



Difference in spatiotemporal patterns of wildlife road-crossings and wildlife-vehicle collisions

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ABSTRACT

Human-wildlife conflicts like wildlife-vehicle collisions pose major challenges for the management and conservation of mobile wildlife in human-dominated landscapes, particularly when large species are involved. Mitigation measures to reduce risk of collisions may be based on information given by wildlife movement and collision data. To test whether movement and collision data indicate different spatiotemporal risk zones, we predicted year-around probabilities of road-crossings of GPS-marked female moose (*Alces alces*) ($n = 102$), and compared them with spatiotemporal patterns of police recorded moose-vehicle collisions ($n = 1158$). Probability of moose road-crossings peaked in May, June, and between mid November and the beginning of January, i.e. during moose migration. Moose-vehicle collisions were more likely during autumn and winter. Comparing environmental attributes of crossing and collision sites showed significant differences. The likelihood of collisions increased with the abundance of human-modified areas and higher allowed speed, and was lower on forest roads. We found that animal movement data alone are insufficient to predict collision risk zones, while analyses of collision data alone overestimate the collision risk in certain habitats. Our findings suggest that higher collision risk is largely due to low light and poor road surface conditions rather than to more animal road-crossings. This suggests that efforts to reduce wildlife collisions should focus on driver attitudes and road conditions rather than animal movement, and any efforts to model the collision risk will require actual collision data, and not just movement data.

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1. Introduction

Roads fragment wildlife habitat, facilitate human access into remote areas, and can have negative impact on wildlife abundance (Forman and Alexander, 1998; Martínéz-Abraín et al., 2009; Benítez-Lopéz et al., 2010). Roads are of particular concern for wide-ranging wildlife because higher road density increases wildlife mortality rates non-linearly due to an enhanced risk of collisions (Frair et al., 2008) and may lower social acceptance when large mammals pose risks to human safety (Lavsund and Sandegren, 1991). Furthermore, the frequency of wildlife-vehicle collisions in general, and especially of collisions with ungulates, is likely to increase as road networks continue to expand, many ungulate populations continue to grow, and traffic volume

increases (Groot Bruinderink and Hazebroek, 1996; Hawbaker et al., 2006; Bergström and Danell, 2009). Yet, for rare species threatened by traffic-related mortality, collision samples may be small (Colino-Rabanal et al., 2011), which may bias mitigation measures based on small samples. However, the use of movement data alone may be inappropriate to predict “hot-spots” for an effective management and conservation. Moreover, for cryptic species affected by traffic-related mortality such as the southern pudu (*Pudu puda*) movement data might be difficult to obtain (Silvia-Rodríguez et al., 2010), and thus, management mitigation measure have to rely on collision data. Therefore, in order to accurately adjust the evaluation of risk for conservation and traffic safety the assessment of whether or not animal movement and collision data indicate different spatiotemporal risk zones is significant. This is important when mitigation measures to reduce collision risk are based on either collision or movement data alone.

Wildlife-vehicle collision probabilities depend on animal movement patterns, landscape and road features (Seiler, 2005; Dussault et al., 2007; Gunson et al., 2011; Lewis et al., 2011). Animal

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movement patterns are the result of decision-making among behavioral trade-offs including an individual's internal state, and its environment at different spatiotemporal scales (Johnson et al., 2002; Nathan et al., 2008). Wildlife such as ungulates can be persistent in their use of established travel routes for migration or daily movement (Bruggeman et al., 2007; Bunnefeld et al., 2011). When roads or railway lines intersect movement routes, these patterns can create zones of higher risk for wildlife conservation and human safety (Gundersen and Andreassen, 1998; Bruggeman et al., 2007; Gunson et al., 2011).

High risk zones for traffic safety and wildlife conservation occur when and where wildlife crossings intersect with high probability for wildlife–vehicle collisions and are thus restricted in time and space. Earlier studies either predicted the risk of wildlife–vehicle collisions based on accident data (Seiler, 2005; Danks and Porter, 2010; Found and Boyce, 2011), or used wildlife movement data to predict road-crossings (Lewis et al., 2011). However, either data set alone may differently indicating high risk at a given time in a given location (Dussault et al., 2007). If collision and movement data are available, then the relative frequency for collisions in space and time can be calculated as the occurrence of a collision at a given place or time relative to the occurrence of animal locations at the given locale or time. Such analyses are significant to identify whether, where and when distribution probabilities for wildlife road-crossings and for collisions differ, and will help to target preventive measures more efficiently. For some species, the use of an expert-opinion or literature-based model might be an excellent alternative (Clevenger et al., 2002). Yet, for species where little information about their movement ecology is available or which exhibit large difference in movement ecology among areas, such an approach may not be a satisfying alternative.

Wildlife with abundant movement and collision data provide opportunity to test for different hypotheses about spatiotemporal distributions of high risk zones between animal movement and collisions data. Here, we compared year-around spatiotemporal frequencies of wildlife road-crossings and collisions using data of migratory moose (*Alces alces*) along a gradient from Low Alpine and Interior to Coastal areas in northern Sweden. Our goal was first, to investigate when and where moose are most likely to cross a road, and second to compare spatiotemporal movement patterns with observed spatiotemporal patterns of moose–vehicle collisions. Based on prior studies, we predicted (1) that moose road-crossings occur when moose are more active, e.g., during migration, rutting, hunting season, and twilight hours; (2) that moose road-crossings take place in preferred moose habitat; and (3) that patterns of moose road-crossings and moose–vehicle collisions differ in time

and space as increased road-crossing frequency may not necessarily result in more collisions at a given time and place.

