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Spatial and Temporal Variation in Moose- (*Alces alces*) Road Crossings

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Natural Resources Management
Submission date: June 2012
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Master of Science Thesis in Natural Resource Management

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Summary

This study examined what separates a crossing site from an available crossing site and investigate when and where roads are more likely to be crossed by moose (*Alces alces*). Five seasonal models for two sexes were selected using an information-theoretic approach based on Akaike's Information Criteria. Crossings were expected to be more likely during times of increased moose activity, and in areas of preferred moose habitat.

There were clear temporal effects of moose road-crossing probability, both within and between seasons: crossings were most likely to occur during the twilight hours. The influence of habitat and climate was much lower than expected, which lead to difficulties in creating spatially predictive statistical models. Nevertheless, high quality forage attracted crossings, while ruggedness, human disturbance and snow depth dissuaded them. It is therefore possible to predict spatially varying crossing probabilities across varying seasons, but it is difficult to produce management recommendations on this basis. Moose-vehicle collision-mitigating actions should therefore be focused on the temporal scale and management of the moose population density.

Introduction

Moose-vehicle collisions (MVCs) are a growing problem in Norway. Over two thousand moose are killed per year as a result of these collisions (SSB, 2011). Drivers often suffer vehicular- and bodily damage, at times mental trauma, and in a few cases per year death. A prime natural resource, the moose population is in this way becoming an increasing cost to society, as well as suffering decreased welfare themselves. The region of Nord-Trøndelag is experiencing both a historically high population density of moose and about 200 annual MVCs (Solberg et al., 2009), and the need for further mitigating measures is sure to increase as road networks expand and traffic density increases (Groot Bruinderink & Hazebroek, 1996).

Three elements combine to create a MVC; a moose and a vehicle occupying the same location at the same time, and a driver who is unable to prevent the collision. The probability of an MVC occurring can be expressed as P(MVC) = P(moose) + P(vehicle) + (P(evasion|crossing). These three elements are affected by several known factors. Road- and weather conditions can affect the driver's perception. This, coupled with the speed of the vehicle, affects the driver's evasion ability and the likelihood of turning an animal crossing into a collision (Van Langevelde & Jaarsma, 2004). While traffic density determines the frequency of vehicles, moose population density and habitat selection determine the spatial and temporal distribution of moose (Andersen & Sæther, 1996). The wildlife and transportation authorities primarily employ three actions to mitigate MVCs. The first is hunting, because moose population size has been shown to have a strong effect on MVCs, as more moose lead to more crossings and therefore more collisions (Joyce and Mahoney, 2001; Seiler, 2005; Rolandsen et al., 2012). The second is erection of wildlife fences, clearing of road-side vegetation, and establishment of feeding stations to draw moose away from transportation corridors (Solberg et al., 2009). The third is the setting of speed limits and the marking of certain stretches of road as 'high probability of moose crossing' with warning signs. This last action is both relatively cheap and highly visible (it is apparent to all who see the signs that local authorities have taken action regarding MVCs).

The setting of speed limits and the placement of warning signs rely upon the assumption that moose crossings of roads are not randomly distributed in space, but rather that there are certain areas where the moose are more likely to cross (i.e. 'hot-spots' of crossing). The identification and marking of these areas then becomes critical, both to ensure this precautionary information reaches the drivers and that the drivers have confidence in the validity of the warning signs' claims as to act upon them.

It has already been shown that moose movement rates and habitat selection varies greatly both spatially and temporally (Dussault et al., 2004; Herfindal et al., 2009; Lykkja et al., 2009; Nikula et al., 2004), and this is also likely to be the case for crossing site selection (Dussault et al., 2007). Human impact on the habitat quality of an area, such as increasing traffic density or decreasing distance to human disturbance, while not a direct predation threat nevertheless tends to drive moose away (Lykkja et al., 2009; Dussault et al., 2005). Regardless, increased traffic density is shown to have a strong positive effect on crossing and collision probability (Seiler, 2005; Danks & Porter, 2010). Collisions and crossings have also been found to be more likely to occur in areas with high quality forage (LeBlanc et al., 2005; Dussault et al., 2007), be it wild vegetation or farmland (Seiler, 2005). Dussault et al. (2007) also found that crossings were more likely to occur in valley floors, supported by the MVC studies that show a negative relationship between the ruggedness of the surrounding terrain and the probability of MVCs on a stretch of road (Seiler, 2005; Gunson et al., 2006; Hurley et al., 2007). Snow depth has also been shown to have significant correlations with the amount of MVCs (Gundersen & Andreassen, 1998; Rolandsen et al., 2010), fuelling the theory that moose may treat roads as snow-free movement corridors in winter, much the same way they use rails (Child, 1983). A summary of the spatial characteristics found to be related to ungulate vehicle collisions (UVCs) is shown in table 1.

Table 1: Direction of relationship between spatial predictors and UVCs.

Predictor type	Species	Effect on UVCs	Source
Animal-based predictors			
Population Density	Moose	+	Joyce and Mahoney, 2001; Dussault et al., 2006; Seiler, 2005; Rolandsen et al., 2011.
Terrain-based predictors			
Proximity to or proportions of forest stands	Moose, White-tailed deer, Mule deer, Red deer, Roe deer, wild boar	+	Bashore et al., 1985; Finder et al., 1999; Hubbard et al., 2000; Malo et al., 2004; Seiler, 2005; LeBlanc et al., 2005; Hurley et al., 2007; Danks & Porter, 2010.
Size or proportions of open areas	Moose, White-tailed deer	+	Hubbard et al., 2000; Seiler, 2005,
Proportion wetlands	Moose	-	Seiler, 2005.
Proportion agriculture	Moose, Wite-tailed deer	-	Hubbard et al., 2000; Seiler, 2005
Proportion, count or area of urban buildings	Moose, White-tailed deer, Mule deer, Red deer, Roe deer, Wild boar	-	Bashore et al., 1985; Nielsen et al., 2003; Malo et al., 2004; Seiler, 2005
Landscape diversity: Shannon's, Simpson's, count or ecotone presence	Moose, White-tailed deer, Mule deer, Red Deer, Roe deer, Wild	Mixed	Puglisi et al., 1974; Bashore et al., 1985; Finder et al., 1999; Nielsen et al., 2003; Malo et al.,

	boar		2004, Seiler, 2005; Gunson et al., 2009; Danks & Porter, 2010
Proportion or count of public land patches	White-tailed deer & Mule deer	+	Finder et al., 1999; Nielsen et al., 2003
Specific habitat use – presence of brackish pools	Moose	+	Dussault et al., 2004
Road based predictors			
Ruggedness of road-side topography	Moose, White-tailed deer, Mule deer, Red deer, Roe deer, Wild boar	-	Gundersen & Andreassen, 1998; Malo et al., 2004; Seiler, 2005, LeBlanc et al., 2005; Gunson, 2006; Dussalt et al., 2006; Hurley, 2007; Gunson et al., 2009
Presence, proximity to, and length of barriers & guardrails	White-tailed deer, Mule deer, Red deer, Roe deer, Wild boar	-	Malo et al., 2004; Gunson et al., 2009
Shortest visibility	White-tailed deer	-	Bashore et al., 1985
Traffic volume or Speed limit	Moose, White-tailed deer	+ (- for white-tailed deer)	Bashore et al., 1985; Seiler, 2005; Hurley et al., 2007; Danks & Porter, 2010
Road width	White-tailed deer	+	Hubbard et al., 2000
Presence or length of fencing	Moose, White-tailed deer	Mixed	Puglisi et al., 1974; Bashore et al., 1985; Seiler, 2005
Intersecting roads	Moose, Roe deer, Red deer, Wild Boar	+	Malo et al., 2004; Seiler, 2005
Riparian corridor, presence, proximity or count	Moose, White-tailed deer, Mule deer	+	Finder et al., 1999; Hubbard et al., 2000; Dussault et al., 2006; Gunson et al 2009.
Climatic predictors			
Temperature	Moose	+	Gundersen & Andreassen,1998; Rolandsen et al., 2010
Snow depth	Moose	+	Gundersen & Anreassen, 1998; Rolandsen et al., 2010

Temporally, moose are driven by time-dependent habitat selection, both within biannual cycles of migration and within daily cycles of forage quality and shelter trade-offs (Godvik et al., 2009; Bjørneraas et al., 2011). Crossing probability varies with time of day, but peaks during the twilight hours and remains high during the night (Neumann et al., 2012). More MVCs have also been found to occur at night than any other period of the day (Joyce and Mahoney, 2001; Solberg et al., 2009), but the effect of daylight on moose activity and crossing probability has not been separated from driver- or road impacts on MVCs, such as traffic volume, vehicle speed and driver visibility, which are all dependent on or highly correlated with amount of daylight. The overlap between the spatial and temporal effects further complicates the identification of crossing hot-spots, as the characteristics of one such spot may be highly local and be subject to seasonal change. Moreover, also considerable variation in MVC probability exists between moose individuals of different sex or age, and this too is subject to temporal variation, for example during the rut, during calving, or during the time of abandonment of yearlings (Groot Burinderink & Hazebroek, 1996; Danks & Porter, 2010). Additionally, there is a sex difference in the aforementioned daily patterns of habitat selection, as male moose select for greater forage quality and poorer cover quality than female moose (Bjørneraas et al., 2011).

The relationship between moose movement patterns, their daily to annual variations, and MVC components such as traffic density and habitat have already been examined on spatial scales ranging from municipal to regional (Solberg et al., 2009; Herfindal et al., 2009; Gundersen et al., 1998). Previous studies have predicted MVCs and/or crossings on the basis of collision (Seiler, 2005; Danks & Porter, 2010) or movement data (Dussalt et al., 2004; Grosman et al., 2010). Neumann et al. (2012), however, broke new ground and examined moose-road crossings and MVCs at an unprecedented level of combined spatial and temporal detail. Their approach was to compare two predictive models of MVCs. First, using moose movement data they created a crossing probability model. They then created a collision risk model based on recorded collision data. Comparing the two, they found that while movement data could be used to predict crossings on fine spatial and temporal scales, crossing probability alone proved a poor predictor for collisions. Nevertheless, a moose on a road is the first step towards creating an MVC, and management that deters crossings has the potential of reducing MVCs. To that end, this study will use moose movement data to predict moose-road crossings spatially and temporally.

Contrary to Neumann et al. (2012), this study is first and foremost a road-centred rather than behavioural study, as the characteristics of roads are easier for management authorities to manipulate than moose habitat selection or ranging behaviour. I therefore assume a representative sample from a homogeneous moose population and ask: "what impact do the characteristics of a road and its surroundings have on the probability of a given moose crossing a road?" In particular, I predicted that moose-road crossings were more likely to occur in periods of increased moose activity, such as during the twilight hours (P1). In addition, I expected moose-road crossings to be more likely to take place in areas with preferred moose habitat, i.e. areas providing forage during feeding, and areas with cover and fewer disturbances during rest (P2), and that road crossings will occur more often on less trafficked roads (P3), and in less rugged terrain, like valley bottoms (P4). During the winter season, I also expected an important effect of snow depth on the probability to cross a road, i.e. roads with a lot of snow around them will be crossed less (P5). Finally, I expected important sex differences, especially so because the forage-cover trade-off is different between the sexes (P6): Males will favour forage more than females, and females favour cover more than males, particularly in close proximity to human disturbance.

Methods:

In this study, I follow a similar approach as Neumann et al. (2012) and examine moose crossings at a high level of detail. Moose data are from the Norwegian Institute for Natural Research (NINA)'s Nord Trøndelag moose-collaring project, *Elgundersøkelse i Nord-Trøndelag, Bindal og Rissa* (Rolandsen et al., 2010). In this study, the movement of a large number of GPS-collared moose of both sexes were followed for several years, allowing for an examination of crossings on a fine spatial and temporal scale. In order to map the spatial and temporal patterns of crossings, I included all roads in Nord-Trøndelag and all crossing-relevant characteristics of every stretch of road with recorded moose crossings. My goal was to identify what separates a crossing site from an available crossing site and to investigate when and where roads were more likely to be crossed by marked moose. Throughout this study, crossing probability refers to the crossing probability of a moose given access to a road, or P(cross|road).

Study Area:

The Norwegian county of Nord-Trøndelag (22,412 km^2) is home to approximately 12,000 moose (Rolandsen et al., 2010). It is shaped by the predominantly south-west to north-east running fjords and valleys in the Caledonian mountain range. The coastal areas and lower altitudes are dominated by wide agricultural areas on top of ice-age silt and sand that range up to 200 meters above sea level. Further inland the landscape changes to broad, forest-rich valleys separated by low mountains. The Norwegian Sea and the Trondheim fjord buffer the climate, with monthly mean winter temperatures ranging from 0 to -10 degrees, up to only 13-15 degrees C in summer. Annual precipitation reaches 2000 mm in the coastal mountains, while the inner valleys are screened and seldom reach even half of this. Towards the eastern Swedish border the climate shifts to a typical continental climate with moderate precipitation and cold winters, the mountains grow to 1200-1500 meters above sea level, but only 2 % of the county's area has an altitude above 900 meters, making Nord-Trøndelag one of the least elevated counties in Norway. Nevertheless, nearly half (49 %) of the county lies above the border of economically productive forest. The forests are a heterogeneous mix of spruces, pines and birch, interspersed with sparsely forested bogs. The County is sparsely populated with a human population density of 5.9 per km^2, with population centres concentrated along the fjords and lakes (Store Norske, 2012).

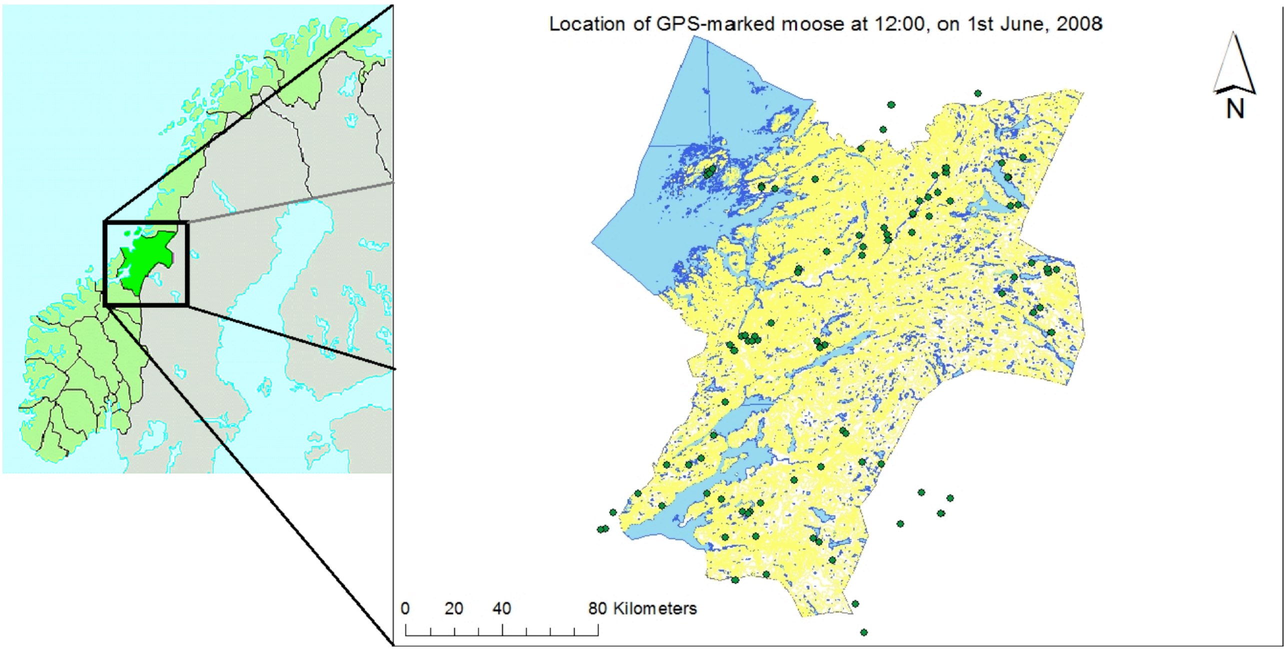

Figure 1. Distribution of GPS-collared moose in Nord-Trøndelag and surrounding areas.

Some of the moose in Nord-Trøndelag are migratory and cover vast distances during their two migration periods, moving between lower altitude winter habitat and higher altitude summer habitat to avoid snow and spatially follow the phenological development of plants, respectively (Hanssen, 2008). Fall migration in Nord-Trøndelag begins in late November and spring migration in May, averaged across age categories and sexes. However, roughly half of the population are resident and remain within a relatively small habitat for their entire lives (Rolandsen et al., 2010).
Moose in the region follow a circadian activity pattern with peak activity during the twilight hours, as the animals move between forage-rich feeding habitat and daytime resting areas with more cover (Rolandsen et al., 2010), in response to perceived predation risk and thermal stress (Dussault et al., 2004; Nikula et al., 2004; Lykkja et al., 2009).

Data collection:

GPS data from NINA's radio-collaring project in Nord-Trøndelag was used to measure movement patterns of the moose population. The animals were tranquillized from helicopter and then equipped with radio collars. Positions were recorded at 2-hour intervals from 2006 to 2010, and consist of over 2.1 million map-positions from 171 GPS-collars (Rolandsen et al., 2010). An example of the spatial distribution of GPS-collared moose is shown in Figure 1.

Individual variable:

Male moose are found to be overrepresented in MVC data (Joyce & Mahoney, 2001; Solberg et al., 2009), and accordingly, Rolandsen et al. (2010) found that the male moose in Nord-Trøndelag crossed public roads 1,4 times more often than females, on average every 4,6 days as opposed to every 6,6 days. However, movement-data based studies of moose-road crossings are often limited to a female-only analysis (Dussault et al., 2007; Neumann et al., 2012). I therefore included the recorded sex of the animals to test whether sex differences in the amount of crossings could contribute to the sex-bias in MVCs.

Temporal variable:

I also included light regime as an important explanatory variable, both as circadian light patterns follow moose activity levels and rates of movement, and as the value of spatial characteristics for moose such as cover vary with varying amount of daylight (Godvik et al., 2009; Lykkja et al., 2009; Neumann et al., 2012). To give me a good estimate of light regime, I used the R-package Maptools to calculate the angle of the sun relative to the horizon at the meteorological site in Levanger for crossing locations date and time. This allows me to precisely categorise the crossings by relative time of day, as light regimes vary according to the time of year.

Spatial variables:

The road network present on the Norwegian Mapping Authorities N50 maps (www.statkart.no) contained classes of roads. While roads are classified for administrative purposes, their classification is nevertheless highly correlated with traffic density (Solberg et al., 2009; Rolandsen et al., 2010). In the absence of direct measures, I therefore included the type of road at the crossing site as a proxy of traffic density, much like Neumann et al.'s (2012) 'major roads' and 'all roads' classification. The road classes in descending order of approximated traffic density are: European roads, National roads, County roads and Municipal roads (Table 2).

Digital Terrain Model (DTM) of Norway from the Norwegian mapping authorities (www.statkart.no) is a 25x25m representation of elevation above sea level. Altitude has been included in previous studies (Hurley et al., 2007) as moose migrate from areas of high altitude in summer to lower altitude in winter (Hanssen, 2008; Rolandsen et al., 2010), but to my knowledge has not been found significant for either crossings nor collisions. From this DTM I extracted both mean slope in degrees and mean standard deviation of the slope for each crossing location and buffer size. Mean slope and standard deviation of slope gives me a measure of the ruggedness of the terrain, known to affect moose movement patterns (Gundersen & Andreassen, 1998; Hurley et al., 2007).

Previous studies have shown a high correlation of moose avoidance of all forms of human disturbance. Therefore, distance to physical structures provides me with a fair measure of human disturbance even when not accounting for disturbance density (Malo et al., 2004; Seiler, 2005; Lykkja et al., 2009). The shortest distance to the nearest registered building was extracted from N50 maps for each of the crossing locations.

Ungulate space use is affected by both accesses to forage and cover during respectively feeding and resting bouts. Therefore, I created cover and forage categories based on Bjørneraas et al. (2011) and Rolandsen et al. (2010) vegetation categories. Using ArcMap 10, NORUT enhanced land cover maps (Northern Research Institute, www.norut.no) were combined with the more detailed vegetation maps of SATSKOG (Norwegian Institute of Forest and Landscape, www.skogoglandskap.no), based on LandSat satellite data. SATSKOG's data on dominant tree species, level of productivity and dominant age category were converted to 30x30m raster cells. These were then combined with the NORUT map of the same resolution. SATSKOG was given priority and replaced NORUT's vegetation data wherever the two maps conflicted. The resulting land-cover map divided the landscape into 25 categories, while all forest areas of the map were further divided into 15 categories according to age category and dominant species (Appendix D). These vegetation categories were further reclassified into two scales, one for quality of moose forage, and the other for quality of cover. Both scales ranged from 1 - open cover or poor forage, and through 2 - intermediate cover and fair forage, to 3 - full cover and good forage. These rough scales were based on Bjørneraas et al. (2011), Rolandsen et al. (2010) and E. Solberg's expert opinion on moose habitat preferences. My study thereby has the advantage of assigning both cover and a forage values to every forest stand, rather than making both these qualities mutually exclusive in one dimension. Additionally, forage and cover quality within buffers were in this way recorded as continuous, linear variables, rather than as categories, facilitating both the statistical modelling and interpretation of results. Because cover and forage characteristics of a stand can vary greatly throughout the year, I specified these characteristics by season. Scots Pine (*Pinus sylvestris* L.), for example, is an important winter browse species for the moose (Bjørneraas et al., 2011), and forests dominated by pine have a higher forage value in winter than in summer. I divided the year into five seasons, which I defined as: early winter from 16th of November to 15th of January, which is marked by winter's first heavy snowfalls, late winter from 16th of January to 15th of April, which is the period with most snow cover, spring from 16th of April to 15th of June, which is characterized by vegetation green-up and calving, summer from 16th of June to 15th of September, with high agricultural productivity and forage maturation, and finally, fall from 16th of September to 15th of November, the rutting and hunting season. This seasonal split is based upon expert opinion and reflects periods of varying moose activity and environmental conditions expected to be relevant for MVCs, namely the two periods of migration, the rut, calving and the dispersal of yearlings (Groot Bruinderink & Hazebroek, 1996; Danks & Porter, 2010; Rolandsen et al., 2010; Neumann et al., 2012). The result was four maps, one for each season and a combined winter map, of cover quality and four maps of forage quality, each with three categories of relative quality. This seasonal split had the added benefit of easing my analysis by avoiding time as a cyclical variable and allowing me a rough comparison between the different 'blocks' of the year without concerning myself with interactions between the various temporal variables. Using the 1.2 million crossing and available crossing points, I then extracted mean cover and forage values for each season and for each point from a buffer with 100m radius.

Spatio-temporal variables:

Temperature and snow depth have been shown to be highly correlated with MVCs (Gundersen & Andreassen, 1998; Solberg et al., 2009), and I wished to examine whether these spatio-temporal climatic variables had an impact on crossing probability. Additionally, Rolandsen et al. (2010) found a spike in MVCs occurring during the early snowfalls. As this would not be captured by the spatial distribution of temperature or snow depth, I included precipitation and used this together with temperature to differentiate between rain- and snowfall. Climatic data was taken from eKlima (Norwegian Meteorological Institute, www.met.no), where mean daily temperatures were extrapolated across a grid of 1km^2 squares. Daily estimates of precipitation and snow depth were also provided. All three of these variables were extracted by location on a point-by-point basis. The explanatory variables I extracted are shown in Table 2.

Table 2: Spatial variables measured at each crossing and available crossing site to model the factors that influence moose-road crossings in Nord Trøndelag.

