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Differential barrier and corridor effects of power lines, roads and rivers on moose (*Alces alces*) movements

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Abstract. Building new power lines is required to satisfy increasing demands for the transmission of electricity, and at the same time the road network is expanding. To provide guidelines for the routing of new power lines and roads, it is essential to test whether linear features deter or attract movements of animals in different landscape settings. Using GPS relocation data from 151 moose (*Alces alces* L.) in central Norway, we tested for barrier and corridor effects of roads, power lines and rivers and accounted for forest cover, the topographical orientation of linear features and the placement of other nearby linear features. We predicted step selection probabilities for different movement options at varying distances from linear features and linear feature combinations. Barrier and corridor effects of linear features altered moose movements, although effects were minor compared to the effects of topography and forest cover. Moose did not avoid crossing power lines, unless the placement of power lines along contour lines impeded movements across them. In contrast, moose avoided crossing of roads and rivers in forests. Moose more likely moved along linear features when getting closer to linear features. Barrier and corridor effects were higher for road/river combinations compared to single linear features. Likewise, the barrier and corridor effects were higher for road/power line combinations, but not power line/river combinations compared to single linear features, when moose were close to the edge of those features. The inconsistent pattern could be due to the low sample size. We found indications of higher disturbance potential of roads compared to power lines and rivers. Managing vegetation in power line rights-of-way to provide abundant browse could counteract possible disturbance, while wildlife overpasses could mitigate road fragmentation effects.

Key words: *Alces alces*; barrier; corridor; moose; movement; Norway; power lines; rivers; roads; step selection function.

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Introduction

Building new power lines is required to transport the increasing electricity produced by renewable energy sources (REN21 2013), at the same time as the road network is expanding (The World Bank 2012). Investments of 70 billion € in Europe (European Commission 2011) and ~4.5 billion € (40 billion NOK) in Norway alone (Statnett SF 2010) are expected to be necessary for onshore electricity transmission systems until 2020. In Norway, circa 200–300 km of new power lines will be constructed per year until 2020 (Statnett SF 2010). Road densities have been increasing in 70% of countries with road density data available between 2005 and 2010 (The World Bank 2012). To provide guidelines for the routing of new power lines and roads, it is essential to test whether linear features deter or attract movements of animals. These effects may be influenced by their disturbance potential, the surrounding landscape and other linear features in the same area.

Allowing movement of animals among fragments is important to maintain overall population productivity in fragmented landscapes (Pulliam 1988, Burkey 1989, Dias 1996), which may otherwise decline due to environmental and demographic stochasticity, and genetic effects in local sub-populations (Lacy and Lindenmayer 1995). Wide-ranging ungulates can in particular be expected to be vulnerable to fragmentation of their habitat (Bartzke et al. 2014). Migratory ungulate movements may enhance production of offspring (Rolandsen et al. 2012), possibly facilitated by seasonal use of habitats (Bjørneraas et al. 2011). Moreover, increasing area use through movements may compensate for reduced resources caused by habitat loss, such as decreased food availability (van Beest et al. 2011) and habitat productivity (Bjørneraas et al. 2012).

Roads, power lines and water bodies such as canals and rivers may potentially act as barriers (Joyal et al. 1984, Vistnes et al. 2004, Epps et al. 2005, Laurian et al. 2008) or corridors (Brown et al. 2006, Latham et al. 2011) for movements. Ungulates may be less likely to use or move through areas with high development of human infrastructure (Nellemann et al. 2003, Vistnes et al. 2004, Sawyer et al. 2012), and ungulate migrations have been reported to decline globally along with increasing human encroachment (Harris et al. 2009). Curatolo and Murphy (2002) found that caribou (*Rangifer tarandus* L.) avoided crossing pipelines paralleled with roads but did not avoid crossing single pipelines or roads. This raises the question if we should avoid building new power lines and roads along existing linear features because it could make such barriers less permeable. Alternatively, this may be a good strategy as it avoids splitting remaining habitat fragments into smaller pieces.

Animals may move along linear features because: (1) they avoid crossing them (Vanak et al. 2010), (2) linear features are aligned along preferred travel routes (Kie et al. 2005, Bruggeman et al. 2007), (3) animals find favorable foraging or cover habitats along linear features (Dusek et al. 1989, Eldegard et al. 2012, Bartzke et al. 2014) or (4) reduced snow cover along linear features facilitates easy travel in winter (Collins and Helm 1997). However, while power lines, roads and rivers all tend to follow lower elevation ranges and provide foraging opportunities along edges (Mould 1979, Ricard and Doucet 1999, Rea 2003), they may have different disturbance potential (Flydal et al. 2009, Montgomery et al. 2012). Rivers may for instance impede ungulate movements because of the physical constraints to overcome such features (Coulon et al. 2006), but rivers should not be disturbing.

Barrier and corridor effects could also result in a concentration of animals near linear features. As a consequence, accumulation of ungulates near linear features may have societal and economic impacts through increased ungulate-vehicle collisions on roads (Seiler 2005, Kenneth 2007), forest damage due to high browsing pressure (Storaas et al. 2001, Edenius et al. 2002), but also reduced need for power line rights-of-way (ROW) clearing and higher sales of hunting licenses (Storaas et al. 2001).

In this study, we compared differential barrier and corridor effects of power lines, roads and rivers on the movements of a large herbivore, the moose (*Alces alces* L.), and tested if the placement of different linear features in the same area altered crossing ability and travel direction. We selected moose in Norway as our model species for ungulates (e.g., red deer *Cervus elaphus* L., roe deer *Capreolus capreolus* L.) because moose move over large areas (Bunnefeld et al. 2011, Bjørneraas et al. 2012) and are therefore likely to encounter such features in isolation and in combination with each other in different landscape settings. We also had an extensive dataset available for this species. The willingness of moose to cross roads and power lines may be influenced by the surrounding forest cover (Forman et al. 2003), the disturbance caused by road traffic (Alexander et al. 2005) or the noise and visual distraction of power lines (Flydal et al. 2010). We included rivers for comparison with anthropogenic features, and because roads are often routed along rivers.