2. Methods

2.1. Study area

Our study area [127,000 km²] in the Provinces of Västerbotten and Norrbotten in Northern Sweden was subdivided into three regions with respect to moose distribution: Coastal ($n = 18$ moose), Interior ($n = 22$), and Low Alpine regions ($n = 62$) (Fig. 1).

The Coastal region (63°42'N 19°40'E, WGS84) had a human density of 18 people km⁻² (Statistics Sweden, 2008), a road density of 1.2 km roads km⁻² (0.4 km km⁻² major roads; Swedish Land Survey, 2008), and was comprised of boreal forest with patches of deciduous trees and agricultural activity in flat to gently rolling terrain (mean: 95 m (range 0–305 m); Swedish Land Survey, 2008). The Interior (64°28'N 19°45'E, WGS84) was dominated by monocultures of Scots Pine (*Pinus sylvestris*) on gently rolling terrain with an average elevation of 227 m (range 11–498 m; Swedish Land Survey, 2008). Human density averaged 12 people km⁻² (Statistics Sweden, 2008) and road density was 1 km roads km⁻² (0.3 km km⁻² major roads; Swedish Land Survey, 2008). The Low Alpine region (65°29'N 16°44'E, WGS84) consisted of boreal coniferous and mountainous birch forest, partly above the tree line, with an average elevation of 561 m (range 42–1760 m). It had an average human density of 1 person km⁻² (Statistics Sweden, 2008) and a road density of 0.4 km road km⁻² (0.1 km km⁻² major roads; Swedish Land Survey, 2008). Moose in the Low Alpine region migrate, on average, further than in the Coastal and Interior regions (Bunnefeld et al., 2011). Hunting season starts in September and lasts until the end of December for adult moose, but most hunting activity and harvest takes place in the first three weeks of September.

2.2. Environmental attributes

We reclassified 25-m resolution Swedish land cover data into eight habitats based on moose biology (Ball et al., 2001; Swedish Land Survey, 2008; Bjørneraas et al., 2011): (1) *deciduous forest* (DEC), (2) *old coniferous forest* (CON), (3) *mixed forest* (MIXED), (4) *young coniferous forest/clear-cuts* (YOUNG), (5) *marsh/open pasture* (MARSH), (6) *mires* (MIRE), (7) *open water* (WATER), and (8) *non-moose habitat* (NON-HABITAT) (dominated by developed and other human-modified areas, with minor contribution of bare rock, sparse vegetation, beach, glaciers, and perpetual snow). We used

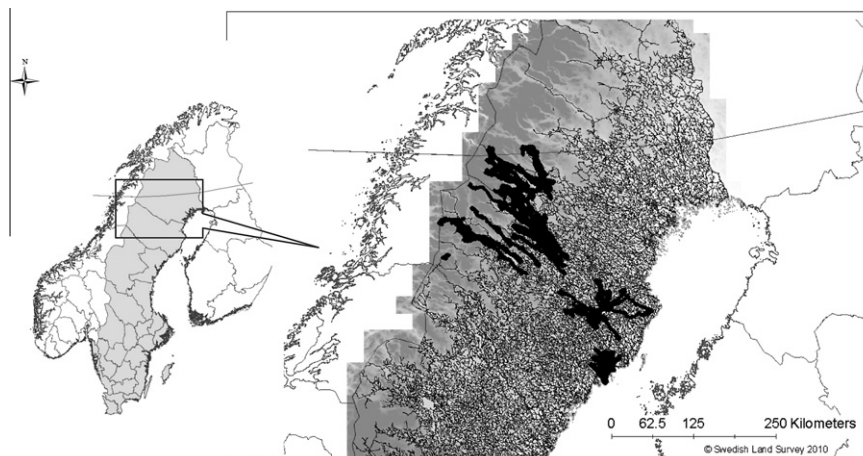


Fig. 1. Map of Fennoscandia, Sweden in gray, and the current road network in northern Sweden. Black dots represent moose GPS locations. Female moose ranged in low alpine, interior and coastal regions (west to east), Provinces of Västerbotten and Norrbotten, Sweden, 2004–2007.

principal component analysis (PCA) to identify the habitats that captured most of the variance.

To balance high spatial resolution and practical restrictions, and in agreement with average moose movement rates per hour (Fig. 2), we applied a 250×250 m grid, calculating for each cell the abundance of the eight habitats and road density [m , 62500 m^{-2}] using the Swedish road map (Beyer, 2008; Swedish Land Survey, 2008). Following previous research, we calculated a terrain ruggedness index for each cell to represent topographic heterogeneity (Riley et al., 1999; Nellemann et al., 2007; NSTC, 2008). Ruggedness varied between 0 and 369, which represents level to moderately rugged terrain (Riley et al., 1999).

Quantitative estimates of traffic volume were not available for most parts of our study area. Therefore, we classified the road network into: (1) “major roads” (≥ 5 m wide) and (2) “all roads” (major roads plus smaller unpaved roads with less traffic and lower speed limits). To investigate the cumulative effect of roads, we calculated for each moose GPS location: (1) the distance to the nearest major road, and (2) the distance to any road. Only few wildlife fences occurred in our study area and they were not evaluated.

