Spatio-temporal variation in moose-vehicle collisions: the effect of varying traffic intensity and light conditions

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Abstract

In order to find effective mitigating measures against the large number of moose-vehicle collisions (MVCs) in the Nordic countries, it is important to learn more about the underlying mechanisms causing their spatio-temporal variation. While many studies have looked at the effects of varying moose density, traffic volume and weather conditions on the seasonal and yearly variation in MVCs, previous research has rarely studied the same questions based on MVC data collected at the temporal scales of date and hour. However, because the circadian activity of moose is closely related to the variation in daylight, the road-crossing probability of moose may differ between light periods (dusk, dawn, night and daytime) – which timing and extent vary with month and latitude. Conversely, the circadian variation in traffic intensity seems to follow a fixed daily pattern in all of Norway. This indicates that the overlap between high crossing probability and high traffic intensity will show a predictable pattern across months and latitudes. To test this hypothesis, I examined to what extent the probability of MVC in a municipality was related to varying traffic intensity within light period during the year, while simultaneously controlling for spatial variation in moose density (harvest per km²) and traffic volume (number of cars). My results demonstrated that the probability of MVC for a given traffic intensity was lowest during the day, which concurs with previous findings that moose are more active at dawn, dusk and night. However, while the probability of MVC increased with increasing traffic intensity at dawn and night, as expected, the relationship was negative at daytime and dusk. The latter two periods coincide with hours of the day with the on average highest traffic intensity, which may suggest that moose may increasingly perceive roads as barriers when the traffic intensity exceeds a certain level. The circadian relationship also explained parts of the latitudinal and monthly variation in MVCs, particularly in November-January. My findings suggest that high probability of MVC is partly associated with the time of the year when high traffic intensity extends into the dark and twilight periods of the day. These results can be used to provide management authorities and the public better information about when and where an MVC is more likely to occur.
Sammendrag
Det er viktig med kunnskap om de underliggende mekanismene for den romlige og temporære variasjonen i det store antallet elgpåkjørsler i Norden for å kunne iverksette effektive avbøtende tiltak. Mange studier har sett på hvordan elgtetthet, trafikkmengde og værforhold påvirker sesongmessig og årlig variasjon i elgpåkjørsler, men denne forskningen har sjeldent studert de samme spørsmålene basert på dato og klokkeslett for påkjørsler. Et viktig mønster kan derfor ha blitt oversett, ettersom daglig elgaktivitet samvarierer med døgnvariasjonene i dagslys, mens trafikkintensitet derimot følger et fast mønster gjennom døgnet. Dette fører til at overlappet mellom elgens aktivitetsperioder og trafikkintensitet vil følge et forutsigbart mønster over måned og breddegrad. Følgelig vil også sannsynligheten for en elgpåkjørsel kunne predikeres. Denne hypotesen testet jeg ved å undersøke hvordan sannsynligheten for elgpåkjørsler blir påvirket av varierende trafikkintensitet i de ulike dagperiodene (dagtid, daggry, skumring, natt), samtidig som jeg kontrollerte for romlig variasjon i elgtetthet (høsting per km²) og trafikkvolum (antall biler). Resultatene viste at sannsynligheten for elgpåkjørsler var lavest på dagtid, noe som stemmer overens med tidligere funn om høyere elgaktivitet ved daggry, skumring og natt. Forholdet mellom sannsynligheten for elgpåkjørsel og trafikkintensitet var positivt ved daggry og natt, men forholdet var negativt på dagtid og i skumringen. De to sistnevnte periodene sammenfaller med de timene av dagen med den gjennomsnittlig høyeste trafikkintensiteten, noe som indikerer at elgen i økende grad kan oppfatte veiene som barrierer når trafikkintensiteten passerer et visst nivå. Forholdet mellom daglig trafikkintensitet og lysforhold (som samvarierer med elgaktivitet) forklarte også deler av måned- og breddegradvariasjon i elgpåkjørsler, da spesielt i november-januar. Funnene mine antyder at høy sannsynlighet for elgpåkjørsler delvis er knyttet til den tiden av året hvor høy trafikkintensitet strekker seg inn i skumringen og de mørkere timer av dagen. Disse resultatene kan brukes til å gi forvaltningen og allmennheten en bedre forståelse av når og hvor elgpåkjørsler mer sannsynlig inntreffer.
Introduction

Ungulate-vehicle collisions (UVCs) is an increasing road-safety and economic problem in Europe and USA (Bruinderink and Hazebroek 1996). At least half a million collisions occur annually in Europe, causing material damages for over one billion Euro (excluding Russia, Bruinderink and Hazebroek 1996). In addition to the issues of animal welfare, these collisions have socioeconomic consequences and may cause serious and fatal injuries to humans (Child and Stuart 1987; Lavsund and Sandegren 1991; Mysen 1996; Schwabe and Schuhmann 2002).

