Response variable: log-transformed (road distance) or cube-root transformed (house and power line distance).

Moose-road distances, winter range
2 models with 95% confidence level of the AICc weights

Covariate	Estimate	SE	z	p
Intercept	5.39	0.13	42.85	0.00
Lat64	−0.09	0.20	0.46	0.64
Lat65	0.90	0.14	6.23	0.00
Lat66	0.44	0.21	2.06	0.04
Lat67	2.93	0.22	13.16	0.00
s(Hour).1	−2.04	0.01	2.12	0.03
s(Hour).2	−0.02	0.01	1.63	0.10
s(Hour).3	0.02	0.01	1.48	0.14
s(Hour).4	0.06	0.01	5.19	0.00
s(Hour).5	0.06	0.01	4.98	0.00
s(Hour).6	0.02	0.01	1.59	0.11
s(Hour).7	−0.01	0.01	0.53	0.59
s(Hour).8	−0.02	0.00	2.09	0.04
s(DEC).1	0.03	0.05	0.50	0.62
s(DEC).2	0.00	0.08	0.02	0.99
s(DEC).3	0.01	0.03	0.41	0.68
s(DEC).4	0.02	0.05	0.46	0.64
s(DEC).5	0.02	0.03	0.61	0.54
s(DEC).6	−0.02	0.03	0.58	0.56
s(DEC).7	−0.02	0.03	0.67	0.50

Moose-road distances, winter range
2 models with 95% confidence level of the AICc weights

Covariate	Estimate	SE	z	p
s(DEC).8	−0.13	0.10	1.29	0.20
s(DEC).9	0.11	0.04	2.67	0.01
s(YOUNG).1	0.19	0.06	3.02	0.00
s(YOUNG).2	0.14	0.15	0.90	0.37
s(YOUNG).3	0.12	0.06	2.07	0.04
s(YOUNG).4	0.08	0.09	0.86	0.39
s(YOUNG).5	0.08	0.05	1.51	0.13
s(YOUNG).6	−0.09	0.07	1.19	0.23
s(YOUNG).7	−0.07	0.05	1.42	0.16
s(YOUNG).8	−0.17	0.16	1.06	0.29
s(YOUNG).9	−0.27	0.07	3.66	0.00
s(CON).1	0.00	0.00	0.00	0.99
s(CON).2	0.00	0.00	0.00	0.99
s(CON).3	0.00	0.00	0.00	0.99
s(CON).4	0.00	0.00	0.00	0.99
s(CON).5	0.00	0.00	0.00	0.99
s(CON).6	−0.00	0.00	0.00	0.99
s(CON).7	−0.00	0.00	0.00	0.99
s(CON).8	−0.00	0.00	0.00	0.99
s(CON).9	−0.03	0.02	2.04	0.04
Corridor	0.12	0.06	2.10	0.04
Perforated	0.07	0.03	2.22	0.03
Edge	0.08	0.04	1.93	0.05
Non-Forest	0.08	0.03	2.59	0.01

Moose-road distances, migration to summer range
3 models with 95% confidence level of the AICc weights

Covariate	Estimate	SE	z	p
Intercept	5.31	0.08	63.51	0.00
Lat64	0.23	0.01	1.79	0.07
Lat65	0.79	0.10	8.10	0.00
Lat66	0.57	0.15	3.83	0.00
Lat67	2.85	0.16	17.51	0.00
s(Hour).1	0.00	0.00	0.00	0.99
s(Hour).2	0.00	0.00	0.00	0.99
s(Hour).3	0.00	0.00	0.00	0.99
s(Hour).4	0.00	0.00	0.00	0.99
s(Hour).5	0.00	0.00	0.00	0.99
s(Hour).6	−0.00	0.00	0.00	0.99

Moose-road distances, migration to summer range
3 models with 95% confidence level of the AICc weights

Covariate	Estimate	SE	z	p
s(Hour).7	−0.00	0.00	0.00	0.99
s(Hour).8	−0.00	0.00	0.00	0.99
s(DEC).1	−0.00	0.00	0.00	0.99
s(DEC).2	−0.00	0.00	0.00	0.99
s(DEC).3	−0.00	0.00	0.00	0.99
s(DEC).4	−0.00	0.00	0.00	0.99
s(DEC).5	−0.00	0.00	0.00	0.99
s(DEC).6	0.00	0.00	0.00	0.99
s(DEC).7	0.00	0.00	0.00	0.99
s(DEC).8	0.00	0.00	0.00	0.99
s(DEC).9	0.04	0.01	2.55	0.01
s(YOUNG).1	0.00	0.00	0.04	0.97
s(YOUNG).2	0.00	0.00	0.02	0.98
s(YOUNG).3	0.00	0.00	0.04	0.97
s(YOUNG).4	0.00	0.00	0.03	0.98
s(YOUNG).5	0.00	0.00	0.04	0.97
s(YOUNG).6	−0.00	0.00	0.04	0.97
s(YOUNG).7	−0.00	0.00	0.04	0.97
s(YOUNG).8	−0.00	0.00	0.04	0.97
s(YOUNG).9	−0.05	0.02	2.85	0.00
s(CON).1	0.00	0.00	0.01	0.99
s(CON).2	0.00	0.00	0.00	0.99
s(CON).3	0.00	0.00	0.01	0.99
s(CON).4	0.00	0.00	0.01	0.99
s(CON).5	0.00	0.00	0.01	0.99
s(CON).6	−0.00	0.00	0.01	0.99
s(CON).7	−0.00	0.00	0.01	0.99
s(CON).8	−0.00	0.00	0.01	0.99
s(CON).9	−0.01	0.01	0.91	0.37
Corridor	0.07	0.05	1.46	0.14
Perforated	0.02	0.02	0.65	0.52
Edge	0.03	0.03	1.10	0.27
Non-Forest	0.06	0.03	1.99	0.05

Moose-road distances, summer range
2 models with 95% confidence level of the AICc weights

Covariate	Estimate	SE	z	p
Intercept	5.54	0.21	26.48	0.00
Lat64	0.12	0.31	0.37	0.71
Lat65	1.73	0.24	7.25	0.00
Lat66	0.58	0.35	1.66	0.10
Lat67	3.28	0.35	9.45	0.00
s(Hour).1	−0.01	0.00	1.85	0.07
s(Hour).2	0.00	0.00	0.77	0.44
s(Hour).3	0.02	0.00	2.52	0.01
s(Hour).4	0.03	0.00	3.69	0.00
s(Hour).5	0.03	0.00	3.76	0.00
s(Hour).6	0.02	0.00	2.65	0.01
s(Hour).7	0.00	0.00	0.58	0.56
s(Hour).8	−0.01	0.00	2.32	0.02
s(DEC).1	−0.00	0.00	0.00	0.99
s(DEC).2	0.00	0.00	0.00	0.99
s(DEC).3	0.00	0.00	0.00	0.99
s(DEC).4	0.00	0.00	0.00	0.99
s(DEC).5	0.00	0.00	0.00	0.99
s(DEC).6	−0.00	0.00	0.00	0.99
s(DEC).7	−0.00	0.00	0.00	0.99
s(DEC).8	−0.00	0.00	0.00	0.99
s(DEC).9	0.00	0.01	0.21	0.84
s(YOUNG).1	0.04	0.05	0.85	0.40
s(YOUNG).2	0.08	0.11	0.69	0.49
s(YOUNG).3	0.02	0.03	0.68	0.50
s(YOUNG).4	0.03	0.05	0.58	0.56
s(YOUNG).5	0.02	0.03	0.71	0.48
s(YOUNG).6	−0.03	0.05	0.64	0.52
s(YOUNG).7	−0.02	0.03	0.70	0.49
s(YOUNG).8	−0.07	0.12	0.57	0.57
s(YOUNG).9	−0.09	0.04	2.47	0.01
s(CON).1	0.03	0.03	1.06	0.29
s(CON).2	0.09	0.08	1.08	0.28
s(CON).3	0.03	0.02	1.49	0.14
s(CON).4	0.04	0.05	0.98	0.33
s(CON).5	0.03	0.02	1.31	0.19

Moose-road distances, summer range
2 models with 95% confidence level of the AICc weights

Covariate	Estimate	SE	z	p
s(CON).6	−0.04	0.04	1.07	0.29
s(CON).7	−0.02	0.02	1.24	0.21
s(CON).8	−0.15	0.10	1.45	0.15
s(CON).9	−0.03	0.03	0.99	0.32
Corridor	0.04	0.04	1.12	0.26
Perforated	−0.03	0.02	1.57	0.12
Edge	0.02	0.03	0.67	0.50
Non-Forest	0.00	0.01	0.35	0.72

Moose-road distances, migration to winter range
2 models with 95% confidence level of the AICc weights