2.3. Moose data

We immobilized 102 free-ranging adult female moose from a helicopter with a dart gun that injected a mixture of etorphine-acpromazine and xylazine (Kreeger and Arnemo, 2007). We equipped each moose with a neck collar with a Global Positioning System (GPS) receiver (Vectronic Aerospace GmbH, Berlin, Germany). To monitor detailed year-around movement behavior, the GPS calculated positions every full hour and for each moose we collected a full year of data, resulting in 8302 ± 0.4 SE fixes per individual. Average dilution of precision was 3.9 ± 2.4 , indicating a good fix quality, and 5.5 ± 1.1 satellites were used for position calculation. We collected data from March 2004 to February 2007. We estimated movement activity by dividing the Euclidean distance between successive locations by the time elapsed [$m \text{ hr}^{-1}$]. Each moose location was assigned to its corresponding 250-m cell to analyze observations in relation to environmental parameters. None of the study animals were killed by vehicles during the study.

2.4. Data sets

We analyzed two different data sets: (1) We classified each moose GPS location as either a moose road-crossing (1) or not (0) by calculating moose movement paths as straight-line connections (Beyer, 2008). Locations, which movement path segment intersected with a road were defined as crossings. Animals some-

times crossed roads several times forth and back, and we therefore classified both locations that intersected with a road as a crossing. To evaluate the attributes of the sites where a moose crossed the road, we identified the point where the estimated movement path intersected with the road, hereafter called site (Beyer, 2008). (2) We compared the spatiotemporal patterns of moose road-crossings with patterns of police-documented moose-vehicle collisions by comparing their distributions in time and by comparing the sites at which crossings and collisions, respectively, happened (Swedish NPB, 2009).

2.5. Spatiotemporal patterns of moose-road crossings

To evaluate the temporal distribution of moose-road crossings, we calculated the relative observed frequency of moose road-crossings in a given week of the year and hour of the day by dividing the amount of crossings by the sum of both crossings and non-crossings in that given week and hour. We tested for non-linear temporal probability of moose road-crossings by fitting a generalized additive model (*gam*) with non-parametric smoothers using the calculated relative frequency of road-crossings as a function of a given week and hour (R Package *mgcv* 1.4-1.1; Wood, 2006). Both explanatory variables were smoothed using the cyclic spline function to account for the similarity between start and end points for weeks of the year and hours of the day (Wood, 2006).

Moose in our study area were migratory, resulting in considerable differences in annual movement patterns (Bunnefeld et al., 2011). Based on the temporal probability of moose road-crossings, and according to the movement ecology paradigm proposed by Nathan et al. (2008), we identified distinct periods of high- and low-probability of moose road-crossings and analyzed those separately. We identified breakpoints of the movement periods using segmented regression with the estimated frequency of a road crossing as a function of the interaction of week and hour as given by the *gam* (R package *segmented* 0.2-7.2; Muggeo, 2007). Thus, we tested for each period whether the probability that a given moose location with a given mix of environmental parameters represented a road-crossing, using equal-sized samples of moose road-crossings and non road-crossing locations in a 30% random subsample of the original data set (sampled without replacement). We used a generalized linear mixed model with logit link and binomial error distribution fit using Laplace approximation (*glmer*; R Package *lme4* 0.999375-39; Pinheiro and Bates, 2000; Crawley, 2007). We tested all possible simple combinations of our suitable set of explanatory variables to identify the important determinants for moose road-crossings (ruggedness; day, night, and twilight hours; region (Coastal, Interior or Low Alpine); moose movement

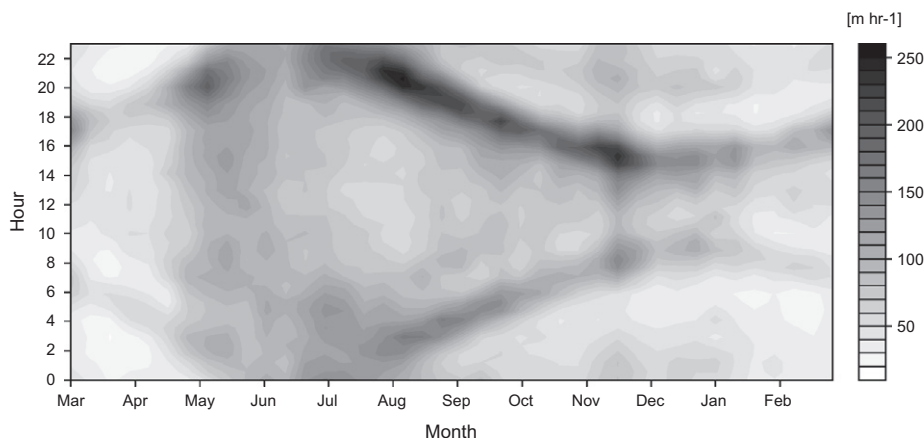


Fig. 2. Average movement activity [$m \text{ h}^{-1}$] of female moose over the course of the year and time of the day.

activity; moose road proximity; and the land cover types indicated by PCA, i.e. percentage of CON, YOUNG, DEC). We included moose proximity to the road in our analysis because moose can range closely to a road without ever crossing it, while utilizing near-road habitat (Laurian et al., 2008). Only moose locations within 1 km of the nearest road were included. Because we wanted to test for differences between regions and the regions where moose were marked were not randomly chosen, we included region as a fixed effect. We included moose individuals as a random effect to control for differences among individuals (Bolker et al., 2009). Because individual moose always remained in the same region, we nested the individual moose random effect within the region where they ranged. The model was evaluated for spatial autocorrelation by computing empirical variograms (R Package *geoR* 1.6–32; Ribeiro and Diggle, 2001). No spatial autocorrelation was found.