In Norway, moose-vehicle collisions (MVCs) are considered most serious from an economic and human welfare point of view. Each year approximately 2000 moose are involved in traffic accidents (www.hjortevilt.no), with societal costs exceeding NOK 200 million (Solstad 2007). This has led to much effort in finding effective mitigating measures. However, because appropriate action must be based on a good understanding of the underlying mechanisms, there is still a need to identify the main factors causing the spatio-temporal variation in MVCs.

MVCs will occur whenever moose and vehicles intersect in time and space, and the driver and moose are unable to prevent the collision. As more moose and vehicles are likely to increase the probability of an intersection, moose density and traffic intensity are among the most important factors affecting the probability of MVC (Mccaffery 1973; Lavsund and Sandegren 1991; Seiler 2004; Rolandsen et al. 2010; Rolandsen et al. 2011). This is also evident in Norway, where the number of collisions have increased during the last four decades, in close correspondence with increasing traffic volume and moose density (Solberg et al. 2009).

In addition to the general effect of traffic volume, the spatial and temporal distribution of MVCs is influenced by local driving conditions. Humans ability to detect objects and individuals decreases with reduced light conditions (Owens and Sivak 1996), resulting in less time to react to animal crossings (Thomas 1995; Sullivan 2011). Likewise, the detection probability and response time may be reduced by dense roadside vegetation (Rea 2003), and higher speed limits and poor road surface conditions (snow, ice) may increase the stopping time (Frate and Spraker 1991; Gunson et al. 2003; Seiler 2005; Sullivan 2011).
Besides affecting the driving conditions, weather conditions can also affect the number of MVCs through its effect on the spatial distribution of moose (Ball et al. 2001; Rolandsen et al. 2011). For instance, more moose seem to be killed during snow rich winters in Norway, probably because moose tend to congregate along roads under such conditions (Odden et al. 1996; Solberg et al. 2009; Rolandsen et al. 2010). In areas with in general low snow depths, moose are less inclined to migrate to lowland and road-dense areas during winter (Hjeljord 2001), possibly explaining why the collision rate are less sensitive to varying snow depth in such areas (Rolandsen et al. 2010; Rolandsen et al. 2011). Because the extent of snow cover and snow depth tend to increase from south to north in Scandinavia, the effect of snow is also suggested to generate latitudinal differences in the distribution of MVCs (Lavsund and Sandegren 1991).

Previously, the effects of moose activity and traffic intensity on the number of MVCs have been analyzed on the temporal scale of days, months or years. However, moose activity and traffic intensity also vary considerably within the day. Moose are crepuscular, i.e. they are most active during dusk and dawn, followed by night (Renecker 1987; Henriksson 2008; Rolandsen et al. 2010), and several studies indicate that more road-crossings by moose occur during the periods where moose are most active (Rolandsen et al. 2010; Neumann et al. 2012). Because the timing of dusk and dawn in Norway varies with season and from north to south, moose are likely to vary their activity pattern correspondingly throughout the year and across latitudes (Rolandsen et al. 2010). In contrast, humans are most active during the lightest part of the day, and are less inclined to change their activity according to varying light conditions (Wever 1979). The typical pattern is that human activities start between 6 and 8 in the morning and ends between 20 and 22 in the evening, and the same pattern is present with respect to the traffic intensity, i.e. the number of cars on the road.