Based on the known reluctance of moose to cross roads (Dussault et al. 2007, Laurian et al. 2008, Beyer et al. 2013), as well as the potential disturbance effect of power lines and movement constraints of rivers, we hypothesized that moose

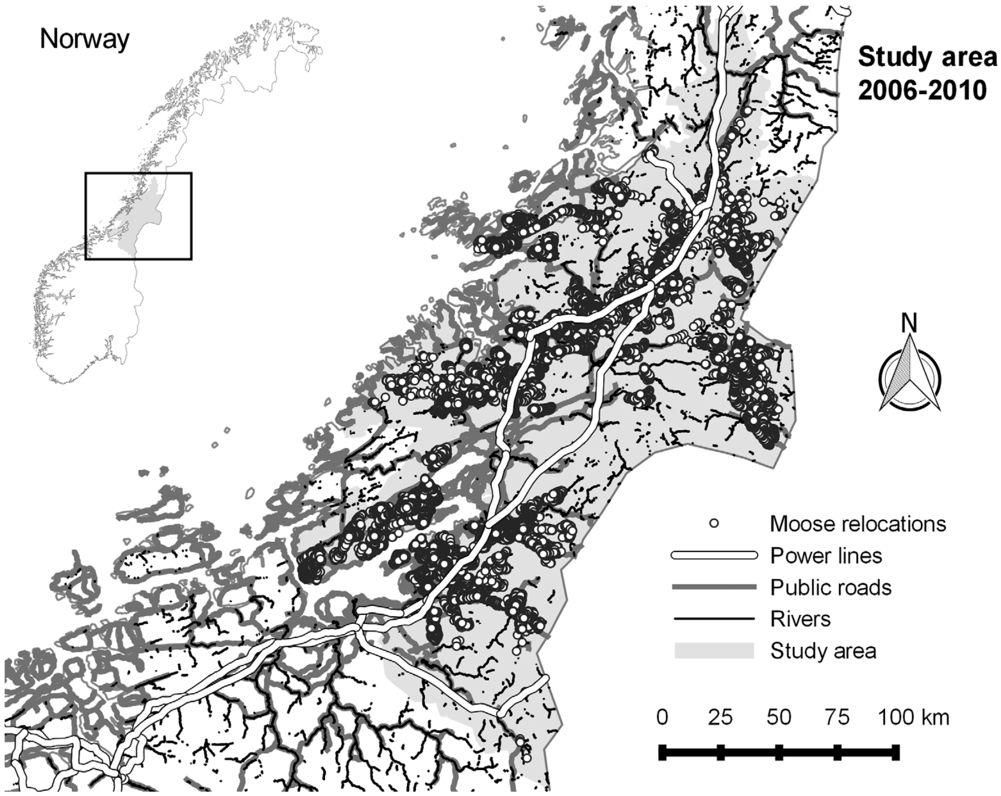

Fig. 1. Study area in the county of Nord-Trøndelag, central Norway. GPS relocation data (2006–2010) of 151 moose (circles) was used to study corridor and barrier effects of power lines (double line), roads (thick grey lines) and rivers (thin grey lines) as well as linear feature combinations on moose movements.

would show reluctance to cross central-grid power lines, roads and rivers, and that these features would rather channel moose movement through the landscape. Among the three features, we predicted power lines to have the least barrier and corridor effects because they provide browsing opportunities and can be easily traversed (P1). Conversely, roads were predicted to have the largest effects because of the disturbance through traffic and other human activity (P2). We predicted combinations of linear features to reduce the probability of crossing and increase the corridor effect even further than for single linear features because of the cumulative barrier effects (P3).

Methods

Study area

The study area (64°30′ N, 12°50′ E, 28,500 km^2) was situated in the county of Nord-Trøndelag and adjacent municipalities in central Norway (Fig. 1). The study area is dominated by spruce forest interspersed with mire, agriculture at lower elevations and open alpine areas. The elevation ranges from the coast to 1,760 m above sea level (asl). Moose can be found throughout the entire area outside urban settlements and below the climatic tree line (at on average 600 m asl; Moen et al. 1999).

We extracted and merged all public roads, i.e., highways, national roads, county roads and municipal roads, from a road database (Norwegian Mapping Authority 2012*b*) regardless of traffic intensity. The Norwegian central grid operator Statnett provided routing data of power lines. A clear-felled corridor with a width of 32–38 m, typical for voltages between 220 and 420 kV (Bevanger and Thingstad 1988), surrounded these power lines. We retrieved major rivers from polygon maps from the Norwegian Water Resources and Energy Directorate (2011) and

Table 1. Count of individual moose with midpoint distances of steps below 2 km from different linear features, as well as those that crossed or were found within respectively 500 m and 25 m from the respective linear feature in central Norway.

Type	$N_{<2000}$	$N_{<500}$	$N_{<25}$
Roads	145	136	114
Power lines	51	47	44
Rivers	127	125	101

removed inflows and lakes by clipping river polylines with river polygons from land cover maps (Norwegian Mapping Authority 2012*a*). In total, 5,113 km roads, 770 km central-grid power lines and 2,658 km rivers were traversing potential moose ranges, i.e., outside urban settlements and below 600 m elevation, in the study area.

The average elevation of roads (131 m ± 131 SD), central-grid power lines (284 m ± 136 SD) and rivers (229 m ± 167 SD) was below the average elevation of the study area (322 m ± 165 SD), i.e., the potential moose ranges. There were also 1,184 km of low voltage power lines in the area (Norwegian Water Resources and Energy Directorate), but they were not included because of inaccurate routing data. These low-voltage power lines were on average 1.0 (±1.2) km away from roads and 2.3 (±2.4) km away from rivers.

Moose data

In total 169 moose were captured between February 2006 and March 2008 and equipped with GPS collars of the types GPS PLUS/GPS Pro Light (Vectronic Aerospace, Germany) and GPS Tellus (Followit Lindesberg AB, former Televilt, Sweden). This was done as a part of a moose field research project aiming to increase the knowledge of moose ecology in the study area and to strengthen the basis for local and regional moose management (Rolandsen et al. 2010). We then followed the movement of each animal over various time spans (depending on battery life and collar/radio durability) to the end of 2010. Erroneous relocations were removed by employing the method of Bjørneraas et al. (2010). Only relocations were included in the analyses that were on Norwegian mainland further than five kilometers away from the Swedish border to minimize influence of unknown features outside Norway as well as restricted of movements on islands. To minimize bias following capture and to standardize the analysis only individuals with at least 1,000 relocations in hourly intervals were included, whereby only steps of more than 10 m length were considered to represent movements.