Covariate	Estimate	SE	z	p
Intercept	5.61	0.19	28.78	0.00
Lat64	0.02	0.29	0.06	0.95
Lat65	2.03	0.23	9.00	0.00
Lat66	0.50	0.33	1.47	0.14
Lat67	3.51	0.36	9.86	0.00
s(Hour).1	−0.00	0.00	0.42	0.67
s(Hour).2	0.02	0.01	1.52	0.13
s(Hour).3	0.03	0.01	2.72	0.01
s(Hour).4	0.04	0.01	2.99	0.00
s(Hour).5	0.03	0.01	2.93	0.00
s(Hour).6	0.03	0.01	2.17	0.03
s(Hour).7	−0.00	0.01	0.01	0.98
s(Hour).8	−0.03	0.00	2.91	0.00
s(DEC).1	−0.00	0.00	0.00	0.99
s(DEC).2	0.00	0.00	0.00	0.99
s(DEC).3	0.00	0.00	0.00	0.99
s(DEC).4	0.00	0.00	0.00	0.99
s(DEC).5	0.00	0.00	0.00	0.99
s(DEC).6	−0.00	0.00	0.00	0.99
s(DEC).7	−0.00	0.00	0.00	0.99
s(DEC).8	−0.00	0.00	0.00	0.99
s(DEC).9	−0.03	0.02	1.76	0.08
s(YOUNG).1	0.04	0.04	1.09	0.28
s(YOUNG).2	0.02	0.11	0.21	0.83
s(YOUNG).3	0.02	0.03	0.62	0.53
s(YOUNG).4	0.04	0.06	0.65	0.52
s(YOUNG).5	0.02	0.03	0.79	0.43
s(YOUNG).6	−0.03	0.05	0.59	0.56
s(YOUNG).7	−0.02	0.03	0.74	0.46
s(YOUNG).8	−0.13	0.14	0.97	0.33
s(YOUNG).9	−0.13	0.04	3.11	0.00
s(CON).1	0.00	0.00	0.00	0.99
s(CON).2	0.00	0.00	0.00	0.99
s(CON).3	0.00	0.00	0.00	0.99
s(CON).4	0.00	0.00	0.00	0.99
s(CON).5	0.00	0.00	0.00	0.99
s(CON).6	−0.00	0.00	0.00	0.99
s(CON).7	−0.00	0.00	0.00	0.99
s(CON).8	−0.00	0.00	0.00	0.99
s(CON).9	−0.10	0.02	5.08	0.00
Corridor	0.03	0.06	0.55	0.59
Perforated	0.04	0.04	1.12	0.26
Edge	0.08	0.04	1.85	0.06
Non-Forest	−0.03	0.03	0.91	0.36

Moose-road distances, stationary
2 models with 95% confidence level of the AICc weights

Covariate	Estimate	SE	z	p
Intercept	4.99	0.08	62.85	0.00
Lat58	0.12	0.12	0.97	0.33
Lat63	0.31	0.31	1.01	0.32
Lat64	0.36	0.17	2.16	0.03
Lat65	4.18	0.32	13.14	0.00
Lat66	0.08	0.19	4.17	0.00
Lat67	3.88	0.17	22.74	0.00
s(Hour).1	−0.03	0.00	3.98	0.00
s(Hour).2	0.00	0.00	0.25	0.81
s(Hour).3	0.03	0.00	3.99	0.00

Moose-road distances, stationary
2 models with 95% confidence level of the AICc weights

Covariate	Estimate	SE	z	p
s(Hour).4	0.04	0.08	4.85	0.00
s(Hour).5	0.03	0.00	4.28	0.00
s(Hour).6	0.03	0.00	3.98	0.00
s(Hour).7	0.02	0.00	2.49	0.01
s(Hour).8	−0.01	0.00	1.57	0.12
s(DEC).1	0.00	0.00	0.00	0.99
s(DEC).2	0.00	0.00	0.00	0.99
s(DEC).3	0.00	0.00	0.00	0.99
s(DEC).4	0.00	0.00	0.00	0.99
s(DEC).5	0.00	0.00	0.00	0.99
s(DEC).6	−0.00	0.00	0.00	0.99
s(DEC).7	−0.00	0.00	0.00	0.99
s(DEC).8	−0.00	0.00	0.00	0.99
s(DEC).9	0.00	0.01	0.64	0.53
s(DRYMIXED).1	−0.00	0.00	0.00	0.99
s(DRYMIXED).2	−0.00	0.00	0.00	0.99
s(DRYMIXED).3	−0.00	0.00	0.00	0.99
s(DRYMIXED).4	−0.00	0.00	0.00	1.00
s(DRYMIXED).5	−0.00	0.00	0.00	0.99
s(DRYMIXED).6	0.00	0.00	0.00	0.99
s(DRYMIXED).7	0.00	0.00	0.00	0.99
s(DRYMIXED).8	0.00	0.00	0.00	0.99
s(DRYMIXED).9	0.05	0.01	4.52	0.00
s(CON).1	−0.00	0.00	0.00	0.99
s(CON).2	−0.00	0.00	0.00	1.00
s(CON).3	−0.00	0.00	0.00	1.00
s(CON).4	−0.00	0.00	0.00	1.00
s(CON).5	−0.00	0.00	0.00	1.00
s(CON).6	0.00	0.00	0.00	1.00
s(CON).7	0.00	0.00	0.00	1.00
s(CON).8	0.00	0.00	0.00	1.00
s(CON).9	0.02	0.01	1.35	0.18
Corridor	−0.12	0.04	2.94	0.00
Perforated	−0.04	0.03	1.07	0.28
Edge	−0.07	0.02	2.96	0.00
Non-Forest	−0.12	0.02	4.93	0.00

Moose-house distances, winter range
4 models with 95% confidence level of the AICc weights

Covariate	Estimate	SE	z	p
Intercept	9.63	0.21	45.05	0.00
Lat64	0.88	0.33	2.65	0.01
Lat65	1.79	0.24	7.29	0.00
Lat66	1.88	0.37	5.14	0.00
Lat67	3.87	0.38	10.26	0.00
s(Hour).1	0.00	0.00	0.00	0.99
s(Hour).2	0.00	0.00	0.00	0.99
s(Hour).3	0.00	0.00	0.00	0.99
s(Hour).4	0.00	0.00	0.00	0.99
s(Hour).5	0.00	0.00	0.00	0.99
s(Hour).6	−0.00	0.00	0.00	0.99
s(Hour).7	−0.00	0.00	0.00	0.99
s(Hour).8	−0.00	0.00	0.01	0.99
s(DEC).1	0.00	0.00	0.00	0.99
s(DEC).2	0.00	0.00	0.00	0.99
s(DEC).3	0.00	0.00	0.00	0.99
s(DEC).4	0.00	0.00	0.00	0.99
s(DEC).5	0.00	0.00	0.00	0.99
s(DEC).6	−0.00	0.00	0.00	0.99
s(DEC).7	−0.00	0.00	0.00	0.99
s(DEC).8	−0.00	0.00	0.01	0.99
s(DEC).9	0.00	0.00	1.21	0.22
s(YOUNG).1	0.00	0.00	0.00	0.99
s(YOUNG).2	0.00	0.00	0.00	0.99
s(YOUNG).3	0.00	0.00	0.00	0.99
s(YOUNG).4	0.00	0.00	0.00	0.99

Moose-house distances, winter range
4 models with 95% confidence level of the AICc weights

Covariate	Estimate	SE	z	p
s(YOUNG).5	0.00	0.00	0.00	0.99
s(YOUNG).6	−0.00	0.00	0.00	0.99
s(YOUNG).7	−0.00	0.00	0.00	0.99
s(YOUNG).8	−0.00	0.00	0.01	0.99
s(YOUNG).9	0.00	0.00	2.06	0.04
s(CON).1	0.00	0.00	0.00	0.99
s(CON).2	0.00	0.00	0.00	0.99
s(CON).3	0.00	0.00	0.00	0.99
s(CON).4	0.00	0.00	0.00	0.99
s(CON).5	0.00	0.00	0.00	0.99
s(CON).6	−0.00	0.00	0.00	0.99
s(CON).7	−0.00	0.00	0.00	0.99
s(CON).8	0.00	0.00	0.01	0.99
s(CON).9	0.00	0.00	0.07	0.94
Corridor	0.02	0.01	1.35	0.18
Perforated	−0.00	0.00	0.22	0.82
Edge	0.02	0.01	2.19	0.03
Non-Forest	0.01	0.00	1.61	0.11

Moose-house distances, migration to summer range
3 models with 95% confidence level of the AICc weights

Covariate	Estimate	SE	z	p
Intercept	9.53	0.02	47.07	0.00
Lat64	0.89	0.31	2.83	0.00
Lat65	0.15	0.24	6.40	0.00
Lat66	1.95	0.35	5.56	0.00
Lat67	3.01	0.41	7.34	0.00
s(Hour).1	−0.00	0.00	0.00	0.99
s(Hour).2	0.00	0.00	0.00	0.99
s(Hour).3	0.00	0.00	0.00	0.99
s(Hour).4	0.00	0.00	0.00	0.99
s(Hour).5	0.00	0.00	0.00	0.99
s(Hour).6	0.00	0.00	0.00	0.99
s(Hour).7	−0.00	0.00	0.00	0.99
s(Hour).8	−0.00	0.00	0.00	0.99
s(DEC).1	−0.03	0.02	1.52	0.13
s(DEC).2	−0.02	0.06	2.72	0.01
s(DEC).3	−0.05	0.02	2.53	0.01
s(DEC).4	−0.06	0.05	1.40	0.16
s(DEC).5	−0.06	0.02	2.77	0.01
s(DEC).6	0.06	0.04	1.56	0.12
s(DEC).7	0.06	0.02	2.37	0.02
s(DEC).8	0.02	0.09	2.55	0.01
s(DEC).9	−0.02	0.02	1.03	0.30
s(YOUNG).1	0.00	0.00	0.21	0.84
s(YOUNG).2	0.00	0.00	0.22	0.83
s(YOUNG).3	0.00	0.00	0.49	0.62
s(YOUNG).4	0.00	0.00	0.49	0.62
s(YOUNG).5	0.00	0.00	0.58	0.56
s(YOUNG).6	−0.00	0.00	0.53	0.60
s(YOUNG).7	−0.00	0.00	0.58	0.56
s(YOUNG).8	−0.00	0.01	0.86	0.39
s(YOUNG).9	0.00	0.00	0.57	0.57
s(CON).1	0.02	0.01	1.74	0.08
s(CON).2	0.02	0.02	0.92	0.36
s(CON).3	0.00	0.00	1.27	0.20
s(CON).4	0.01	0.00	1.12	0.26
s(CON).5	0.00	0.00	1.36	0.17
s(CON).6	−0.00	0.00	1.08	0.28
s(CON).7	−0.00	0.00	1.32	0.19
s(CON).8	−0.03	0.02	1.27	0.20
s(CON).9	−0.00	0.01	0.96	0.34
Corridor	−0.02	0.01	1.22	0.22
Perforated	−0.00	0.00	0.50	0.62
Edge	0.02	0.00	1.77	0.08
Non-Forest	−0.00	0.00	0.19	0.85