The different circadian activity pattern of humans and moose suggests that the effect of varying traffic intensity on MVCs may be difficult to detect if traffic intensity is measured on a daily or seasonal scale only. Indeed, the probability of MVC on a given day was not related to the daily road-crossing frequency of moose in Norway and Sweden (Rolandsen et al. 2010; Neumann et al. 2012). If anything, there was a negative relationship, in which months with more road-crossings by moose tended to
have on average less MVCs, while months with lower crossing frequency had more MVCs (Rolandsen et al. 2010). Possibly, this pattern could be due to a poor overlap between the time of the day with peak traffic and peak moose activity (e.g. Frate and Spraker 1991). For instance, because moose are most active in the night time during summer, and most traffic takes place in the period from 08:00 to 22:00, it is unlikely that the generally higher traffic intensity recorded in the summertime should lead to more MVCs. On the other hand, it may also be that the number of MVCs does not increase proportionally with traffic intensity, even for a given moose activity. This was suggested by Seiler (2005), who showed that the number of MVCs increased with increasing traffic to a certain level (c. 4000 vehicles per day), but decreased when the traffic intensity increased even more. Presumably, this is because moose perceive the road as a barrier when the number of vehicles on the road is high. No moose accidents were recorded when the traffic increased to 9000 vehicles per day (Seiler 2005), indicating that such roads are perceived as complete barriers by the moose, and thus not crossed at all.

Using a large dataset on MVC with high spatio-temporal resolution (municipality, time and date), I here examine to what extent circadian variation in traffic intensity and light conditions is important for understanding the spatial, hourly and monthly variation in MVCs. I hypothesize that the probability of MVC is related to the circadian variation in traffic intensity and moose activity throughout the year, and that this variation affects the spatio-temporal distribution of MVCs in Norway. To test this hypothesis, I examined the relationship between the probability of MVC and traffic intensity within light period (dawn, day, dusk, night) and month, while simultaneously controlling for spatial variation in moose density (harvest per km²) and traffic volume (number of cars).

As most studies suggest that moose are most active during dusk and dawn, I predict that (1) the probability of MVC, for a given traffic intensity, is highest during these two periods, followed by night and lowest during daytime. Moreover, as more vehicles increase the chance of an intersection, I predict (2) a positive relationship between the probabilities of MVC and traffic intensity during dawn, dusk and night, but (3) a negative relationship between the probability of MVC and traffic intensity during daytime. The latter relationship was expected because moose are less active at daytime, and may be less willing to cross roads when visually exposed in daylight.
and when the disturbing effect of traffic is high (Seiler 2005). I also predict (4) that the circadian variation in traffic intensity and light conditions will explain part of the variation in MVCs among months and across latitudes. This can be expected because of the spatio-temporal variation in the degree of overlap between moose activity and traffic intensity. Indeed, high moose activity (during dusk and dawn) will more often overlap with high traffic intensity in the darkest months (November-February) than during summer (May-August), and the effect will be larger in the north than the south due to higher monthly variation in the number of daylight hours in the north.
Methods

Study area
The study area included 245 municipalities all across Norway, except in the western region (Fig. 1). In Norway, there is approximately 100,000 moose during winter (Solberg 2005), inhabiting municipalities from 58 to 71 degrees north. Because of the country’s latitudinal position and range, there is much variation in circadian light conditions within and between months. In December, there is no daylight furthest north, while daylight is present for 24-hours in June. In the south, the seasonal variation in light conditions is substantially smaller (www.timeanddate.com).

Moose-vehicle collisions
In this study, I obtained all MVC data from the National Cervid Register (NCR), reported during the years 2007-2012. It is not mandatory to report collision data to NCR, but an increasing number of municipalities do so, as this also allows for reporting data of non-fatal collisions, as well as the location, time and date of the collision. In contrast, all municipalities are obliged to report MVC data to Statistics Norway (www.ssb.no), but only at the scale of municipality and year, and only collisions with a fatal outcome for the moose. As indicated in Fig. 1, the data reported to the different institutions show very much the same geographical variation in the number of MVCs, indicating that data from NCR are fairly representative of the spatial variation in the number of MVCs reported to Statistics Norway.

In total, I used data from 7838 MVCs, with date and time of occurrence. As not all collisions had exact location, all data were assigned the municipality’s geographical center coordinate. The recorded time was given in hours and minutes, but due to reporting errors and rounding off, the accuracy of the minutes was unreliable. For instance, 44% of all collisions occurred at the top of the hour. I therefore ignored minutes, and instead summarized MVCs as an hourly value per month, within year and municipality. Although hourly data were aggregated on month, several collisions only occurred in 13% of the cases (and then mainly two collisions). Therefore, I found it most appropriate to convert the number of MVCs into a binomial response variable, either did a collision occur within an hour (1), or it did not (0). By this procedure, the number of occurrences was reduced from 7838 to 6817.
Fig. 1 Mean number of moose-vehicle collisions (MVCs) per hunting year reported to the National Cervid Register (NCR) or Statistics Norway (SSB). The green stars indicate the location of the traffic counting stations that were used to estimate the average hourly traffic intensity. The map foundation was made by the Norwegian mapping authority.