Variable	Definition	Unit
Building	Distance to nearest human development	Meters
Cover	Mean cover quality within 100m buffer	Min 1, Max 3
Forage	Mean forage quality within 100m buffer	Min 1, Max 3
Precipitation	Mean daily precipitation extrapolated to 1 km^2 grid	Tenths of mm
Road type	Official road class. Proxy for traffic density	European, National, County, Municipal
SDslope	Standard deviation of the slope within 100m buffer	Degrees
Sex	Sex of animal, determined at collaring	Male or Female
Snow depth	Mean daily snow depth extrapolated to 1 km^2 grid	Tenths of mm
Solar elevation	Angle of the sun relative to horizon in Levanger at time of crossing	Degrees
Temperature	Mean daily temperature extrapolated to 1 km^2 grid	Degrees Celsius

Analyses:

The 2-hour locations from each moose could be linked into a continuous directional path map. I created the movement maps for each moose, and then subdivided these for each month. The result was a movement map showing all the directional movement of each moose within each month. Using kernel density estimation (KuD) I created a probability distribution for the presence of each moose (Figure 2). The 99.9 % contour of this distribution provided me with a rough estimate of each moose's monthly home range (Laver & Kelly, 2008). N50 maps from the Norwegian Mapping Authorities provided me with maps of Nord-Trøndelag's road network. Overlaying these contours with the road network from the N50 digital maps allowed me to create a 'crossing' point at each intersection of the moose directional movement lines and the roads. I then created 'available crossing points' every 30 meters along every piece of road that fell within each monthly home range (Figure 3). This enabled me to compare the recorded road crossing locations with all the potential locations where the moose could have crossed the road. I extracted the coordinates of the crossing locations and gave recorded crossings a value of 1, and the available crossing sites a value of 0. Every recorded crossing had a date and two-hour time interval when the crossing occurred; the available crossing sites were given a random date and time within the relevant moose month.

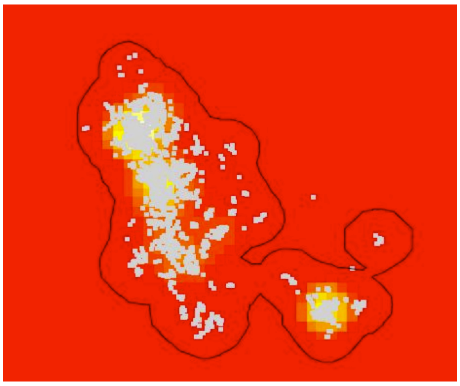

Figure 2: Example of home range estimated by the use of 99.9 % Kernel density estimation (KuD)

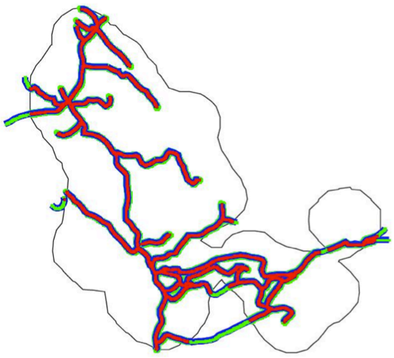

Figure 3. Example of road network overlayed on 99.9% KuD contour from figure 2. Available crossing sites in red

The study encompassed the temporal and spatial analysis of >3000 recorded crossings and >1 million available crossing sites using logistic regression and Akaike's Information Criterion (AIC; Burnham & Anderson, 2002) for model selection.

Statistical Modelling:

My first approach was to build relatively simplified statistical models without random individual

effects. Further research will have to address the validity of this first rough approach, as the analysis of residual-error structures fell outside the scope of this study. To limit the number of interactions, I opted to analyse both sexes separately and estimate all parameters for each sex. I selected the best fitting model based on backward selection from the full model using AIC (Burnham & Anderson, 2002). In addition, I evaluated the predictive power of the models using Receiver Operating Characteristics (ROC) (Hosmer & Lemeshow, 2000). The Area Under the Curve (AUC) of a ROC provides important information on the predictive power of a model. AUC values range from 0.5 to 1. To make interpretation of these AUC values more comparable to those of a R^2, I rescaled these values to range between 0 and 1 (i.e. rescaled AUC = 2*[AUC-0.5]). For each seasonal split separately, the theoretical full model was therefore defined as:
*P(crossing) = light conditions + traffic volume + distance to human disturbance + cover quality + forage quality + ruggedness of the terrain + temperature + precipitation + snow depth + (cover quality * light conditions) + (cover quality * traffic density) + (cover quality * distance to disturbance) + (forage quality * light conditions) + (snow depth * traffic volume) + (temperature * precipitation)* where the dependent variable is the probability of a moose crossing, given access to a road within the monthly home range. This is also referred to as P(cross|road) (as seen in figure 4).

The model contains six interactions which I expected to be important. First, as light conditions affect visibility and therefore the importance of cover, I expected an interaction between light conditions and cover. Second, because disturbance by humans increases perceived predation threat for moose, I included an interaction between cover quality and traffic volume, and a third interaction between cover quality and distance to human disturbance. Fourth, due to the circadian activity patterns of moose, which is tied to their rumination cycles, the attractive power of high forage quality vegetation depends on the moose activity and rumination stage. Therefore, I used light conditions as a proxy for activity levels, and predicted an interaction between light conditions and forage. Fifth, as deep snow impedes moose movement, roads could be treated as snow-free movement corridors; however, the extent of this will depend on traffic volume (hence, a snow – traffic volume interaction). And finally, rainfall *per se* is not expected to have as great effect on crossing probabilities. However, rain coming down as snow is expected to be important, I therefore also included the interaction between rainfall and temperature in the model. Due to the difficulties of modelling cyclical variables, I created a categorical variable to capture the variation between the rising and setting sun. Most of this variation was found within -6 and 12 degrees. The time between -6 and 0 degrees of solar elevation is defined as Civil Twilight. This period was split into dusk and dawn, for the setting and rising solar direction respectively. The time between 0 and 12 degrees was then defined as either morning or evening. This period is characterized by the presence of low light levels, and the absence of direct sunlight in most Nord-Trøndelag valleys. Any other time was assigned the label day (angle > 12 degrees) or night (angle < -6 degrees).

The full model was therefore written as follows:

P (crossing), binomial linear log regression= 6-level daylight factor + 4-level road type factor + (log distance to disturbance +1) + cover buffer + forage buffer + ruggedness SD of the slope buffer + temperature + precipitation + snow depth + cover * daylight factor + cover * road type factor + cover * (log distance to disturbance + 1) + forage * daylight + snow depth * road type factor + temperature * precipitation

This study is intended to be the first step toward unravelling one of the factors that combine to create an MVC (P(moose), P(vehicle), and P(Evasion|crossing)). Although stepwise selection has been the target of criticism due to inflated probabilities of type I errors (false positives) and AIC's tendencies towards overly complex models (Mundry & Nunn, 2009), it is nonetheless seen as a “necessary evil” when alternatives are lacking (Bolker, 2012) and remains widespread in use (Whittingham et al., 2006), for good or ill. At the very least, stepwise selection gives preliminary results that can, when interpreted with caution, be used as both indicators for future studies and illuminate gaps in existing knowledge.

Preliminary Analysis:

Initially, the spatial variables were extracted in four different buffer sizes: 100m, 500m, 1000m and 2500m. The two smaller sizes were intended to provide a high level of detail of the crossing sites, while the larger mimicked the home range size of the moose (Forman & Alexander, 1998; Danks & Porter, 2010; Hurley et al, 2007). However, after preliminary analysis revealed only minor variations between them, I omitted 500m, 1000m and 2500m from my final analysis in the interest of simplicity and brevity.

The literature reports little effects of altitude and in accordance my preliminary analysis did not reveal an important effect either; therefore, I opted to omit this variable from further analysis. This lack of effect in our analysis may be a result of most of the variation in altitude being a product of seasonal moose migration, which was fully captured in the seasonal split between models (i.e. there was little effect of within-seasonal variation in altitude). Additionally, the standard deviation of the slope proved a more robust predictor than the mean slope, which was therefore discarded.

I found that private roads were crossed more than public roads, but since there is little traffic and only 3% of MVCs occur on private roads (Rolanden et al., 2011), I chose to limit my study to the public roads in Nord Trøndelag. Upon doing so, I found that whilst there were more recorded crossings by male moose than female, when controlling for population sex bias female moose had less available road to cross and had a higher probability of crossing a road should they come across one (Figure 4). Building separate male and female models therefore made it possible to avoid any complex three-way interaction effects that would otherwise be present between sex, cover, forage, disturbance, road type and light conditions.

Due to the immense size of the dataset and the statistical power of any analyses, nearly every explanatory variable was significantly correlated with all others. The full correlation matrices can be found in Table 4 in Appendix A. Worthy of special note are the high correlations ($r > 0.828$) between forage and cover quality in early and late winter, because the same vegetation stands provide both high quality cover and the best quality forage available. During the other seasons, cover and forage are negatively correlated.

Results:

Sex differences:

Figure 4 indicates that the average male moose had access to more crossing sites within their monthly home range than female moose, and crossed more roads in every season. However, female moose crossed roads more than expected given their lower access to roads, resulting in a higher probability of crossing given a road, than males. When tested, however, there was no significant difference in absolute number of recorded crossings per individual between sexes: neither, on a yearly scale (Mann-Whitney U Test p-value, $P=0.271$) nor within each season (Mann-Whitney U Tests, p-values, $0.43<P<0.79$). Despite being unable to explicitly test for sex differences in my models, I find that the sex differences in habitat utilisation and predation pressure response are expressed in crossing site selection, as shown in the spatial results below.

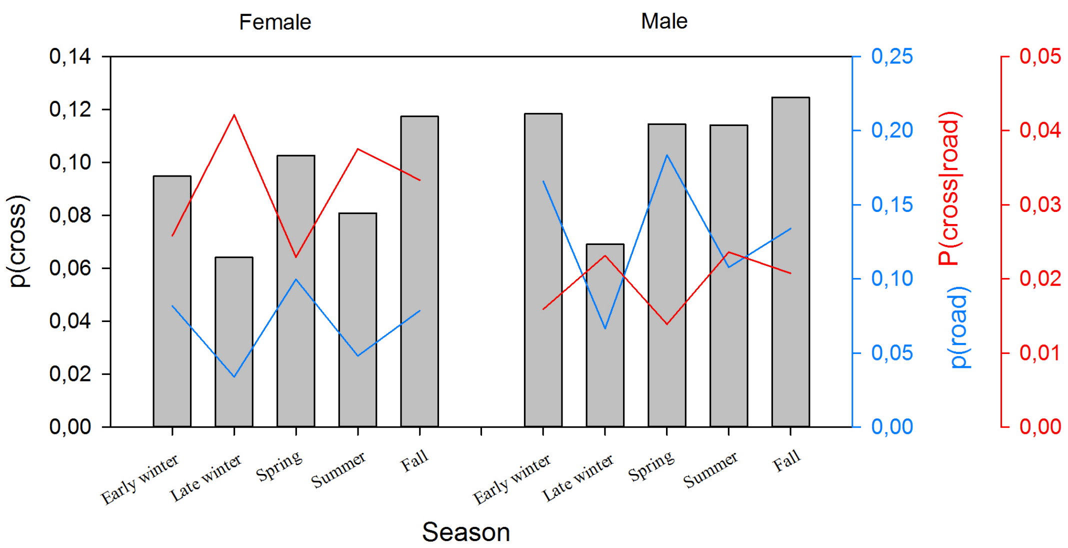

Figure 4. Crossings by female and male moose in different season. P(cross) is the proportion of registered crossings, controlling for population sex bias, sampling effort and collar failure. P(road) is the proportion of randomized available crossing sites, proportional to the length of road. P(cross|road) is the number of crossings divided by the number of available crossing sites. P(road) shows the variation in amount of road-crossing sites the moose had access to within the monthly home range. This and P(cross|road) together shape the pattern of p(cross). The focus of this study is on P(cross|road), how the probability of crossing given access changes both in space and time.

General patterns:

Visual interpretation of the spatial habitat characteristics of forage, cover and ruggedness showed varied relationships with P(cross|road) within each season (Figures 21-26 in Appendix B). Traffic density (as approximated by road type) and the distance to the nearest building both showed no strong relationship with crossing probability P(cross|road) (Figures 12-14 in Appendix B). The temporal and spatial variations in my spatio-temporal variables are not separated and are difficult to discern. Nevertheless, increased snow depth dissuaded crossings (Figures 15 & 16 in Appendix B). In general higher temperatures saw slightly increased probabilities of P(cross|road) outside winter (Figures 17 & 18 in Appendix B), while precipitation had no obvious relationship with crossings (Figures 19 & 20 in Appendix B). By contrast, the variation in P(cross|road) with changing light conditions showed a clear spike during twilight(-6 degrees to 6 degrees) and avoidance of the day (day>12 degrees) (Figure 11 in Appendix A). This led me to expect temporal variation to provide a better explanation for moose-road crossings than habitat characteristics or climatic measures.

Stepwise model selection of my theoretical full model for both sexes and five seasons yielded ten models. The results can be seen in Table 3 in Appendix A.
The light conditions at the time of crossing proved to have the greatest predictive power in my models, explaining nearly half of the model fit by themselves (light conditions only = 0.13<rescaled

AUC<0.39, best fit models = 0.35<rescaled AUC<0.53). AUC of light conditions peaked in summer, and was at its lowest in early winter, when Nord-Trøndelag is at its darkest. A plot of the yearly patterns of moose-road crossings revealed the high degree of temporal variation present between seasons (Figure 5). Regardless, several patterns were consistent across seasons: Crossings were more likely to occur during twilight and night, in forage-rich and less rugged surroundings not too close to buildings, on warmer days with no snow cover, and male moose were less likely to cross roads than females given equal access.

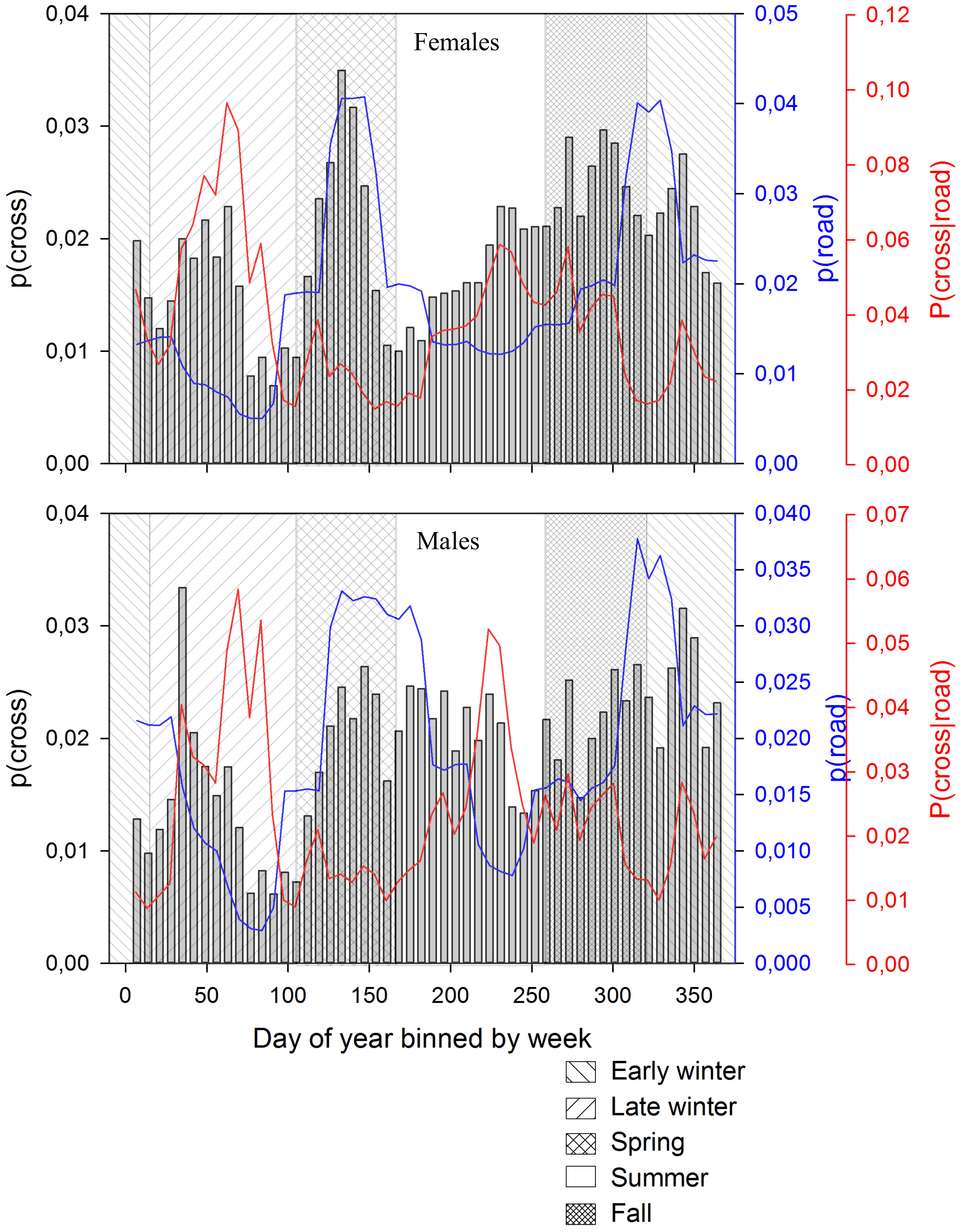

Figure 5. Crossings of male and female moose through the year. P(cross) is the proportion of registered crossings, controlling for population sex bias, sampling effort and collar failure. P(road) is the proportion of randomized available crossing sites, proportional to the length of road. P(cross|road) is the number of crossings divided by the number of available crossing sites. P(road) shows the variation in amount of road-crossing sites the moose had access to within the monthly home range. This and P(cross|road) together shape the pattern of p(cross).

Temporal patterns of road crossings

Road crossings were not evenly distributed throughout the year (Figure 5). Winter saw fewer recorded crossings than summer and fall, whilst in spring females experienced both a dramatic rise and fall in crossings, leading to a lower proportion of crossings in summer than males. The lowest number of crossings occurred between mid-March and mid-April, coinciding with the period of the year in which the moose have the smallest home ranges and lowest movement rates. There is also a sharp dip around day 150 in early June, which marks the peak of calving. These patterns are a result of two underlying individual differences; varying access to roads (p(road)) and varying crossing likelihood given a road (P(cross|road)).

The available crossing locations (and thereby available road) are extracted on a monthly basis. The month of March is clearly visible towards the end of late winter, as the period of the year where moose have the least amount of road within their home ranges (Figure 5). The amount of available crossing locations (p(road)) peaked in May and November. Although these are periods of low crossing probability given a road (P(cross|road)), the large amount of road available nevertheless resulted in a high number or recorded crossings (p(cross)).

For equal access to roads there are a higher number of crossings in late winter and summer than the rest of the year (Figure 5). The probability of crossing given a road (P(cross|road)) peaks in March and August, periods with low access to roads and few actual recorded crossings.

Figure 5 shows how the probability of a moose crossing shifts throughout the year and is captured by the seasonal split of models. I therefore have reason to believe that the attractive or repulsive power of my spatial variables will shift with seasons, as my seasonal split captures the variation in both crossing probability and recorded crossings (p(cross)).

Circadian light conditions greatly affected crossing probability given a road for both sexes. Night was set as the intercept in the models, and day and morning were found to be negatively related to crossing probability compared to night (coefficient estimates, -3.4<day<-0.97, -2.55>morning<-0.87). Evening ranged from being negatively to positively related with crossings compared to night (-0.35 <evening<0.50), and was overall found to have higher probabilities of crossings than its solar elevation counterpart: morning. Dusk and dawn were in some seasons found to positively relate to crossing probability with night as the intercept, but in others showed no significant difference compared to night (-0.83<dusk<0.98, -2.0<dawn<0.67). As expected, increasing light led to a lower probability of crossing, regardless of the road-side habitat forage or cover quality (Figures 27 & 28 in Appendix C). However, these habitat features did impact crossing probability in interaction with light conditions. Day and morning in interaction with cover quality were found to have consistent positive relationships with crossing probability when compared to night in interaction with cover quality (Figures 6, 7, 8, 9 & 10).

In the female moose models, in all seasons besides early winter the period of civil twilight (dusk & dawn) had a higher probability of crossing given a road than any other time of day, regardless of whether the sun was rising or setting (Figures 6, 7, 8, 9 & 10). Early winter is centred on the winter solstice and is the season with the longest periods of darkness. While the rising and setting sun caused similar crossing probability patterns, they differentiated under approach to, during, and immediately after the twilight hours (Evening to Night vs. Night to Morning). There is a general trend across seasons for a higher probability of crossing at dusk just before sunset, and at night just before sunrise. A more detailed view of the untested patterns can be found in Figure 11 in Appendix A.

<u>Spatial patterns of road crossings</u>

An interaction effect was expected between forage quality and light conditions, but moose of both sexes tended to select crossing sites with high forage quality over those with low (coefficient estimates, 0.23<forage<1.00), and this selection was close to uniform throughout the solar day resulting in no significant interaction effect except for during fall and early winter for female moose (absence from Figures 6, 7, 8, 9 & 10). (Figure 27 in Appendix C shows the modelled relationships between light conditions and forage quality.)

The effect of cover is highly dependent upon the proximity to human infrastructures and is as expected stronger in females than in males: all the models of female crossing probability (and all male models except during summer) showed a significant interaction effect between cover quality and distance to disturbance (Figures 6, 7, 8, 9, & 10). Once cross-sections of this interaction are plotted out, we can clearly see how the negative relationship between cover quality and crossing probability persists at greater distances from human disturbance, while weakening at nearer distances (Figure 29 in Appendix C). The interaction of cover quality by distance to disturbance and crossing probability is greatest for females in spring, and lowest in early winter (coefficient estimates, -0.66<cover by disturbance<-0.28). Male moose, on the other hand, are only affected to a significant degree by the cover by disturbance interaction in early winter and in spring (absence from Figures 6, 7. 8, 9, & 10). The strength of this interaction is generally stronger in the female models than the male models (male coefficient estimates in spring = -0.32, and early winter = -0.19). Although cover was found to have a significant interaction effect with road type in all models, there is no uniform trend or pattern between seasons or sexes, as seen by the varied coefficient estimates in Figures 6, 7, 8, 9, & 10.

As expected moose were found to be less likely to cross roads that were surrounded by rugged terrain (coefficient estimates, -0.18<slope<-0.03, Figures 6, 7, 8, 9 & 10). During spring, females parted from the norm and ruggedness did not have any clear relationship with crossing probability, causing step-wise selection to discard ruggedness from the spring female model. Untested patterns of crossings and ruggedness can be found in Figures 25 & 26 in Appendix B.

Spatio-temporal patterns of road crossings

In six of the ten models, temperature and precipitation were found to have a significant interaction (see Figures 6, 8, 9, & 10). While precipitation alone is difficult to interpret (coefficient estimates, -0.007<precipitation<0.018), there is a marked split between daily average temperatures that allow for snowfall (<5 °C) and those where the precipitation must have fallen as rain (>10 °C) as can be seen in Figure 30 in Appendix C. Here we see that moose were found to be more likely to cross roads on days with warm rain than on snowy or clear days, and snowfall dissuaded crossings. The untested patterns of crossings and my spatio-temporal data can be found in Figures 15-20 in Appendix B.

Moose were found to have a higher probability of crossing public roads in areas and/or at times with less snow: snow depth was found to have a significantly negative relationship with crossing probability in the models. However, due to the measurement scale of the variables this is most readily visible in the standardized coefficient plots (Figures 6, 7, 8, 9 & 10). Increased snow depth generally discouraged crossings except for males in early winter, where no relationship was found in the interaction between road type and snow depth (Figure 31 in Appendix C).