Moose-house distances, summer range
4 models with 95% confidence level of the AICc weights

Covariate	Estimate	SE	z	p
Intercept	8.86	0.33	26.54	0.00
Lat64	1.43	0.49	2.89	0.00
Lat65	3.01	0.38	7.89	0.00
Lat66	2.09	0.56	3.74	0.00
Lat67	5.29	0.55	9.59	0.00
s(Hour).1	−0.00	0.00	0.67	0.50
s(Hour).2	0.00	0.00	0.31	0.75
s(Hour).3	0.00	0.00	1.00	0.32
s(Hour).4	0.00	0.00	1.33	0.18
s(Hour).5	0.00	0.00	1.31	0.19
s(Hour).6	0.00	0.00	0.90	0.37
s(Hour).7	0.00	0.00	0.04	0.97
s(Hour).8	−0.00	0.00	0.98	0.33
s(DEC).1	−0.00	0.00	0.06	0.96
s(DEC).2	−0.00	0.01	0.25	0.80
s(DEC).3	−0.00	0.00	0.65	0.52
s(DEC).4	−0.00	0.00	0.75	0.45
s(DEC).5	−0.00	0.00	0.76	0.45
s(DEC).6	0.00	0.00	0.65	0.51
s(DEC).7	0.00	0.00	0.70	0.49
s(DEC).8	0.02	0.01	1.30	0.20
s(DEC).9	0.00	0.00	0.34	0.74
s(YOUNG).1	0.00	0.00	0.00	0.99
s(YOUNG).2	0.00	0.00	0.00	0.99
s(YOUNG).3	0.00	0.00	0.00	0.99
s(YOUNG).4	0.00	0.00	0.00	0.99
s(YOUNG).5	0.00	0.00	0.00	0.99
s(YOUNG).6	−0.00	0.00	0.00	0.99
s(YOUNG).7	−0.00	0.00	0.00	0.99
s(YOUNG).8	−0.00	0.00	0.00	0.99
s(YOUNG).9	0.00	0.00	0.83	0.41
s(CON).1	−0.00	0.00	0.00	0.99
s(CON).2	0.00	0.00	0.00	0.99
s(CON).3	0.00	0.00	0.00	0.99
s(CON).4	0.00	0.00	0.00	0.99
s(CON).5	0.00	0.00	0.00	1.00
s(CON).6	−0.00	0.00	0.00	0.99
s(CON).7	0.00	0.00	0.00	1.00
s(CON).8	0.00	0.00	0.00	0.99
s(CON).9	0.00	0.00	0.43	0.67
Corridor	−0.00	0.00	1.05	0.29
Perforated	−0.00	0.00	1.54	0.12
Edge	−0.00	0.00	0.64	0.52
Non-Forest	−0.00	0.00	1.97	0.05

Moose-house distances, migration to winter range
4 models with 95% confidence level of the AICc weights

Covariate	Estimate	SE	z	p
Intercept	8.64	0.41	20.85	0.00
Lat64	1.15	0.62	1.84	0.07
Lat65	3.45	0.50	7.18	0.00
Lat66	2.29	0.71	3.21	0.00
Lat67	5.22	0.71	7.31	0.00
s(Hour).1	−0.00	0.00	1.10	0.27
s(Hour).2	−0.00	0.00	0.01	0.99
s(Hour).3	0.00	0.00	0.82	0.41
s(Hour).4	0.00	0.00	1.25	0.21
s(Hour).5	0.00	0.00	1.65	0.10
s(Hour).6	0.00	0.00	1.63	0.10
s(Hour).7	0.00	0.00	0.76	0.44
s(Hour).8	−0.00	0.00	0.73	0.46
s(DEC).1	−0.00	0.00	0.00	0.99
s(DEC).2	0.00	0.00	0.00	0.99
s(DEC).3	0.00	0.00	0.00	1.00
s(DEC).4	−0.00	0.00	0.00	0.99
s(DEC).5	−0.00	0.00	0.00	0.99
s(DEC).6	0.00	0.00	0.00	0.99
s(DEC).7	0.00	0.00	0.00	0.99
s(DEC).8	0.00	0.00	0.00	0.99
s(DEC).9	0.02	0.01	1.64	0.10
s(YOUNG).1	−0.00	0.00	0.00	0.99

Moose-house distances, migration to winter range
4 models with 95% confidence level of the AICc weights

Covariate	Estimate	SE	z	p
s(YOUNG).2	−0.00	0.00	0.00	0.99
s(YOUNG).3	−0.00	0.00	0.00	0.99
s(YOUNG).4	−0.00	0.00	0.00	0.99
s(YOUNG).5	−0.00	0.00	0.00	0.99
s(YOUNG).6	0.00	0.00	0.00	0.99
s(YOUNG).7	0.00	0.00	0.00	0.99
s(YOUNG).8	0.00	0.00	0.00	0.99
s(YOUNG).9	−0.00	0.00	0.55	0.58
s(CON).1	0.00	0.00	0.00	0.99
s(CON).2	0.00	0.00	0.00	0.99
s(CON).3	0.00	0.00	0.00	0.99
s(CON).4	0.00	0.00	0.00	0.99
s(CON).5	0.00	0.00	0.00	0.99
s(CON).6	−0.00	0.00	0.00	0.99
s(CON).7	−0.00	0.00	0.00	0.99
s(CON).8	−0.00	0.00	0.00	0.99
s(CON).9	−0.00	0.00	0.75	0.45
Corridor	0.00	0.02	0.37	0.71
Perforated	0.02	0.02	1.43	0.15
Edg	0.00	0.02	0.10	0.92
Non-Forest	−0.02	0.01	1.55	0.12

Moose-house distances, stationary
3 models with 95% confidence level of the AICc weights

Covariate	Estimate	SE	z	p
Intercept	6.97	0.18	38.48	0.00
Lat58	0.27	0.28	0.95	0.34
Lat63	1.81	0.72	2.52	0.01
Lat64	3.80	0.39	9.64	0.00
Lat65	4.11	0.74	5.58	0.00
Lat66	3.97	0.44	9.05	0.00
Lat67	5.83	0.40	14.73	0.00
s(Hour).1	−0.00	0.00	0.00	0.99
s(Hour).2	0.00	0.00	0.00	0.99
s(Hour).3	0.00	0.00	0.00	0.99
s(Hour).4	0.00	0.00	0.00	0.99
s(Hour).5	0.00	0.00	0.00	0.99
s(Hour).6	0.00	0.00	0.00	0.99
s(Hour).7	−0.00	0.00	0.00	0.99
s(Hour).8	−0.00	0.00	0.00	0.99
s(DEC).1	0.00	0.00	0.00	0.99
s(DEC).2	0.00	0.00	0.00	0.99
s(DEC).3	0.00	0.00	0.00	0.99
s(DEC).4	0.00	0.00	0.00	0.99
s(DEC).5	0.00	0.00	0.00	0.99
s(DEC).6	−0.00	0.00	0.00	0.99
s(DEC).7	−0.00	0.00	0.00	0.99
s(DEC).8	−0.00	0.00	0.00	0.99
s(DEC).9	0.01	0.00	2.09	0.04
s(DRYMIXED).1	−0.00	0.00	0.00	0.99
s(DRYMIXED).2	−0.00	0.00	0.00	0.99
s(DRYMIXED).3	−0.00	0.00	0.00	0.99
s(DRYMIXED).4	−0.00	0.00	0.00	0.99
s(DRYMIXED).5	−0.00	0.00	0.00	0.99
s(DRYMIXED).6	0.00	0.00	0.00	0.99
s(DRYMIXED).7	0.00	0.00	0.00	0.99
s(DRYMIXED).8	0.00	0.00	0.00	0.99
s(DRYMIXED).9	0.02	0.00	3.64	0.00
s(CON).1	−0.00	0.00	0.00	0.99
s(CON).2	−0.00	0.00	0.00	0.99
s(CON).3	−0.00	0.00	0.00	0.99
s(CON).4	−0.00	0.00	0.00	0.99
s(CON).5	−0.00	0.00	0.00	0.99
s(CON).6	0.00	0.00	0.00	0.99
s(CON).7	0.00	0.00	0.00	0.99
s(CON).8	0.00	0.00	0.00	0.99
s(CON).9	0.02	0.00	3.19	0.00
Corridor	−0.06	0.02	4.03	0.00
Perforated	−0.03	0.01	2.54	0.01
Edge	−0.05	0.00	5.83	0.00
Non-Forest	−0.07	0.00	6.92	0.00

Moose-power line distances, winter range
4 models with 95% confidence level of the AICc weights