Previously, Bartzke et al. (2014) used the same dataset to analyze step selection towards roads and power lines following Fortin et al. (2005). In that study, we matched five random movement steps, generated from the empirical distribution of step lengths and turning angles, to each observed moose movement step (i.e., choice set). Here, we used the same dataset and selected all choice sets containing steps that ended at least 2.5 km away from urban settlements to minimize the influence of human activity close to linear features. We further selected choice sets containing steps with midpoint distances below 2 km from any linear feature assuming that moose do not respond to the features beyond this distance. Moose response distances to roads reported by Laurian et al. (2008) (500 m), Laurian et al. (2012) (100–250 m) and Bartzke et al. (2014) (1000 m) indicate that this assumption is reasonable. Since only two observed steps crossed three different linear features at the same time we removed choice sets of steps containing such crossings. After selection, 151 individuals remained for analysis with on average 3,120 (±2,356 SD) steps per individual. Moose relocations used to derive movement steps were found at on average 258 (±148 SD) m asl. Most individuals (79–86%) within 2 km from the nearest linear feature were also found at least once less than 25 m from or crossed the respective feature. Less than 10% of the selected individuals never crossed the respective linear feature or entered a buffer below 500 m from that feature (Table 1).

Candidate models and covariates

We started with a "Basic model", including forest to account for moose's known preference for forest (Bjørneraas et al. 2011, Bjørneraas et al. 2012), elevation to account for avoidance of alpine areas and lowland agricultural areas outside the growing season (Bjørneraas et al. 2011), and distance in interaction with the closest linear feature type to separate between responses towards or away from different linear features. Steps where more than half of the step lengths fell within the forest map from the Norwegian Forest and Landscape Institute (Gjertsen 2007), converted into 30×30 m raster, were considered to traverse forest. Elevation at the end point of movement steps was derived from a 25×25 m DEM raster. Distances to different linear features at the midpoint of movement steps were derived from 10×10 m distance rasters created in ArcGIS 10 (ESRI 2011). We included quadratic terms for elevation and distance as we expected non-linear effects in these (Fortin et al. 2005, Laurian et al. 2012, Bartzke et al. 2014). We also included the maximum elevation difference along steps, because we anticipated that moose avoid moving across terrain with altering elevation to save energy (Parker et al. 1984). To reduce bias in step selection due to the distance moved (Hjermann 2000), we followed the suggestion of Forester et al. (2009) and included step length as a covariate (also see May et al. 2010). Longer steps more likely cross linear features (Eftestøl et al. 2014) and can induce stronger changes in selection. By including step length as a covariate we account for changes in movement activity that may influence selection through factors like habitat, time of the day or season.

We then developed three additional candidate models defined as the Basic model plus barrier or corridor effects, or both. We defined barrier effects as the reluctance by moose to cross linear features. Likewise, corridor effects were preferences for moving along linear features over moving away or towards them. We expected the willingness of moose to cross or move along linear features to vary with distance to linear features, forest, and the topographical orientation of linear features, and assigned these covariates to steps. Linear features were considered crossed when steps intersected one or two linear features. We added crossings of different linear feature types, including their interactions with forest, distance to linear features and the orientation of linear features along contour lines ("Barrier model"). Orientation along (versus across) contour lines was defined as the angle between crossed linear feature(s) and closest elevation contour line segment below 45°. Acute segment angles were calculated by splitting linear features and elevation contour lines within 1 km from linear features into 25 m long segments in Secondo (Secondo Team, Department of Computer Science, FernUniversität Hagen, Hagen, North Rhine-Westphalia, Germany). Because less than 250 observed steps crossed several linear features with one movement step, we disregarded interactions with these types of crossing. We developed a "Corridor model" including movement orientation (moving along versus towards/away from linear features), and with the same interactions as the Barrier model. Movement along linear features was defined as acute angles between feature segment and movement step below 45°. Two linear feature segments were considered combined when they were less than 250 m apart (length weighted mean (H. L. Beyer, *available online:* http://www.spatialecology.com/gme/isectlinerst.htm) with an acute angle of less than 45°. Finally, we combined all three models into a "Combined model" including besides the Basic model also barrier and corridor effects and their interactions. We made no explicit distinction between movements towards or away from linear features, but accounted for such movements by including distance to linear features as a covariate in all statistical models. Step selection for or against distance to linear feature indicates whether moose preferred to approach (negative selection for distance) or move away (positive selection for distance). Such effects may become stronger with decreasing distances to linear features.

Modelling approach and model predictions

To determine if moose step selection is best explained by barrier, corridor, a combination of both or neither of these effects, we compared model parsimony of the candidate models from QIC (quasi-likelihood under independence criterion) values. QIC values are similar to AIC values (Akaike 1973) and decline with parsimony (Craiu et al. 2008). QIC were used because we accounted for temporal autocorrelation among steps by clustering steps over individuals (Fortin et al. 2005). We checked whether individuals were moving independently of each other by calculating for each individual the percentage of its steps within a range of 500 m and three hours to each one of the other individuals. This percentage was less than three for all individuals, except 15 individuals that were up to 16% within the given distance and time to one of the other individuals.