We used Akaike's information criterion (AIC) to identify the most parsimonious among competing models (Burnham and Anderson, 2002). For each model we calculated the area under the receiver operating curve (AUC; R package *ROCR* 1.0–4; Sing et al., 2005) to estimate how well a given model was able to predict the data. We evaluated the contribution of the moose within region random effect, i.e., difference among individuals, to the model fit by comparing the best-supported linear mixed model with its counterpart – a generalized linear model without a random effect – using the likelihood ratio test. We also compared the two models less formally using AIC. To evaluate the effect of different road types, we fitted separate models for all roads and for major roads only.

2.6. Comparison of moose road crossings versus moose-vehicle collisions

To test for differences between the spatiotemporal distribution of moose road-crossings and moose-vehicle collisions, we compared moose location data with 1158 police-documented moose-vehicle collisions in our study area (November 2005–December 2007; Swedish NPB, 2009). By law each moose-vehicle collision has to be reported to the police, and generally the local hunter team is responsible for the tracking or taking care of the injured or dead animal. Each record in the national database includes information about the type of collision, coordinates and time. While the temporal accuracy of these data is good, the spatial accuracy varies, and the exact location error is unknown (personal comment A. Sävberger, Swedish NPB, 2009). Varying spatial accuracy in wildlife-collision data may complicate predictions of high risk zones for traffic safety (Gunson et al., 2009). Seiler (2005) reported a location error estimate of ± 500 m for the Swedish police-reported collision data. Our study is located in the boreal zone, which is characterized by relatively little habitat heterogeneity, and large connected homogeneous forest areas. This reduces the bias a location error of a few hundreds of meters would cause. To test for non-linear temporal probability of collisions, we applied a *gam* using the relative frequency of collisions as a function of the interaction of a given week and hour. We calculated the relative frequency by dividing the amount of collisions by the sum of moose road-crossings and collisions in a given week and hour (cyclic spline function; R Package *mgcv* 1.4–1.1; Wood, 2006).

To test for environmental differences between sites where moose crossed roads and collisions happened, we first applied a generalized linear model, with logit link and binomial errors distribution using the event of a moose road crossing (coded as 0) and collision (coded as 1) the response variable. Based on the empirical variogram, the initial model showed evidence of spatial autocorrelation, so we subsequently fit a generalized linear mixed model, with an exponential correlation structure, using penalized quasi-likelihood to an equal-sized 25% subsample of

the original data. We subsampled due to restricted computational capacity (sampled without replacement). Sites were assigned as random effect. We evaluated the occurrence of a moose road-crossing and collision as a function of road density, ruggedness, highest speed allowed, major or forest road, and the land cover categories indicated by PCA (i.e., the percentage of CON, YOUNG, NON-HABITAT) (R Package *stats* 2.8.1; Crawley, 2007). Because generalized linear mixed models fit using penalized quasi-likelihood do not use a true likelihood, we could not use likelihood-based model selection methods. Instead, we used the AUC of the models to identify for each number of parameters the model that best predicted the data (R package *ROCR* 1.0–4; Miller, 1990; Sing et al., 2005).

We used the software ArcGIS 9.3 for all GIS analyses (ESRI, Redlands, CA, USA). All statistical analyses were carried out in R 2.11.1 (R Development Core Team, 2010). We used a statistical significance of $p < 0.05$.

3. Results

Moose showed a bimodal activity pattern with a strong seasonal pattern and were most active for about three hours in the morning and afternoon (Fig. 2).

The probability for moose road-crossings varied both by time of day and among seasons (*all roads*: edf = 28.2, Ref.df = 28.2, *F*-value = 45.6, $p < 0.0001$, adj. $R^2 = 0.51$, deviance explained = 51.6%, Fig. 3A; *major roads*: edf = 27.9, Ref.df = 27.9, *F*-value = 26.9, $p < 0.0001$, adj. $R^2 = 0.37$, deviance explained = 38.6%, Fig. 3B). Within the same day, the probability of a road-crossing followed a bimodal pattern, but this pattern was weaker than the intra-annual pattern (Fig. 3A and B). The probability distribution before and after periods of high hunting activity (first three weeks in September) and rutting season (end of September to mid of October) did not differ (Fig. 3A and B).

Based on initial results, we defined four movement phases (Table 1). We found high probability for moose road-crossings between end of April and end of June ("spring-peak", *all roads* and *major roads* weeks 18–26), and between mid of November and beginning of January ("winter-peak", *all roads* weeks 47–2, *major roads* weeks 47–3; Fig. 3A and B). Between beginning of March and beginning of April ("spring-dip", *all roads* and *major roads* weeks 10–15) and between end of June and mid of August ("summer-dip", *all roads* weeks 27–32, *major roads* weeks 27–34) the probability was particularly low (Fig. 3A and B).

Differences among moose individuals, i.e. the moose within region random effect, contributed to the model fit differently in the four movement phases (Table 1). In all movement phases, the odds-ratio indicated that the probability that a moose crosses a road increased considerably with higher rates of movement (Fig. 4). On the other hand as moose-road distance increased, the probability of a moose crossing a road significantly decreased (Fig. 4). The odds-ratio indicated that this relationship was slightly lower during the winter-peak. Moose in the mountainous region had a higher probability of crossing a road in the winter-peak and summer-dip compared to the two other regions (Fig. 4). Models had AUC scores between 0.92 and 0.98 (Table 1).

The temporal distribution of moose road-crossings and moose-vehicle collisions differed. The predicted probability of collisions was highest from 16:00–20:00 h in fall and early winter (time zone UTC/GMT + 1 h; October to January; edf = 23.6, Ref.df = 26.3, *F*-value = 13.3, $p < 0.0001$, adj. $R^2 = 0.22$, deviance explained = 23.6%; Fig. 5).