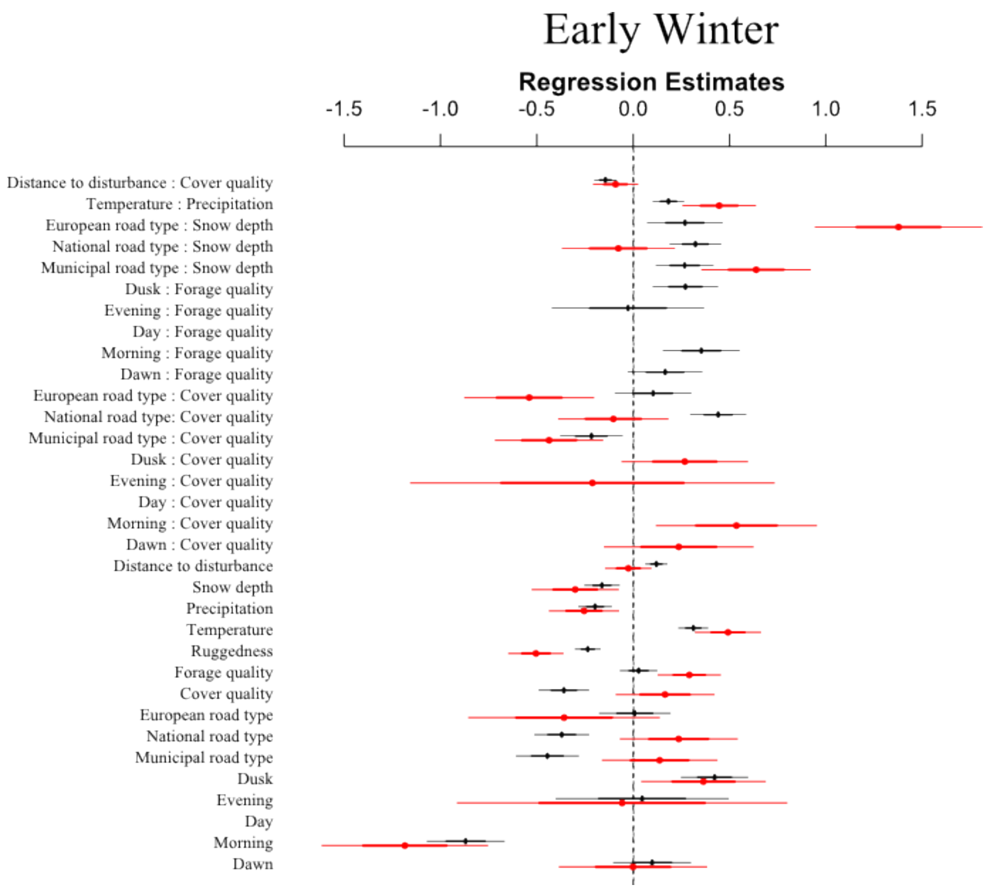

Figure 6 Standardized regression estimates for best fit model in early winter. Males in red.

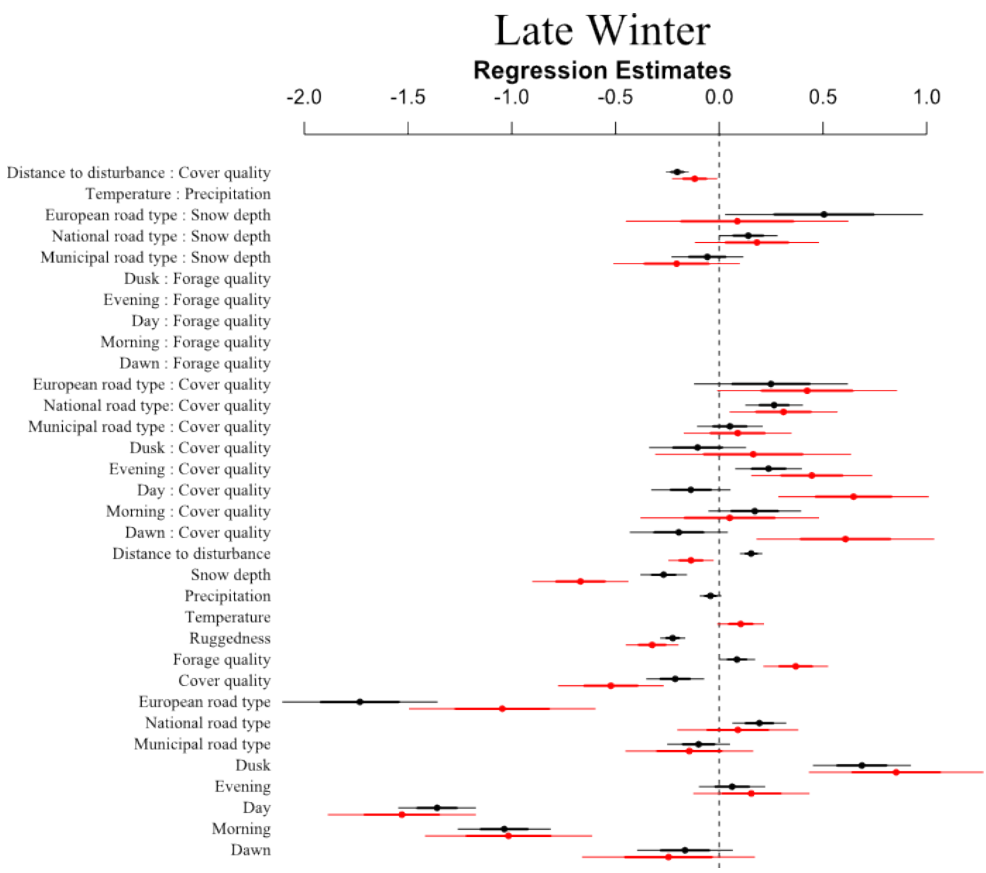

Figure 7 Standardized regression estimates for best fit model in late winter. Males in red.

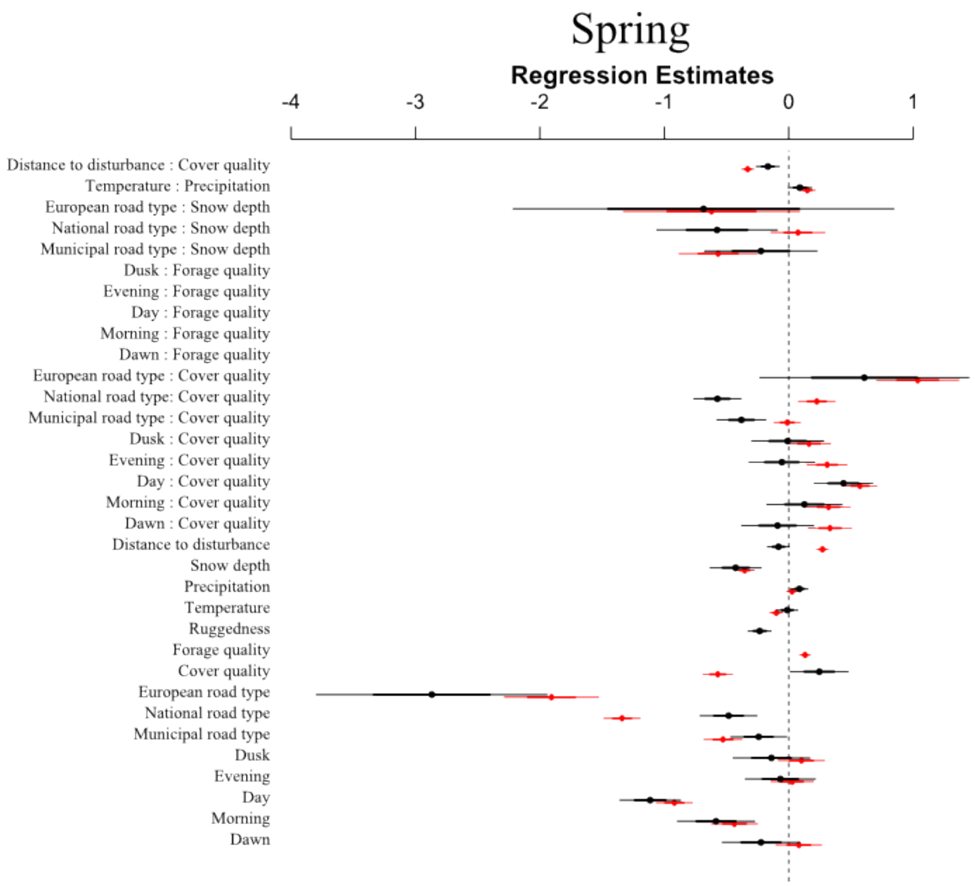

Figure 8 Standardized regression estimates for best fit model in spring. Males in red.

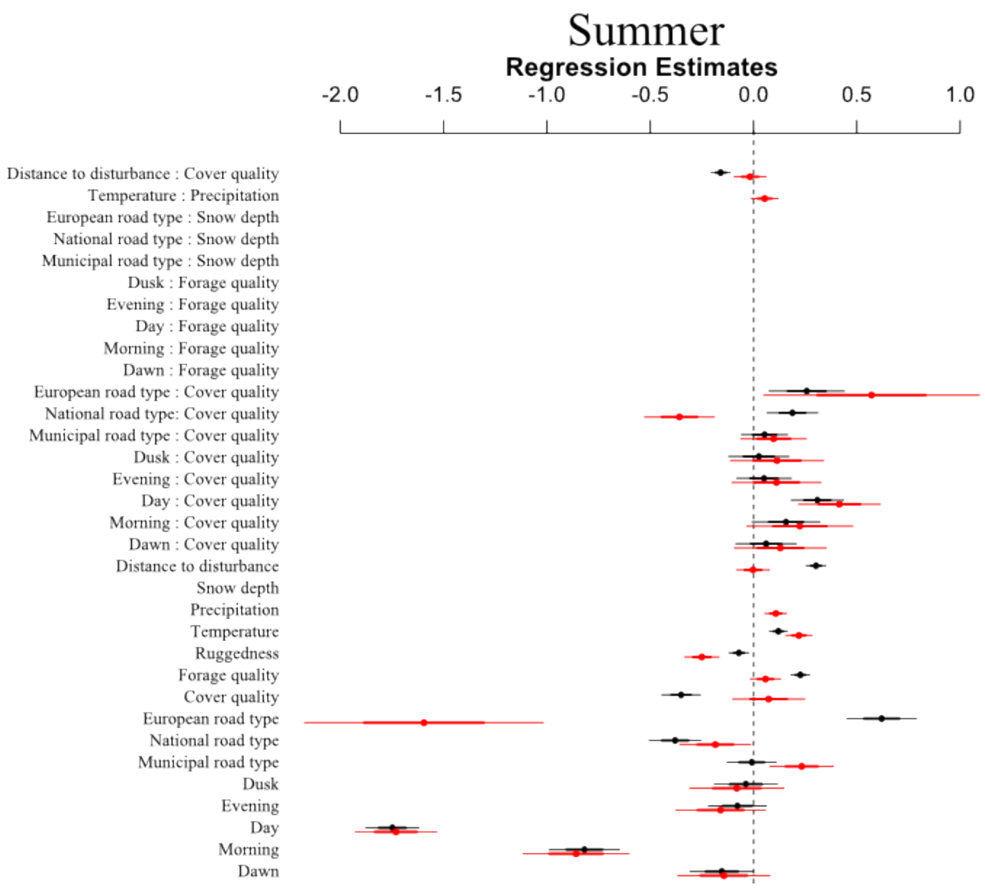

Figure 9 Standardized regression estimates for best fit model in summer. Males in red.

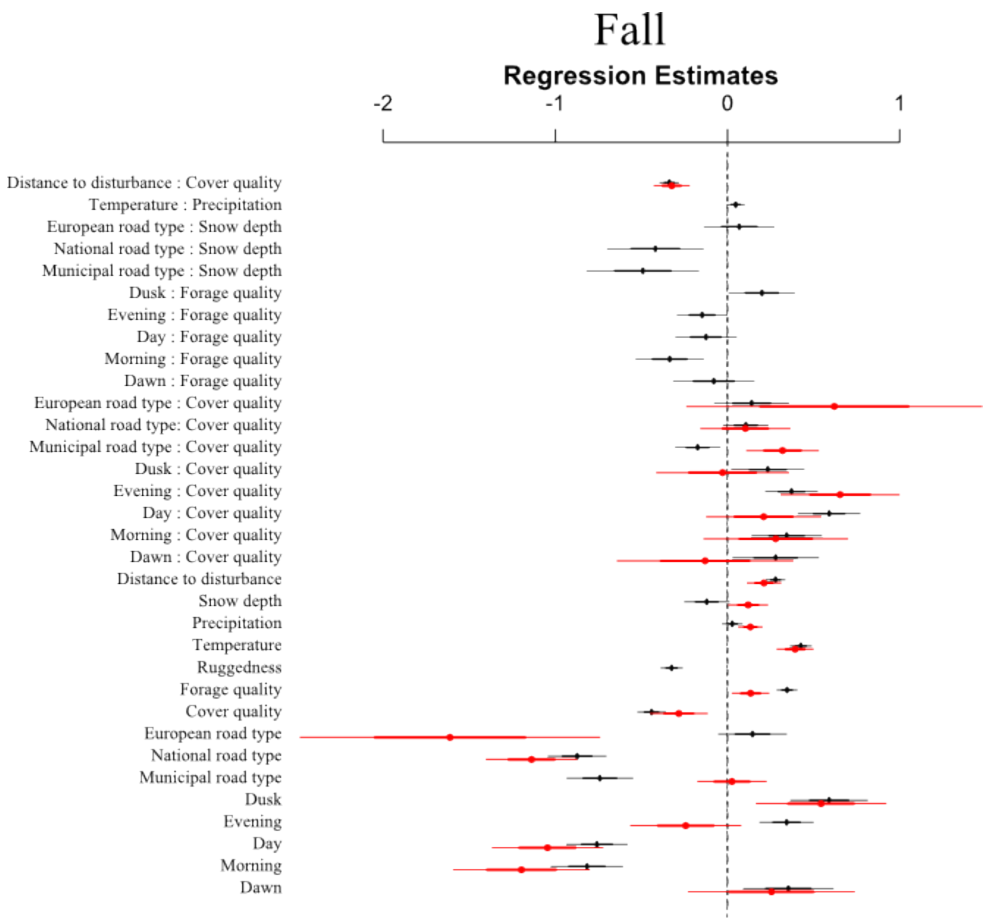

Figure 10 Standardized regression estimates for the best fit model in fall. Males in red.

Discussion

The intention of this study was to compare recorded road-crossing sites with stretches of road that were not crossed. This was carried out with the aim of examining whether crossings were more likely to occur in areas of preferred moose habitat, during times of increased moose activity, and to map how this might be subject to seasonal change.

The results showed that the seasonal split was justified, given the high degree of variation between the seasons observed in most of the explanatory variables (Figures 5, 6, 7, 8, 9 & 10). Initially, I expected the spatial habitat characteristics of a crossing site to carry a greater weight in determining the probability of a crossing, in line with prediction 2 (P2). However, the intra-seasonal circadian variation in light conditions seemed to be more important as it explained between one and two thirds of the seasonal variation in crossing probability. Both sexes of moose were most likely to cross roads during night and the twilight hours, and more likely to cross in the evening than in the morning in all seasons (Figures 6, 7, 8, 9, & 10, and Figures 27 & 28 in Appendix C). This supports my first prediction (P1) that moose would be more likely to cross during periods of increased activity. This allows for straightforward interpretations, unlike the remaining variation that is explained by a host of inter-connected spatial and spatio-temporal effects (Table 3 in Appendix A and Table 5 in Appendix C) which are more often than not confounded. The complexity of these effects limits the possibility of untangling the effect any one particular variable in these simplified linear models.

The results from the temporal data match those of Neumann et al. (2012) for female moose. The bimodal activity pattern, with higher rates of movement during the beginning and end of their daily foraging period, is clearly visible in temporal selection of crossing sites (Figure 27 & 28 in Appendix C). The marked males showed similar behaviour.
Crossing probability was not equally distributed around the daily solar maximum. Morning and dawn both showed consistently lower probabilities of crossing than their counterparts, evening and dusk (Figures 6, 7, 8, 9 & 10). As moose are roaming between different forage patches, I would hypothesise that this roaming behaviour through forage-rich areas would bring the moose into contact with roads, which are then potentially crossed, and that this roaming behaviour is first triggered and then intensified by the setting sun. Conversely, the rising of the sun should see a decrease in roaming behaviour and a more direct movement pattern towards areas of greater cover quality.
Hanssen (2008) found no significant difference in moose movement velocity between dusk and dawn, leading further credence to the hypothesis that my results could stem from the paths taken by the moose during their periods of increased activity. This lack of fit with civil twilight and the differentiation of the setting sun over the rising sun are details that could be of interest to authorities wishing to control or mitigate the effects of moose-road crossings.

I found support for prediction 2 (P2) that moose were more likely to cross in areas of preferred habitat, although the results are not as clear as those for prediction 1(P1) (Figures 27, 28, 29, 31 & 32 in Appendix C). Forage does indeed play a significant role in the probability of a site to become a crossing site in Nord Trøndelag. Increased forage quality increases the risk of crossing for both sexes (Figure 27 in Appendix C). Crossings were always more likely during the night and twilight than during the day, but the selection for forage quality was roughly uniform throughout the solar day, resulting in no significant interaction effect apart from during fall and early winter for females (Figures 6 & 10, and Figure 27 in Appendix C). Seiler (2005), LeBlanc et al. (2005), Hurley et al. (2007) and Danks & Porter (2010) all found a significant effect of the surrounding terrain's forage quality on the probability of MVCs. Despite the exceptions, the absence of significant interaction effects and the consistent positive relationship between forage quality and crossing probability nevertheless shows that forage quality is the most reliable spatial predictor of crossing probability in this study. However, the overall probability of crossing still depends heavily on season and time of day.

Moose appear to come into contact with roads, which are often crossed during periods of increased moose activity. In other words, while roads are not preferred habitat for the moose and are treated as temporary obstacles (Dussault et al., 2007), they do not deter the moose from their foraging behaviour or direct them into less forage-rich habitats. I did not find Seiler's (2005) threshold of traffic density at which roads become major obstacles. Only males showed any consistent preference for public roads with less approximated traffic density (Figure 32 in Appendix C). Road type was a significant predictor of moose-road crossings, but its effect on crossing probability for females perhaps suggests that the road types are not ordered by traffic density after all. This is likely due to the administrative rather than scaled classification of road type, which leads to road type being a poor proxy for traffic density.

The results supported the third prediction (P3), with rugged terrain being found to dissuade crossings for both sexes and in all seasons apart from females in spring (Figures 6, 7, 8, 9, & 10). Dussault et al. (2006) also found this relationship between ruggedness and moose-road crossings, while Seiler (2005) and Hurley et al. (2007) found that increased ruggedness decreased the number of MVCs. This information could direct the attention of road management authorities to the least rugged road-sides of Nord-Trøndelag; the valley floors and agricultural areas.

Temporal variation proved a better predictor for moose-road crossings than spatial variation, as shown above. However, the spatial resolution of the results here is limited by the sampling design, because moose may shift habitats within their monthly home ranges, for example from areas of higher altitudes to areas of lower altitudes in response to increasing snow depth which hinders foraging (Gundersen & Andreassen, 1998). This behaviour shows no major difference between migratory and stationary moose. When the first snowfalls occur, both types move down the altitude gradient (Rolandsen et al., 2010) into the lower reaches of their monthly home ranges, the same valley floors that are home to public roads with high traffic density.

Prediction 5 (P5) was supported in that snowfall, low temperatures and deep snow during early winter all decreased the probability of crossings (Figures 30 & 31 Appendix C). Nevertheless, this period of the first snowfall in November and December is both the yearly peak of MVCs (Solberg et al., 2009; Rolandsen et al., 2010) and shows a high number of recorded crossings(p(cross)), something that also occurs during spring (Figure 5). Both these periods show moose occupying

road-rich habitats, but that they do not show a preference for crossing roads at these times over others (P(cross|road) in Figure 5). An increased number of moose in habitats that are increasingly nearer roads results in more recorded crossings, rather than an increased probability of crossing for the individual moose. Rolandsen et al. (2010) also found that the amount of GPS-locations within 100m of a public road reached their annual peak in early winter. The question is then posed, if early winter and spring both show a high number of crossings and access to road, why do MVCs peak in only the former? With traffic density nearly 50% higher in summer than in winter in Nord Trøndelag, it is clear that neither crossings nor traffic density alone cause MVCs. Rolandsen et al. (2010) suggested that early winter sees an overlap of the circadian peaks of moose activity and the peaks of daily traffic volume, while in summer they are temporally separated. Hanssen (2008) found that moose activity levels, despite temporal shifts from late spring through summer and early fall, continuously peaked outside times of high human activity. As light levels dictate moose activity levels, this temporal split is clearly visible in my results by the continued high probability of crossings during twilight, though the time of twilight changes through the year (Figures 27 & 28 in Appendix C). Additionally, light conditions impact a driver's ability to avoid turning a crossing into a collision (Van Langevelde & Jaarsma, 2004), leading to an expectation of a higher number of MVCs in the darkness of the Scandinavian winter.
I therefore suggest that the 'snow effect' of the first snowfall on MVC probability is not an effect of increased crossing probability, but is mainly a product of increased density of moose near roads combined with higher traffic densities during the peak activity periods of moose in winter. It is also a season where the complex spatial and spatio-temporal variables explain more variation in crossing probability than any other season, weakening predictions based on light conditions alone. Possibly, this is related to on-going fall migration, weakening the predictive power of habitat characteristics as moose move directionally from one area to another, rather than around a local area.

I predicted that sex differences in cover and forage priorities would be reflected in crossing probability (P6). Although finding no significant sex effect on crossings within each season or on the yearly scale simple comparisons (Figures 6, 7, 8, 9 & 10) indicated that sex differences in habitat utilisation might have been present in a combined model. Cover, for instance, had a greater effect on females than males. The interaction effect between distance to disturbance and cover clearly shows how selection for crossing sites with cover increased with decreased distance to buildings (Figure 29 in Appendix C). The two sexes are commonly found to be differently affected by human disturbance, which may be perceived as predation risk by the moose (Frid and Dill, 2002). Accordingly, Lykkja et al., (2009) found that females avoided human infrastructure to a greater degree than males in Nord Trøndelag during summer, and in line with this, I found that female moose had crossed fewer road sites near (<100m) buildings than males (Figures 13 & 14 in Appendix B). In addition, I found females to show overall higher avoidance of human disturbance at crossing sites than males, although the effect was small compared to the effects of light conditions or road type(see Figures 6, 7, 8, 9 & 10). This may in part be due to my measurement of distance to disturbance, as all buildings were assumed a potential source of disturbance. However, a solitary and seldom-used forest cabin may be expected to differ significantly from that of a village centre or a busy household with respect to disturbance. Alternatively, it may be taken as support for prediction 6 (P6).

Moose are more active during night and twilight, when they prioritize forage over cover. Anything that affects the 'value' of cover, such as perceived predation pressure, therefore has limited effect on activity except during the day. Since increased activity is what results in crossings, we should not be surprised by the low predictive power of distance to disturbance on crossings. Cover was found to be more important during the day, as shown by the day by cover interaction coefficient estimates relative to night by cover (Figures 6, 7, 8, 9 & 10). The patterns in the interaction effects in Figure 28 (Appendix C) are difficult to interpret at first glance, because cover and forage are not mutually exclusive. Moose may be present in patches of intermediate cover and high forage, especially during winter when the same patches provide intermediate cover and the seasonal high of forage (Pearson correlations between forage and cover, early winter=0.836 & 0.835, late winter=0.828 & 0.843, for females and males respectively). The negative relationship between cover and crossing probability and the aforementioned reliability of forage quality therefore supports the importance of forage quality in moose habitat selection, as found by Bjørneraas et al. (2011). This further supports the hypothesis that moose may treat roads as obstacles, but that crossings simply occur in those areas the moose roam through: namely those of high forage quality.

Implications for management and potential areas for future study

The combination of both the spatial and temporal patterns of road crossings is necessary for any management authorities attempting to limit the number of MVCs, especially so as most mitigating actions are primarily deployed spatially through the placement of signs and the clearing of road-side vegetation (although Rea (2003) points at the varying impact of clearings at different times of the year). I have shown that moose-road crossings are relatively difficult to predict on a fine spatial scale. Given the aforementioned overlap between daily traffic volume and moose activity in winter (and absence thereof during summer), the importance of crossings alone for MVCs may be called into question. Indeed, Neumann et al. (2012) found that animal movement data alone was insufficient to predict collision risk. If temporal variation is what drives MVC probability, then management based on the fine spatial scale may be in need of re-evaluation. If the validity of a 'danger of moose-crossing' sign is time-dependent, then alternative strategies such as time-specific signs or increased public awareness of collision risk times could be worth examination.