To summarize, the transformed MVC data consisted of a 24-hour vector for each month, year and municipality, with the corresponding presences or absence of collisions, for each municipality’s reporting period. Because there was no information on when municipalities began reporting, I assumed that they started in the hunting year (i.e. May-April) of their first recorded MVC.

Light conditions
To be able to test my predictions, I needed information about the circadian variation in moose activity. I used light conditions as a proxy for moose activity, and assumed that moose were most active during dusk and dawn, followed by night, in all parts of Norway. This assumption has been supported by previous studies on moose behavior (e.g. Rolandsen et al. 2010; Neumann et al. 2012). To create light periods at a monthly basis, I estimated the solar elevation on the 15th of every month for each municipality, employing the software R 2.15.2 (R Core Team 2012) and the R package maptools (Lewin-Koh et al. 2012). The light conditions were divided into four
different light periods based on the solar angle relative to the horizon: daytime (> 0°), night (< -12°), dawn (-12° ≥ 0°) and dusk (0° ≤ -12°).

**Traffic intensity**

As an estimate of hourly traffic intensity, I computed the average hourly traffic intensity estimate (AHTI) based on data from four traffic counting stations operated by the National Public Roads Administration (www.vegvesen.no; Eq. 1) and distributed along main roads in Norway (Fig. 1). The average AHTI estimate was calculated as:

\[
AHTI_h = \frac{\sum_{t=1}^{t=4} \sum_{m=1}^{m=12} \sum_{d=1}^{d_{max}} car_{h,d,m,t}}{4}
\]  

(Eq. 1)

where \( h= \) hour, \( d= \) day, \( m= \) month and \( t= \) traffic counting station. I assumed that this variable was representative for most Norwegian roads, and assigned the same AHTI estimates to all months and municipalities. Although this is a wide generalization, the pattern seemed to be fairly similar at all the traffic stations (Fig. 2), despite their wide geographic distribution (Fig. 1). I therefore considered this to be an adequate representation of the circadian variation in traffic intensity.

![Fig. 2](image.png)

**Fig. 2** Relative hourly traffic intensity (AHTI), computed based on four traffic counting stations distributed along main roads in Norway (Fig. 1). The mean of each traffic station is given in grey, while the overall mean is given in black.
The variation in traffic volume between areas was not accounted for by the AHTI estimates, which only varied through the day. Thus, to account for spatial variation in traffic volume, I included the number of private cars per municipality as a variable in the models. This variable increased by 10% during the study period (www.ssb.no), and was therefore included with yearly variation.

Moose density

As an index of moose density, I used the annual harvest per km² forest and bog in a municipality. A similar index has been employed in previous studies (Mysterud 2004; Seiler 2004; Solberg et al. 2009), and seems to be closely correlated with other estimates of density (Solberg and Sæther 1999; Solberg et al. 2005; Solberg et al. 2006). However, it is not a perfect reflection of the actual population density. Because hunting strongly influences the population dynamics, moose harvested one or two year into the future is often found to be a more accurate measure of the current year’s moose density (Seiler 2004; Solberg et al. 2009). As my MVC data are from the most recent years, I could not use future harvest statistics, but instead I used the year’s harvest as a proxy for moose density. Unfortunately, during the hunting year 2008/2009 data was only published on the level of counties. Thus, to be able to assign data to the level of municipality, I used harvest statistics from 2007/2008 as a proxy for the density in 2008/2009. This was justified by the fact that no significant change in the number of kills per county were recorded during these two hunting years (Paired t-test, \( t_{19} = 0.084, p = 0.9368 \)).