Covariate	Estimate	SE	z	p
Intercept	13.22	1.56	8.49	0.00
Lat64	1.32	2.38	0.55	0.58
Lat65	9.46	1.78	5.31	0.00
Lat66	11.10	2.69	4.12	0.00
Lat67	14.36	2.75	5.22	0.00
s(Hour).1	0.00	0.00	0.00	0.99
s(Hour).2	0.00	0.00	0.00	0.99
s(Hour).3	0.00	0.00	0.00	1.00
s(Hour).4	−0.00	0.00	0.00	0.99
s(Hour).5	−0.00	0.00	0.00	0.99
s(Hour).6	−0.00	0.00	0.00	0.99
s(Hour).7	−0.00	0.00	0.00	0.99
s(Hour).8	−0.00	0.00	0.00	1.00
s(DEC).1	−0.00	0.00	0.00	1.00
s(DEC).2	−0.00	0.00	0.00	1.00
s(DEC).3	−0.00	0.00	0.00	1.00
s(DEC).4	−0.00	0.00	0.00	1.00
s(DEC).5	−0.00	0.00	0.00	1.00
s(DEC).6	0.00	0.00	0.00	1.00
s(DEC).7	0.00	0.00	0.00	1.00
s(DEC).8	0.00	0.00	0.00	1.00
s(DEC).9	0.00	0.00	1.03	0.30
s(YOUNG).1	0.00	0.00	0.00	1.00
s(YOUNG).2	0.00	0.00	0.00	1.00
s(YOUNG).3	0.00	0.00	0.00	1.00
s(YOUNG).4	0.00	0.00	0.00	1.00
s(YOUNG).5	0.00	0.00	0.00	1.00
s(YOUNG).6	−0.00	0.00	0.00	1.00
s(YOUNG).7	−0.00	0.00	0.00	1.00
s(YOUNG).8	−0.00	0.00	0.00	1.00
s(YOUNG).9	0.00	0.00	0.19	0.85
s(CON).1	0.00	0.00	0.00	1.00
s(CON).2	0.00	0.00	0.00	1.00
s(CON).3	0.00	0.00	0.00	1.00
s(CON).4	0.00	0.00	0.00	1.00
s(CON).5	0.00	0.00	0.00	1.00
s(CON).6	−0.00	0.00	0.00	1.00
s(CON).7	−0.00	0.00	0.00	1.00
s(CON).8	−0.00	0.00	0.00	1.00
s(CON).9	−0.00	0.00	0.26	0.80
Corridor	0.00	0.02	0.21	0.84
Perforated	0.00	0.01	0.52	0.60
Edge	0.00	0.02	0.26	0.80
Non-Forest	0.00	0.01	0.43	0.67

Moose-power line distances, migration to summer range
3 models with 95% confidence level of the AICc weights

Covariate	Estimate	SE	z	p
Intercept	13.00	1.13	11.52	0.00
Lat64	2.40	1.73	1.39	0.16
Lat65	6.61	1.32	5.01	0.00
Lat66	11.39	1.99	5.74	0.00
Lat67	15.45	2.04	7.56	0.00
s(Hour).1	0.00	0.00	0.00	0.99
s(Hour).2	0.00	0.00	0.00	0.99
s(Hour).3	0.00	0.00	0.00	0.99
s(Hour).4	0.00	0.00	0.00	0.99
s(Hour).5	0.00	0.00	0.00	0.99
s(Hour).6	−0.00	0.00	0.00	0.99
s(Hour).7	−0.00	0.00	0.01	0.99
s(Hour).8	−0.00	0.00	0.01	0.99
s(DEC).1	0.00	0.00	0.00	0.99
s(DEC).2	0.00	0.00	0.00	1.00
s(DEC).3	0.00	0.00	0.00	0.99
s(DEC).4	0.00	0.00	0.00	0.99
s(DEC).5	0.00	0.00	0.00	0.99
s(DEC).6	−0.00	0.00	0.00	0.99
s(DEC).7	−0.00	0.00	0.00	0.99
s(DEC).8	−0.00	0.00	0.00	0.99
s(DEC).9	−0.00	0.00	0.36	0.72

Moose-power line distances, migration to summer range
3 models with 95% confidence level of the AICc weights

Covariate	Estimate	SE	z	p
s(YOUNG).1	−0.00	0.00	0.00	0.99
s(YOUNG).2	−0.00	0.00	0.01	0.99
s(YOUNG).3	−0.00	0.00	0.01	0.99
s(YOUNG).4	−0.00	0.00	0.00	0.99
s(YOUNG).5	−0.00	0.00	0.01	0.99
s(YOUNG).6	0.00	0.00	0.00	0.99
s(YOUNG).7	0.00	0.00	0.00	0.99
s(YOUNG).8	0.00	0.00	0.00	0.99
s(YOUNG).9	0.00	0.00	0.34	0.73
s(CON).1	0.00	0.00	0.00	0.99
s(CON).2	0.00	0.00	0.00	0.99
s(CON).3	0.00	0.00	0.00	0.99
s(CON).4	0.00	0.00	0.00	0.99
s(CON).5	0.00	0.00	0.00	0.99
s(CON).6	−0.00	0.00	0.00	0.99
s(CON).7	−0.00	0.00	0.00	0.99
s(CON).8	−0.00	0.00	0.00	0.99
s(CON).9	−0.00	0.00	0.37	0.71
Corridor	−0.01	0.01	0.63	0.53
Perforated	0.01	0.01	1.31	0.19
Edge	−0.00	0.01	0.70	0.49
Non-Forest	−0.02	0.00	2.48	0.01

Moose-power line distances, summer range
4 models with 95% confidence level of the AICc weights

Covariate	Estimate	SE	z	p
Intercept	13.58	1.90	7.14	0.00
Lat64	0.35	3.06	0.11	0.91
Lat65	9.30	2.16	4.30	0.00
Lat66	5.73	3.26	1.76	0.08
Lat67	11.38	3.25	3.50	0.00
s(Hour).1	−0.00	0.00	0.01	0.99
s(Hour).2	−0.00	0.00	0.02	0.99
s(Hour).3	−0.00	0.00	0.01	0.99
s(Hour).4	−0.00	0.00	0.01	0.99
s(Hour).5	−0.00	0.00	0.00	0.99
s(Hour).6	0.00	0.00	0.00	0.99
s(Hour).7	0.00	0.00	0.00	0.99
s(Hour).8	0.00	0.00	0.00	0.99
s(DEC).1	0.00	0.00	0.00	0.99
s(DEC).2	0.00	0.00	0.00	1.00
s(DEC).3	0.00	0.00	0.00	0.99
s(DEC).4	0.00	0.00	0.00	0.99
s(DEC).5	0.00	0.00	0.00	0.99
s(DEC).6	−0.00	0.00	0.00	0.99
s(DEC).7	−0.00	0.00	0.00	0.99
s(DEC).8	0.00	0.00	0.00	0.99
s(DEC).9	0.00	0.00	0.03	0.98
s(YOUNG).2	0.00	0.01	0.18	0.86
s(YOUNG).3	0.00	0.00	0.35	0.73
s(YOUNG).4	0.00	0.00	0.31	0.76
s(YOUNG).5	−0.00	0.00	0.36	0.72
s(YOUNG).6	−0.00	0.00	0.32	0.75
s(YOUNG).7	−0.00	0.00	0.37	0.71
s(YOUNG).8	−0.00	0.02	0.44	0.66
s(YOUNG).9	−0.01	0.00	1.28	0.20
s(CON).1	−0.00	0.00	0.00	0.99
s(CON).2	−0.00	0.00	0.00	0.99
s(CON).3	−0.00	0.00	0.00	0.99
s(CON).4	−0.00	0.00	0.00	0.99
s(CON).5	−0.00	0.00	0.00	0.99
s(CON).6	0.00	0.00	0.00	0.99
s(CON).7	0.00	0.00	0.00	0.99
s(CON).8	0.00	0.00	0.00	0.99
s(CON).9	0.00	0.00	0.00	0.38
Corridor	−0.03	0.02	1.68	0.09
Perforated	−0.00	0.01	0.81	0.42
Edge	−0.04	0.01	2.48	0.01
Non-Forest	−0.03	0.01	2.83	0.00

Moose-power line distances, migration to winter range
3 models with 95% confidence level of the AICc weights

Covariate	Estimate	SE	z	p
Intercept	13.43	1.67	8.05	0.00
Lat64	0.64	2.53	0.25	0.80
Lat65	11.45	1.95	5.88	0.00
Lat66	8.37	2.94	2.85	0.00
Lat67	11.31	2.93	3.85	0.00
s(Hour).1	−0.00	0.00	0.00	0.99
s(Hour).2	0.00	0.00	0.00	0.99
s(Hour).3	0.00	0.00	0.00	0.99
s(Hour).4	0.00	0.00	0.00	0.99
s(Hour).5	0.00	0.00	0.00	0.99
s(Hour).6	0.00	0.00	0.00	0.99
s(Hour).7	−0.00	0.00	0.00	0.99
s(Hour).8	−0.00	0.00	0.00	0.99
s(DEC).1	0.00	0.00	0.00	0.99
s(DEC).2	0.00	0.00	0.00	0.99
s(DEC).3	0.00	0.00	0.00	0.99
s(DEC).4	0.00	0.00	0.00	0.99
s(DEC).5	0.00	0.00	0.00	0.99
s(DEC).6	−0.00	0.00	0.00	0.99
s(DEC).7	−0.00	0.00	0.00	0.99
s(DEC).8	−0.00	0.00	0.00	0.99
s(DEC).9	−0.00	0.01	0.64	0.52
s(YOUNG).2	0.06	0.04	1.71	0.09
s(YOUNG).3	−0.00	0.12	0.04	0.97
s(YOUNG).4	−0.00	0.04	0.13	0.90
s(YOUNG).5	−0.00	0.07	0.01	0.99
s(YOUNG).6	−0.00	0.04	0.04	0.97
s(YOUNG).7	−0.00	0.06	0.00	0.99
s(YOUNG).8	−0.00	0.04	0.01	0.99
s(YOUNG).9	0.05	0.14	0.38	0.71
s(CON).1	0.00	0.00	0.00	0.99
s(CON).2	0.00	0.00	0.00	0.99
s(CON).3	0.00	0.00	0.00	0.99
s(CON).4	0.00	0.00	0.00	0.99
s(CON).5	0.00	0.00	0.00	0.99
s(CON).6	−0.00	0.00	0.00	0.99
s(CON).7	−0.00	0.00	0.00	0.99
s(CON).8	−0.00	0.00	0.00	0.99
s(CON).9	−0.00	0.01	0.63	0.53
Corridor	0.03	0.04	0.92	0.36
Perforated	−0.02	0.02	0.65	0.52
Edge	0.02	0.03	0.81	0.42
Non-Forest	0.02	0.02	0.69	0.52

