

Large-scale spatiotemporal variation in road mortality of moose: Is it all about population density?

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Abstract. Ungulate-vehicle collisions (UVC) constitute a widespread and increasing problem in large parts of the world. This has generated an intensive search for mitigating measures, but often based on a weak understanding of the underlying spatiotemporal factors. We examined the effects of harvest density (a proxy for moose density), traffic-related variables and climate on the spatiotemporal variation in number of moose-vehicle collisions (MVC) in 14 Norwegian counties based on 31 year of data. Moose density was the most important factor explaining the variation in MVC, both within and between counties. In addition, the spatiotemporal variation in MVC was positively related to traffic volume (private car mileage) and snow depth, and negatively related to winter temperature. The relationship between traffic volume and temporal variation in MVC was stronger in counties with general low traffic volume, possibly because high traffic volume can act as a barrier to moose road crossings. Likewise, the temporal effect of snow depth was mainly present in counties with on average deep snow, i.e., where it constitutes a constraint on moose movement and space use during winter. Our study highlights the different importance between areas of the factors underlying the spatiotemporal variation in MVC. A notable exception was the variation in moose density, which follows an isometric scaling to the variation in MVC in all counties. Thus, a given percentage decrease in moose density is likely to return a similar percentage decrease in MVC. A significant population reduction may therefore be an efficient mitigating measure to reduce the number of MVC in Norway. From a harvesting and conservation point of view, other possible preventive measures to reduce MVC should also be considered. However, because of the strong temporal effects of moose density and snow depth, evaluations of other mitigating actions should always seek to control for temporal variation in these variables.

Key words: *Alces alces*; climate; mitigating measures; mixed effect models; moose; moose-vehicle collisions; Norway; population density; road mortality; traffic volume; ungulate-vehicle collisions.

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INTRODUCTION

During the last 50 years there has been a strong increase in many ungulate populations in Europe (e.g., Apollonio et al. 2010) and North America

(e.g., McShea et al. 1997), and with that a number of new human-wildlife conflicts have appeared. A serious conflict concerns ungulate-vehicle collisions (UVCs), which in many areas are taking a high and increasing toll of animals

(e.g., Bruinderink and Hazebroek 1996, Conover 1997). In Norway, for instance, the annual number of UVCs, with fatal outcome for the animal, has steadily increased from about 500 in the early 1970s to about 7000 ungulate (moose, *Alces alces*, red deer, *Cervus elaphus*; roe deer, *Capreolus capreolus*; and wild reindeer, *Rangifer tarandus tarandus*) mortalities the last years (Solberg et al. 2009). UVCs also cause human injuries, in worst case fatal, as well as large socio-economical cost. In many countries the increase in UVC has activated an intensive search for mitigating measures, but often based on a weak understanding of the underlying mechanisms. To be able to implement the appropriate actions it is vital to first identify which factors are causing the UVCs to vary in time and space.

Proximately, UVCs are the outcome of ungulates and vehicles being at the same spot at the same time. More UVCs are therefore likely to happen when ungulates are frequently crossing busy roads (or rails) and when the driving conditions are poor. Consequently, previous research has documented that the number of UVCs is related to factors such as crossing frequency, traffic volume (e.g., number of cars per time unit) and driving conditions (Bruinderink and Hazebroek 1996, Joyce and Mahoney 2001, Seiler 2005). For instance, the numbers of UVCs often seem to peak at dawn and dusk (Allen and McCullough 1976, Haikonen and Summala 2001), probably because of higher movement activity of ungulates during such periods and because the driving conditions (visibility) are generally less good (Haikonen and Summala 2001). Similarly, the number of UVC is often higher during rutting, dispersal and migration (Lavsund and Sandegren 1991, Bruinderink and Hazebroek 1996)—which are periods of high movement activity—and when weather conditions are difficult. The latter may involve periods of snow fall or deep snow, which make ungulates to congregate in low altitude areas (e.g., Ball et al. 2001), closer to rails and roads.

At the current stage, most of our understanding of UVC is based on studies conducted at relatively small spatial and temporal scales, whereas only a few studies have explored the variation in UVCs over several years and over larger geographical areas (Mysterud 2004, Seiler 2004). However, such larger scale studies are

important because many of the presumably most important causal factors may only be detectable at large spatial and temporal scales. Large ungulates can use extensive areas during the year, and local variations in UVCs can therefore be influenced by processes occurring far from the area of interest. In particular, this may be so for migratory species where the proportion, timing and extent of migration depend on prevailing environmental conditions in a given year and season. In the course of several decades the conditions leading to UVC may also vary over a much larger range, making it possible to detect the influence of factors that are normally not varying much over short periods of time (e.g., population density).