Statistical analyses

All statistical analyses were done using R 2.15.2 (R Core Team 2012). I used a binomial mixed model approach (GLMM) with logit link function to model the data, utilizing the R package lme4 (Bates et al. 2012). Because of repeated measures within each spatial unit and for all years, municipality and year were included as random factors in the models. To account for the spatio-temporal differences in moose density and traffic volume, I also included the number of private cars (traffic volume), and the annual number of moose harvested per km² forest and bog within municipality (moose density) as fixed factors in all my models. These variables were log transformed to ensure model convergence, and to reduce the impact of extreme values on the fitted probabilities.
To identify any spatio-temporal variation in MVCs in Norway, I first created a model with the binomial MVC response variable, and with month (categorical), latitude (continuous) and their two-way interaction as explanatory variables (Model 1). A significant interaction term would indicate different latitudinal variation among months in the probability of MVC.

Model 1: $P(\text{MVC}) = \text{Month} + \text{Latitude} + (\text{Month} \times \text{Latitude}) + \ln(\text{Private cars}) + \ln(\text{Moose harvest})$

Next, to test my predictions, I created model 2 by adding light period and traffic intensity to model 1, as well as their two-way interactions. First, I assessed the fit of the new model by using a likelihood-ratio test. Second, I tested the variation in probability of MVC among the four day periods for a given traffic intensity, as I predicted a higher probability of MVC during dusk and dawn compared to night and day (Prediction 1). This was done by comparing the predicted probability of MVC (on logit scale) at the overall mean traffic intensity, using a two sample z-test. Third, I used the slope estimates of Light period*AHTI in model 2, to examine if the probability of MVC increased significantly with traffic intensity during dawn, dusk and night (Prediction 2), and decreased during daytime (Prediction 3).

Model 2: $P(\text{MVC}) = \text{Month} + \text{Latitude} + \text{Light period} + \text{AHTI} + (\text{Month} \times \text{Latitude}) + (\text{Light period} \times \text{AHTI}) + \ln(\text{Private cars}) + \ln(\text{Moose harvest})$

Finally, I tested if traffic intensity and light conditions explained parts of the spatio-temporal distribution in MVCs (Prediction 4) by comparing model 1 and 2. This was done by first predicting the probability of MVC for latitudes between 58°N-70°N (by intervals of 2°N) each month, in model 1 and 2. Next, by using a two sample z-test, I compared the probability estimates (on logit scale) between the models at a given latitude. I reported the result of the z-tests with a 95% confidence interval, combining them to form a continuous interval along the latitudes 58°N-70°N for each month. This would indicate whether the estimated probabilities of MVC in model 1 and 2 were significantly different ($p < 0.05$) at any given latitude within a month. In addition, I extracted the slope estimates of Month*Latitude in model 2 to examine if the probability of MVC was significantly related to latitude in each month. All values are reported on logit scale, unless otherwise stated.
**Results**

As expected, the probability of MVC was positively related to the number of private cars ($\beta = 0.227 \pm 0.066, z = 3.453, p < 0.001$) and to the number of moose harvested per km$^2$ forest and bog ($\beta = 0.437 \pm 0.062, z = 7.000, p < 0.001$). Controlling for these variables, I still found significant spatio-temporal variation in MVCs in Norway (Fig. 3). Generally, the probability of MVC was positively related to latitude (increased from south to north) in November-March, whereas the relationship was negative in May-September (Fig. 3). In April and October, which lies between these two periods, there was no significant spatial variation (Fig. 3). Consequently, as the highest and lowest probability of MVC was found in the north (Fig. 3), there was more monthly variation in the probability of MVC in the north than in the south.

The fit of model 1 increased significantly when light conditions and traffic intensity were included, creating model 2 ($F_{7,28} = 2796.6, p < 0.001$). The probability of MVC increased with increasing traffic intensity at dawn ($\beta = 31.41 \pm 2.77, z = 11.35, p < 0.001$) and night ($\beta=28.53 \pm 0.70, z = 40.90, p < 0.001$; Fig. 4), as expected from prediction 2. At dusk, there was a negative relationship between the probability of MVC and traffic intensity ($\beta = -11.77 \pm 1.95, z = -6.04, p < 0.001$; Fig. 4), opposite of what I predicted. A negative relationship between the probability of MVC and traffic

![Fig. 3 Predicted relationships between the probability of a moose-vehicle collision (P(MVC)) and latitude (°N) within months, based on a binomial mixed model (model 1, see Methods). Spatial variation in moose harvest and number of vehicles is kept constant at mean values. Significance of slope estimates, $p < 0.1 \ (*)$, $p < 0.05 \ (*)$, $p < 0.01 \ (**)$ and $p < 0.001 \ (***)$](image-url)
Fig. 4 Predicted relationships between the probability of moose-vehicle collision (P(MVC)) and the hourly traffic intensity in four different light periods, based on a binomial mixed model (see Methods, model 2). Spatial variation in moose harvest and number of vehicles is kept constant at mean values. The vertical line represents the overall mean hourly traffic intensity, while the grey dots represent the mean hourly traffic intensity in each light period.