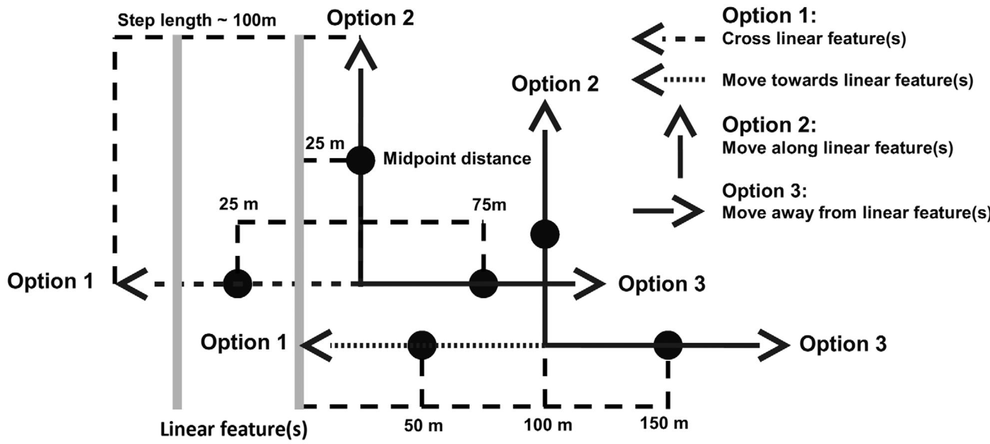

Fig. 2. Moose movement options in response to linear features. The probability of crossing linear feature(s) (upper double line) over moving along (thin lines) or away from (thick line) linear feature(s) were predicted for situations when moose were in close enough proximity to cross linear features (25 m, close to the edge), assuming a step length of 100 m. At further distances (≥100 m) the three possible options were moving towards (lower double line), along (thin lines) or away from (thick lines) linear features without the option to cross linear features.

To find out if crossing probabilities of rivers could have been influenced by ice cover, we also applied the top-ranking model to a dataset excluding the coldest period January-March. We applied an equivalent model but excluding effects of linear feature combinations to a dataset of that period. All statistical analyses were done in R version 3.1.0 (R Development Core Team 2014). We used a cox proportional hazard model (cph) from the R-package rms version 4.2-0 (Harrell 2014) to model step selection probabilities (Supplement).

From the most parsimonious model we predicted step selection probabilities following Manly et al. (2002):

$$P_{ij} = \frac{\exp(\beta_1 \times x_{ij1} + \beta_2 \times x_{ij2} + \ldots + \beta_p \times x_{ijp})}{\sum_{j=1}^{3} \exp(\beta_1 \times x_{ij1} + \beta_2 \times x_{ij2} + \ldots + \beta_p \times x_{ijp})}. \quad (1)$$

Step selection probability is the probability of selecting movement step j at the ith choice over three alternative movement steps dependent on the coefficients β_p and the environmental variable x_{ijp}. The alternative movement options which moose were assumed to select from near the edge of linear features (25 m distance) were crossing, moving along, or moving away from linear features (Fig. 2). At distances of at least 100 m from linear features, the alternatives were moving along, towards or moving away from linear features, but not the option of crossing linear features (Fig. 2). We assumed a step length of 100 m, which is approximately the mean step length of observed movement steps (99 m ± 179 SD), and adjusted distances to linear features accordingly (Fig. 2). We assumed angles of 0 degrees between steps and linear features for movements along those features. Angles of 90 degrees were assumed for steps that crossed, moved towards or away from linear features (Fig. 2).

We predicted step selection probabilities for movements along linear features irrespective of the direction in which animals could move along linear features. If animals were moving randomly, the probability of choosing one of three movement options would be 0.33, providing that other variables along steps are equal. We kept step length, forest cover, elevation and maximum elevation difference along steps at equal values for the three movement options. We defined avoidance or attraction to be a step selection probability below or above 0.33.

Results

Model selection

The most parsimonious model explaining moose step selection included the effects of

Table 2. Predicted step selection probabilities (P) from Eq. 1 and sample size (n_o/n_r) for moose crossing, moving along or away from roads (Rd), power lines (Pl), rivers (Ri) in response to forest versus open habitat and the alignment of linear features along contour lines in central Norway.

	Crossing			Moving along			Moving away†		
Statistics	Rd	Pl	Ri	Rd	Pl	Ri	Rd	Pl	Ri
Forest habitat									
Not aligned to contours									
P	0.23	0.35	0.26	0.39	0.33	0.37	0.38	0.33	0.37
n_o	374	567	290	23,606	7,104	12,966	22,401	7,235	12,257
n_r	2,327	2,014	1,482	56,608	18,504	30,674	51,538	16,418	27,997
Aligned to contours									
P	0.22	0.26	0.23	0.40	0.39	0.39	0.38	0.35	0.37
n_o	1,409	606	1,207	84,778	11,395	62,713	76,068	9,512	56,086
n_r	10,059	2,969	7,021	171,475	25,084	124,626	165,632	22,947	121,577
Open habitat									
Not aligned to contours									
P	0.37	0.39	0.34	0.32	0.30	0.33	0.32	0.31	0.33
n_o	374	13	86	2,536	198	1,238	2,454	181	1,192
n_r	1,265	57	348	8,605	921	4,274	7,781	829	4,033
Aligned to contours									
P	0.35	0.30	0.31	0.33	0.36	0.35	0.32	0.34	0.34
n_o	764	14	230	6,740	403	4,420	6,098	384	3,878
n_r	3,161	84	977	21,195	1,551	13,107	19,900	1,577	12,957

Notes: Predictions were made from the Combined model (Appendix A) testing for the effects of environmental variables as well as barrier and corridor effects of linear features on step selection of 151 moose using GPS relocation data. A step selection probability below 0.33 indicates avoidance. The sample sizes are choice sets containing different types of observed (n_o)/random (n_r) movement steps.

† The sample sizes (n_o/n_r) are choice sets containing steps towards or away from linear features without crossing or moving along them.

distance to linear features, as well as barrier and corridor effects (the Combined model: QIC = 1,674,272). Although the other three models all had ΔQIC values >2, the difference in parsimony between the Combined model and the Barrier model was smallest (ΔQIC = 136) compared to the Corridor (ΔQIC = 1,417) or Basic model (ΔQIC = 1,649).

Significance of selected variables

In general, moose avoided crossing linear features and linear feature combinations ($P < 0.05$), except for power lines and power line/river combinations, while they preferred moving along roads and road/river combinations ($P < 0.05$). Moose avoided steps towards linear features and more so when the closest linear feature was a road, indicated by a significant interaction of distance and roads. Apart from the effects of linear features, moose avoided steps traversing predominantly open habitats and steps along relatively steep terrain (elevation difference) ($P < 0.001$). Moreover, they avoided low elevations ($P < 0.001$) that were probably associated with high human activity. The full model is listed in Appendix A.