Within the study area, 64% ($n = 736$) of all moose-vehicle collisions occurred on major roads although these comprised only 29% of all roads. Comparing sites of moose road-crossings and collisions

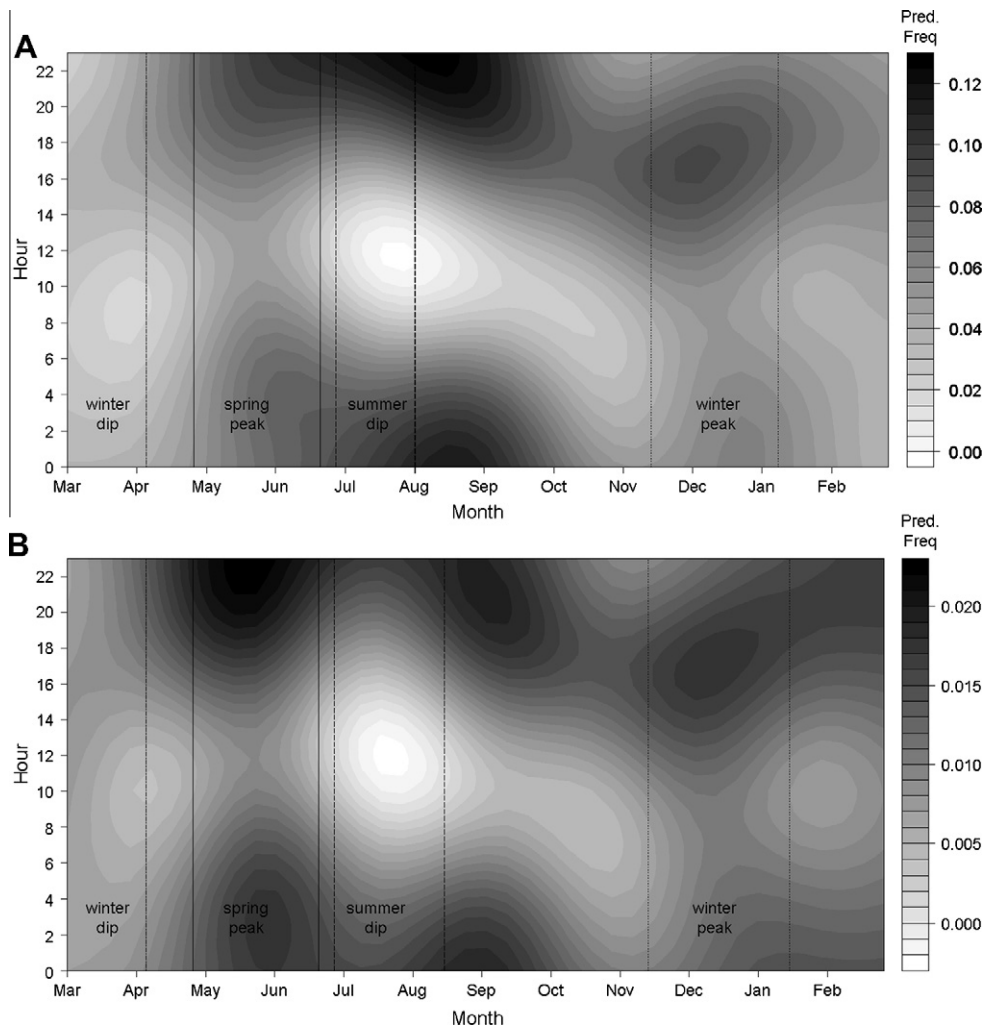


Fig. 3. Predicted probability of female moose road-crossing on a daily and seasonal basis for *all roads* (A) and *major roads* (B). The vertical lines represent the breakpoints of the four movement phases (solid: *spring-peak*, dotted: *winter-peak*, two dash: *winter-dip*, long dash: *summer-dip*).

Table 1
Generalized linear mixed model predicting moose road-crossings for *all roads* and for *major roads* in the four movement phases. Breakpoints for movement phases indicated by segmented regression. Δ AIC between glmer and glm, and likelihood ratio test to evaluate the contribution of the random effect, i.e., the difference among moose, to the model fit.

Data set	Movement phase	Fixed factors	AUC	Random effect to the model fit, $df = 2$
All roads	Spring-peak, week 18–26	Rdist*** mhr*** DEC*** CON*	0.92	Δ AIC = -27.3; $lr = 31.3$, $p < 0.0001$
	Winter-peak, week 47–2	Rdist*** mhr*** Rugged ^a Region Mountainous* Region Inland ^a	0.93	Δ AIC = -6.3; $lr = 10.3$, $p = 0.006$
	Spring-dip, week 10–15	Rdist*** mhr*** Rugged* CON**	0.95	Δ AIC = -1.3; $lr = 5.4$, $p = 0.07$
	Summer-dip, week 27–32	Rdist*** mhr*** DEC*** Region-Mountainous** Region-Inland ^a	0.92	Δ AIC = -15.6; $lr = 19.6$, $p < 0.0001$
Major roads	Spring-peak, week 18–26	Rdist*** mhr*** CON*	0.96	Δ AIC = 3.1; $lr = 0.9$, $p = 0.6$
	Winter-peak, week 47–3	Rdist*** mhr*** YOUNG*	0.96	Δ AIC = -4.8; $lr = 8.8$, $p = 0.01$
	Spring-dip, week 10–15	Rdist*** mhr***	0.98	Δ AIC = 2.1; $lr = 1.9$, $p = 0.4$
	Summer-dip, week 27–34	Rdist*** mhr*** DEC*** Region-Mountainous** Region-Inland	0.97	Δ AIC = -0.04; $lr = 4.0$, $p = 0.1$

Rdist = moose distance to road; mhr = moose movement activity; Rugged = terrain ruggedness index; DEC = deciduous forest; CON = old coniferous forest; YOUNG = young coniferous forest; Region = region where moose range; Rdist, mhr, Rugged = log-transformed.