While moose-road crossings are an irreplaceable component of MVCs, the probability to find a moose close to a road is also important. Studies exploring the effects of population density on MVCs (Joyce & Mahoney, 2001; Seiler 2005; Rolandsen et al., 2011) suggest that a larger spatial scale and a focus on the probability of a moose using an area (i.e. P(moose)) as opposed to the probability of a moose crossing, given a road (i.e. P(cross|road|moose)) may be an alternative way to capture the moose component of MVC variation.

Further study should be given to the other two components of MVCs, the probability of a vehicle on the road, P(car), and the reaction of the driver (i.e. P(evasion|crossing)). The temporal pattern of traffic density and its overlap with moose-road crossings has the potential of explaining the majority of MVC variation. While road type is shown to be a poor proxy for traffic density, and counting stations are few and far between, the importance of P(car) must not be overlooked.
My results showing the importance of forage and the weaker effect of cover may give reason to doubt the effectiveness of road-side vegetation clearing as a crossing-preventative measure. Rea (2003) found that vegetation clearing practices increased the forage quality of the road-side vegetation stands, potentially causing more crossings and MVCs. Unfortunately, the resolution of the digital vegetation maps used in this study do not allow me to capture variation between roads where vegetation clearing is practiced and those where it is not. Regardless of its potentially counter-productive effect on crossing probability, however, road-side vegetation clearing is thought to have the potential of increasing visibility and thereby driver reaction time (Gunson et al., 2009).

This study provides a general overview of various road-side characteristics and the seasonal changes in their influence on moose-road crossing probability. There is considerable potential for future research, and this study merely points at general trends and areas of interest. I would also point out two additional directions for future studies. First, the early winter season contains the majority of MVCs, a high number of crossings, and a lower than usual contribution of temporal explanation. An in-depth analysis into the effects of the first snowfall, the following migration and its changes in habitat and crossing site utilization and how these interact with winter traffic has the possibility of identifying precisely what makes this time of year so dangerous for road-crossing moose.

Secondly, the shift in crossing probability between the rising and the setting of the sun hints at distinct patterns in daily moose movement. Further study into how moose move during dawn and dusk, in conjunction with how moose treat roads during these different periods, might reveal why moose-road crossings are biased towards the setting sun, and in turn reveal whether dusk is a more dangerous time than dawn to be driving in Nord Trøndelag.

Reservations

These analyses of crossing probability may be limited by the sampling design. Male moose in Nord-Trøndelag have, on average, larger home ranges and faster movement rates than females (Hanssen 2008; Rolandsen et al., 2012). This could result in a larger amount of available crossing sites without necessarily increasing the rate at which the individual moose 'meets' a road. A sampling method that includes a measure of frequency of the GPS-locations to be within a certain proximity of roads, within each monthly home range sample to evaluate the relevance of each available crossing site, is suggested is being discussed regarding any further examination of the current data set. This would be similar to the Neumann et al. (2012) inclusion of all GPS-points within 1 km of a crossing site as available crossing sites, while retaining the road-centred focus of this study. This limitation could be critical for a causational behavioural study, but it may be questionable whether the effect on a road-centred study would be worthy of concern, or whether there are preferable alternative sampling designs.

Additionally, as mentioned with regard to the ‘snow effect’ (above), the sampling design concerning monthly home-range crossing site extractions did not afford the possibility to capture internal variation within each month. The amount of available crossing sites, p(road), is proportional to the length of road within each monthly home-range, but it does not differentiate between varying patterns of the road network within each home range. The inclusion of recorded kernel density use estimates in the models would provide a measure of each individual moose’s probability of encountering each crossing site, providing a measure of the movement patterns of each moose within every monthly home range.

Another issue to consider is that of spatial autocorrelation. There is only 30 meters between the road crossing points, the buffer zones therefore overlap other sampling points, as well as other buffer zones. Every sampled moose month is expected to be highly autocorrelated, both spatially and temporally, as the data points are not independent. Additionally, a crossing might have occurred at the same coordinates as an available crossing site, a problem common in habitat selection (Keating and Cherry, 2004). However the large number of available crossing points makes this a highly unlikely event. In line with Johnson et al. (2006), I can perhaps be confident that the occurrence of such a contamination will be low, and the potential bias in my results negligible.

The predictive powers of the statistical models were relatively good, but any interpretation was complicated and should perhaps be carried out with caution. Not only have they been subjected to information-based step-wise selection and are victim to a high covariance between certain explanatory variables, the very nature of the models is so conditional that they should only serve as an indicator of patterns, not as a clear predictive tool. In accord with the warnings of Mundry and Nunn (2009), it appears here that the use of information criteria and stepwise selection has led to the retention of explanatory variables that would otherwise have been found non-significant in a classic Wald-test (see the low estimates in Figures 6, 7, 8, 9 & 10).

As an initial study into moose-road crossings, this study strongly suggests that further work is necessary. The next step must be an investigation into residual patterns. The potential for systematic individual differences, as well as spatial and temporal autocorrelation in the model residuals has not been investigated. The models presented here remain preliminary at least until they are accounted for.

Conclusion

This study set out to explore what separates a crossing site from an available crossing site and to investigate when and where roads were more likely to be crossed by marked moose.
I found clear temporal effects of moose road-crossing probability, both within and between seasons, but the influence of habitat and climate was much lower than expected, which lead to difficulties in creating spatially predictive statistical models. As the results show, it is possible to predict varying crossing probabilities across varying seasons, but the differences in explanatory power are slight, and the impact of a single variable so difficult to trace, that it is difficult to produce management recommendations on this basis. The large-scale uniformity yet local variation of the landscape leads to further difficulties for fine scale spatial management. However, the way in which the moose respond to the landscape was subject to high temporal variation. I have shown that while spatial prediction cannot be recommended, I am able to predict the effect of changing seasons and time of day on the probability of moose crossings. My management recommendation is therefore to focus MVC-mitigating actions towards the temporal scale and management of the moose population density.

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Appendices table of contents:

Appendix A: Model selection results and light conditions

Table 3: Model selection results:

Early winter

Sex	Model	AIC	ΔAIC	# Parameters	AUC rescaled to 0-1
Female	Full fit	12712	6	34	
	Stepwise	12706	0	26	0,35
	Light conditions	13108	402	1	0,13
Male	Full fit	4187	6	34	
	Stepwise	4181	0	26	0,43
	Light conditions	4373	192	1	0,14

Late winter

Sex	Model	AIC	ΔAIC	# Parameters	AUC rescaled to 0-1
Female	Full fit	12851	6	34	
	Stepwise	12845	0	26	0,42
	Light conditions	13279	434	6	0,26
Male	Full fit	4540	20	34	
	Stepwise	4530	0	26	0,53
	Light conditions	4862	332	6	0,26

Spring

Sex	Model	AIC	ΔAIC	# Parameters	AUC rescaled to 0-1
Female	Full fit	18003	6	34	
	Stepwise	17997	0	27	0,47
	Light conditions	19091	1094	6	0,24
Male	Full fit	7091	11	34	
	Stepwise	7080	0	27	0,48
	Light conditions	7412	332	6	0,25

Summer

Sex	Model	AIC	ΔAIC	# Parameters	AUC rescaled to 0-1
Female	Full fit	16986	12	34	
	Stepwise	16974	0	22	0,5
	Light conditions	17444	470	6	0,39
Male	Full fit	8699	13	34	
	Stepwise	8686	0	24	0,49
	Light conditions	8907	221	6	0,38

Fall

Sex	Model	AIC	ΔAIC	# Parameters	AUC rescaled to 0-1
Female	Full fit	14401	0	34	
	Stepwise	14401	0	34	0,53
	Light conditions	15749	1348	6	0,20
Male	Full fit	4961	12	34	
	Stepwise	4949	0	23	0,48
	Light conditions	5202	253	6	0,22

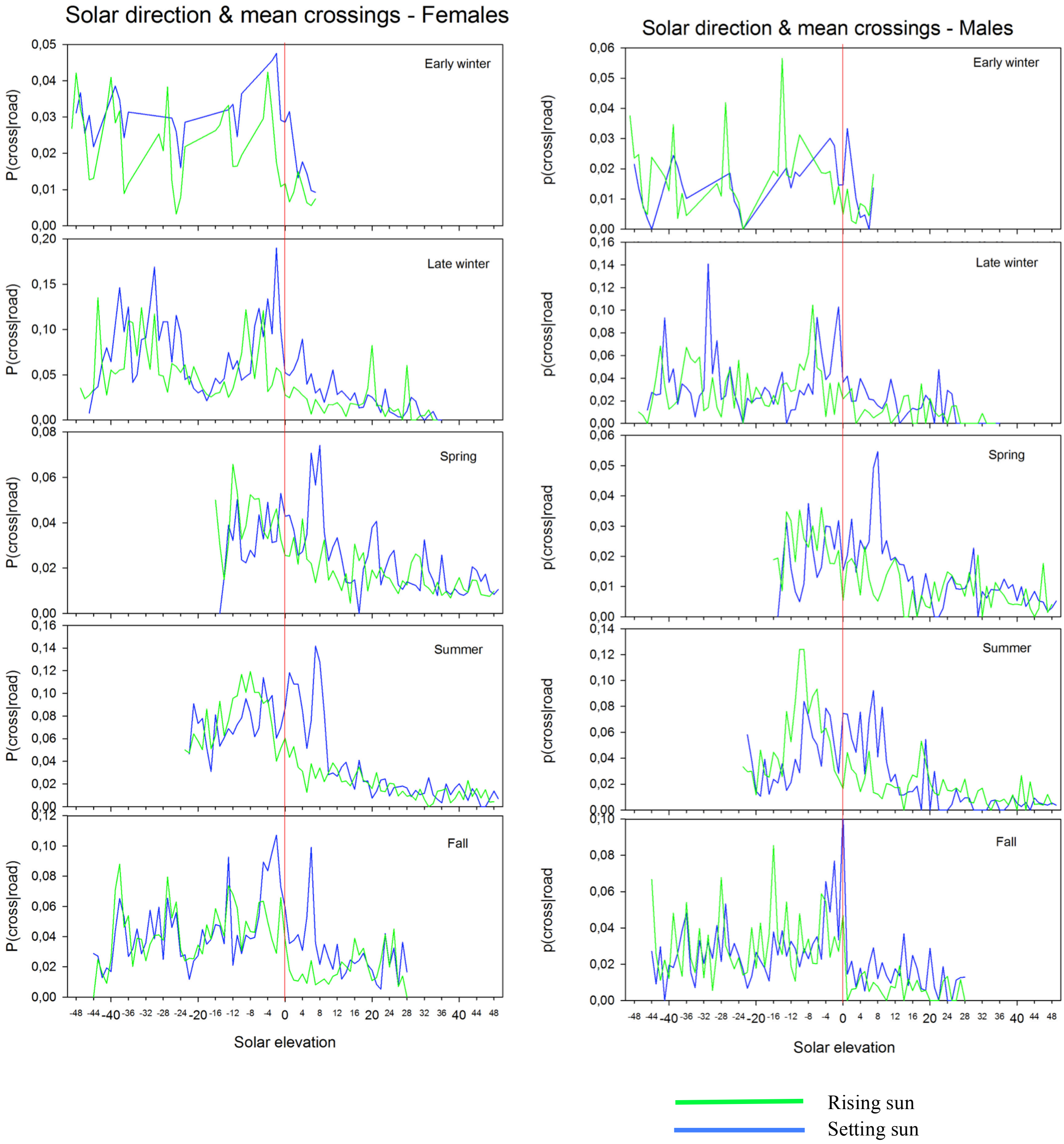

Figure 11. Mean crossings, P(cross|road), versus the rising and setting sun. Mean crossings is the sum of recorded crossings divided by the sum of potential crossing sites within the monthly home range... The red vertical line marks sunrise and sunset, at 0 degrees solar elevation.

Early winter is symmetrically distributed across the winter solstice, while every other season is asymmetrically related to the nearest solstice. Early winter is therefore a season with less change in daily solar elevation cycles than any other season. Since our data points are recorded at two-hour intervals, the lack in intra-seasonal variation in solar elevation leads to the segregated solar elevation estimates and is the cause of the sharp spikes and dips visible in the early winter figures.

Appendix B: Descriptive patterns.

Data presentation

In keeping with the road-centred focus, I plotted the internal variation in moose crossing probability within each of my recorded variables. The distribution of recorded crossings is influenced by four factors: (1) the probability of a moose having access to a road, (2) the probability of that moose crossing a road given access, (3) the movement speed of the moose and (4) the pattern and shape of road distribution within the monthly home range. To shed light on some of these underlying factors, I plotted the two road-centred p(road), P(cross|road) and their combined influence in p(cross) for my variables in Figures 12 through 26.

All figures were given three y-axes;
p(cross) – The proportion of registered crossings.
p(road) – The proportion of randomized available crossing sites.
P(cross|road) – The number of crossings divided by the number of available crossing sites

p(cross) - Proportion of recorded crossings within each bin. For temporal variables I divided by the number of GPS locations registered that day. This controls for temporal sampling effort and potential collar failure. I do not expect this temporal bias to be present in my spatial data, as collar failure and temporal sampling bias is not biased with respect to region and other spatial characteristics. In figures, the total area under the bars on the plot sum to one.

p(road) - Proportion of available crossing sites within each bin. This is a rough estimate of probability of being close to road, as available crossing sites are recorded every 30 meters along all roads in each moose's monthly home range, the count is proportional to the length of road. For temporal variables I controlled for sampling effort and collar failure. In figures, the area under the curve sums to one.

P(cross|road) - This measure, or mean crossing value, is the probability of crossing given a road. As the number of available crossing sites is proportional to the amount of road within the monthly home range, I can control for individual differences in road amount within home range by dividing the number or recorded crossings (controlling for number of GPS locations) by the number of available crossing sites within the same variable value bins.

The resulting figures revealed the patterns present in the data and served as basis for the statistical models. However, care should be taken with any interpretation, because the lack of a uniform error estimate leaves only the central tendencies reliable. Any patterns in crossing probability not rooted in a solid proportion of available crossing points should be ignored. Additionally, the many different pieces of software involved have resulted in a schizophrenic use of both comma and point as decimal delimitation in the figures. I apologize for any confusion this may cause.

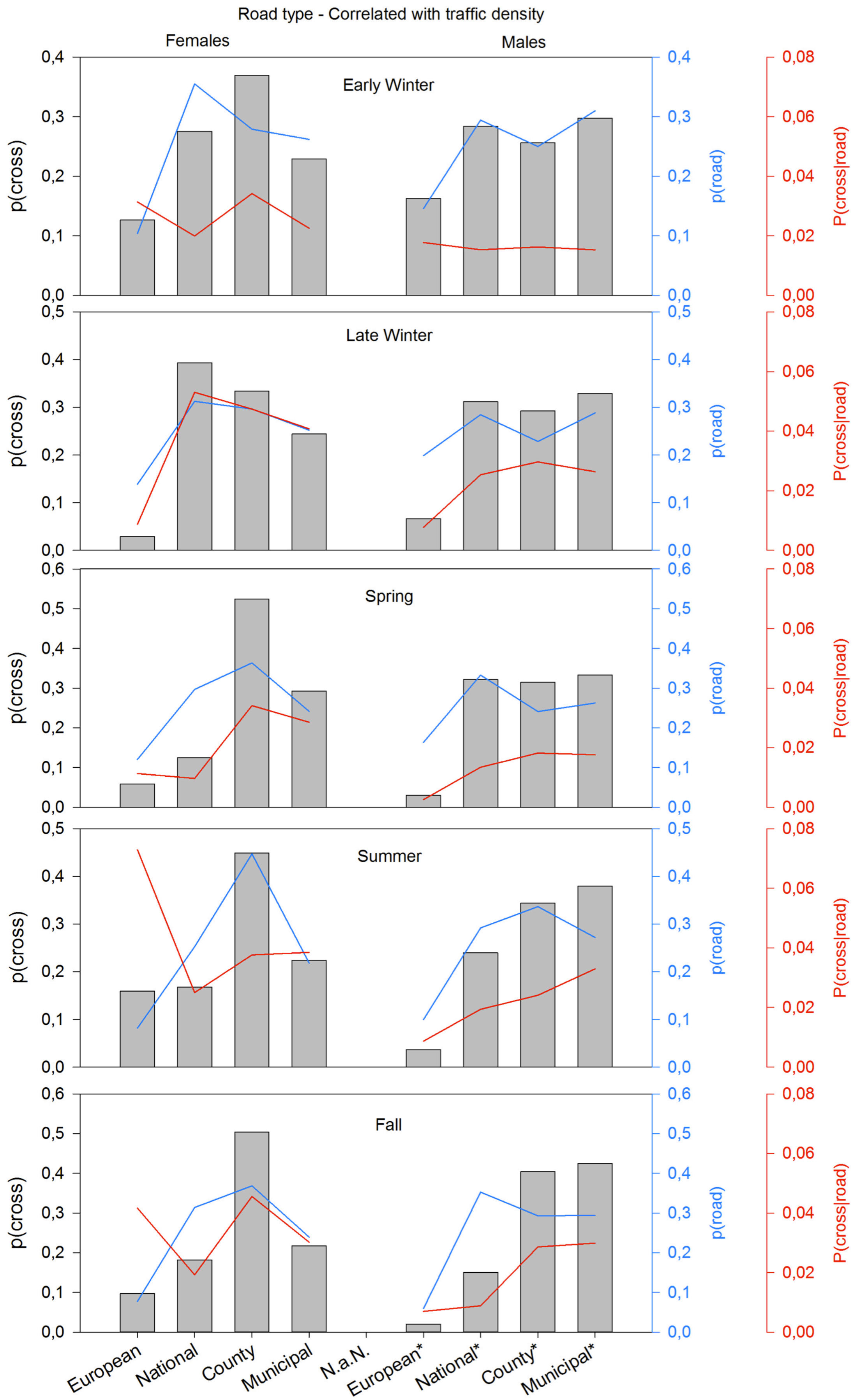

Figure 12. Crossings & Public Road Type, a proxy for traffic density. Road types are sorted in ascending order of assumed traffic density

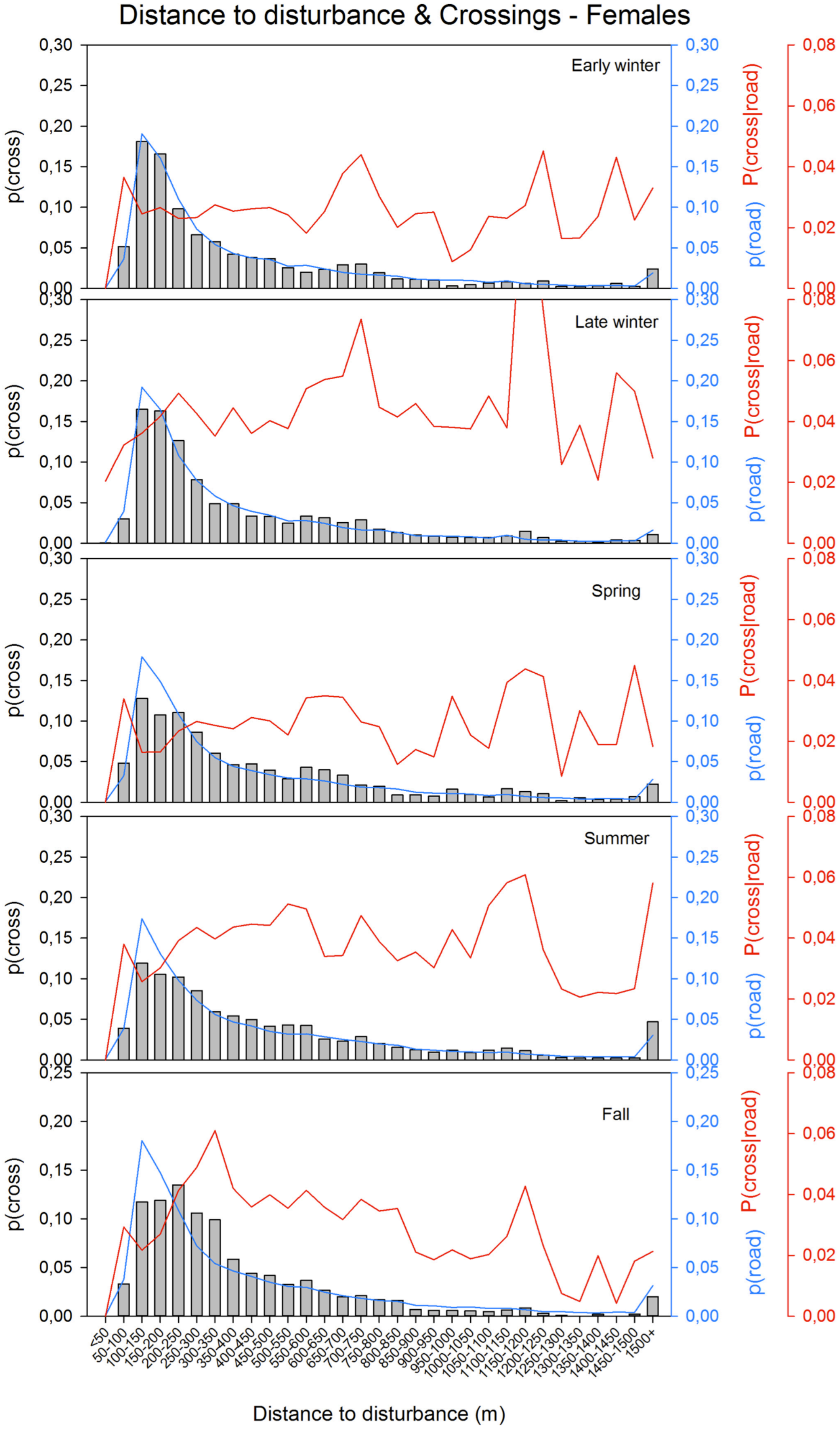

Figure 13. Crossings & Distance to nearest human construction. Females.