Moose-power line distances, stationary
3 models with 95% confidence level of the AICc weights

Covariate	Estimate	SE	z	p
Intercept	15.17	1.11	13.73	0.00
Lat58	−2.75	1.72	1.60	0.11
Lat63	2.65	2.41	0.60	0.55
Lat64	0.41	2.47	0.16	0.87
Lat65	19.79	4.78	4.14	0.00
Lat66	10.81	2.78	3.90	0.00
Lat67	15.62	2.46	6.35	0.00
s(Hour).1	−0.00	0.00	0.01	0.99
s(Hour).2	−0.00	0.00	0.00	0.99
s(Hour).3	−0.00	0.00	0.00	0.99
s(Hour).4	0.00	0.00	0.00	0.99
s(Hour).5	0.00	0.00	0.00	0.99
s(Hour).6	0.00	0.00	0.01	0.99
s(Hour).7	0.00	0.00	0.00	0.99
s(Hour).8	0.00	0.00	0.00	0.99
s(DEC).1	0.00	0.00	0.00	0.99
s(DEC).2	0.00	0.00	0.00	1.00
s(DEC).3	0.00	0.00	0.00	0.99
s(DEC).4	0.00	0.00	0.00	0.99
s(DEC).5	0.00	0.00	0.00	1.00
s(DEC).6	−0.00	0.00	0.00	1.00
s(DEC).7	−0.00	0.00	0.00	1.00
s(DEC).8	−0.00	0.00	0.00	1.00
s(DEC).9	−0.00	0.00	0.07	0.94
s(DRYMIXED).1	−0.00	0.00	0.00	0.99
s(DRYMIXED).2	−0.00	0.00	0.00	1.00

Moose-power line distances, stationary
3 models with 95% confidence level of the AICc weights

Covariate	Estimate	SE	z	p
s(DRYMIXED).3	−0.00	0.00	0.00	0.99
s(DRYMIXED).4	−0.00	0.00	0.00	0.99
s(DRYMIXED).5	−0.00	0.00	0.00	0.99
s(DRYMIXED).6	0.00	0.00	0.00	0.99
s(DRYMIXED).7	0.00	0.00	0.00	0.99
s(DRYMIXED).8	0.00	0.00	0.00	0.99
s(DRYMIXED).9	−0.00	0.00	2.07	0.04
s(CON).1	−0.00	0.00	0.00	0.99
s(CON).2	−0.00	0.00	0.00	0.99
s(CON).3	−0.00	0.00	0.00	0.99
s(CON).4	−0.00	0.00	0.00	0.99
s(CON).5	−0.00	0.00	0.00	0.99
s(CON).6	−0.00	0.00	0.00	0.99
s(CON).7	−0.00	0.00	0.00	0.99
s(CON).8	−0.00	0.00	0.00	0.99
s(CON).9	−0.00	0.00	1.40	0.16
Corridor	−0.00	0.01	0.03	0.97
Perforated	−0.00	0.00	0.40	0.69
Edge	−0.00	0.00	0.08	0.93
Non-Forest	−0.00	0.00	1.25	0.21

Appendix 3.

Model-averaged coefficients for alternative models within the 95% confidence level of the AICc weights. Covariates were found to be correlated to moose movement rates to the nearest infrastructure objects (roads, houses, power lines) using a generalized additive mixed model. Moose movement rates [m h^{-1}] as a function of time-of-day, distance to the nearest infrastructure object, and environmental characteristics for stationary moose, and in the four movement phases of migratory moose. Moose were applied as random effect, nested in region. Non-parametric smoothed terms are indicated by s( ). Region: area where moose ranged; Hour: time of the day; Road: moose distance to the nearest road; House: moose distance to the nearest house; Power: moose distance to the nearest power line; DEC: deciduous forest; YOUNG: young coniferous forest; CON: old coniferous forest; DRYMIXED: mixed forest on low productive ground; MSPA: features of forest connectivity. Response variable: log-transformed.

Moose movement rates, winter range
1 model with 95% confidence level of the AICc weights

Covariate	Estimate	SE	z	p
Intercept	3.06	4.61	66.39	0.00
Lat64	−0.03	0.07	0.48	0.63
Lat65	−0.21	0.05	3.81	0.00
Lat66	−0.05	0.08	0.59	0.56
Lat67	−0.33	0.09	3.84	0.00
s(Hour).1	−0.30	0.04	7.59	0.00
s(Hour).2	−0.15	0.04	3.95	0.00
s(Hour).3	0.18	0.04	4.61	0.00
s(Hour).4	−0.14	0.04	3.64	0.00
s(Hour).5	0.54	0.04	13.74	0.00
s(Hour).6	0.52	0.04	12.98	0.00
s(Hour).7	−0.22	0.04	5.63	0.00
s(Hour).8	0.10	0.04	2.46	0.01
s(Road).1	−0.11	0.06	1.77	0.08
s(Road).2	0.05	0.03	1.90	0.06
s(Road).3	0.05	0.04	1.38	0.17
s(Road).4	−0.03	0.01	2.28	0.02
s(Road).5	−0.04	0.03	1.46	0.14
s(Road).6	0.05	0.02	2.65	0.01
s(Road).7	−0.05	0.02	1.80	0.07
s(Road).8	−0.31	0.17	1.88	0.06
s(Road).9	−0.07	0.06	1.13	0.26
s(House).1	0.00	0.00	0.00	0.99
s(House).2	−0.00	0.00	0.00	0.99
s(House).3	−0.00	0.00	0.00	0.99
s(House).4	0.00	0.00	0.00	0.99
s(House).5	0.00	0.00	0.00	0.99

Moose movement rates, winter range
1 model with 95% confidence level of the AICc weights

Covariate	Estimate	SE	z	p
s(House).6	−0.00	0.00	0.00	0.99
s(House).7	−0.00	0.00	0.00	0.99
s(House).8	−0.00	0.00	0.00	0.99
s(House).9	−0.04	0.01	2.81	0.00
s(Power).1	0.01	0.06	0.24	0.81
s(Power).2	−0.04	0.09	0.38	0.71
s(Power).3	0.04	0.04	1.25	0.21
s(Power).4	−0.04	0.06	0.68	0.50
s(Power).5	0.02	0.03	0.58	0.56
s(Power).6	−0.04	0.05	0.72	0.47
s(Power).7	0.02	0.03	0.75	0.46
s(Power).8	−0.18	0.18	1.02	0.31
s(Power).9	−0.04	0.06	0.61	0.54
s(DEC).1	−0.00	0.00	0.00	0.99
s(DEC).2	−0.00	0.00	0.00	0.99
s(DEC).3	0.00	0.00	0.00	0.99
s(DEC).4	0.00	0.00	0.00	0.99
s(DEC).5	0.00	0.00	0.00	0.99
s(DEC).6	−0.00	0.00	0.00	0.99
s(DEC).7	−0.00	0.00	0.00	0.99
s(DEC).8	−0.00	0.00	0.00	0.99
s(DEC).9	0.03	0.02	1.62	0.10
s(YOUNG).1	0.04	0.05	0.70	0.49
s(YOUNG).2	0.06	0.09	0.75	0.46
s(YOUNG).3	0.02	0.03	0.74	0.46
s(YOUNG).4	0.04	0.05	0.85	0.40
s(YOUNG).5	0.03	0.03	0.97	0.33
s(YOUNG).6	−0.04	0.04	1.05	0.29
s(YOUNG).7	−0.28	0.24	1.14	0.25
s(YOUNG).8	−0.17	0.10	1.75	0.08
s(YOUNG).9	−0.08	0.05	1.66	0.10
s(CON).1	−0.00	0.00	0.00	0.99
s(CON).2	−0.00	0.00	0.00	0.99
s(CON).3	−0.00	0.00	0.00	0.99
s(CON).4	−0.00	0.00	0.00	0.99
s(CON).5	−0.00	0.00	0.00	0.99
s(CON).6	0.00	0.00	0.00	0.99
s(CON).7	0.00	0.00	0.00	0.99
s(CON).8	0.00	0.00	0.00	0.99
s(CON).9	0.05	0.02	2.46	0.01
Corridor	0.15	0.10	1.47	0.14
Perforated	0.06	0.06	1.15	0.25
Edge	0.12	0.07	1.67	0.10
Non-Forest	0.29	0.05	5.90	0.00

Moose movement rates, migration to summer range
3 models with 95% confidence level of the AICc weights