* $p < 0.05$.

** $p < 0.01$.

*** $p < 0.0001$.

^a n.s.: not significant.

showed that these two sites differed considerably in their environmental attributes. The model with the highest AUC score included three significant variables (AUC = 0.88; Table 2). The odds-ratio denoted higher odds of collision at sites where speed and the abun-

dance of human-modified area were higher, while the odds-ratio decreased at sites on forest roads (Table 2). There was also a slightly negative effect of the abundance of old coniferous forest (Table 2).

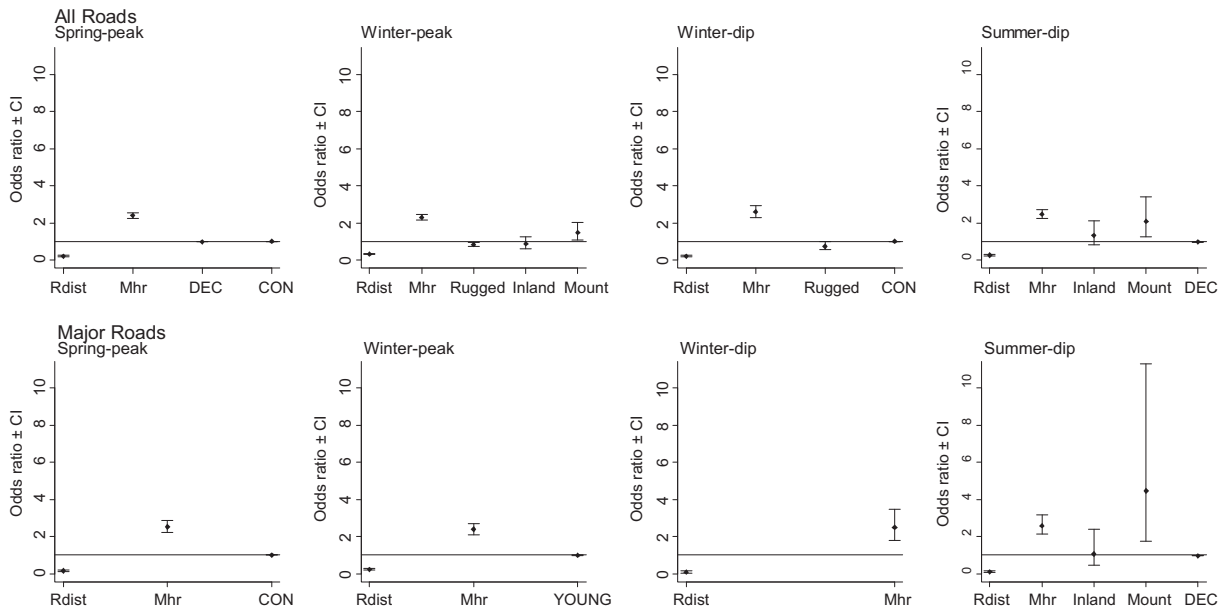


Fig. 4. The odds-ratio with 95% confidence interval of the best-supported generalized linear mixed model predicting moose road crossings in a given movement phase. The black line indicates an odds-ratio of 1 (no effect). Rdist = moose distance to road; mhr = moose movement activity; Rugged = terrain ruggedness index; DEC = deciduous forest; CON = old coniferous forest; YOUNG = young coniferous forest; Region = region where moose range; Rdist, mhr, Ruggedness = log-transformed.

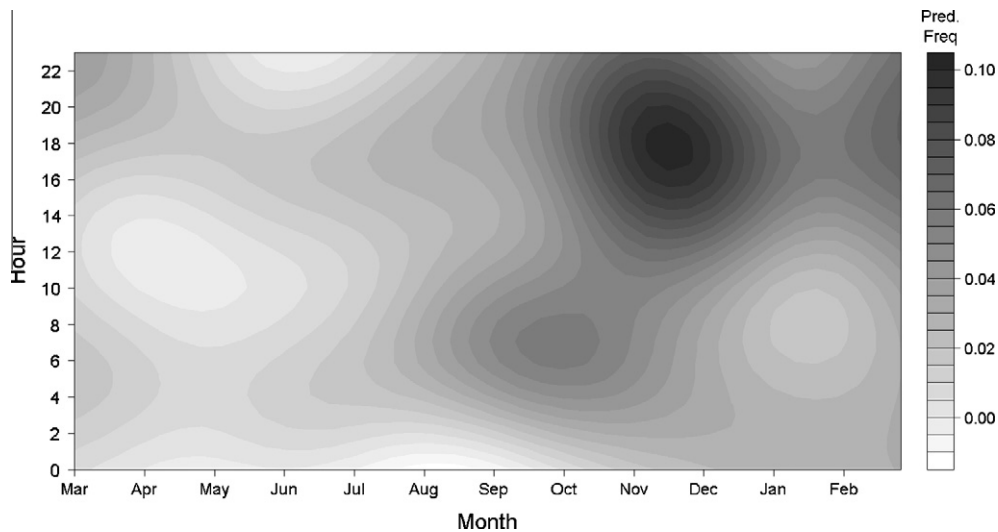


Fig. 5. Temporal predicted probabilities for moose-vehicle collision in relation to the occurrence of moose road crossings.