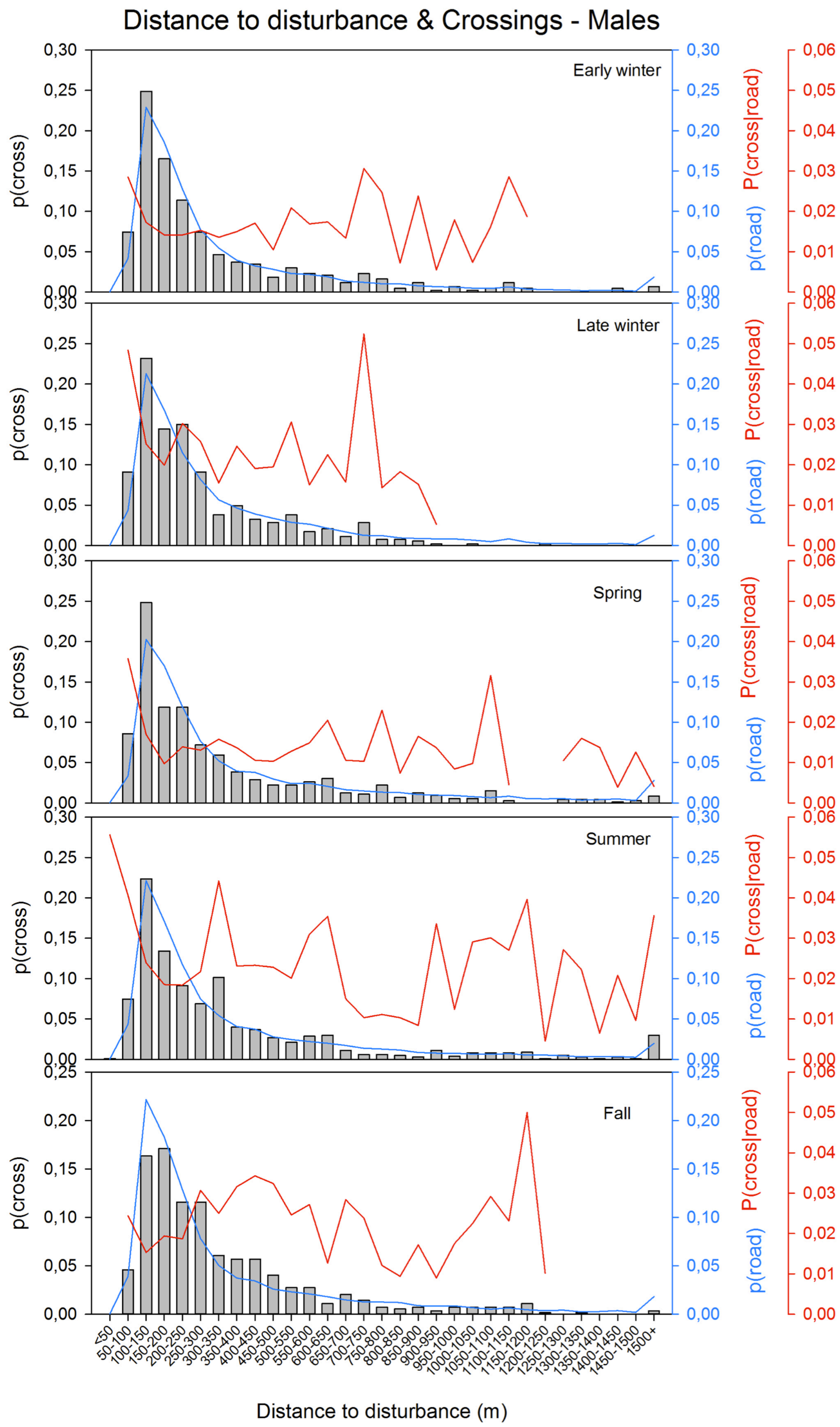

Figure 14. Crossings & Distance to disturbance. Males

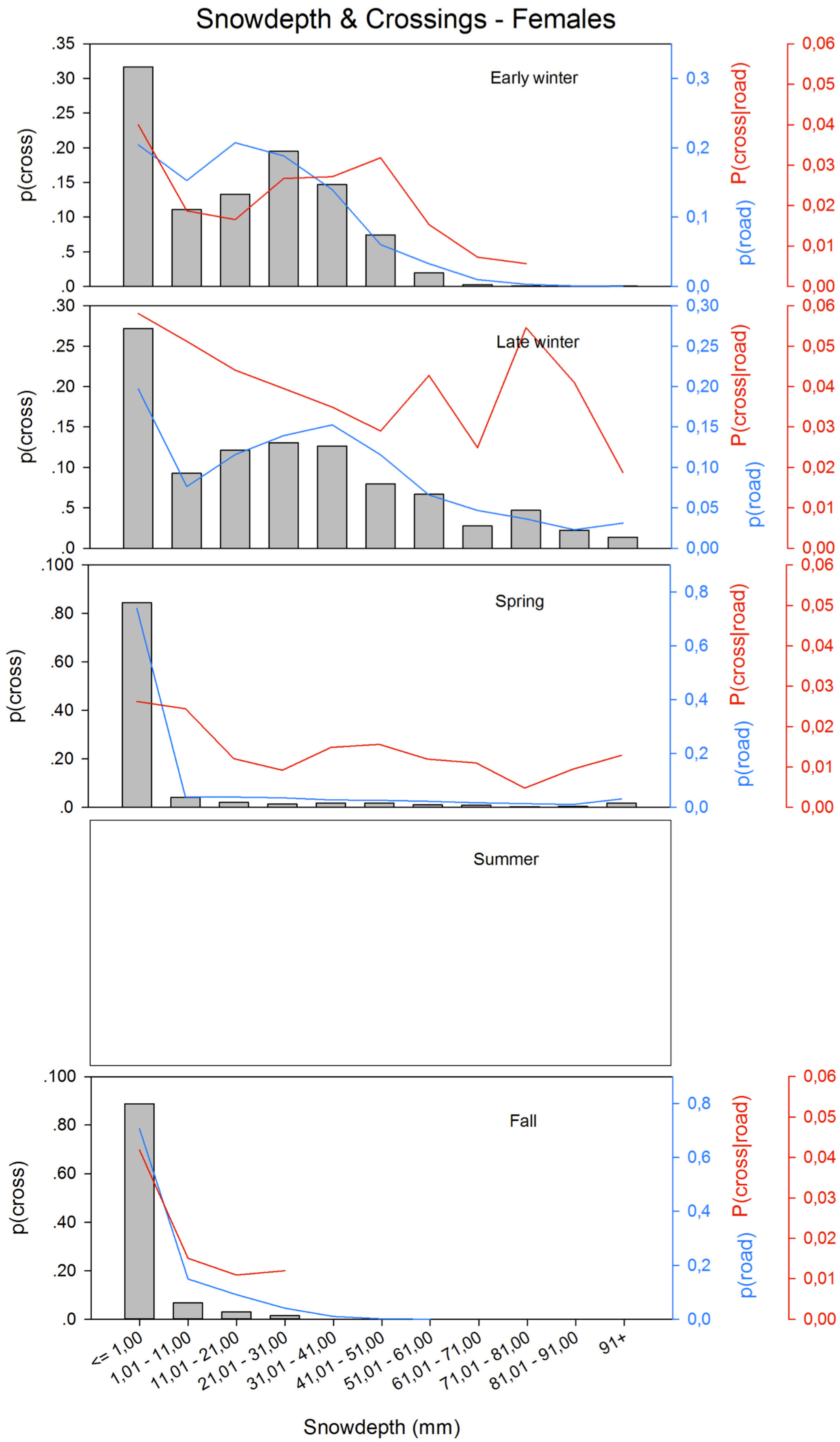

Figure 15. Crossings & Daily Snow Depth. Females

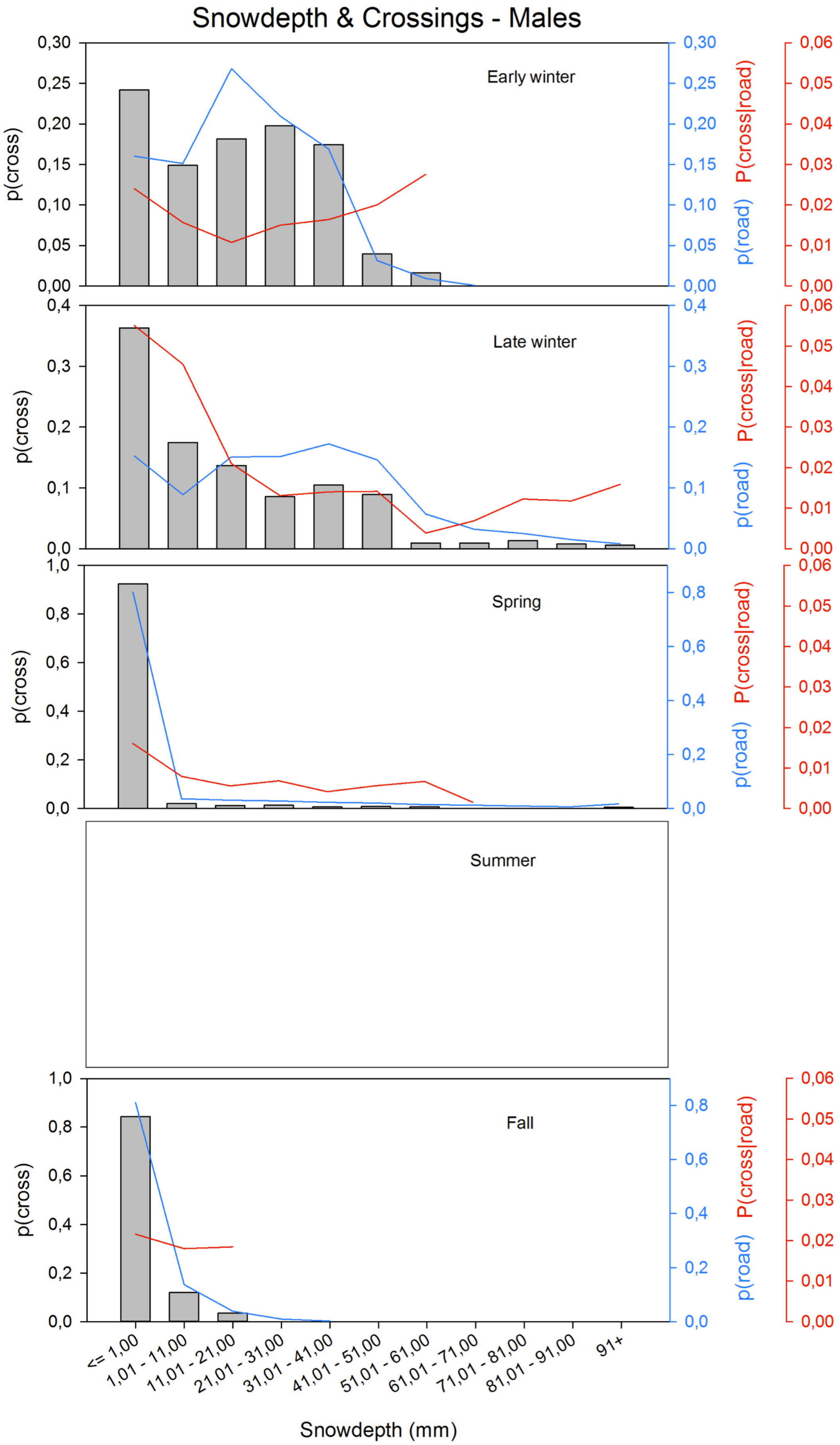

Figure 16. Crossings & Snow Depth. Males

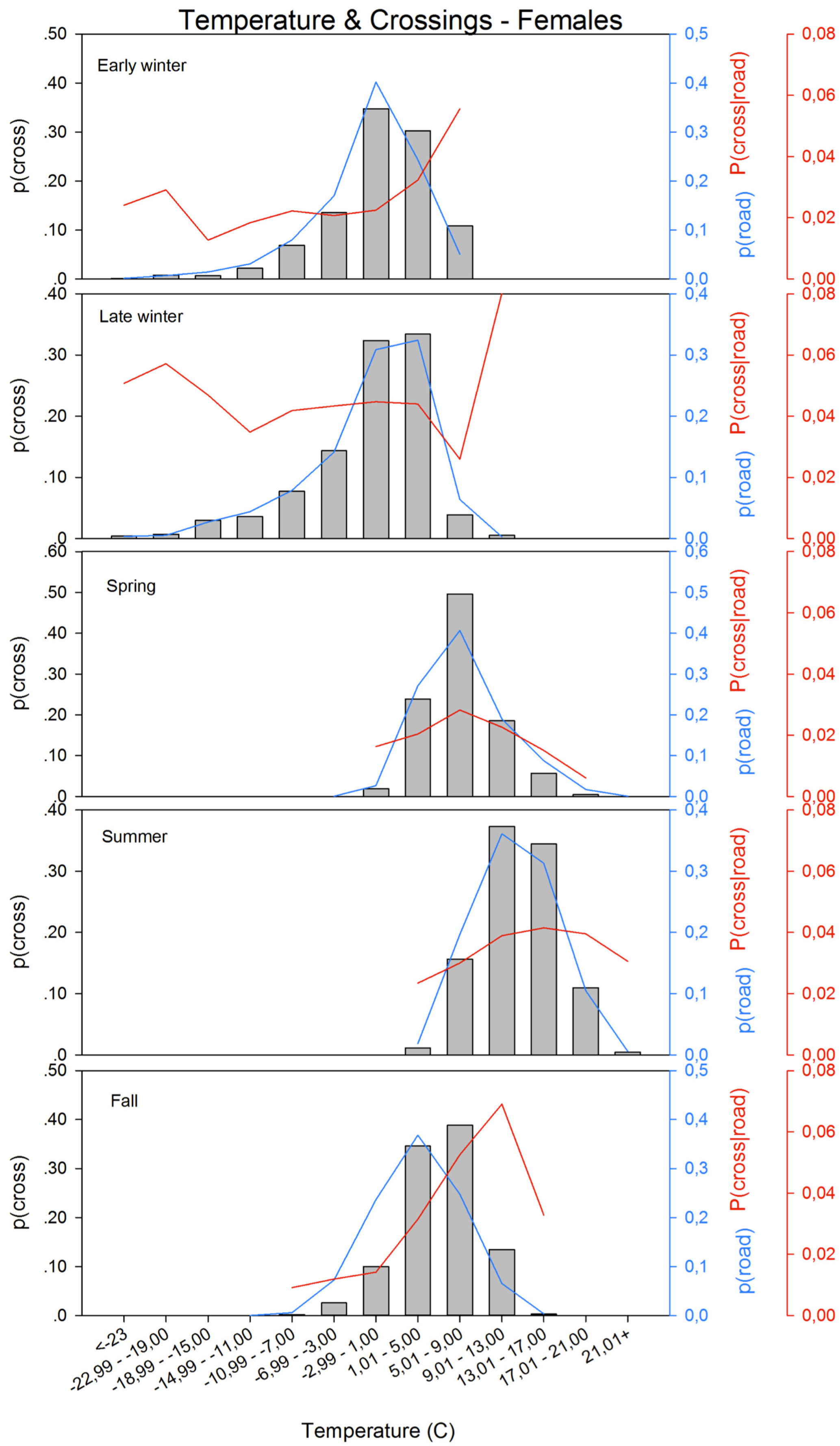

Figure 17. Crossings & Mean daily temperature. Females

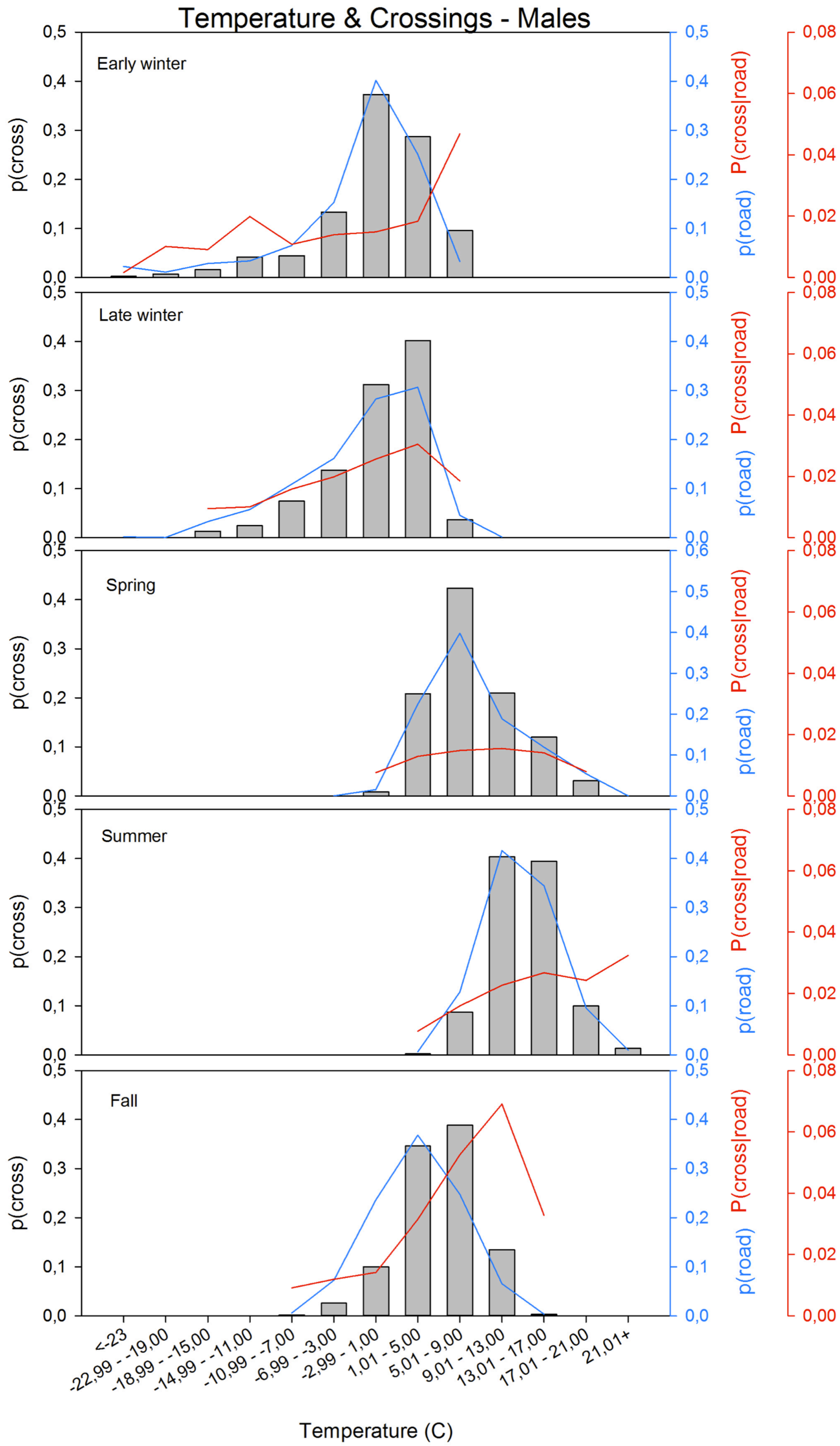

Figure 18. Crossings & Mean daily temperature. Males

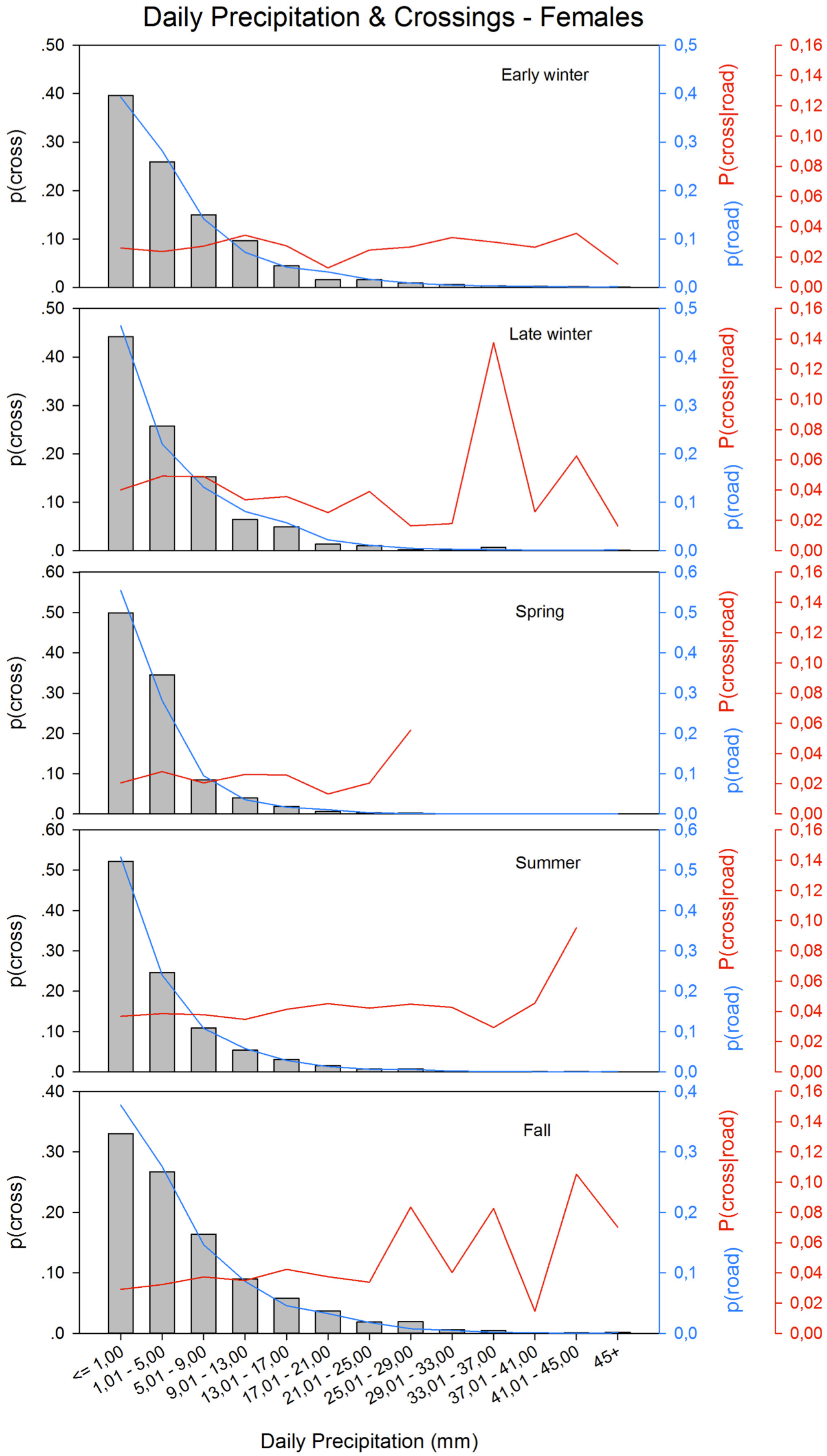

Figure 19. Crossings & Total daily precipitation. Females

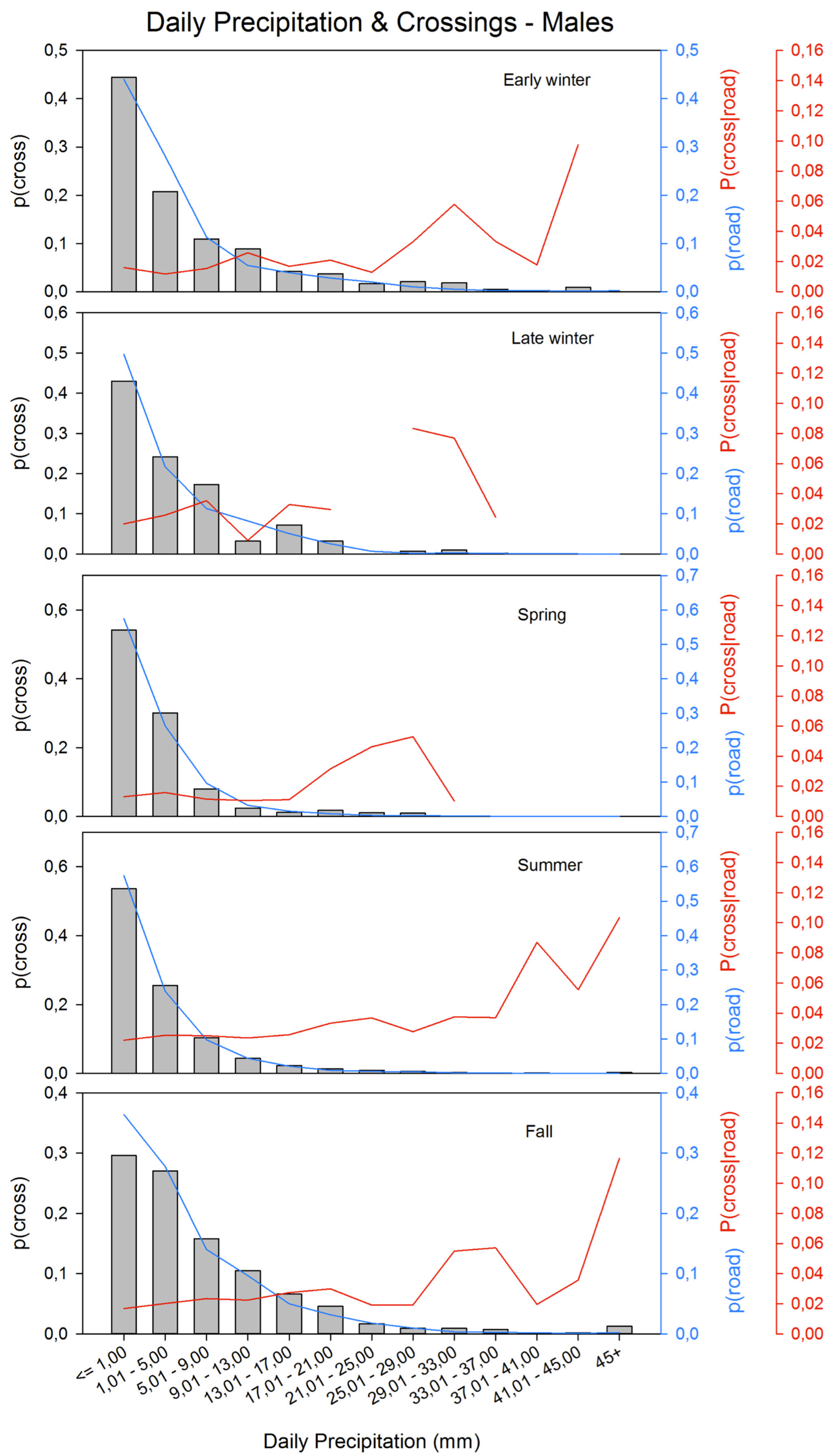

Figure 20. Crossings & total daily precipitation. Males

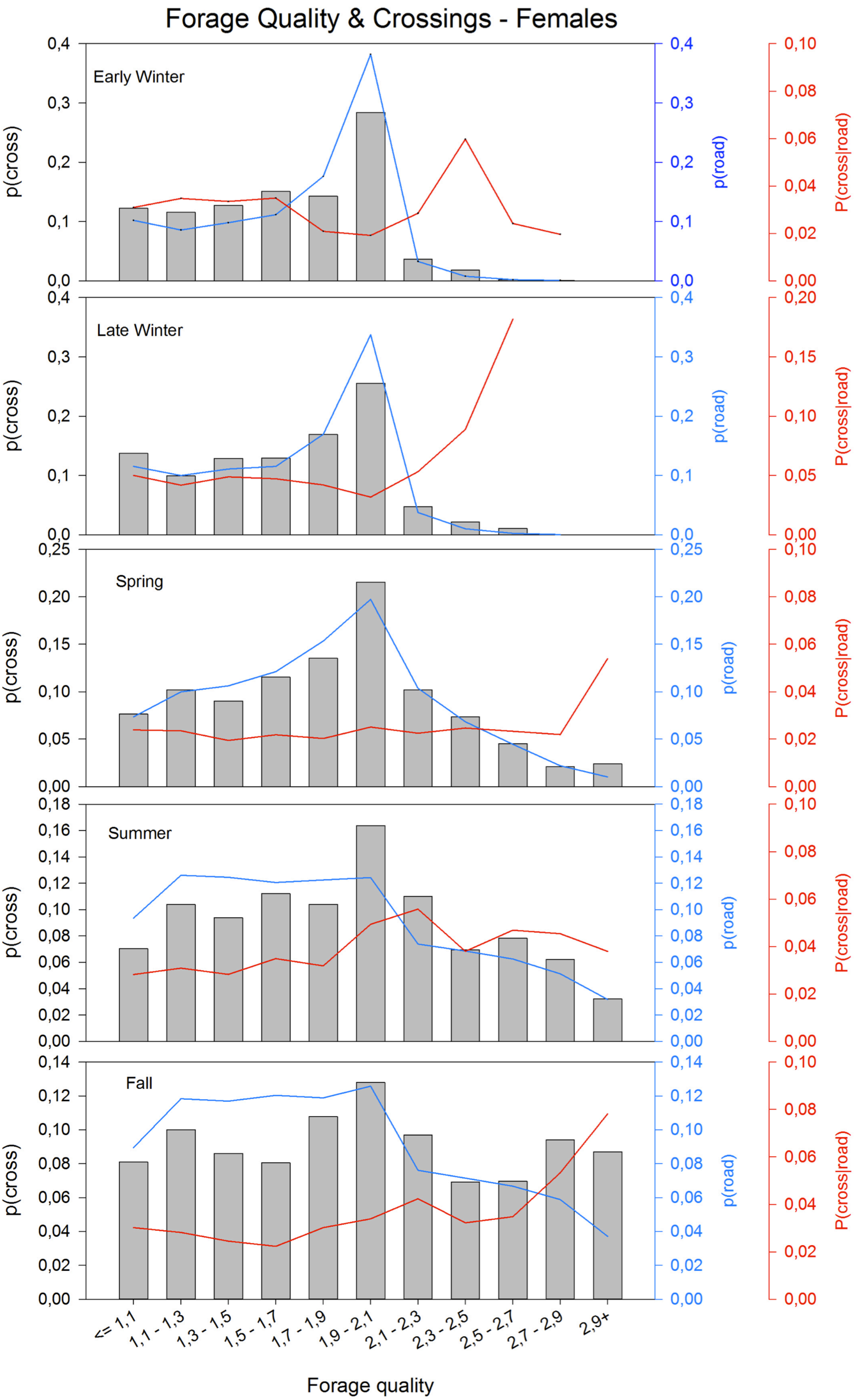

Figure 21. Crossings & Forage quality. Females

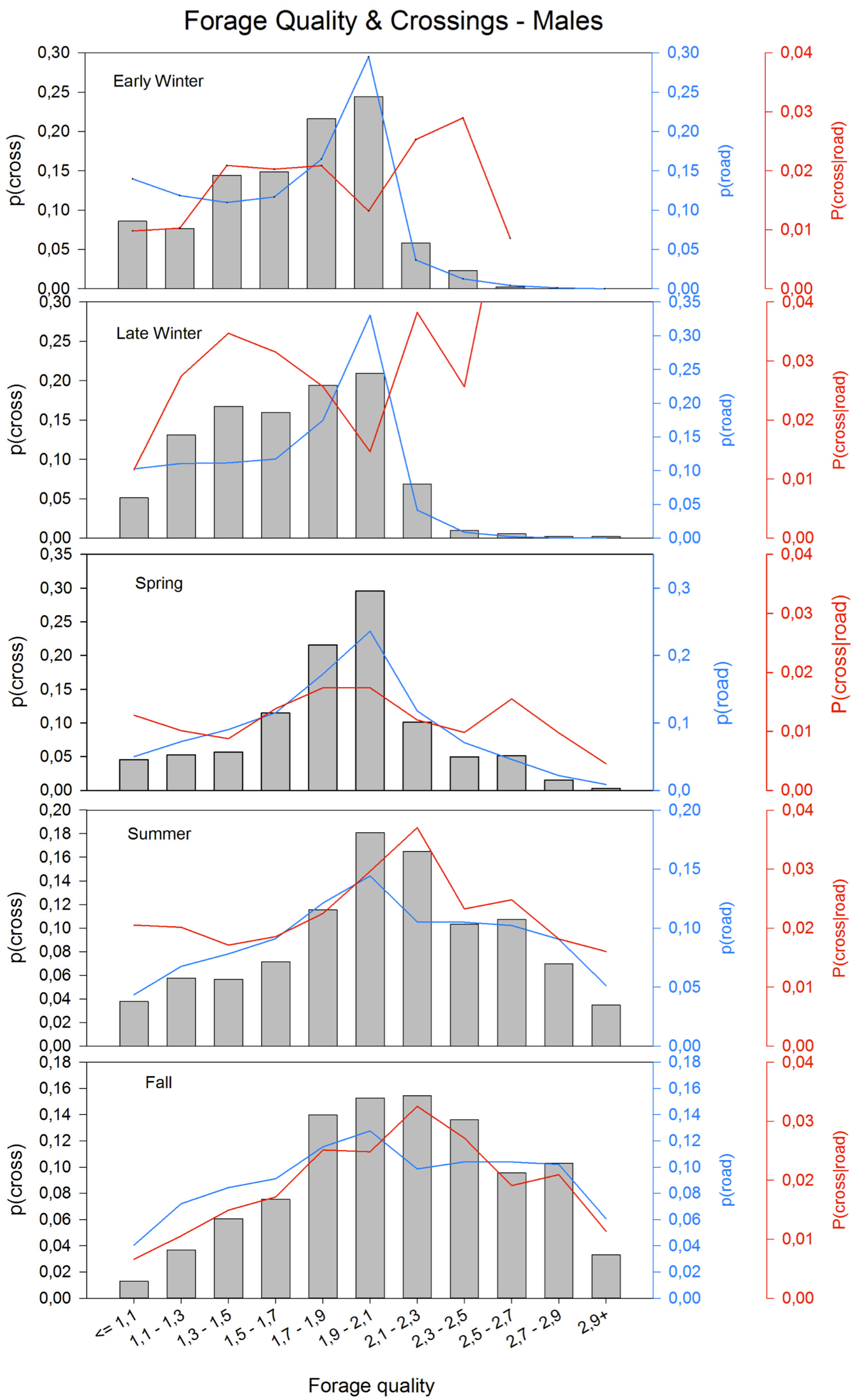