Predictions of crossing versus other movements in close proximity to linear features

A deviation from a step selection probability of 0.33 in Tables 2 and 3 indicates that those movement steps were non-random and influenced by linear features. In forests, moose avoided crossing roads and rivers. Instead they preferred to move along or away from these linear features in forest. Moose avoided crossing and preferred moving along power lines in forests when those were aligned along contour lines. In open habitat when linear features were aligned along the contour lines, moose seemingly preferred to cross roads, while they moved along power lines and rivers. When not aligned along contour lines, moose crossed linear features in open habitat. Moose less likely crossed and more likely moved along or away from road/power line and road/river combinations compared to single linear features (Table 3). In contrast, moose most likely crossed and least likely moved along power line/river combinations (Table 3). During winter, moose more likely crossed roads in open habitat compared to the rest of the year (Tables B1 and B3 in Appendix B). Moose refrained more from crossing power lines during winter in open

Table 3. Predicted step selection probabilities (P) from Eq. 1 and sample size (n_o/n_r) for moose crossing, moving along or away from combinations of roads (Rd), power lines (Pl) and rivers (Ri) in central Norway.

	Crossing			Moving along			Moving away†		
Statistics	Rd/Ri	Rd/Pl	Pl/Ri	Rd/Ri	Rd/Pl	Pl/Ri	Rd/Ri	Rd/Pl	Pl/Ri
P	0.10	0.14	0.44	0.47	0.43	0.29	0.44	0.43	0.27
n_o	139	16	85	26,549	105	1,103	22,672	87	985
n_r	2,319	85	280	51,521	268	2,228	49,296	214	2,092

Notes: Predictions were made from the Combined model (Appendix A) testing for the effects of environmental variables as well as barrier and corridor effects of linear features on step selection of 151 moose using GPS relocation data. A step selection probability below 0.33 indicates avoidance. The sample sizes are choice sets containing different types of observed (n_o)/random (n_r) movement steps. The feature in combinations assumed closest to steps is named first.

† The sample sizes are choice sets containing steps towards or away from linear feature combinations without crossing or moving along them.

habitat, especially when aligned along contour lines, rather preferring to move along them. In open habitats, moose were also less likely to cross rivers during winter compared to the rest of the year; they rather moved along or away from those.

Prediction of step selection probabilities with distance from linear features

Moose shifted from mostly moving towards linear features to moving along or away from linear features at distances below approximately 1 km, when linear features were not aligned along contour lines (Fig. 3A, C, E, G, I, K). Moose responded more strongly towards roads (Fig. 3A, C) and power lines (Fig. 3E, G) than rivers (Fig. 3I, K), indicated by the change in step selection probabilities with distance from linear features.

Among linear features, moving along power lines (Fig. 3E, G) was least preferred while moving along roads (Fig. 3A, C) was most preferred below approximately 1 km distance. Moving along power lines became the most likely movement option at approximately 100 m distance to power lines in forests, when power lines were not aligned along contour lines (Fig. 3E). Overall, moose more likely moved along linear features in forests and those aligned along contour lines (Fig. 3A–L).

Similar to single linear features, moose increased movements along and reduced movements towards linear feature combinations in their proximity (Fig. 4A–C). Movements along road/river combinations (Fig. 4A) and power line/river combinations (Fig. 4C) were overall more likely and extended over larger distances compared to single linear features (Fig. 3A–L).

Discussion

We analyzed movement preferences of 151 moose in central Norway and found differences in barrier and corridor effects between roads, power lines and rivers whilst accounting for forest cover, elevation and the topographical orientation of linear features. The comparison of candidate models indicated that both barrier and corridor effects of linear features affected moose movements, although the effects were minor compared to the effects of topography and forest cover. The comparatively small reduction in model parsimony when accounting for only crossing compared to both crossing and moving along linear features indicates that moose moved along linear features partly because they avoided crossing them.

Moose avoided crossing roads and rivers, but not power lines, hence only partly supporting our hypothesis. While the model predicted that moose avoided crossing of roads and rivers only in forests, previous studies have detected increased probabilities for road crossings (Dussault et al. 2007, Laurian et al. 2008) and accident with vehicles (Seiler 2005) in forests. This apparent contradiction, however, may be explained by a general preference of moose for forests, thus increasing the probability for crossing roads in forests, rather than a higher preference for crossing roads in forests itself. Possibly, the gap created by linear features in forests prevents moose from crossing them.

Browsing opportunities inside power line ROWs may have reduced the reluctance of moose to overcome these gaps. Similarly, Joyal et al. (1984) found that moose did not avoid