Covariate	Estimate	SE	z	p
Intercept	3.41	0.07	50.45	0.00
Lat64	−0.02	0.10	0.26	0.80
Lat65	−0.21	0.08	2.67	0.01
Lat66	−0.18	0.12	1.50	0.13
Lat67	−0.53	0.16	3.29	0.00
s(Hour).1	−0.02	0.05	0.37	0.71
s(Hour).2	−0.06	0.05	1.03	0.30
s(Hour).3	0.04	0.05	0.81	0.42
s(Hour).4	0.17	0.06	2.97	0.00
s(Hour).5	0.26	0.06	4.62	0.00
s(Hour).6	0.28	0.05	5.09	0.00
s(Hour).7	0.43	0.05	7.98	0.00
s(Hour).8	−0.08	0.05	1.43	0.15
s(Road).1	0.14	0.09	1.49	0.14
s(Road).2	−0.07	0.03	2.06	0.04
s(Road).3	−0.03	0.04	0.63	0.53
s(Road).4	0.04	0.02	1.67	0.09
s(Road).5	0.04	0.03	1.20	0.23
s(Road).6	0.06	0.04	1.59	0.11
s(Road).7	−0.05	0.03	1.33	0.18
s(Road).8	−0.31	0.26	1.18	0.24
s(Road).9	−0.13	0.08	1.58	0.11
s(House).1	0.00	0.00	0.00	0.99
s(House).2	−0.00	0.00	0.00	0.99

Moose movement rates, migration to summer range
3 models with 95% confidence level of the AICc weights

Covariate	Estimate	SE	z	p
s(House).3	−0.00	0.00	0.00	0.99
s(House).4	0.00	0.00	0.00	0.99
s(House).5	0.00	0.00	0.00	0.99
s(House).6	0.00	0.00	0.00	0.99
s(House).7	0.00	0.00	0.00	0.99
s(House).8	−0.00	0.00	0.00	0.99
s(House).9	−0.05	0.03	2.08	0.04
s(Power).1	0.14	0.11	1.37	0.17
s(Power).2	−0.02	0.20	0.10	0.92
s(Power).3	0.02	0.06	0.30	0.76
s(Power).4	−0.08	0.13	0.63	0.53
s(Power).5	−0.02	0.05	0.49	0.62
s(Power).6	−0.05	0.11	0.49	0.62
s(Power).7	−0.00	0.04	0.19	0.85
s(Power).8	−0.23	0.39	0.59	0.55
s(Power).9	0.09	0.15	0.63	0.53
s(DEC).1	0.00	0.00	0.00	0.99
s(DEC).2	0.00	0.00	0.00	0.99
s(DEC).3	0.00	0.00	0.00	0.99
s(DEC).4	0.00	0.00	0.00	0.99
s(DEC).5	0.00	0.00	0.00	0.99
s(DEC).6	−0.00	0.00	0.00	0.99
s(DEC).7	−0.00	0.00	0.00	0.99
s(DEC).8	−0.00	0.00	0.00	0.99
s(DEC).9	−0.00	0.03	0.13	0.89
s(YOUNG).1	0.00	0.00	0.00	0.99
s(YOUNG).2	0.00	0.00	0.00	0.99
s(YOUNG).3	0.00	0.00	0.00	0.99
s(YOUNG).4	0.00	0.00	0.00	0.99
s(YOUNG).5	0.00	0.00	0.00	0.99
s(YOUNG).6	−0.00	0.00	0.00	0.99
s(YOUNG).7	−0.00	0.00	0.00	0.99
s(YOUNG).8	−0.00	0.00	0.00	0.99
s(YOUNG).9	−0.06	0.03	1.94	0.05
s(CON).1	−0.00	0.00	0.00	0.99
s(CON).2	−0.00	0.00	0.00	0.99
s(CON).3	−0.00	0.00	0.00	0.99
s(CON).4	−0.00	0.00	0.00	0.99
s(CON).5	−0.00	0.00	0.00	0.99
s(CON).6	−0.00	0.00	0.00	0.99
s(CON).7	−0.00	0.00	0.00	0.99
s(CON).8	−0.00	0.00	0.00	0.99
s(CON).9	−0.01	0.03	0.41	0.68
Corridor	0.02	0.02	0.14	0.89
Perforated	−0.01	0.09	0.14	0.89
Edge	0.05	0.11	0.46	0.64
Non-Forest	0.45	0.07	6.06	0.00

Moose movement rates, summer range
3 models with 95% confidence level of the AICc weights

Covariate	Estimate	SE	z	p
Intercept	3.63	0.06	59.70	0.00
Lat64	0.06	0.08	0.72	0.47
Lat65	−0.09	0.07	1.17	0.24
Lat66	0.17	0.10	1.70	0.09
Lat67	0.04	0.12	0.36	0.72
s(Hour).1	0.21	0.04	4.61	0.00
s(Hour).2	−0.23	0.04	5.33	0.00
s(Hour).3	−0.23	0.04	5.25	0.00
s(Hour).4	−0.28	0.04	6.34	0.00
s(Hour).5	−0.26	0.04	5.82	0.00
s(Hour).6	−0.04	0.04	1.07	0.29
s(Hour).7	0.43	0.04	9.78	0.00
s(Hour).8	0.31	0.04	7.00	0.00
s(Road).1	0.18	0.83	2.21	0.03
s(Road).2	0.08	0.05	1.58	0.11
s(Road).3	0.00	0.04	0.01	0.99
s(Road).4	−0.02	0.02	1.17	0.24
s(Road).5	−0.00	0.04	0.24	0.81
s(Road).6	0.02	0.02	0.91	0.36
s(Road).7	0.02	0.04	0.69	0.49

Moose movement rates, summer range
3 models with 95% confidence level of the AICc weights

Covariate	Estimate	SE	z	p
s(Road).8	−0.22	0.31	0.71	0.48
s(Road).9	−0.21	0.10	2.12	0.03
s(House).1	−0.21	0.12	1.75	0.08
s(House).2	−0.05	0.12	0.39	0.70
s(House).3	0.01	0.08	0.18	0.90
s(House).4	−0.00	0.08	0.03	0.98
s(House).5	−0.02	0.07	0.25	0.81
s(House).6	0.01	0.07	0.21	0.84
s(House).7	0.02	0.07	0.31	0.76
s(House).8	0.25	0.34	0.72	0.47
s(House).9	−0.18	0.11	1.56	0.12
s(Power).1	0.00	0.00	0.00	0.99
s(Power).2	0.00	0.00	0.00	0.99
s(Power).3	−0.00	0.00	0.00	0.99
s(Power).4	0.00	0.00	0.00	0.99
s(Power).5	−0.00	0.00	0.00	0.99
s(Power).6	0.00	0.00	0.00	0.99
s(Power).7	−0.00	0.00	0.00	0.99
s(Power).8	0.00	0.00	0.00	0.99
s(Power).9	0.00	0.03	0.26	0.79
s(DEC).1	0.00	0.00	0.00	0.99
s(DEC).2	−0.00	0.00	0.00	1.00
s(DEC).3	0.00	0.00	0.00	0.99
s(DEC).4	0.00	0.00	0.00	0.99
s(DEC).5	0.00	0.00	0.00	0.99
s(DEC).6	−0.00	0.00	0.00	0.99
s(DEC).7	−0.00	0.00	0.00	0.99
s(DEC).8	−0.00	0.00	0.00	0.99
s(DEC).9	0.00	0.00	0.03	0.99
s(YOUNG).1	0.00	0.00	0.00	0.99
s(YOUNG).2	0.00	0.00	0.00	0.99
s(YOUNG).3	0.00	0.00	0.00	0.99
s(YOUNG).4	0.00	0.00	0.00	0.99
s(YOUNG).5	0.00	0.00	0.00	0.99
s(YOUNG).6	−0.00	0.00	0.00	0.99
s(YOUNG).7	−0.00	0.00	0.00	0.99
s(YOUNG).8	−0.00	0.00	0.00	0.99
s(YOUNG).9	0.00	0.02	0.38	0.70
s(CON).1	0.00	0.00	0.00	0.99
s(CON).2	0.00	0.00	0.00	0.99
s(CON).3	0.00	0.00	0.00	0.99
s(CON).4	0.00	0.00	0.00	0.99
s(CON).5	−0.00	0.00	0.00	0.99
s(CON).6	−0.00	0.00	0.00	0.99
s(CON).7	−0.00	0.00	0.00	0.99
s(CON).8	−0.00	0.00	0.00	0.99
s(CON).9	0.00	0.02	0.39	0.70
Corridor	0.01	0.10	0.12	0.91
Perforated	−0.04	0.06	0.73	0.47
Edge	−0.02	0.08	0.22	0.83
Non-Forest	0.15	0.04	3.61	0.00

Moose movement rates, migration to winter range
3 models with 95% confidence level of the AICc weights