Figure 22. Crossings & Forage quality. Males

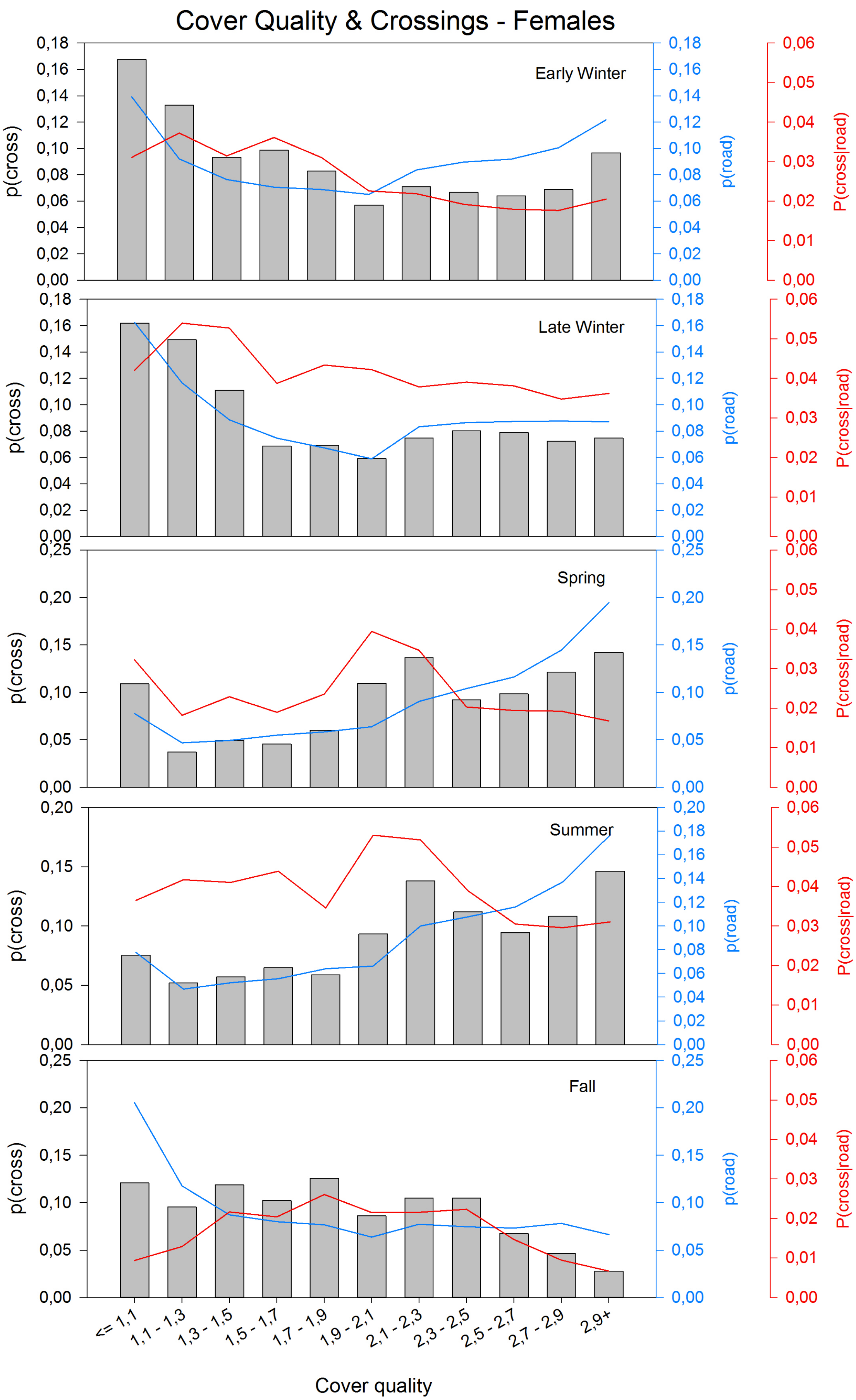

Figure 23. Cover quality and crossings. Females

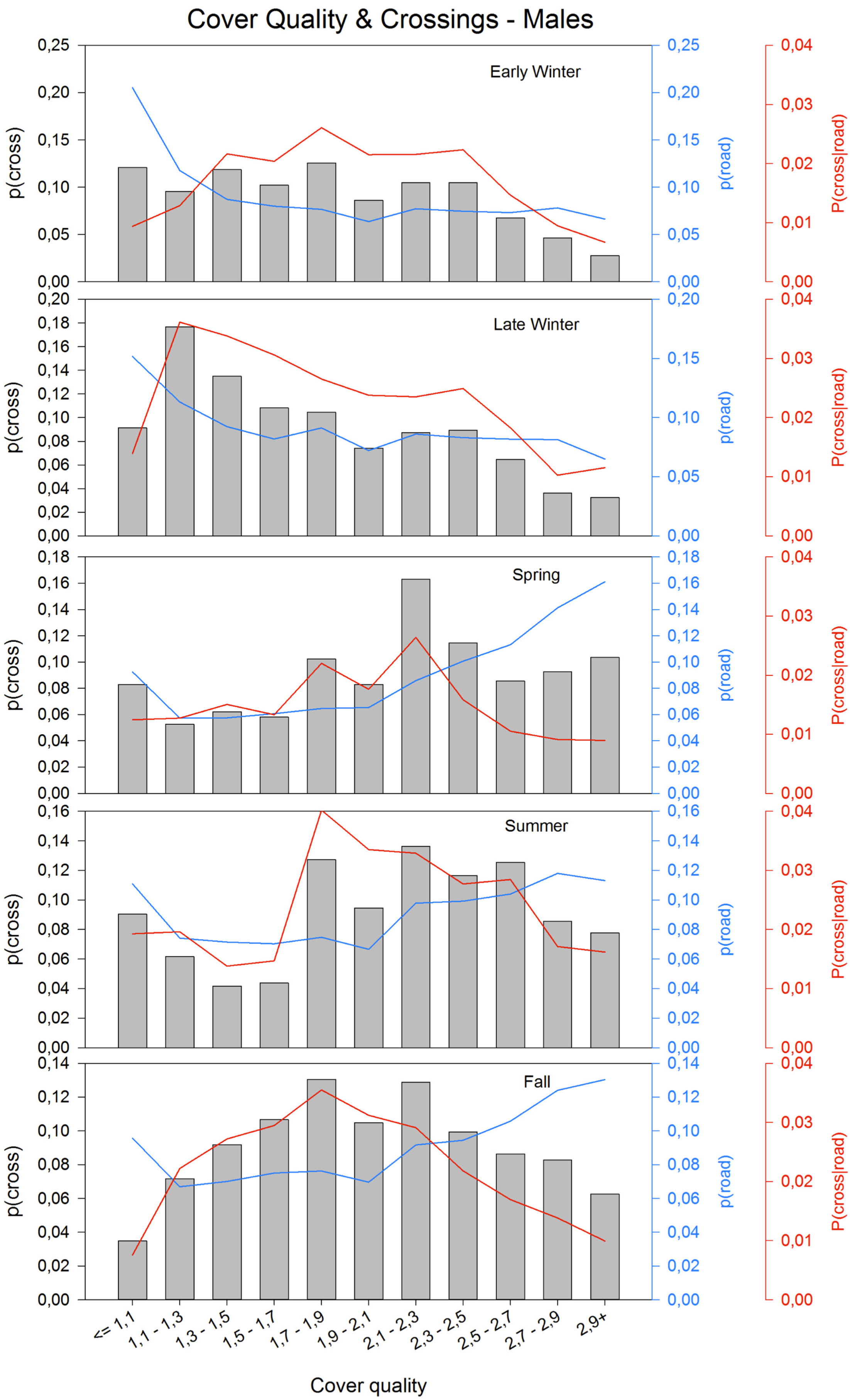

Figure 24. Crossings & Cover quality. Males

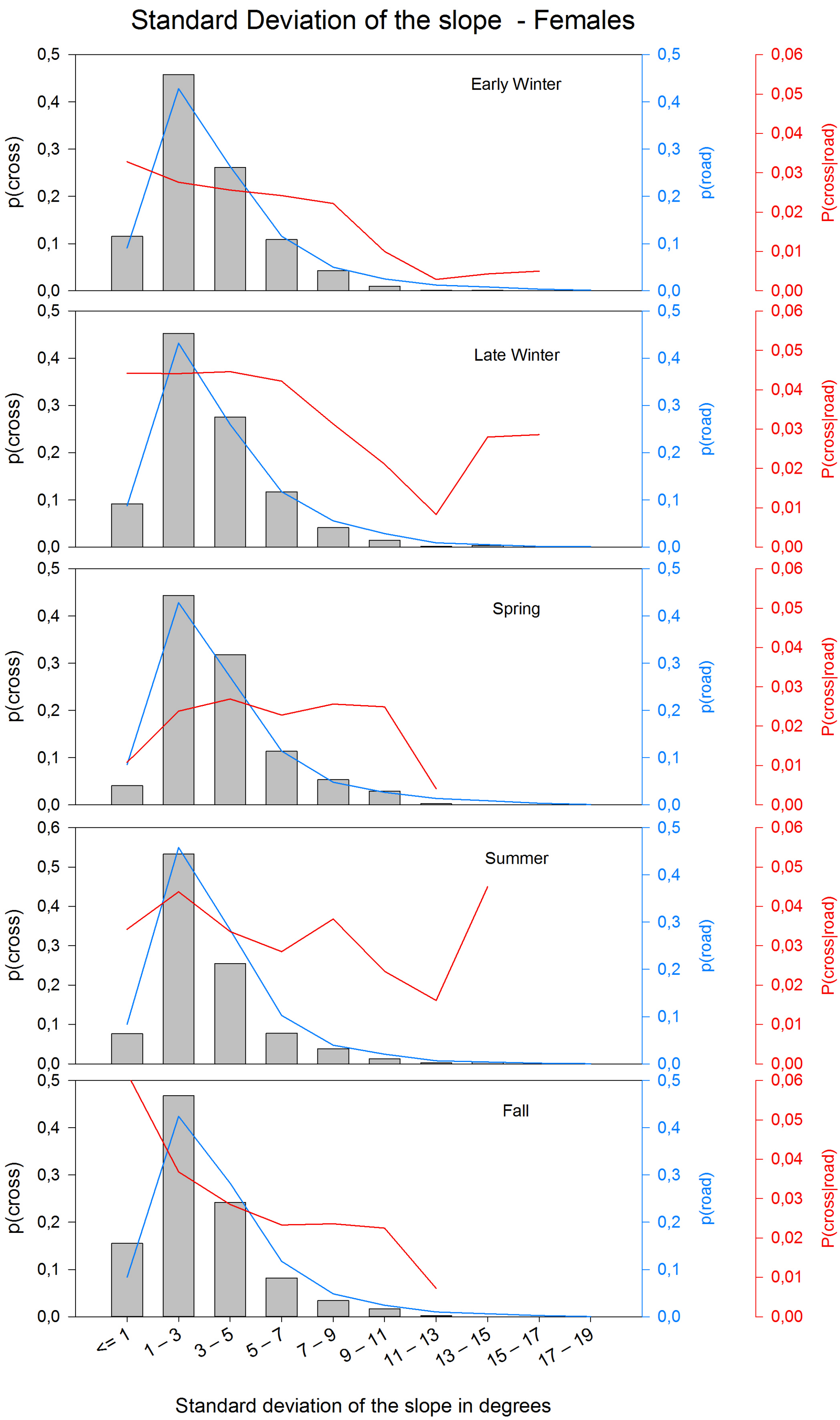

Figure 25. Crossings and the standard deviation of the slope within 100m buffer. Females

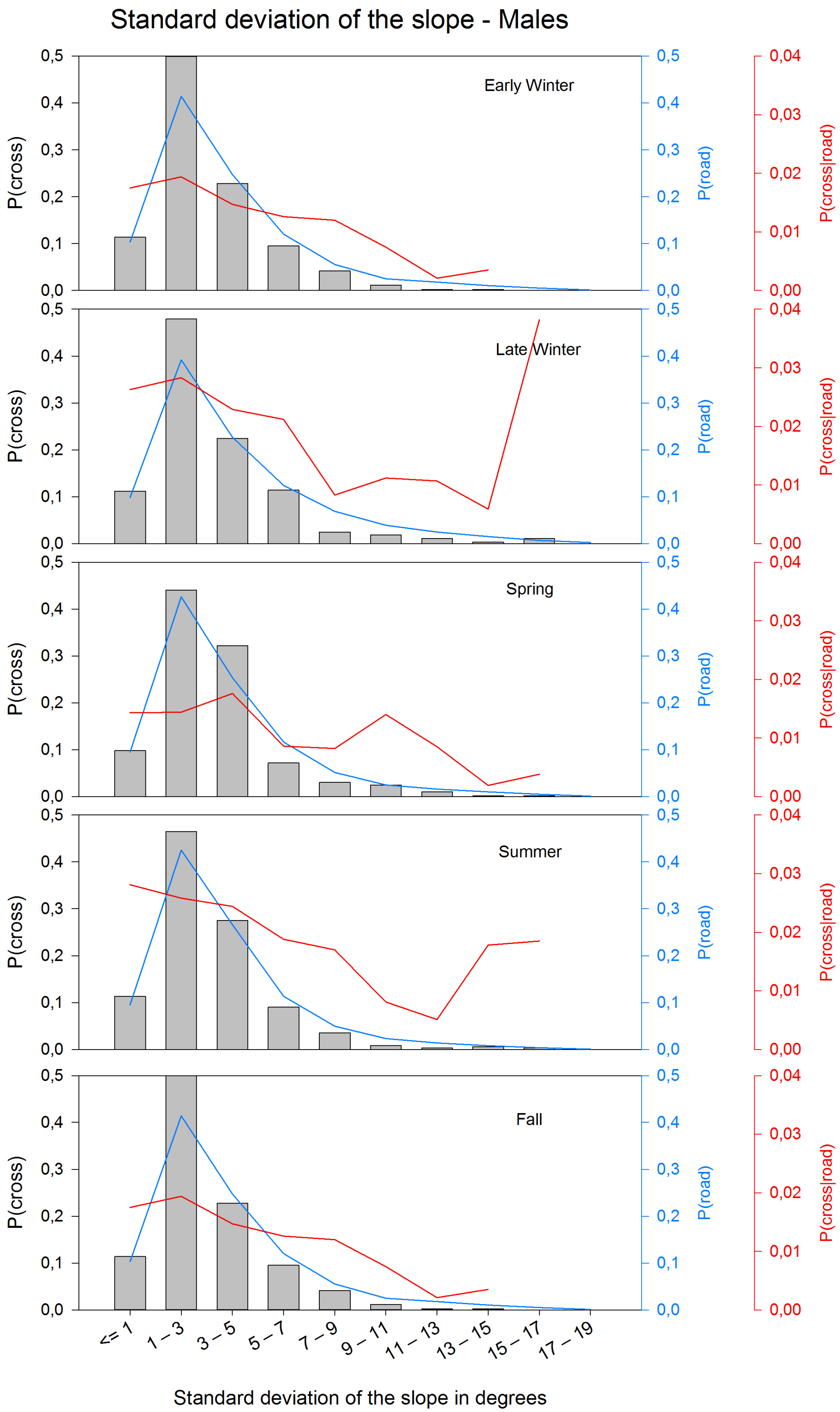

Figure 26. Crossings and the standard deviation of the slope within 100m buffer. Males

Appendix C: Interaction plots and coefficient estimates

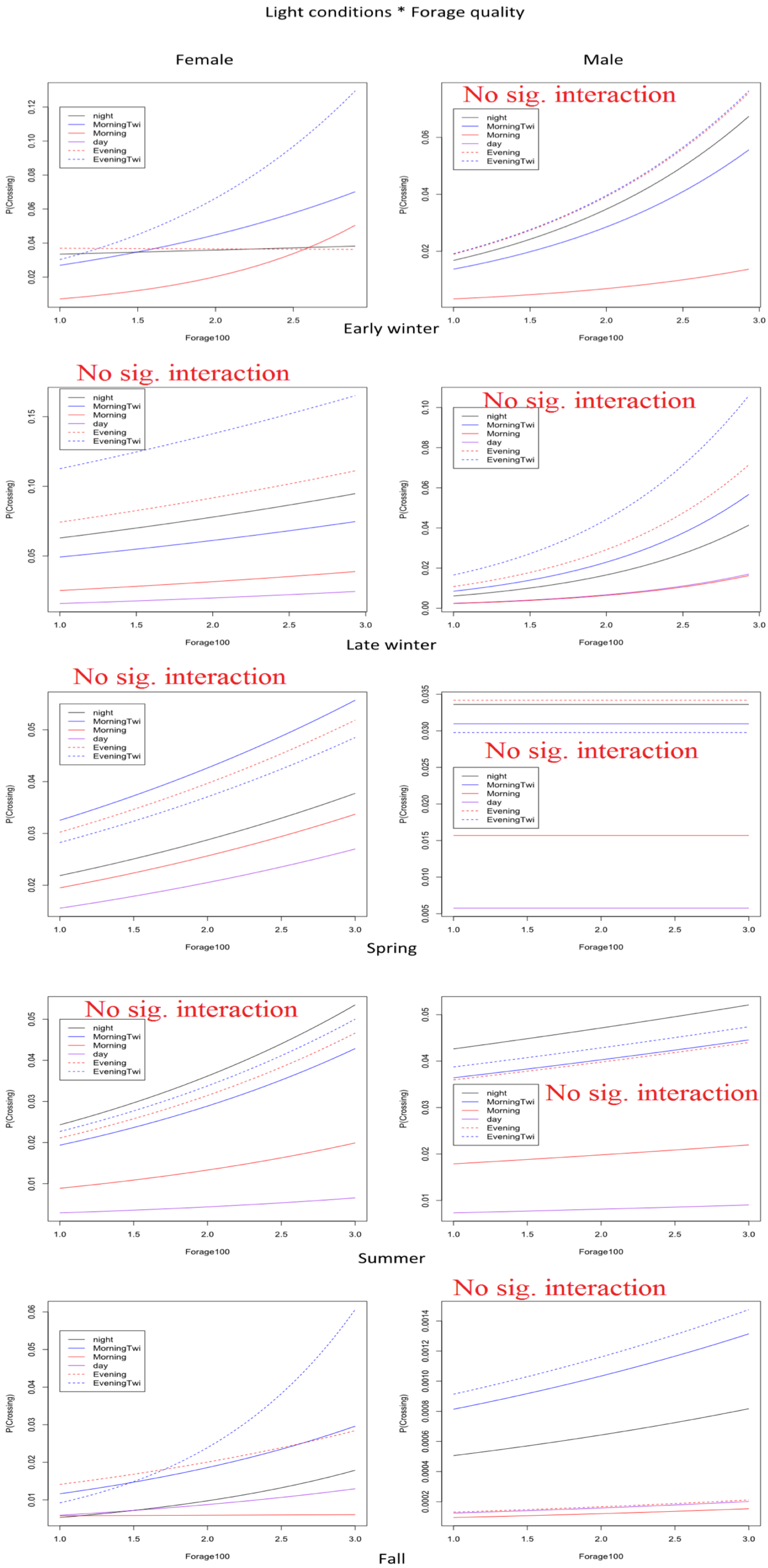

Figure 27. Interaction patterns after model selection. Forage quality and light conditions relationship with probability of crossing given a road. Varying scales on y-axis allow comparison between seasons.