Intensity was also found at daytime ($\beta = -12.80 \pm 1.04$, $z = -12.29$, $p < 0.001$; Fig. 4; supporting Prediction 3).

Comparing the probability of MVC at the overall mean traffic intensity (vertical line in Fig. 4) for the four light periods indicates that the probability was significantly higher at dawn than at dusk and night (Fig 5), and all these light periods had significantly higher probabilities than at daytime (Fig. 5). This was partly in accordance with prediction 1; that moose are more active at dusk and dawn compared to at night and daytime, and suggest that moose are more likely to cross roads and be killed in traffic during the former light periods.
Fig. 5 Comparison of the probability of MVC (on logit scale) at the overall mean traffic intensity (see vertical line Fig.4) for the four light periods. If the confidence interval overlap zero, the estimates are not significantly different.

The outcome of the two spatio-temporal models, model 1 and model 2 is presented in Fig. 6 (grey and black lines, respectively). There were significant differences in the estimated probability of MVC between the two models in November, December and January, except at southern latitudes (Fig. 6). This indicates that the effect of traffic intensity and light condition primarily affected MVCs in the months with little daylight, and more so at northern latitudes. However, there was almost no change in the probability estimates of the two models in February, except for a small decline in the relationship between the probability of MVC and latitude (Fig. 6). In the summer season, May to September, the effect of traffic intensity and light conditions did not significantly affect the variation in MVCs (Fig.6). Still, the spatio-temporal differences were reduced in model 2, mainly because of a reduction in predicted probability of MVC at northern latitudes during November - January (Fig. 6). Although these results are in accordance with prediction 4, it is obvious that much spatio-temporal variation remained unexplained even after accounting for circadian variation in traffic intensity and light conditions (Fig. 6).
Fig. 6 Predicted relationships between the probability of a moose-vehicle collision (P(MVC)) and latitude (°N) within months, based on binomial mixed models. The black lines represent a model with day period and traffic intensity included (see Methods, model 2), whereas grey lines represent the model without these variables (see Methods, model 1). The variation in moose harvest and number of vehicles is kept constant at mean values. Significantly differences in the predicted probability of MVC between the two models are marked by grey shading (see Appendix 1 for details). Significance of slope estimates, $p < 0.1$ (*), $p < 0.05$ (**), $p < 0.01$ (***), and $p < 0.001$ (****).


Discussion

In this study, I demonstrated that there is a significant relationship between the probability of moose-vehicle collision (MVC) and the circadian variation in traffic intensity and light conditions (Fig. 4), and that these relationships can explain parts of the spatio-temporal variation in MVCs (Fig. 6). Thus, to better predict the temporal (hourly and monthly) and spatial (latitudinal) distribution of MVCs, it is important to account for circadian variation in traffic intensity and light conditions (as an index of moose activity). For a given traffic intensity, I found that the probability of MVC was highest at dawn, followed by dusk and night, and with the lowest probability at daytime (Prediction 1, Fig 5). This suggests that there is a positive relationship between the probability of MVC and the road-crossing frequency of moose, although the probability differed between light periods of assumed similar moose activity (dusk and dawn). Moreover, there was a positive relationship between the probability of MVC and traffic intensity at dawn and night, while at dusk and day the relationship was negative (Prediction 2 and Prediction 3, Fig 4). This indicates that the probability of MVC is not only a product of road-crossings frequency of moose and the number of intersecting cars, but that a high number of cars may also deter moose from crossing. Although circadian variation in traffic intensity and light conditions explained parts of the spatio-temporal variation in the probability of MVC (Prediction 4; Fig. 6), much variation remained unexplained. This suggests that additional factors are important to fully understand why the probability of MVC varies across Norway and between months.