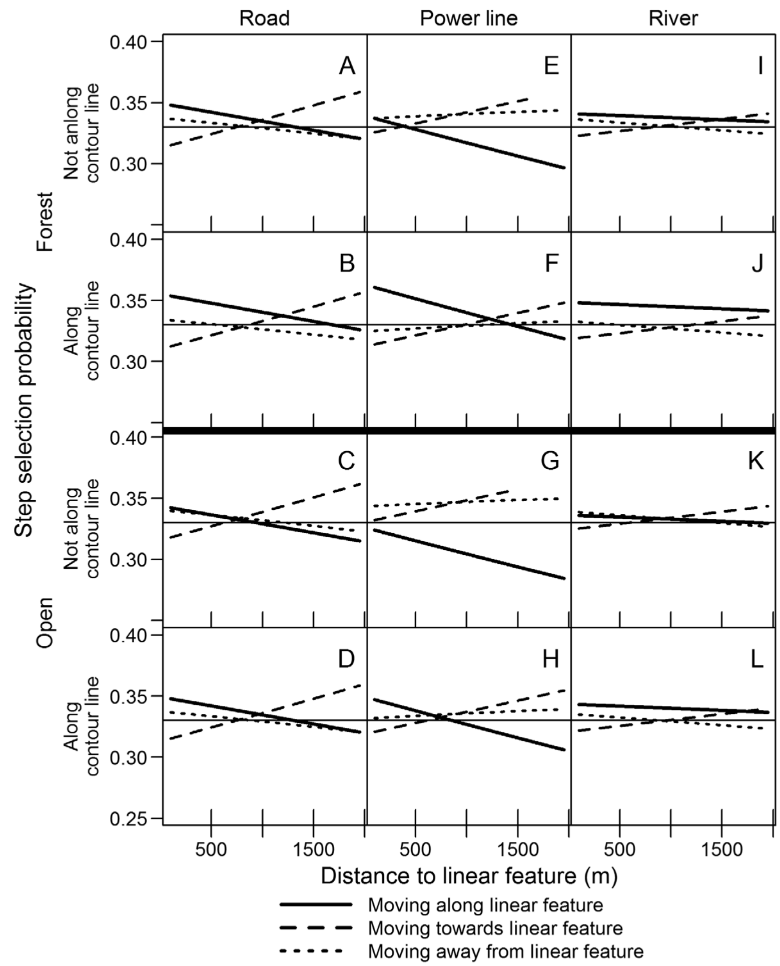

Fig. 3. Predicted step selection probabilities (Eq. 1) from a Combined model (Appendix A) for moose movements along (straight lines), towards (dashed lines) and away (dotted lines) from roads, power lines and rivers in relation to distance to linear features in central Norway. It was assumed that moose did not have the option to cross linear features at a distance equal or above 100 m from linear features. Predictions were made for movements in forests and open habitats and for situations when linear features were aligned along contour or not. A step selection probability below 0.33 indicates avoidance.

crossing power line ROWs of 90 m width. Avoidance of moving across terrain with varying elevation may explain why moose avoided crossing power lines when those were aligned along contour lines. Correspondingly, moose-vehicle collisions are less likely in areas with high variation in elevation (Seiler 2005).

Although the model predicted that moose did not avoid crossing linear features in open habitats, they were less likely to move towards them when being closer. This could prevent moose from even getting close enough to cross such features. Moose changed from moving towards power lines and roads at a distance above approximately 1 km, to moving away from or along such features at lower distances. As a result, moose may progressively abandon areas close to linear features. Similarly, Panzacchi et al. (2013) found that female reindeer (*Rangifer tarandus tarandus* L.) reduced area use below distances of 1 km from power lines and roads while Laurian et al. (2008) showed that moose home ranges increased with the density of roads inside, possibly because they compensated for reduced area use near roads.

Although power lines had the least barrier and

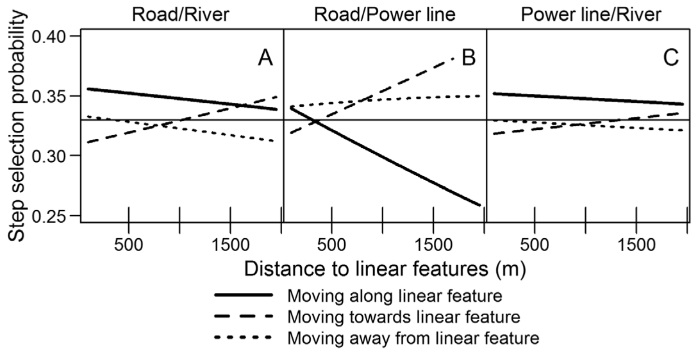

Fig. 4. Predicted step selection probabilities (Eq. 1) from a Combined model (Appendix A) for moose movements along (straight lines), towards (dashed lines) and away (dotted lines) from road/river, road/power line and power line/river combinations dependent on distance to the closest linear feature in central Norway. The description is identical to Fig. 3.

corridor effects when moose were in close proximity as described by P1, we cannot rule out a disturbance potential of power lines. Moose changed their movements more strongly with varying distances to power lines compared to rivers. Moose may have reacted to the power line structure or less preferred habitats surrounding power lines. The strongest effects were found near roads as described by P2, although other human activities close to roads could also have influenced this pattern (Lykkja et al. 2009).

Although most individuals came into close proximity to linear features, a few (2–9%) were never found closer than 500 m to linear features during the study period. If and how moose perceive linear features at a distance above 500 m can be discussed, although empirical findings do suggest an effect even at substantial distances from roads. For instance, moose responded to highways at distances up to 750 m in Canada (Laurian et al. 2012). Surprisingly, even larger response distances were reported for forest roads (Jiang et al. 2009, Laurian et al. 2012). In Sweden, moose moved faster only at distances below 125 m from roads, and not power lines (Neumann et al. 2013). Response distances of most other species towards roads were found to range from less than 100 m up to approximately 1 km (Forman et al. 2003: Fig. 11.6). Reindeer were suspected to be disturbed by roads (Forman et al. 2003: Fig. 11.6) and power lines (Vistnes and Nellemann 2001) up to distances of several kilometers.

Moose may also have responded to environmental variables other than linear features. Neither roads, rivers or power lines are randomly distributed in the landscape, but are typically found at lower elevations. Accordingly, most moose habitats may be found at elevations higher than the linear features, which could affect the daily movement of moose, e.g., if access to forage were higher at lower elevations due to higher primary production. The average elevation of power lines and rivers was similar to that of moose relocations, but roads were traversing lower areas. Hence, the tendency of moose to move towards roads at distances above 1 km could be due to better feeding conditions at lower elevations. Indeed, as the browsing pressure is also likely to be lower, higher supply of food may attract moose towards roads, particularly during low disturbance periods (e.g., the night; Lykkja et al. 2009).

We found increased barrier effects for simultaneous road/power line crossings and increased barrier and corridor effects in road/river combinations as described by P3. The predictions for linear feature combinations including power lines were however not consistent. Barrier and corridor effects increased for power line/road combinations, but the opposite was predicted by the model for power line/river combinations when moose were close to the edge of to those features. A possible reason could have been our inability to account for the topographical orientation of linear feature combinations and forest cover because of the low sample size.