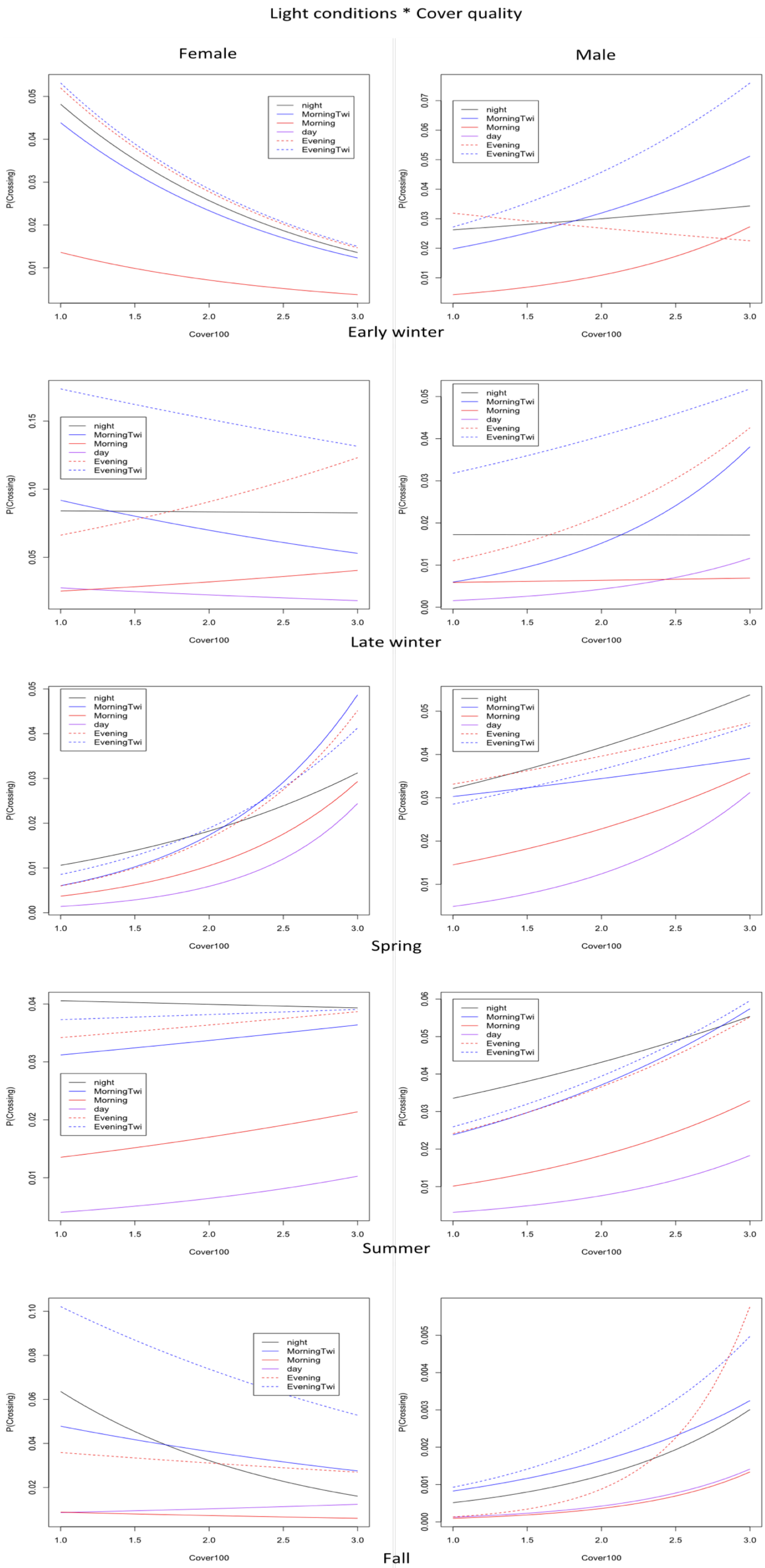

Figure 28. Interaction patterns after model selection. Cover quality and light conditions relationship with probability of crossing given a road. Varying scales on y-axis allow for comparison between seasons.

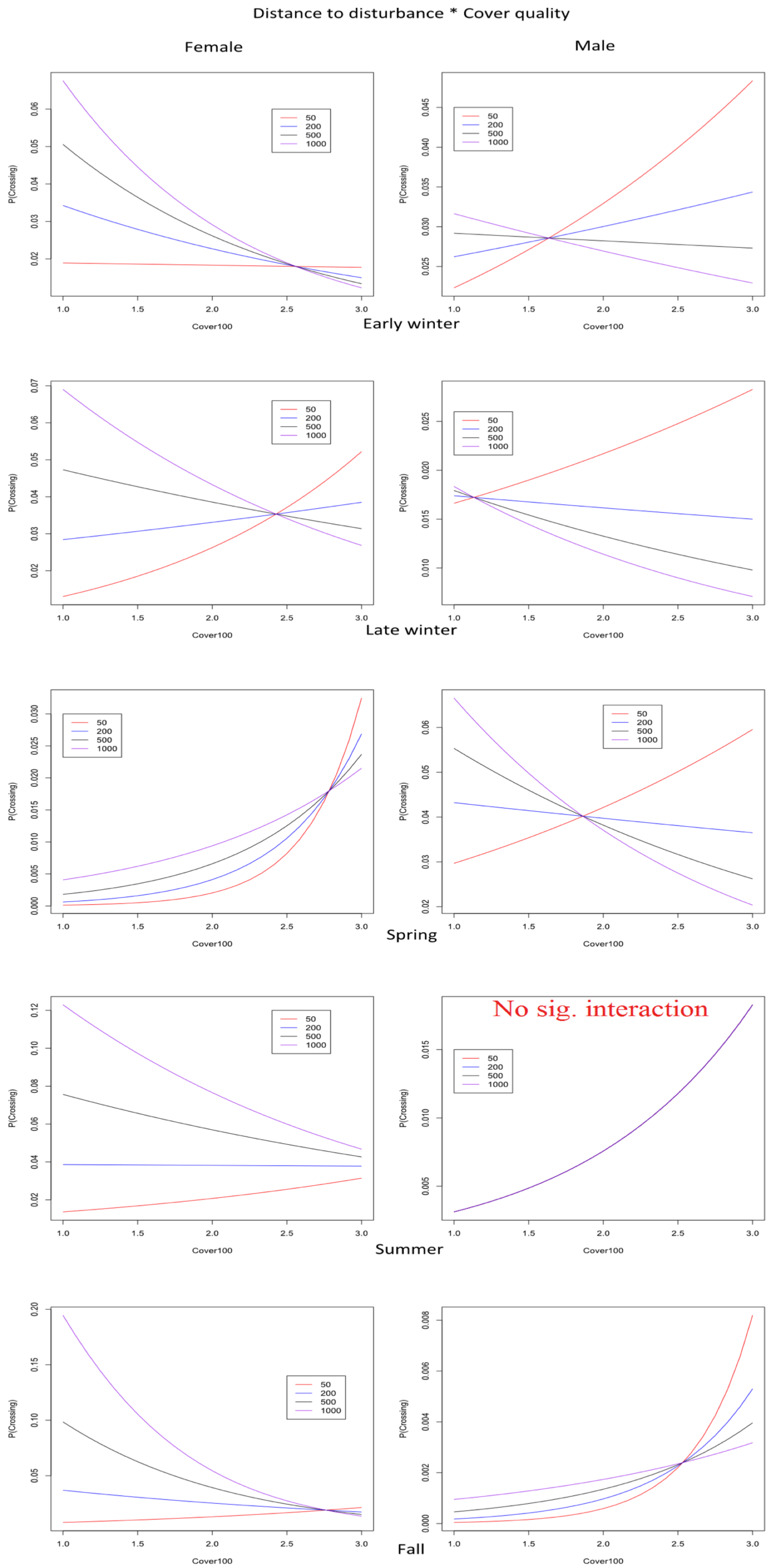

Figure 29. Interaction patterns after model selection. Cover quality and 4 distances to nearest disturbance. 50m, 200m, 500m & 1km and their relationship with probability of crossing given a road.

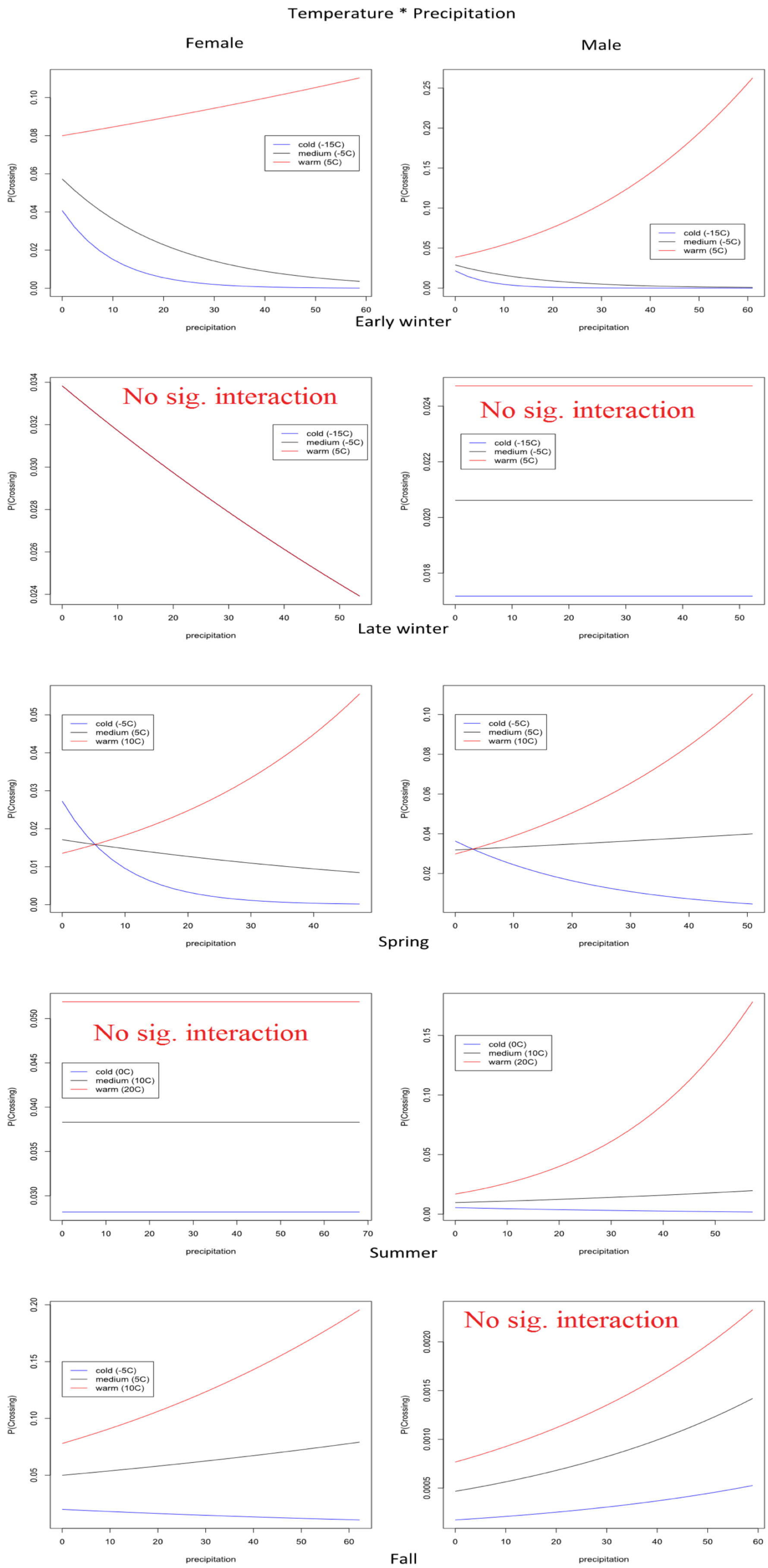

Figure 30. Interaction patterns after model selection. Mean daily temperature and total daily precipitation. Three varying temperatures representing seasonal warm, medium & cold, separating snow and rain in the snowy seasons, and their relationship with probability of crossing given a road

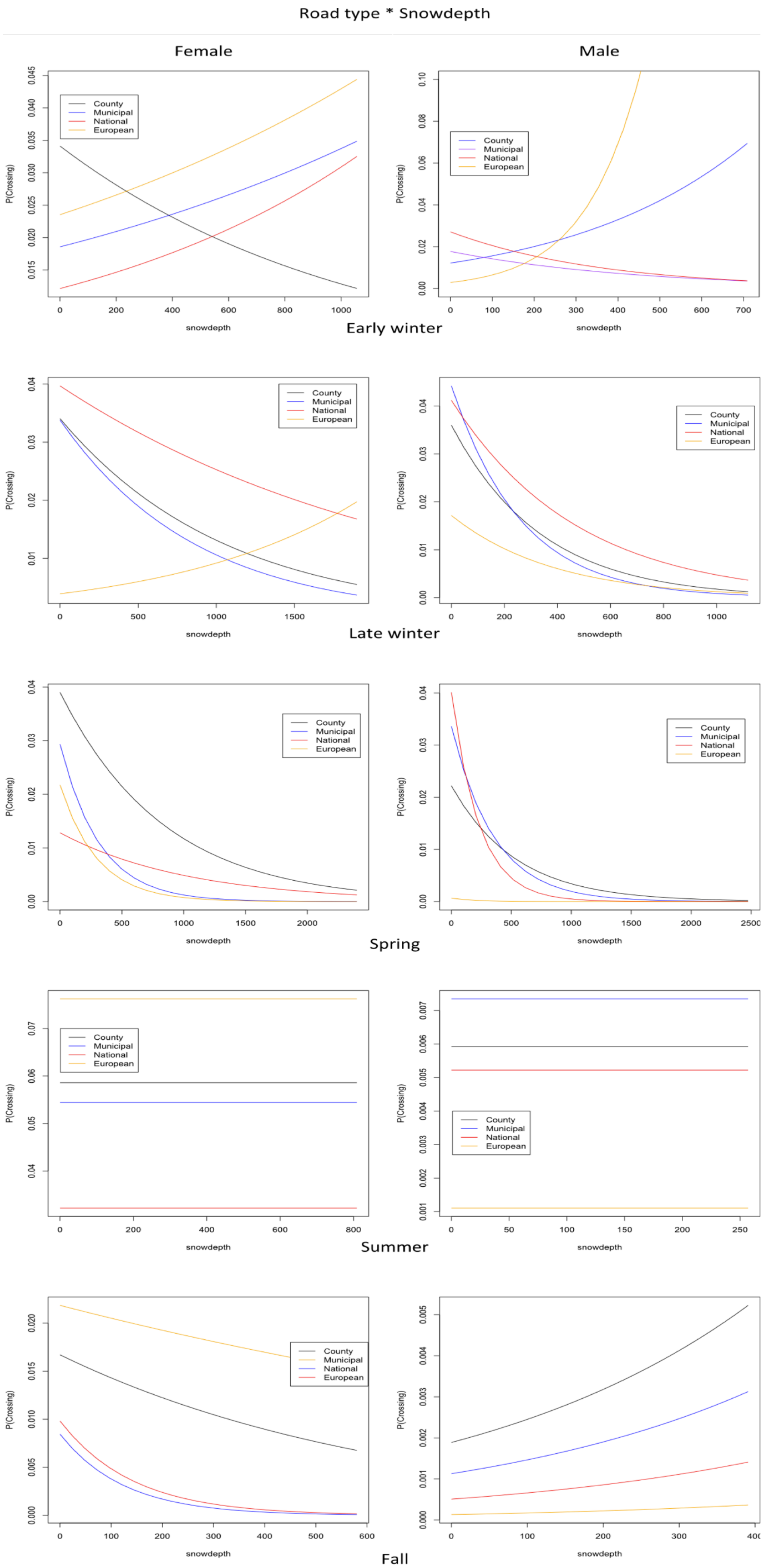

Figure 31. Interaction patterns after model selection. Public road type, snow depth and their relationship with crossing probability given access to a road.

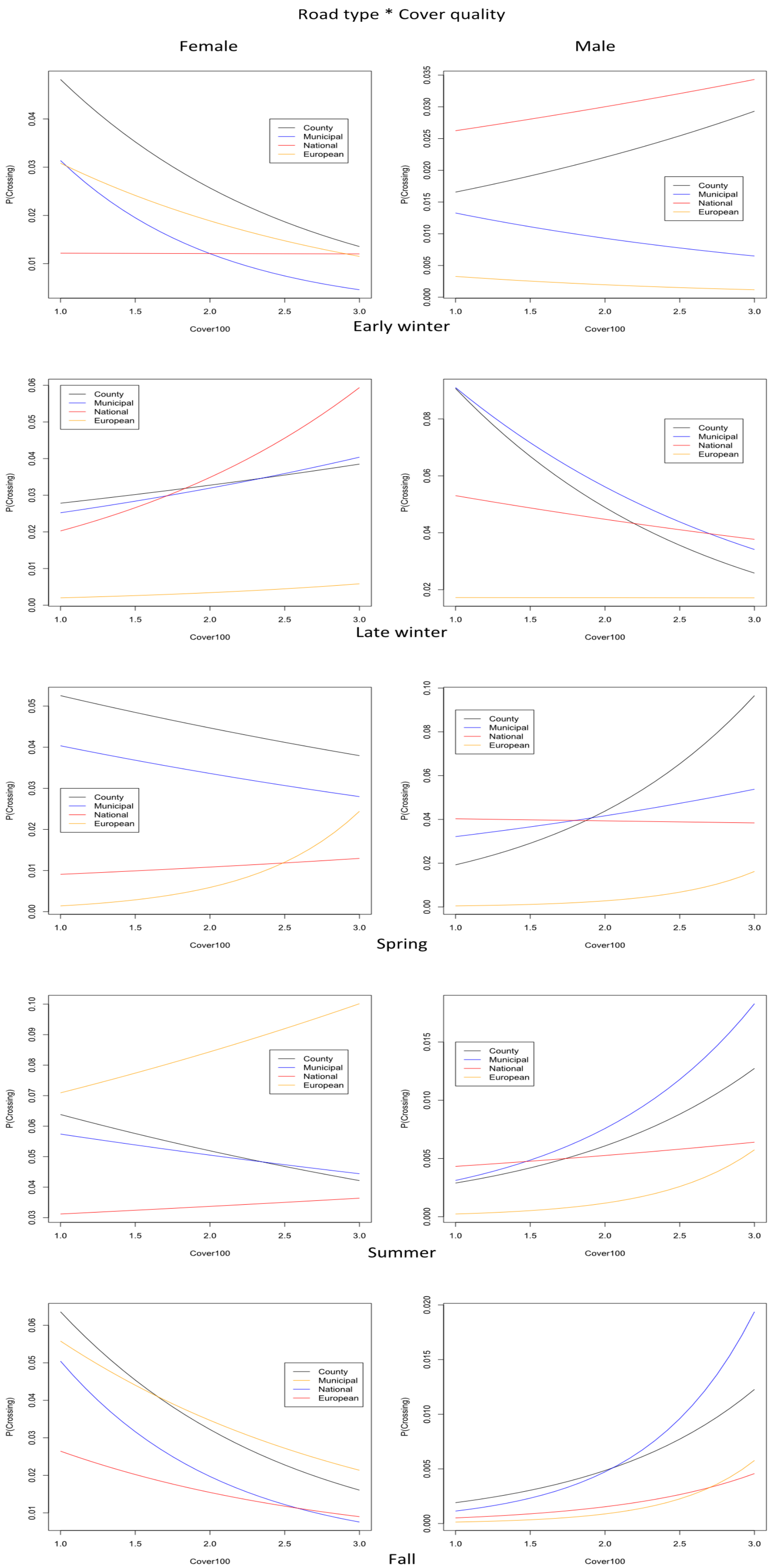

Figure 32. Interaction patterns after model selection. Public road type by cover quality relationship with crossing probability given access to a road.