Covariate	Estimate	SE	z	p
s(Road).6	0.02	0.02	0.95	0.34
s(Road).7	−0.04	0.04	1.00	0.32
s(Road).8	−0.37	0.37	0.99	0.32
s(Road).9	−0.21	0.12	1.79	0.07
s(House).1	−0.00	0.00	0.00	0.99
s(House).2	−0.00	0.00	0.00	0.99
s(House).3	0.00	0.00	0.00	0.99
s(House).4	0.00	0.00	0.00	0.99
s(House).5	0.00	0.00	0.00	0.99
s(House).6	−0.00	0.00	0.00	0.99
s(House).7	−0.00	0.00	0.00	0.99
s(House).8	0.00	0.00	0.00	0.99
s(House).9	0.02	0.03	0.69	0.49
s(Power).1	0.00	0.00	0.00	0.99
s(Power).2	−0.00	0.00	0.00	0.99
s(Power).3	0.00	0.00	0.00	0.99
s(Power).4	0.00	0.00	0.00	0.99
s(Power).5	0.00	0.00	0.00	0.99
s(Power).6	−0.00	0.00	0.00	0.99
s(Power).7	−0.00	0.00	0.00	0.99
s(Power).8	0.00	0.00	0.00	0.99
s(Power).9	−0.00	0.03	0.08	0.93
s(DEC).1	−0.00	0.00	0.00	0.99
s(DEC).2	−0.00	0.00	0.00	0.99
s(DEC).3	−0.00	0.00	0.00	0.99
s(DEC).4	−0.00	0.00	0.00	0.99
s(DEC).5	−0.00	0.00	0.00	0.99
s(DEC).6	0.00	0.00	0.00	0.99
s(DEC).7	0.00	0.00	0.00	0.99
s(DEC).8	0.00	0.00	0.00	0.99
s(DEC).9	−0.01	0.05	1.76	0.08
s(YOUNG).1	0.00	0.00	0.00	0.99
s(YOUNG).2	0.00	0.00	0.00	0.99
s(YOUNG).3	0.00	0.00	0.00	0.99
s(YOUNG).4	0.00	0.00	0.00	0.99
s(YOUNG).5	0.00	0.00	0.00	0.99
s(YOUNG).6	−0.00	0.00	0.00	0.99
s(YOUNG).7	−0.00	0.00	0.00	0.99
s(YOUNG).8	−0.00	0.00	0.00	1.00
s(YOUNG).9	−0.06	0.04	1.42	0.16
s(CON).1	−0.00	0.00	0.00	0.99
s(CON).2	−0.00	0.00	0.00	0.99
s(CON).3	−0.00	0.00	0.00	0.99
s(CON).4	−0.00	0.00	0.00	0.99
s(CON).5	−0.00	0.00	0.00	0.99
s(CON).6	0.00	0.00	0.00	0.99
s(CON).7	0.00	0.00	0.00	0.99
s(CON).8	−0.00	0.00	0.00	0.99
s(CON).9	−0.06	0.05	1.19	0.23
Corridor	0.50	0.18	2.76	0.01
Perforated	0.34	0.12	2.88	0.00
Edge	0.12	0.13	0.89	0.37
Non-Forest	0.31	0.81	3.84	0.00

Moose movement rates, migration to winter range
3 models with 95% confidence level of the AICc weights

Covariate	Estimate	SE	z	p
Intercept	3.47	0.08	41.56	0.00
Lat64	−0.12	0.10	1.20	0.23
Lat65	−0.11	0.10	1.09	0.28
Lat66	−0.09	0.12	0.75	0.45
Lat67	−0.07	0.02	0.39	0.70
s(Hour).1	0.01	0.08	0.14	0.89
s(Hour).2	0.58	0.81	7.15	0.00
s(Hour).3	−0.46	0.80	5.70	0.00
s(Hour).4	0.06	0.08	0.72	0.47
s(Hour).5	0.06	0.08	0.68	0.50
s(Hour).6	0.99	0.082	12.03	0.00
s(Hour).7	0.00	0.08	0.11	0.91
s(Hour).8	−0.11	0.08	1.28	0.20
s(Road).1	−0.17	0.10	1.65	0.10
s(Road).2	0.05	0.06	0.87	0.38
s(Road).3	0.03	0.05	0.59	0.56
s(Road).4	−0.02	0.02	1.14	0.25
s(Road).5	−0.03	0.04	0.82	0.41

Moose movement rates, stationary
1 model with 95% confidence level of the AICc weights

Covariate	Estimate	SE	z	p
Intercept	3.23	0.04	72.69	0.00
Lat58	−0.01	0.06	0.20	0.84
Lat63	0.27	0.14	1.98	0.05
Lat64	0.05	0.08	0.61	0.54
Lat65	−0.52	0.18	2.82	0.00
Lat66	−0.13	0.09	1.52	0.13
Lat67	−0.00	0.13	0.05	0.96
s(Hour).1	−0.01	0.03	0.42	0.68
s(Hour).2	−0.06	0.03	2.13	0.03
s(Hour).3	−0.22	0.03	7.28	0.00
s(Hour).4	−0.24	0.03	8.12	0.00
s(Hour).5	0.04	0.03	1.41	0.16
s(Hour).6	0.26	0.03	8.67	0.00
s(Hour).7	0.22	0.03	7.41	0.00
s(Hour).8	0.13	0.03	4.43	0.00
s(Road).1	−0.07	0.05	1.50	0.13

s(Road).2	−0.00	0.02	0.57	0.57
s(Road).3	−0.02	0.02	0.99	0.32
s(Road).4	0.02	0.01	1.81	0.07
s(Road).5	0.02	0.02	1.19	0.23
s(Road).6	0.02	0.01	1.73	0.08
s(Road).7	−0.02	0.02	1.34	0.18
s(Road).8	−0.13	0.10	1.21	0.23
s(Road).9	−0.11	0.05	2.41	0.02
s(House).1	0.28	0.16	1.80	0.07
s(House).2	−0.12	0.11	1.10	0.27
s(House).3	−0.09	0.09	0.96	0.33
s(House).4	−0.00	0.01	0.27	0.78
s(House).5	0.08	0.07	1.26	0.21
s(House).6	−0.03	0.02	1.58	0.11
s(House).7	0.09	0.07	1.34	0.18
s(House).8	−0.28	0.25	1.13	0.26
s(House).9	−0.05	0.08	0.65	0.51
s(Power).1	0.00	0.00	0.00	1.00
s(Power).2	0.00	0.00	0.00	0.99
s(Power).3	−0.00	0.00	0.00	1.00
s(Power).4	0.00	0.00	0.00	0.99
s(Power).5	−0.00	0.00	0.00	1.00
s(Power).6	0.00	0.00	0.00	0.99
s(Power).7	−0.00	0.00	0.00	0.99
s(Power).8	0.00	0.00	0.00	0.99
s(Power).9	0.06	0.04	1.64	0.10
s(DEC).1	−0.08	0.07	1.31	0.19
s(DEC).2	−0.08	0.12	0.69	0.49
s(DEC).3	−0.03	0.05	0.65	0.51
s(DEC).4	−0.03	0.06	0.44	0.66
s(DEC).5	−0.01	0.04	0.33	0.74
s(DEC).6	0.02	0.05	0.32	0.75
s(DEC).7	0.02	0.04	0.45	0.66
s(DEC).8	−0.09	0.15	0.62	0.54
s(DEC).9	0.15	0.05	2.86	0.00
s(DRYMIXED).1	0.00	0.00	0.00	0.99
s(DRYMIXED).2	−0.00	0.00	0.00	0.99
s(DRYMIXED).3	0.00	0.00	0.00	0.99
s(DRYMIXED).4	0.00	0.00	0.00	0.99
s(DRYMIXED).5	0.00	0.00	0.00	0.99
s(DRYMIXED).6	−0.00	0.00	0.00	0.99
s(DRYMIXED).7	−0.00	0.00	0.00	0.99
s(DRYMIXED).8	−0.00	0.00	0.00	0.99
s(DRYMIXED).9	−0.01	0.01	0.66	0.51
s(CON).1	−0.00	0.00	0.00	0.99
s(CON).2	−0.00	0.00	0.00	0.99
s(CON).3	−0.00	0.00	0.00	0.99
s(CON).4	−0.00	0.00	0.00	0.99
s(CON).5	−0.00	0.00	0.00	0.99
s(CON).6	0.00	0.00	0.00	0.99
s(CON).7	0.00	0.00	0.00	0.99
s(CON).8	0.00	0.00	0.00	0.99
s(CON).9	0.07	0.02	4.42	0.00
Corridor	0.32	0.09	3.69	0.00
Perforated	0.18	0.06	2.99	0.00
Edge	0.06	0.05	1.21	0.23
Non-Forest	0.29	0.04	7.31	0.00

References

Ball, J. P., Nordengren, C., & Wallin, K. (2001). Partial migration by large ungulates: Characteristics of seasonal moose *Alces alces* ranges in northern Sweden. *Wildlife Biology*, 7, 39–47.

Bartón, K. (2012). *MuMIn package: Model selection and model averaging based on information criteria*. Available from http://cran.r-project.org/

Berger, J. (2007). Fear, human shields and the redistribution of prey and predators in protected areas. *Biology Letters*, 3, 620–623.

Bergström, R., & Danell, K. (2009). Mer vilt i dag än för 50 år sedan [More wildlife today than 50 years ago]. *Vilt och fisk fakta*, 2009, 4.

Bjorheden, R. (2007). Possible effects of the hurricane Gudrun on the regional Swedish forest energy supply. *Biomass & Bioenergy*, 31, 617–622.

Bjørneraas, K., Solberg, E., Herfindal, I., Van Moorter, B., Rolandsen, C. M., Tremblay, J. P., et al. (2011). Moose *Alces alces* habitat use at multiple temporal scales in a human-altered landscape. *Wildlife Biology*, 17, 44–54.

Bowman, J., Ray, J. C., Magoun, A. J., Johnson, D. S., & Dawson, F. N. (2010). Roads, logging, and the large-mammal community of an eastern Canadian boreal forest. *Canadian Journal of Zoology*, 88, 454–467.

Brown, J. S., & Kotler, B. P. (2007). Foraging and the ecology of fear. In D. W. Stephens, J. S. Brown, & R. C. Ydenberg (Eds.), *Foraging: Behavior and ecology* (pp. 437–480). Chicago & London: University of Chicago Press.

Bruggeman, J. E., Garrott, R. A., White, P. J., Watson, F. G. R., & Wallen, R. (2007). Covariates affecting spatial variability in bison travel behavior in Yellowstone National Park. *Ecological Applications*, 17, 1411–1423.