Spatio-temporal variation in MVCs

In general, I observed a higher probability of MVC during November-February, confirming previous studies from Norway (Gundersen and Andreassen 1998; Rolandsen et al. 2010), northern Sweden (Lavsund and Sandegren 1991; Neumann et al. 2012) and Alaska (Frate and Spraker 1991). These areas are located at approximately the same latitudes as Norway. In contrast, further south a predominance of collisions seems to occur during June-September (i.e. 44°N to 57°N; Newfoundland (Joyce and Mahoney 2001), southern Sweden (Skolving 1987; Lavsund and Sandegren 1991), USA (Danks and Porter 2010; Sullivan 2011) and Quebec (Dussault et al. 2006)). This latitudinal difference in the monthly distribution of MVC seems to be in accordance with my results and hypothesis, with a higher
probability of MVC further south in summer, and with a higher probability of MVC further north in winter (Fig. 3). However, this spatio-temporal pattern is not consistent in all studies. In Finland, for instance, there was a peak in MVCs in September (Haikonen and Summala 2001) and not around December as expected, despite Finlands position at the same latitude as Norway. Hence, the seasonal distribution of MVCs cannot be derived by only using latitudinal location and month, indicating that a more complex combination of factors influence the probability of MVC.

**Traffic intensity and moose activity**

At the overall mean traffic intensity, the probability of MVC was higher at dawn than at night and dusk, and in all these light periods the probability of MVC was higher than at daytime (Fig. 5). This suggests that moose cross roads more frequently during dawn than in other light periods. However, Hanssen (2008) did not find any difference in crossing frequency between dusk and dawn, while Fliflet (2012) found that moose crossed roads more often at dusk. An alternative is therefore that factors related to the car drivers, such as awareness and perception (Dussault et al. 2006), also may influence the probability of MVC at dawn. For instance, car drivers may be less alert in the morning than they are at dusk, despite the similar light conditions. In addition, there may be a barrier effect imbedded in this pattern as indicated by the different responses to varying traffic intensity in the different light periods (Fig. 4). There was a positive relationship between the probability of MVC and traffic intensity at dawn and night, but a negative relationship at dusk and daytime (Prediction 2 and 3; Fig. 4). Because of the substantially higher average traffic intensity during the two latter periods (Fig. 4), moose may perceive roads mostly as a barrier at dusk and daytime, and increasingly so as traffic intensity increases (Seiler 2005). Although this mechanism can explain why the effect of traffic intensity differs between dawn and night on the one hand, and dusk and day on the other, it is less clear why the same pattern is present during periods of similar traffic intensity (Fig. 4). Possibly, moose may behave less cautiously around roads at dawn, since this is a period usually preceded by low traffic intensity (Fig. 2). In addition, moose are often using areas closer to human settlements during night (e.g. Lykkja et al. 2009) and will thus have to cross roads to be able to retreat to safer areas during the day.

I used light conditions as a proxy for moose activity in this study. It was thus not possible for me to disentangle the effect of reduced visibility and moose activity on
the probability of MVC. Several studies propose that reduced visibility may be an important factor influencing MVCs (Frate and Spraker 1991; Dussault et al. 2006; Neumann et al. 2012), and not just moose activity. During dusk, dawn and night, reduced visibility decreases the ability to detect crossing moose, thereby increasing the probability of MVC. (Hills 1980; Frate and Spraker 1991; Owens and Sivak 1996). Accordingly, one could argue that visibility per se can induce the relationship between traffic intensity and light conditions, and not necessarily moose activity. However, a more likely explanation is that a combination of the two variables affects MVCs (Haikonen and Summala 2001). This is supported by my findings, as the highest probability of MVC at the overall mean traffic intensity occurred at dawn (Fig. 5). If only the visibility was important, I would expect that traffic intensity at night, when it is dark, would lead to an even higher probability of MVC. Based on my study, however, it is impossible to quantify what correlate of the light period (visibility or moose activity) that is the most influential on the number of MVCs.