4. Discussion

As predicted, the patterns of peaks for moose road-crossings differed considerably in both space and time from those of collisions. Thus, while animal movement data identify sites where wildlife preferably cross roads (Lewis et al., 2011), and thereby give valuable information for future road development, models to predict zones of high collision risk require actual collision data, not only movement data.

Temporally our results suggest that poorer light and road surface conditions, and not necessarily higher animal road-crossing activity, may be the main factor increasing the risk of a collision in our study area. Moose road-crossings peaked from May to June, and from mid of November to January, and in these periods often occurred throughout the day, corresponding to female moose migration patterns (Bunnefeld et al., 2011). Daily, moose road-

crossings closely followed moose activity patterns, with higher probabilities for road-crossings occurring with peak movement phases. In contrast, most moose vehicle-collisions happened in autumn and winter, i.e., from October to January, and from the late afternoon into the early evening hours. The daily distribution of collisions in our study area corresponded with findings by Danks and Porter (2010), but the seasonal differed as the authors found most moose-vehicle collisions happened between May and October. These seasonal differences may be due to difference in light conditions. While Danks and Porter (2010) study took place at a latitude of 45°, our study areas ranged in latitudes from 63–65°, providing 24-h daylight during summer but very few hours of daylight during winter. Because their study lacked corresponding animal movement data, as is the case for most wildlife-vehicle collision studies, unfortunately relative frequencies of road-crossings resulting in collisions are not available.

Table 2
Distribution of the odds ratios with 95% CIs of the generalized linear mixed model with penalized quasi-likelihood predicting moose road-crossings and moose-vehicle collisions. An odds-ratio of 1 indicates no effect. For each number of fixed factors, the model with the highest AUC value is given. Same random effects structure for all model combinations. Model with the highest AUC value in bold.

Odds ratio with 95% CIs and significance of the fixed factors, crossings (coded as 0) vs. collisions (coded as 1)								AUC
Average	Road type 25% vs. 75% on a major road	Speed 71 km h ⁻¹ ± 0.4 vs. 73 km h ⁻¹ ± 1	Rden 279 m ± 6 vs. 327 m ± 10 per 250 x 250 m	Rugged 32 ± 2 vs. 25 ± 1	NON-HABITAT 2% ± 1 vs. 28% ± 2	CON 47% ± 2 vs. 31% ± 2	YOUNG 30% ± 2 vs. 9% ± 1	
1								0.43
2	0 ^{***}				Inf ^{***}	0.99 ^{***} (0.98–0.99)		0.77
3		1.10 ^{***} (1.08–1.13)			1.09 ^{***} (1.06–1.12)	0.99 [*] (0.99–1.0)		0.83
4		1.10 ^{***} (1.07–1.12)			1.06 ^{***} (1.04–1.08)	0.98 ^{***} (0.97–0.99)	0.97 ^{***} (0.96–0.98)	0.87
5		1.09 ^a (1.07–1.10)	0.94 ^{***} (0.89–1.0)	0.82 [*] (0.59–1.12)	1.08 ^{***} (1.06–1.10)		0.98 ^{***} (0.97–0.99)	0.86
6	0.21^{***} (0.13–0.33)	1.08^{***} (1.06–1.11)	0.95^a (0.90–1.00)	0.77^a (0.56–1.06)	1.08^{***} (1.06–1.11)	0.99[*] (0.96–1.00)		0.88
7	0 ^a	Inf ^{***}	0 ^a	0 ^a	Inf ^{***}	0 ^a	0 ^a	0.80

Speed = highest allowed speed on the given road segment; Road Type = site on forest road (coded as 3) or major road (intercept, coded as 1), 68 out of 273 sites on a major road (25%; crossings) vs. 186 out of 249 sites on a major road (75%; collisions); NON-HABITAT = predominantly developed areas; CON = old coniferous forest; YOUNG = young coniferous forest; Rden = road density of the given road segment (squared rooted in the model); Rugged = terrain ruggedness index (log-transformed in the model).

* $p < 0.05$.

** $p < 0.01$.

*** $p < 0.0001$.

^a n.s.: not significant.

Patterns of collision differ not only with area, but also with sex and age (Groot Bruinderink and Hazebroek, 1996). Unfortunately, our collision data did not distinguish among accidents involving adult male, female, or subadult moose. We analyzed movement data of only adult female moose. This may have affected our findings of the spatiotemporal differences between sites of moose road-crossings and collisions if adult females differ in their road-crossing behavior from subadult or male moose. To further improve the predictive power when analyzing animal movement and collision data, we recommend future research if possible to include study animals of different ages and each gender, reflecting the present population structure.

None of the tagged moose was killed by traffic during the course of the study. Such lack of fatal events when crossing a road may indicate that the overall number of animals that cross roads in high risk zones or at risky times is relatively small. Yet, we cannot fully exclude a bias in detection rate of the tagged animals due to their reflective neck collar, which may let tagged moose on the road being earlier recognized in darkness than their un-tagged conspecifics. This may have reduced the relative risk of tagged moose of being involved in a collision.