Bunnefeld, N., Borger, L., Van Moorter, B., Rolandsen, C., Dettki, H., Solberg, E. J., et al. (2011). A model-driven approach to quantify migration patterns: Individual, regional and yearly differences. *Journal of Animal Ecology*, 80, 466–476.

Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multi-model inference: A practical information-theoretic approach*. New York: Springer-Verlag.

Calenge, C. (2007). Exploring habitat selection by wildlife with adehabitat. *Journal of Statistical Software*, 22(6).

Coulon, A., Morellet, N., Goulard, M., Cargnelutti, B., Angibault, J.-M., & Hewison, A. J. M. (2008). Inferring the effects of landscape structure on roe deer (*Capreolus capreolus*) movements using a step selection function. *Landscape Ecology*, 23, 603–615.

Crawly, M. J. (2007). *The R book*. England: John Wiley and Sons.

Cushman, S. A., Raphael, M. G., Ruggiero, L. F., Shirk, A. S., Wasserman, T. N., & O'Doherty, E. C. (2011). Limiting factors and landscape connectivity: The American marten in the Rocky Mountains. *Landscape Ecology*, 26, 1137–1149.

Dussault, C., Ouellet, J.-P., Laurian, C., Courtois, R., Poulin, M., & Breton, L. (2007). Moose movement rates along highways and crossing probability models. *Journal of Wildlife Management*, 71, 2338–2345.

Eldegard, K., Lyngved, J. T., & Hjeldjord, O. (2012). Coping in a human-dominated landscape: Trade-off between foraging and keeping away from roads by moose (*Alces alces*). *European Journal of Wildlife Research*, 58, 969–979.

Ericsson, G., & Wallin, K. (2001). Age-specific moose *Alces alces* mortality in a predator-free environment: Evidence for senescence in females. *Ecoscience*, 8, 157–163.

Forester, J. D., Ives, A. R., Turner, M. G., Anderson, D. P., Fortin, D., Beyer, H. L., et al. (2007). State-space models link elk movement patterns to landscape characteristics in Yellowstone National Park. *Ecological Monographs*, 77, 285–299.

Forman, R. T. T., & Alexander, L. E. (1998). Roads and their major ecological effects. *Annual Review of Ecology and Systematics*, 29, 207–231.

Frid, A., & Dill, L. (2002). Human-caused disturbance stimuli as a form of predation risk. *Conservation Ecology*, 6, 11.

Godvik, I. M. R., Loe, L. E., Vik, J. O., Veiberg, V., Langvatn, R., & Mysterud, A. (2009). Temporal scales, trade-offs, and functional responses in red deer habitat selection. *Ecology*, 90, 699–710.

Harrell, F. (2009). *Design package: Variance inflation factor as of collinearity*. Available from http://cran.r-project.org/

Hawbaker, T. J., Radeloff, V. C., Clayton, M. K., Hammer, R. B., & Gonzalez-Abraham, C. E. (2006). Road development, housing growth, and landscape fragmentation in Northern Wisconsin: 1937–1999. *Ecological Applications*, 16, 1222–1237.

Ingold, P. (2005). (*Recreational activities in the habitat of the Alpine animals*) Freizeitaktivitäten im Lebensraum der Alpentiere. Switzerland: Haupt Publisher.

Jiang, G., Ma, J., Zhang, M., & Stott, P. (2009). Multiple spatial-scale resource selection function models in relation to human disturbance for moose in northeastern China. *Ecological Research*, 24, 423–440.

Jiang, G., Ma, J., Zhang, M., & Stott, P. (2010). Multi-scale foraging habitat use and interactions by sympatric cervids in northeastern China. *Journal of Wildlife Management*, 74, 678–689.

Kreeger, T. J., & Arnemo, J. M. (2007). *Handbook of wildlife chemical immobilization*. Wyoming, USA: Terry J Kreeger.

Kuemmerle, T., Perzanowski, K., Chaskovskyy, O., Ostapowicz, K., Halada, L., Bashta, A.-T., et al. (2010). European Bison habitat in the Carpathian Mountains. *Biological Conservation*, 143, 908–916.

Laurian, C., Dussault, C., Ouellet, J.-P., Courtois, R., Poulin, M., & Breton, L. (2008). Behavior of moose relative to a road network. *Journal of Wildlife Management*, 72, 1550–1557.

Lavsund, S., Nygrén, T., & Solberg, E. J. (2003). Status of moose populations and challenges to moose management in Fennoscandia. *Alces*, 39, 109–130.

Leblond, M., Dussault, C., & Quellet, J. P. (2010). What drives fine-scale movements of large herbivores? A case study using moose. *Ecography*, 33, 1102–1112.

Lottker, P., Rummel, A., Traube, M., Stache, A., Sustr, P., Muller, J., et al. (2009). New possibilities of observing animal behaviour from a distance using activity sensors in GPS-collars: An attempt to calibrate remotely collected activity data with direct behavioural observations in red deer *Cervus elaphus*. *Wildlife Biology*, 15, 425–434.

Lykkja, O. N., Solberg, E. J., Herfindal, I., Wright, J., Rolandsen, C. M., & Hanssen, M. G. (2009). The effects of human activity on summer habitat use by moose. *Alces*, 45, 109–124.

Martin, J., Basille, M., Van Moorter, B., Kindberg, J., Allaine, D., & Swenson, J. E. (2010). Coping with human disturbance: Spatial and temporal tactics of the brown bears (*Ursus arctos*). *Canadian Journal of Zoology*, 88, 875–883.

Muggeo, V. M. R. (2007). *Segmented package: Segmented relationships in regression models*. Available from http://cran.r-project.org/

Neumann, W. (2009). *Moose Alces alces behaviour related to human activity*. PhD thesis, Swedish University of Agricultural Sciences, p. 64.

Neumann, W., Ericsson, G., & Dettki, H. (2009). The non-impact of hunting on moose *Alces alces* movement, diurnal activity, and activity range. *European Journal of Wildlife Research*, 55, 255–265.

Neumann, W., Ericsson, G., Dettki, H., Bunnefeld, N., Keuler, N. S., Helmers, D. P., et al. (2012). Difference in spatiotemporal patterns of wildlife road-crossings and wildlife-vehicle collisions. *Biological Conservation*, 145, 70–78.

Olsson, M., Cox, J. J., Larkin, J. L., Widen, P., & Olovsson, A. (2011). Space and habitat use of moose in southwestern Sweden. *European Journal of Wildlife Research*, 57, 241–249.

Persson, E. (2003). Transmission line corridors as habitat for large herbivores. Exam work. *Swedish University of Agricultural Sciences*, 96, 27.

Pinheiro, J. C., & Bates, D. M. (2000). *Mixed effects models in S and S-Plus*. New York: Springer-Verlag.

R Development Core Team. (2012). *R: A language and environment for statistical computing*. Available from http://cran.r-project.org/

Raab, B., & Vedin, H. (1995). *National atlas of Sweden. Climate, lakes and rivers*. Stockholm: Almqvist & Wiksell International.

Rea, R. V., Child, K. N., Spata, D. P., & MacDonald, D. (2010). Road and rail side vegetation management implications of habitat use by moose relative to brush cutting season. *Environmental Management*, 46, 101–109.

Ribeiro, P. J., Jr., & Diggle, P. J. (2001). *GeoR package: A package for geostatistical analysis*. Available from R-NEWS, ISSN 1609-3631.

Rivrud, I. M., Loe, L. E., & Mysterud, A. (2010). How does local weather predict red deer home range size at different temporal scales? *Journal of Animal Ecology*, 79, 1280–1295.

Roever, C. L., Boyce, M. S., & Stenhouse, G. B. (2010). Grizzly bear movement relative to roads: Application of step selection functions. *Ecography*, 33, 1113–1122.

Schneider, R. R., & Wasel, S. (2000). The effect of human settlement on the density of moose in northern Alberta. *Journal of Wildlife Management*, 64, 513–520.

Singh, N. J., Borger, L., Dettki, H., Bunnefeld, N., & Ericsson, G. (2012). From migration to nomadism: Movement variability in a northern ungulate across its latitudinal range. *Ecological Applications*, 22, 2007–2020.

Stankowich, T. (2008). Ungulate flight responses to human disturbance. A review and meta-analysis. *Biological Conservation*, 141, 2159–2173.

Stedman, R., Diefenbach, D. R., Swope, C. B., Finley, J. C., Luloff, A. E., Zinn, H. C., et al. (2004). Integrating wildlife and human-dimensions research methods to study hunters. *Journal of Wildlife Management*, 68, 762–773.

Swedish Land Survey. (2010). *Digital data maps of land cover, elevation and infrastructure*. Available from www.lantmateriet.se

Van Ballenberghe, V., & Miquelle, D. G. (1990). Activity of moose during spring and summer in interior Alaska, USA. *Journal of Wildlife Management*, 54, 391–396.

Vistnes, I., & Nellemann, C. (2008). The matter of spatial and temporal scales: A review of reindeer and caribou response to human activity. *Polar Biology*, 31, 399–407.

Vogt, P., Riitters, K. H., Estreguil, C., Kozak, J., Wade, T. G., & Wickham, J. D. (2007). Mapping spatial patterns with morphological image processing. *Landscape Ecology*, 22, 171–177.

Wood, S. (2006). *Generalized additive models – An introduction with R*. USA: Chapman and Hall/CRC.

WRAM. (2010). *WRAM 2011. Wireless Remote Animal Monitoring (WRAM)*. http://www.slu.se/WRAM/ (last accessed: 21.08.10).