The effect of traffic intensity and moose activity on the spatio-temporal variation in MVCs

Sullivan (2011) demonstrated that MVCs follow the sun’s annual cycle, with a peak in collisions at twilight hours during winter, and thus suggested that MVCs were closely correlated to the degree of overlap in moose activity and traffic intensity. However, he emphasized that the observed pattern was the net effect of several factors. This corresponds well with my results, as the overlap between traffic intensity and moose activity only explained parts of the spatio-temporal variation in MVCs (Fig. 6). Hence, parts of the seasonal variation in MVC may arise due to varying degree of overlap between traffic intensity and moose activity (Rolandsen et al. 2010), but additional factors are also important. Traffic intensity and moose activity (light period) explained the latitudinal variation in MVC significantly only in November-January (Fig. 6), which are months with high latitudinal variation in circadian light conditions. However, a similar large variation exists in May-July, but during these months, the circadian variation in traffic intensity and moose activity did not explain much of the latitudinal variation in MVC (Fig. 6). A contributing cause is probably that moose tend to congregate along roads in November-January when deep snow reduces mobility and food access at higher altitudes (Rolandsen et al. 2011), and in the same period there is a larger overlap between high activity periods of moose and traffic intensity. Hence,
a higher proportion of the moose population may be exposed to the traffic hazards in November–January compared to May–July. In the latter period, moose tend to use the entire forested area and may also behave differently, e.g. due to calving (Rolandsen et al. 2010).

Besides explaining why more moose are more often killed on roads in the winter than summer, the effects of snow may also explain why the probability of MVC was higher in the north than in the south (Fig. 6). In general, winters are longer in the north and more precipitation is likely to fall as snow (Moen 1999). Combined with the rugged landscape structure, a large proportion of the moose population may therefore congregate in valleys close to roads. In the south, the concentration effect of snow is likely to be less prevalent because of on average lower altitudes (Moen 1999), less snow and shorter winters (Moen 1999). Although moose density (harvest per km²) was included in the models, this variable is not able to reflect such local variation in moose density.

**Management implications**

I have demonstrated that the probability of MVC are not uniformly distributed throughout the day, the year, and across latitudes, and that parts of this variation can be explained by circadian variation in traffic intensity and moose activity. These results should be used to give the management authorities and the public better information about when and where MVCs are more likely to occur. In order to reduce the number of MVCs, it is also essential to consider traffic intensity and moose activity when evaluating what mitigating measures to implement. One mitigating measure that could be considered is a reduction in speed limits (Bertwistle 1999) in combination with warning signs (Stanley et al. 2006). However, to reduce its impact on the traffic efficiency, such measures should primarily be implemented in areas and during periods when high traffic intensity is likely to overlap with periods of high moose activity. This may be achieved by introducing dynamic speed limit and warning signs (Mastro et al. 2008), i.e. signs that display a different warning message in periods of high and low risk of MVC, respectively. The public should also be made more aware of these periods (Rogers 2004), and the effectiveness of such measures should be evaluated.
Concluding remarks
I found that the probability of MVC varied with circadian light conditions and traffic intensity (Fig. 4 and Fig. 5), and that this relationship partly explained the spatio-temporal variation in MVCs (Fig. 6). However, there was much unexplained variation (Fig. 6), indicating that additional variables are necessary to explain why MVCs show such a large variation in probability of MVC from south to north and during the year. In particular, there are two relationships that should be assessed by future studies. Firstly, the probability of MVC should also be analyzed in relation to snow depth and topography as this might further improve our understanding of the spatio-temporal variation in MVCs. Secondly, a non-linear modeling approach should be explored, as increasing traffic intensity seems to have a positive effect on the probability of MVC below certain traffic intensities, and a negative effect above (Fig. 4). Lastly, I recommend studies of traffic accidents involving other wildlife to also consider the use of circadian traffic intensity and light conditions as explanatory variables. According to my results, this may help to predict the probability of an accident at a given place and time, and ultimately help to increase road safety and reduce the number of wildlife-traffic accidents.
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Appendix 1

Comparison of the predicted probabilities between the model with (model 2) and without (model 1) traffic intensity and light period included. This comparison was done by first predicting the probability of MVC for latitudes between 58°N-70°N (by intervals of 2°N) each month, both in model 1 and 2. Next, by using a two sample z-test, I compared the probability estimates between the models for all the given latitudes. Lastly, I reported the result of the z-tests with a 95% confidence interval, combining them to form a continuous interval along the latitudes 58°N-70°N for each month. The results indicate whether the predicted probabilities of MVC in model 1 and 2 were significantly different (not overlapping with zero) or not (overlapping with zero).
Appendix 2

Hourly distribution of collisions according to latitude and month per municipality