Coefficient estimates:

Tables 5.0-5.4, Females:

Table 5.0: Female Early Winter

Coefficients:

	Estimate	*Std, Error*	*z value*	*Pr(>|z|)*	
(Intercept)	-5.9764008	0.6721353	-8.892	< 2e-16	***
Dawn	-0.6811215	0.4660835	-1.461	0.143913	
Morning	-2.5529463	0.4966045	-5.141	2.74E-007	***
Evening	0.1845352	0.8979605	0.206	0.837178	
Dusk	-0.8552841	0.4159456	-2.056	0.039759	*
Municipal roads	-0.1242273	0.2092013	-0.594	0.552635	
National roads	-2.0585534	0.2171403	-9.48	< 2e-16	***
European roads	-0.6140298	0.3245694	-1.892	0.058514	,
Distance to disturbance	0.7303276	0.1183451	6.171	6.78E-010	***
Cover	1.0895511	0.3482816	3.128	0.001758	**
Forage	0.072433	0.1370361	0.529	0.597104	
Ruggedness	-0.0888449	0.012622	-7.039	1.94E-012	***
Temperature	0.0358068	0.0072296	4.953	7.31E-007	***
Precipitation	-0.0208732	0.0051852	-4.026	5.68E-005	***
Snow Depth	-0.0009986	0.0002804	-3.561	0.000369	***
Municipal roads:Cover	-0.3221978	0.1198215	-2.689	0.007167	**
National roads:Cover	0.6460117	0.1072588	6.023	1.71E-009	***
European roads:Cover	0.1494227	0.1463656	1.021	0.307308	
Distance to disturbance:Cover	-0.2854037	0.0569571	-5.011	5.42E-007	***
Dawn:Forage	0.4567055	0.271035	1.685	0.09198	,
Morning:Forage	0.9818982	0.2794967	3.513	0.000443	***
Evening:Forage	-0.0822545	0.5532073	-0.149	0.881801	
Dusk:Forage	0.7510266	0.2379528	3.156	0.001598	**
Municipal roads:Snow Depth	0.001611	0.0004562	3.531	0.000414	***
National roads:Snow Depth	0.0019517	0.0004102	4.758	1.95E-006	***
European roads:Snow Depth	0.0016201	0.000599	2.705	0.006836	**
Temperature:Precipitation	0.0053827	0.0012266	4.388	1.14E-005	***

Table 5.1: Female Late Winter
Coefficients:

	Estimate	Std, Error	z value	Pr(>|z|)	
(Intercept)	-7.5359572	0.6522907	-11.553	< 2e-16	***
Dawn	0.3844064	0.3217104	1.195	0.232133	
Morning	-1.5194143	0.3391708	-4.48	7.47E-006	***
Day	-0.9739454	0.2633509	-3.698	0.000217	***
Evening	-0.6082721	0.247103	-2.462	0.013831	*
Dusk	0.9822536	0.3208552	3.061	0.002203	**
Municipal roads	-0.1768491	0.1981478	-0.893	0.372119	
National roads	-0.7158164	0.1834004	-3.903	9.50E-005	***
European roads	-3.0236069	0.6321799	-4.783	1.73E-006	***
Distance to disturbance	0.9852406	0.1143741	8.614	< 2e-16	***
Cover	1.9811516	0.339625	5.833	5.43E-009	***
Forage	0.2295921	0.1191994	1.926	0.05409	,
Ruggedness	-0.0864161	0.0116727	-7.403	1.33E-013	***
Precipitation	-0.0066581	0.0042469	-1.568	0.116943	
Snow Depth	-0.0009761	0.0002062	-4.733	2.21E-006	***
Dawn:Cover	-0.2874324	0.1746654	-1.646	0.099843	,
Morning:Cover	0.2527817	0.1650978	1.531	0.125744	
Day:Cover	-0.2019586	0.1410414	-1.432	0.152169	
Evening:Cover	0.3507964	0.1189469	2.949	0.003186	**
Dusk:Cover	-0.1541392	0.1728619	-0.892	0.372559	
Municipal roads:Cover	0.0755539	0.1172596	0.644	0.519361	
National roads:Cover	0.3903991	0.1026578	3.803	0.000143	***
European roads:Cover	0.367692	0.2739263	1.342	0.179498	
Distance to disturbance:Cover	-0.4058464	0.0560649	-7.239	4.52E-013	***
Municipal roads:Snow Depth	-0.0002091	0.0003166	-0.661	0.508873	
National roads:Snow Depth	0.0005095	0.0002576	1.978	0.047967	*
European roads:Snow Depth	0.0018392	0.0008694	2.116	0.034384	*

Table 5.2: Female Spring
Coefficients:

	Estimate	Std, Error	z value	Pr(>|z|)	
(Intercept)	-1.14E+001	7.18E-001	-15.844	< 2e-16	***
Dawn	-1.08E+000	3.02E-001	-3.573	3.53E-004	***
Morning	-1.55E+000	3.02E-001	-5.151	2.60E-007	***
Day	-2.92E+000	2.37E-001	-12.343	< 2e-16	***
Evening	-1.05E+000	2.75E-001	-3.826	1.30E-004	***
Dusk	-4.70E-001	2.93E-001	-1.604	1.09E-001	
Municipal roads	-2.40E-001	1.85E-001	-1.302	1.93E-001	
National roads	-2.15E+000	2.77E-001	-7.757	8.68E-015	***
European roads	-5.27E+000	6.92E-001	-7.615	2.64E-014	***
Distance to disturbance	1.84E+000	1.21E-001	15.181	< 2e-16	***
Cover	2.90E+000	3.03E-001	9.549	< 2e-16	***
Forage	2.81E-001	5.01E-002	5.61	2.03E-008	***
Temperature	-4.77E-002	7.20E-003	-6.624	3.50E-011	***
Precipitation	-6.10E-002	1.50E-002	-4.069	4.72E-005	***
Snow Depth	-1.23E-003	1.38E-004	-8.931	< 2e-16	***
Dawn:Cover	5.14E-001	1.37E-001	3.743	1.82E-004	***
Morning:Cover	4.96E-001	1.38E-001	3.592	3.28E-004	***
Day:Cover	8.89E-001	1.09E-001	8.189	2.63E-016	***
Evening:Cover	4.79E-001	1.27E-001	3.765	1.67E-004	***
Dusk:Cover	2.53E-001	1.37E-001	1.847	6.48E-002	,
Municipal roads:Cover	-1.90E-002	8.50E-002	-0.224	8.23E-001	
National roads:Cover	3.50E-001	1.17E-001	2.982	2.86E-003	**
European roads:Cover	1.61E+000	2.59E-001	6.218	5.04E-010	***
Distance to disturbance:Cover	-6.59E-001	5.11E-002	-12.906	< 2e-16	***
Municipal roads:Snow Depth	-1.97E-003	5.51E-004	-3.579	3.45E-004	***
National roads:Snow Depth	2.56E-004	3.82E-004	0.671	5.02E-001	
European roads:Snow Depth	-2.16E-003	1.23E-003	-1.747	8.07E-002	,
Temperature:Precipitation	9.17E-003	2.02E-003	4.54	5.62E-006	***

Table 5.3: Female Summer
Coefficients:

	Estimate	*Std, Error*	*z value*	*Pr(>|z|)*	
(Intercept)	-8.656604	0.709547	-12.2	< 2e-16	***
Dawn	-0.367956	0.265315	-1.387	0.16548	
Morning	-1.374916	0.301352	-4.562	5.06E-006	***
Day	-2.840775	0.235888	-12.043	< 2e-16	***
Evening	-0.257544	0.237299	-1.085	0.27778	
Dusk	-0.127775	0.262647	-0.486	0.62662	
Municipal roads	-0.196381	0.195246	-1.006	0.3145	
National roads	-1.048115	0.228909	-4.579	4.68E-006	***
European roads	-0.294037	0.380379	-0.773	0.43952	
Distance to disturbance	1.096971	0.116394	9.425	< 2e-16	***
Cover	1.288461	0.288791	4.462	8.14E-006	***
Forage	0.409334	0.043145	9.487	< 2e-16	***
Ruggedness	-0.031267	0.010845	-2.883	0.00394	**
Temperature	0.031786	0.006034	5.268	1.38E-007	***
Dawn:Cover	0.095689	0.118011	0.811	0.41745	
Morning:Cover	0.248908	0.131937	1.887	0.05922	,
Day:Cover	0.489012	0.101914	4.798	1.60E-006	***
Evening:Cover	0.080028	0.106342	0.753	0.45172	
Dusk:Cover	0.040319	0.117561	0.343	0.73162	
Municipal roads:Cover	0.083609	0.090717	0.922	0.35672	
National roads:Cover	0.298398	0.099267	3.006	0.00265	**
European roads:Cover	0.407319	0.146648	2.778	0.00548	**
Distance to disturbance:Cover	-0.319492	0.048528	-6.584	4.59E-011	***

Table 5.4: Female Fall
Coefficients:

	Estimate	*Std, Error*	*z value*	*Pr(>|z|)*	
(Intercept)	-1.30E+001	7.56E-001	-17.168	< 2e-16	***
Dawn	-3.35E-001	5.92E-001	-0.566	0.571255	
Morning	-8.77E-001	4.95E-001	-1.773	0.076265	,
Day	-2.33E+000	4.51E-001	-5.17	2.34E-007	***
Evening	-4.33E-001	3.72E-001	-1.165	0.244199	,
Dusk	-8.59E-001	5.28E-001	-1.627	0.103744	*
Municipal roads	7.86E-002	1.91E-001	0.412	0.680112	**
National roads	-1.03E+000	2.11E-001	-4.855	1.21E-006	***
European roads	-3.64E-001	4.14E-001	-0.878	0.379804	***
Distance to disturbance	1.80E+000	1.24E-001	14.475	< 2e-16	***
Cover	3.07E+000	3.18E-001	9.631	< 2e-16	***
Forage	6.13E-001	5.37E-002	11.417	< 2e-16	***
Ruggedness	-1.28E-001	1.29E-002	-9.941	< 2e-16	***
Temperature	9.51E-002	8.63E-003	11.012	< 2e-16	***
Precipitation	-1.19E-003	6.89E-003	-0.173	0.862942	
Snow Depth	-1.58E-003	8.73E-004	-1.806	0.070964	,
Dawn:Cover	4.26E-001	1.90E-001	2.242	0.024935	*
Morning:Cover	5.23E-001	1.55E-001	3.378	0.000729	***
Day:Cover	8.96E-001	1.37E-001	6.529	6.63E-011	***
Evening:Cover	5.65E-001	1.15E-001	4.898	9.70E-007	***
Dusk:Cover	3.57E-001	1.61E-001	2.219	0.026458	*
Municipal roads:Cover	-2.59E-001	9.96E-002	-2.604	0.009224	**
National roads:Cover	1.64E-001	9.97E-002	1.646	0.099796	,
European roads:Cover	2.15E-001	1.65E-001	1.307	0.191309	*
Distance to disturbance:Cover	-6.51E-001	5.45E-002	-11.953	< 2e-16	***
Dawn:Forage	-1.37E-001	2.08E-001	-0.659	0.509685	
Morning:Forage	-5.89E-001	1.76E-001	-3.351	0.000805	***
Day:Forage	-2.17E-001	1.57E-001	-1.381	0.167135	
Evening:Forage	-2.56E-001	1.30E-001	-1.975	0.048252	*
Dusk:Forage	3.56E-001	1.70E-001	2.1	0.035726	*
Municipal roads:Snow Depth	-6.51E-003	2.17E-003	-3.001	0.002694	**
National roads:Snow Depth	-5.53E-003	1.86E-003	-2.971	0.00297	**
European roads:Snow Depth	9.33E-004	1.36E-003	0.687	0.492335	**
Temperature:Precipitation	1.82E-003	9.71E-004	1.873	0.061076	,

Tables 5.5-5.9 Males:

Table 5.5: Male Early Winter

Coefficients:

	Estimate	*Std, Error*	*z value*	*Pr(>|z|)*	
(Intercept)	-6.5732926	1.3871943	-4.739	2.15E-006	***
Dawn	-0.6433711	0.5839839	-1.102	0.270595	
Morning	-2.6417294	0.6854302	-3.854	0.000116	***
Evening	0.5175646	1.2882273	0.402	0.687857	
Dusk	-0.3636434	0.5017666	-0.725	0.46862	
Municipal roads	0.4281063	0.4133346	1.036	0.300325	
National roads	0.6236971	0.4057345	1.537	0.124243	
European roads	-0.8258392	0.6716797	-1.23	0.218879	
Distance to disturbance	0.3107512	0.257938	1.205	0.228299	
Cover	1.3015444	0.7180898	1.813	0.069908	,
Forage	0.7465103	0.2107463	3.542	0.000397	***
Ruggedness	-0.1766149	0.0252293	-7	2.55E-012	***
Temperature	0.0298368	0.0105424	2.83	0.004652	**
Precipitation	-0.0118836	0.0087909	-1.352	0.176436	
Snow Depth	-0.0022619	0.0008538	-2.649	0.008069	**
Dawn:Cover	0.3537133	0.2912107	1.215	0.224507	
Morning:Cover	0.8018726	0.3130136	2.562	0.010414	*
Evening:Cover	-0.3164876	0.7080817	-0.447	0.6549	
Dusk:Cover	0.400911	0.2460469	1.629	0.103227	
Municipal roads:Cover	-0.6531876	0.2108228	-3.098	0.001946	**
National roads:Cover	-0.1536673	0.2146118	-0.716	0.473976	
European roads:Cover	-0.8071229	0.2523933	-3.198	0.001384	**
Distance to disturbance:Cover	-0.1901413	0.1228952	-1.547	0.121819	
Municipal roads:Snow Depth	0.0048015	0.0010705	4.485	7.29E-006	***
National roads:Snow Depth	-0.0005775	0.001105	-0.523	0.601218	
European roads:Snow Depth	0.01036	0.0016359	6.333	2.41E-010	***
Temperature:Precipitation	0.0095441	0.0020466	4.663	3.11E-006	***

Table 5.6: Male Late Winter
Coefficients:

	Estimate	Std, Error	z value	Pr(>|z|)	
(Intercept)	-4.0911113	1.289483	-3.173	0.00151	**
Dawn	-2.0165629	0.6954618	-2.9	0.003736	**
Morning	-1.1646199	0.613264	-1.899	0.057558	,
Day	-3.4123445	0.5826532	-5.857	4.73E-009	***
Evening	-1.1471986	0.4507778	-2.545	0.01093	*
Dusk	0.3701012	0.6344324	0.583	0.559652	
Municipal roads	-0.1380877	0.3704803	-0.373	0.709352	
National roads	-1.060992	0.3680093	-2.883	0.003938	**
European roads	-2.3984823	0.7770892	-3.086	0.002025	**
Distance to disturbance	0.2867065	0.238193	1.204	0.228716	
Cover	0.6065739	0.703202	0.863	0.388364	
Forage	1.0098897	0.2127703	4.746	2.07E-006	***
Ruggedness	-0.0995745	0.0197513	-5.041	4.62E-007	***
Temperature	0.0186161	0.0099046	1.88	0.06017	,
Snow Depth	-0.0030363	0.0005304	-5.724	1.04E-008	***
Dawn:Cover	0.9454409	0.3321663	2.846	0.004423	**
Morning:Cover	0.0819462	0.3338635	0.245	0.806109	
Day:Cover	1.0059236	0.2808481	3.582	0.000341	***
Evening:Cover	0.6946546	0.2262018	3.071	0.002134	**
Dusk:Cover	0.2574566	0.366003	0.703	0.481789	
Municipal roads:Cover	0.1417602	0.2012819	0.704	0.481254	
National roads:Cover	0.4837352	0.2018937	2.396	0.016576	*
European roads:Cover	0.6598234	0.335862	1.965	0.049464	*
Distance to disturbance:Cover	-0.2530016	0.1196025	-2.115	0.0344	*
Municipal roads:Snow Depth	-0.000925	0.0006961	-1.329	0.183901	
National roads:Snow Depth	0.0008401	0.0006824	1.231	0.218324	
European roads:Snow Depth	0.0004077	0.0012238	0.333	0.739006	

Table 5.7: Male Spring
Coefficients:

	Estimate	*Std, Error*	*z value*	*Pr(>|z|)*	
(Intercept)	-7.1086879	1.257765	-5.652	1.59E-008	***
Dawn	0.0752321	0.4673546	0.161	0.872114	
Morning	-1.0050385	0.5071047	-1.982	0.047489	*
Day	-2.5806576	0.3985217	-6.476	9.45E-011	***
Evening	0.1152357	0.4288784	0.269	0.788168	
Dusk	-0.1098771	0.4720393	-0.233	0.815939	
Municipal roads	1.1055325	0.3358313	3.292	0.000995	***
National roads	1.6335201	0.3276085	4.986	6.16E-007	***
European roads	-4.6446334	1.7537253	-2.648	0.008086	**
Distance to disturbance	0.6138799	0.2253009	2.725	0.006436	**
Cover	2.2382568	0.5439226	4.115	3.87E-005	***
Ruggedness	-0.0830079	0.0172624	-4.809	1.52E-006	***
Temperature	-0.0136458	0.0098543	-1.385	0.166126	
Precipitation	-0.0181664	0.0196934	-0.922	0.356289	
Snow Depth	-0.0018928	0.0004655	-4.066	4.78E-005	***
Dawn:Cover	-0.1363392	0.2233741	-0.61	0.541622	
Morning:Cover	0.1921162	0.2336856	0.822	0.411012	
Day:Cover	0.6708964	0.1817126	3.692	0.000222	***
Evening:Cover	-0.0834912	0.2042507	-0.409	0.68271	
Dusk:Cover	-0.0131561	0.2230035	-0.059	0.952956	
Municipal roads:Cover	-0.5789344	0.1524407	-3.798	0.000146	***
National roads:Cover	-0.8726091	0.1478057	-5.904	3.55E-009	***
European roads:Cover	0.9251189	0.6428865	1.439	0.150148	
Distance to disturbance:Cover	-0.3294613	0.0950693	-3.465	0.000529	***
Municipal roads:Snow Depth	-0.0009911	0.0010122	-0.979	0.327489	
National roads:Snow Depth	-0.0025569	0.0010831	-2.361	0.018238	*
European roads:Snow Depth	-0.0030389	0.0034051	-0.892	0.372149	
Temperature:Precipitation	0.0045591	0.0025449	1.791	0.073227	,

Table 5.8: Male Summer
Coefficients:

	Estimate	*Std,Error*	*z-value*	*Pr(>|z|)*	
(Intercept)	-3.829209	0.357788	-10.702	< 2e-16	***
Dawn	-0.549345	0.363501	-1.511	0.130721	
Morning	-1.561705	0.432729	-3.609	0.000307	***
Day	-3.03737	0.333253	-9.114	< 2e-16	***
Evening	-0.507834	0.348092	-1.459	0.144591	
Dusk	-0.436348	0.367727	-1.187	0.235383	
Municipal roads	-0.071023	0.269478	-0.264	0.792121	
National roads	0.952652	0.27565	3.456	0.000548	***
European roads	-3.359094	1.059795	-3.17	0.001527	**
Cover	0.115777	0.13304	0.87	0.384169	
Forage	0.105269	0.067418	1.561	0.118422	
Ruggedness	-0.093898	0.016133	-5.82	5.88E-009	***
Temperature	0.056085	0.010695	5.244	1.57E-007	***
Precipitation	-0.019081	0.024753	-0.771	0.440787	
Dawn:Cover	0.19591	0.170926	1.146	0.251724	
Morning:Cover	0.339082	0.19731	1.719	0.085701	,
Day:Cover	0.630362	0.152403	4.136	3.53E-005	***
Evening:Cover	0.168255	0.165745	1.015	0.310038	
Dusk:Cover	0.171288	0.17341	0.988	0.323268	
Municipal roads:Cover	0.146244	0.122316	1.196	0.231843	
National roads:Cover	-0.549085	0.130399	-4.211	2.54E-005	***
European roads:Cover	0.851942	0.395509	2.154	0.031237	*
Temperature:Precipitation	0.003169	0.001957	1.62	0.105334	

Table 5.9: Male Fall
Coefficients:

	Estimate	*Std, Error*	*z value*	*Pr(>|z|)*	
(Intercept)	-13.074457	1.480423	-8.832	< 2e-16	***
Dawn	0.674964	0.809292	0.834	0.40427	
Morning	-2.10148	0.713858	-2.944	0.003242	**
Day	-1.722819	0.558616	-3.084	0.002042	**
Evening	-2.353525	0.62671	-3.755	0.000173	***
Dusk	0.634907	0.620619	1.023	0.306297	*
Municipal roads	-1.005889	0.340086	-2.958	0.003099	**
National roads	-1.472781	0.437766	-3.364	0.000767	***
European roads	-3.614658	1.714504	-2.108	0.035007	*
Distance to disturbance	1.731954	0.25227	6.865	6.63E-012	***
Cover	3.377942	0.626205	5.394	6.88E-008	***
Forage	0.239912	0.097436	2.462	0.013807	*
Temperature	0.099287	0.013657	7.27	3.60E-013	***
Precipitation	0.018897	0.005131	3.683	0.00023	***
Snow Depth	0.002613	0.001269	2.059	0.039483	*
Dawn:Cover	-0.1993	0.393602	-0.506	0.612612	
Morning:Cover	0.429741	0.322202	1.334	0.182282	,
Day:Cover	0.321821	0.256977	1.252	0.210448	***
Evening:Cover	1.002411	0.265222	3.78	0.000157	***
Dusk:Cover	-0.043555	0.296583	-0.147	0.883245	***
Municipal roads:Cover	0.489993	0.161842	3.028	0.002465	**
National roads:Cover	0.159039	0.201691	0.789	0.430386	*
European roads:Cover	0.951134	0.659081	1.443	0.148986	
Distance to disturbance:Cover	-0.683915	0.110652	-6.181	6.38E-010	***

Appendix D: Mapping categories

Table 7. Cover and Forage classification of Satskog digital maps.

Forest age & type	Cover, sp, su, au, wi	Forage, sp, su, au, wi
Young mixed forest	I, I, I, I	G, G, G, F
Young pine	I, I, I, I	P, P P, G
Young decideous	I, I, I, I	G, G, G, F
Young mixed coniferous	I, I, I, I	G, G, G, G
Young spruce	I, I, I, I	G, G, G, F
Intermediate mixed forest	C, C, C, I	F, F, F, F
Intermediate pine	I, I, I, I	P, P, P, F
Intermediate decideous	C, C, C, I	G, G, G, F
Intermediate mixed coniferous	C, C, C, C	F, F, F, F
Intermediate spruce	C, C, C, C	F, F, F, F
Old mixed forest	C, C, C, I	P, P, P, F
Old pine	I, I, I, I	P, P, P, P
Old decideous	C, C, C, I	G, G, G, F
Old mixed coniferous	C, C, C, C	P, P, P, F
Old spruce	C, C, C, C	P, P, P, F

*sp=spring, su=summer, au=fall, wi=winter
**C=cover, I=intermediate, O=open, G=good, F=fair, P=Poor

Table 8. Cover and Forage classifications of Norut digital maps.

Cell category	Cover, sp, su, au, wi	Forage, sp, su, au, wi
Barskog – tett tresjikt	C, C, C, C	F, F, F, F
Barskog og blandingsskol – åpent tresjikt	I, I, I, I,	F, F, F, G
Lavrik furuskog	I, I, I, I,	P, P, P, G
Lågurtskot og edellauvskog	C, C, C, O	F, F, F, F
Høgstaude- og storebregnelaubskog	C, C, C, O	G, G, G, F
Blåbær- og småbregnebjørkeskog	C, C, C, O	F, F, F, F
Kreklingbjørkeskog	C, C, C, O	P, P, P, P
Lavrik bjørkeskog	C, C, C, O	P, P, P, P
Tuemyr og lågvokst fastmattemyr	O, O, O, O	P, P, P, P
Høgvokst mattemyr (høgstarrmyr)	O, O, O, O	P, P, P, P
Blautmyr og åpen sumpvegetasjon	O, O, O, O,	P, P, P, P
Eksponerte rabber, blokkmark, berg i dalen (låglan)	O, O, O, O	P, P, P, P
Gras- og frytlerabb	O, O, O, O	P., P, P, P
Lavhei	O, O, O, O	P, P, P, P
Lyngrik leside	O, O, O, O	P, P, P, P
Lynghei og frisk rishei (lågland og fjell)	O, O, O, O	P, P, P, P
Urterik eng (lågland og fjell)	O, O, O, O	F, F, F, P
Gras- og musøresnøleie	O, O, O, O	P, P, P, P
Ekstremsnøleier	O, O, O, O	P, P, P, P
Bre, snødekt mark	O, O, O, O	P, P, P, P
Vann	O, O, O, O	P, P, P, P
Dyrka mark	O, O, O, O	F, G, G, P
By, tettsted	O, O, O, O	P, P, P, P
Uklassifisert/skygge	-	-