Moreover, nearly 80% of power line/river crossings occurred at only one location by one individual. There was no spatial clustering for other power line/river crossings. Thus the high probability for simultaneous power line/river crossing does not necessarily reflect the general preference of the moose population in the study area. Incorporating the effects of lower-voltage power lines would have helped to clarify the effects of power lines in combination with other linear features, but unfortunately we had no access to accurate routing data for lower-voltage power lines.

Our results indicate that power lines do not pose barriers to moose movements. In contrast, Vistnes et al. (2004) concluded that power lines pose migration barriers to reindeer, although this conclusion has been challenged (Reimers et al. 2007). Being primarily adapted to forests, moose are reluctant to use open areas (Bjørneraas et al. 2011), but probably to lesser extents when gaps are small. The benefits of additional browsing resources in power line ROWs may also outweigh the disadvantage of removing forest cover and the possible disturbance of power lines to moose. Managing power line ROWs in a way that provides abundant browse could be the best strategy to reduce possible aversion and barrier effects (Joyal et al. 1984, Ricard and Doucet 1999).

Roads have a greater potential to reduce the access of moose to seasonal feeding and cover habitats (Seiler et al. 2003) and may pose constraints on reproduction (Rolandsen et al. 2012) and genetic diversity (Epps et al. 2005, Coulon et al. 2006). This study and the fact that about 4,000 moose per year are involved in traffic accidents in Norway (Rolandsen et al. 2011), however, indicates that roads do not block moose crossings entirely. Increasing the food availability in the proximity of roads is not recommended, as this may increase the risk of moose-vehicle collisions (Rea 2003, Rea et al. 2010). Making roads more penetrable, e.g., by creating over or under passes (Olsson and Widen 2008), may therefore be the only way of reducing the barrier and corridor effects, at least for roads with heavy traffic.

Conclusions

We compared barrier and corridor effects of roads, rivers and power lines on movements of a large herbivore, the moose, in central Norway. We found that roads and combinations of roads with other linear features had the strongest effects. Moose more likely moved along linear features when getting closer, although moved randomly when in close proximity to power lines. The results indicate that power lines do not pose a barrier to moose movements, which contrast to the barrier effects of linear forest openings of roads and rivers.

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Supplemental Material

Appendix A

Table A1. Beta-coefficients, robust standard errors, Wald χ^2 and significance of variables of the Combined model testing for the effects of environmental variables as well as barrier and corridor effects of linear features and linear feature combinations on moose step selection in central Norway.

Variable	β	SE	χ^2	P
Step length	1.4e−03	7.5e−05	359.7	<0.001
Elevation difference	−1.6e−02	9.2e−04	294.6	<0.001
Forest = no	−3.4e−01	2.3e−02	222.8	<0.001
Elevation	3.1e−03	6.4e−04	23.6	<0.001
Elevation^2	−4.0e−06	1.1e−06	14.5	<0.001
Distance	3.9e−04	1.6e−04	5.8	0.016
Distance^2	−2.1e−07	1.2e−07	3.1	0.078
Distance : feature type = road	3.7e−04	1.3e−04	8.1	0.004
Distance : feature type = river	6.4e−05	1.4e−04	0.2	0.654
Distance^2 : feature type = road	−2.7e−07	1.2e−07	5.1	0.024
Distance^2 : feature type = river	−3.1e−08	1.3e−07	0.1	0.810
Crossing type = road	−3.9e−01	6.9e−02	30.8	<0.001
Crossing type = power line	1.4e−01	1.5e−01	0.9	0.339
Crossing type = river	−3.1e−01	1.2e−01	6.1	0.013
Crossing type = road & river	−1.4e+00	2.6e−01	26.6	<0.001
Crossing type = road & power line	−1.1e+00	2.3e−01	23.3	<0.001
Crossing type = power line & river	7.2e−01	3.0e−01	5.8	0.016
Forest : crossing type = road	6.2e−01	6.8e−02	83.6	<0.001
Forest : crossing type = power line	1.4e−01	2.2e−01	0.4	0.510
Forest : crossing type = river	3.9e−01	1.3e−01	8.4	0.004
Feature orientation : crossing type = road	−4.1e−02	6.6e−02	0.4	0.540
Feature orientation : crossing type = power line	−3.5e−01	1.1e−01	10.3	0.001
Feature orientation : crossing type = river	−1.1e−01	1.0e−01	1.1	0.284
$\mathrm{Distance_{Cr}}$: crossing type = road	−2.2e−03	3.4e−04	41.3	<0.001
$\mathrm{Distance_{Cr}}$: crossing type = power line	−2.2e−03	5.6e−04	15.1	<0.001
$\mathrm{Distance_{Cr}}$: crossing type = river	−1.0e−03	3.9e−04	7.1	0.008
$\mathrm{Distance_{Cr}}$: crossing type = road & river	−4.4e−03	1.3e−03	11.9	0.001
$\mathrm{Distance_{Cr}}$: crossing type = road & power line	2.5e−03	1.9e−03	1.8	0.178
$\mathrm{Distance_{Cr}}$: crossing type = power line & river	−8.2e−03	1.3e−03	37.0	<0.001
Corridor type = road	7.1e−02	2.2e−02	10.5	0.001
Corridor type = power line	2.7e−02	9.5e−02	0.1	0.779
Corridor type = river	3.5e−02	3.1e−02	1.2	0.270
Corridor type = road & river	1.0e−01	4.2e−02	5.9	0.015
Corridor type = road & power line	4.8e−02	9.0e−02	0.3	0.593
Corridor type = power line & river	8.4e−02	7.7e−02	1.2	0.276
Forest : corridor type = road	−2.6e−02	2.8e−02	0.8	0.369
Forest : corridor type = power line	−5.9e−02	5.8e−02	1.0	0.308
Forest : corridor type = river	−2.2e−02	2.7e−02	0.6	0.431
Feature orientation : corridor type = road	2.5e−02	1.5e−02	2.9	0.088
Feature orientation : corridor type = power line	1.0e−01	2.6e−02	16.3	<0.001
Feature orientation : corridor type = river	3.2e−02	2.4e−02	1.8	0.180
$\mathrm{Distance_{Co}}$: corridor type = road	−6.6e−05	1.9e−05	12.1	0.001
$\mathrm{Distance_{Co}}$: corridor type = power line	−1.0e−04	6.8e−05	2.2	0.139
$\mathrm{Distance_{Co}}$: corridor type = river	−1.5e−05	2.5e−05	0.4	0.546
$\mathrm{Distance_{Co}}$: corridor type = road & river	−4.0e−05	5.2e−05	0.6	0.441
$\mathrm{Distance_{Co}}$: corridor type = road & power line	−2.1e−04	3.8e−04	0.3	0.583
$\mathrm{Distance_{Co}}$: corridor type = power line & river	−2.1e−05	4.6e−05	0.2	0.658

Notes: ":" stands for first-order interactions. Linear feature combinations are indicated with a "&" between them. For a description of the variables, see *Methods*.