The chance for a moose to cross a road increased with proximity to a road. This fact itself was not surprising, but has implications for collision risk for moose occupying home ranges with high road density. Next, it means that moose in our study seldom ranged in road-near habitat when not crossing roads as moose locations not related to a road-crossing were on average further away from a road. This observed behavior suggests a lower utilization of habitats in road proximity by moose in our study area. In moose, selection of road-near habitat might be a scale-dependent trade-off 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 treasured resources (Laurian et al., 2008; Shanley and Pyare, 2011). Habitat near roads may provide increased forage for a species such moose that benefits from disturbed habitats (Bowman et al., 2010; Rea et al., 2010). In human-dominated landscapes, harvested wildlife utilize road-near habitats in a circadian pattern with higher use of those habitats during times of lower human activity (Martin et al., 2010). During the winter-peak movement phase we found the relationship between moose-road proximity and probability for a road crossing to be slightly less distinct compared to the other times as indicated by the odds ratios. This suggests that moose may utilize habitat near roads during winter to a greater degree

than during other times. Such change in behavior may in turn increase the risk for moose-vehicle collisions, especially when snow is deep and moose utilize roads or railway tracks as easy pathways (Lavsund and Sandegren, 1991; Gundersen and Andreassen, 1998).

We did not find evidence that disturbances by hunting increased the probability of road-crossing, supporting findings by Lavsund and Sandegren (1991). Thus, momentary higher movement activity and spatial displacement due to hunting disturbance do not necessarily result in more moose road-crossings (Neumann, 2009). However, we found a slight increase in moose-vehicle collisions during daytime in September and October, suggesting a relatively higher risk of accidents when moose cross roads during these months, potentially due to higher traffic in the hunting season as suggested by Sudharsan et al. (2006) for deer-vehicle collisions.

In contrast to other studies (Lavsund and Sandegren, 1991; Groot Bruinderink and Hazebroek, 1996; Sudharsan et al., 2006), we did not find that the risk for moose-vehicle collisions or the probability of road-crossings peaked during rutting season, with the exception of a slight increase in collisions during daytime. Unlike in Southern Sweden, moose harvest in Northern Sweden starts before the rutting season, resulting in noticeably reduced population numbers when the rut starts. This may explain the lack of a major peak in collisions in Northern parts of the country as lowered numbers of ungulate-vehicle collisions correlate with reduced ungulate population numbers (Groot Bruinderink and Hazebroek, 1996; Mysterud, 2004).

Movement reflects a decision-making process including individual differences and behavioral change over time (Morales and Ellner, 2002; Hawkes, 2009). In line with the current paradigm in movement ecology (Nathan et al., 2008), we found that individual behavior was an important determinant of the probability of a moose crossing a road. Yet, differences among individuals contributed differently to the model fit in different movement phases. Individual differences were more important when moose crossed any road, while individuals appeared to be more uniform in their behavior when crossing major roads. This suggests that individual differences in habitat use affect the probability of moose crossing a road when it is any road, i.e., most commonly smaller roads, while moose respond more uniformly towards major roads.

Moose movement activity was an important factor in each movement phase. The probability that a moose crosses the road increased considerably with higher rates of movement. This suggests

that road-crossings preferably take place during the period of the day when moose are most active, but may also indicate that road-crossings are non-trivial events for moose, supporting findings by Dussault et al. (2007) who reported that moose moved faster when crossing a road.

We found that the environmental characteristics of moose road-crossings sites and the actual collision sites differed substantially. While collisions occurred predominantly at sites with high abundance of human-modified areas and where higher speed was allowed, moose crossed roads predominantly when they were forest roads and at sites that had abundant old coniferous forest. This suggests a general higher risk for moose-vehicle collisions in proximity to human settlements, which can be an artifact of higher traffic activity close to developed areas, but may also reflect lower driver awareness for wildlife-vehicle collisions risk. In our study, the probability for collisions increased with higher speed limit, although the difference in average speed limits between sites where moose crossed preferably roads and where collisions happened were small. For moose, Seiler (2005) found that most collisions happened on roads with speed limits of 90 km h⁻¹, whereas roads with lower or higher speed limits were associated with fewer collisions. Interestingly, our results partly contrast findings of studies that compared road intercepts of wildlife-vehicle collisions with random road intercepts (and not with wildlife movement data). Those studies found that collisions happened more often at sites that were relatively undeveloped, but had high habitat diversity, and were close to forests (Danks and Porter, 2010; Gunson et al., 2011). As spatial accuracy of our collision data did not always match the accuracy of animal GPS-location data (personal comment A. Sävberger, Swedish NPB, 2009), there remain some uncertainties in their spatial differences. Such uncertainties may complicate conclusions about the strength and direction of environmental variables on risk for collisions (Gunson et al., 2009). To minimize these uncertainties, we recommend future sampling of collision data to intensify efforts for spatial accuracy.

5. Conclusions

Our study emphasizes that the spatiotemporal conclusions for high risk zones for collisions given by animal movement and collision data are very different. Each data set alone would under- or overrate given factors, but combining these data sets highlighted the relative risk during a given time and at given site. “Hot-spots” for conservation and safety occur when and where wildlife road-crossing activity overlaps with conditions for higher collisions risk (Seiler, 2005; Gunson et al., 2011; Lewis et al., 2011). Identifying these two components accurately will facilitate targeting preventive measures more efficiently, it will help to identify whether measures should focus on wildlife or driver parameters, and whether warning efforts can focus on certain times of the year to have the maximum impact on driver alertness. In particular, movement data can help to recognize movement corridors that may provide a higher risk for collisions (Lewis et al., 2011). This may be especially valuable where roads are being developed because migratory ungulates can be quite persistent in their use of traditional migration routes despite anthropogenic alterations (Bruggeman et al., 2007). Such analyses may be help to identify favorable places for mitigation measures to reduce collision risk.

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