Appendix B

Table B1. Predicted step selection probabilities (P) from Eq. 1 and sample size (n_o/n_r) for moose crossing, moving along or away from roads, power lines, rivers in response to forest versus open habitat and the alignment of linear features along contour lines in central Norway in the period April–December.

	Crossing			Moving along			Moving away†		
Statistic	Rd	Pl	Ri	Rd	Pl	Ri	Rd	Pl	Ri
Forest									
Not aligned to contours									
P	0.24	0.36	0.26	0.39	0.32	0.37	0.37	0.32	0.36
n_o	316	455	253	19,356	5,394	11,075	18,180	5,478	10,363
n_r	1,813	1,526	1,220	46,223	13,971	26,061	42,063	12,417	23,816
Aligned to contours									
P	0.22	0.28	0.24	0.40	0.38	0.39	0.38	0.34	0.37
n_o	1,199	472	1,101	70,458	7,985	53,229	62,554	6,328	46,770
n_r	8,150	2,085	5,882	141,813	17,543	104,801	137,083	15,932	102,337
Open									
Not aligned to contours									
P	0.36	0.39	0.36	0.32	0.29	0.32	0.32	0.32	0.32
n_o	279	11	82	2,189	163	1,044	2,078	154	1,014
n_r	1,005	39	287	7,230	724	3,578	6,556	644	3,422
Aligned to contours									
P	0.35	0.31	0.33	0.33	0.35	0.34	0.32	0.34	0.33
n_o	634	10	212	5,875	305	3,726	5,316	290	3,201
n_r	2,588	66	819	18,289	1,153	10,947	17,071	1,183	10,846

Notes: Predictions were made from the Combined model (equivalent to Appendix A) testing for the effects of environmental variables as well as barrier and corridor effects of linear features on step selection of 145 moose using GPS relocation data. A step selection probability below 0.33 indicates avoidance. The sample sizes are choice sets containing different types of observed (n_o)/random (n_r) movement steps.

† The sample sizes (n) are choice sets containing steps towards or away from linear features without crossing or moving along them.

Table B2. Predicted step selection probabilities (P) from Eq. 1 and sample size (n_o/n_r) for moose crossing, moving along or away from combinations of roads, power lines and rivers in central Norway in the period April–December.

	Crossing			Moving along			Moving away†		
Statistic	Rd/Ri	Rd/Pl	Pl/Ri	Rd/Ri	Rd/Pl	Pl/Ri	Rd/Ri	Rd/Pl	Pl/Ri
P	0.10	0.14	0.46	0.47	0.44	0.28	0.43	0.43	0.26
n_o	124	15	83	21,854	103	1,041	18,129	83	953
n_r	1,875	74	236	41,972	257	2,102	40,062	202	1,986

Notes: Predictions were made from the Combined model (equivalent to Appendix A) testing for the effects of environmental variables as well as barrier and corridor effects of linear features on step selection of 145 moose using GPS relocation data. A step selection probability below 0.33 indicates avoidance. The sample sizes are choice sets containing different types of observed (n_o)/random (n_r) movement steps. The feature in combinations assumed closest to steps is named first.

† The sample sizes are choice sets containing steps towards or away from linear feature combinations without crossing or moving along them.

Table B3. Predicted step selection probabilities (P) from Eq. 1 and sample size (n_o/n_r) for moose crossing, moving along or away from roads, power lines, rivers in response to forest versus open habitat and the alignment of linear features along contour lines in central Norway in the period January-March.

	Crossing			Moving along			Moving away†		
Statistic	Rd	Pl	Ri	Rd	Pl	Ri	Rd	Pl	Ri
Forest									
Not aligned to contours									
P	0.24	0.35	0.24	0.38	0.33	0.37	0.38	0.32	0.39
n_o	48	111	34	4,125	1,702	1,870	4,127	1,751	1,878
n_r	466	480	234	10,008	4,504	4,542	9,160	3,980	4,123
Aligned to contours									
P	0.24	0.26	0.22	0.39	0.39	0.38	0.37	0.35	0.40
n_o	185	128	101	14,099	3,390	9,379	13,367	3,160	9,222
n_r	1,682	865	1,050	29,005	7,481	19,454	28,078	6,960	18,987
Open habitat									
Not aligned to contours									
P	0.39	0.37	0.20	0.31	0.32	0.39	0.30	0.31	0.40
n_o	56	2	3	337	35	186	358	27	171
n_r	214	18	53	1,305	197	666	1,184	185	597
Aligned to contours									
P	0.38	0.28	0.18	0.32	0.38	0.41	0.30	0.35	0.41
n_o	100	4	15	847	98	684	771	94	674
n_r	481	18	131	2,820	397	2,132	2,784	392	2,095

Notes: Predictions were made from Combined model (equivalent to Appendix A, but excluding the effects of linear feature combinations) testing for the effects of environmental variables as well as barrier and corridor effects of linear features on step selection of 142 moose using GPS relocation data A step selection probability below 0.33 indicates avoidance. The sample sizes are choice sets containing different types of observed (n_o)/random (n_r) movement steps.

† The sample sizes (n) are choice sets containing steps towards or away from linear features without crossing or moving along them.

Supplement

R script for analyzing the effects of environmental variables, linear features (roads, power lines, rivers) and linear feature combinations on moose step selection (*Ecological Archives*, http://dx.doi.org/10.1890/ES14-00278.1.sm).