In this study, we examined the large-scale spatiotemporal variation in UVCs based on 31 year of data from 14 Norwegian counties. More specifically, we tested to what extent the number of moose vehicle collisions (MVC) was related to moose density, traffic volume and climate. Based on previous studies we expected (1) the number of MVC to be higher in years and counties with high population density and (2) high traffic volume. This is because these factors are likely to be associated with the number of moose crossings and frequency of intersecting vehicles, respectively. Previous findings indicate that the number of MVC increase in periods with much snow along roads (Lavsund and Sandegren 1991) and rails (Andersen et al. 1991, Modafferi 1991, Gundersen and Andreassen 1998), possibly because snow depth affects the spatial distribution and movement rate of moose. Therefore, we expected the number of MVC to (3) be higher in years and areas with deeper snow. Varying movement rates could also be the reason why the number of UVC is sometimes reported to covary with other weather variables. For instance, higher numbers of moose-train collisions are reported in cold periods during winter (Andersen et al. 1991, Gundersen and Andreassen 1998), which could mean that moose are more active when temperatures are low. Being physiologically adapted to cold environments moose can be easily heat stressed during warm periods (Renecker and Hudson 1986, Dussault et al. 2004). Hence, we also expected MVC to occur less often in years and counties with relatively warm (4) winters and (5) summers.



Fig. 1. The 14 counties in Norway that were included in the study: 1, Finnmark; 2, Troms; 3, Nordland; 4, Nord-Trøndelag; 5, Sør-Trøndelag; 6, Hedmark; 7, Oppland; 8, Buskerud; 9, Oslo–Akershus; 10, Østfold; 11, Vestfold; 12, Telemark; 13, Aust-Agder; 14, Vest-Agder.

METHODS

Study area

The study area covers all counties in Norway, except for the counties in western Norway (Fig. 1) where moose densities are low and very few moose are killed on roads (on average < 1.1 moose killed per year and county). In the remaining counties, moose are present in all types of forests and are regularly killed in traffic.

Most of the study area is in the boreal vegetation zones, with small parts covering the boreonemoral and nemoral zone in the very south (Moen 1999). Downy birch (*Betula pubescens*) and to a lesser extent Scots pine (*Pinus sylvestris*) dominate the forests in the two northernmost counties, whereas Norway spruce

(*Picea abies*) and Scots pine become the dominating tree species further south. In the southern counties, forests consist mainly of Scots pine, Norway spruce and birch in the interior, and coniferous trees mixed with birch, oak (*Quercus robur*) and to some extent beech (*Fagus sylvatica*) along the coast (Moen 1999).

In general, the length of the winter season increases from south to north and from coast to inland. In the very south, snow normally covers the ground for less than 3 months, while in the north it may stay for 6 months or more (Moen 1999). However, because of large altitudinal gradients, there are large variation in the duration of snow cover and snow depth in most counties. Exceptions are the county of Østfold

(Fig. 1: area 10), Oslo–Akershus (area 9) and Vestfold (area 11), where almost all land suitable for moose (i.e., forests and bogs) are found at relatively low altitudes (<300 m asl) and where the average snow depth is quite low (Moen 1999). During the study period, the mean snow depth was $41.9 \text{ cm} \pm 19.4 \text{ SD}$ within county and year, whereas the mean summer temperature was $12.2^\circ\text{C} \pm 2.0 \text{ SD}$, and mean winter temperature was $-3.0^\circ\text{C} \pm 2.5 \text{ SD}$. All meteorological data were collected by the Norwegian Meteorological Institute (<http://met.no/>).

Road mortality of moose

The number of moose-vehicle collisions (MVC) within each county was obtained from Statistics Norway (<http://www.ssb.no>) for the period 1977/1978–2007/2008. These data are compulsory reported by the municipality wildlife board to Statistics Norway each year (i.e., April 1–March 31 the following year) and involves moose killed on impact or moose injured in the accident and later dispatched by wildlife officials. Moose that are visually assessed to be unharmed by the wildlife officials or not seen after the accident are not included. Based on data from a restricted number of municipalities and years, about 50–60% of all collisions involving moose lead to the death of the animal (Solberg et al. 2009).

Moose density

As a relative measure of population density, we used the annual number of harvested moose per km^2 of moose inhabitable land (undeveloped areas below the tree line) within county. Harvest density has previously been found to quite closely follow the variation in moose density in Norway at a regional scale (Solberg et al. 1999, Austrheim et al. 2008), although often with a time-lag of 1–2 years relative to a change in population size (Solberg et al. 1999, Fryxell et al. 2010). To get an idea of how well harvest density relates to moose density, and with what time lag, we used a subset of years (1990–2007) for which we also possessed data on moose seen per hunter-day. This index is based on a large number of moose observations recorded by moose hunters each year and is found to correlate closely with moose density (Ericsson and Wallin 1999, Solberg and Sæther 1999, Sylven 2000, Solberg et al. 2006, Ronnegard et

al. 2008). The correlation between moose seen per hunter-day and harvest density in the same year was on average positive (mean $r = 0.52$, range: -0.61 – 0.90), indicating that harvest density was quite well tracking the variation in moose density within county. However, the correlations became even higher when adding a time lag of one (mean $r = 0.72$, range: 0.31 – 0.96) or two years (mean $r = 0.73$, range: 0.47 – 0.98) to the response in harvest density. To account for potential time lags, we therefore also examined the fit of models where harvest density was included with a time lag of one (year $t + 1$) or two years (year $t + 2$), as an alternative to the effect in the current year (year t).

Length of public roads and traffic volume

Counties in Norway vary in size and density of roads. In the analysis, we therefore included as a covariate the total length of public roads (State road, County road and Municipality roads) within county. We used the current road density, but acknowledge that the density has probably increased during the study period due to construction of new roads. However, based on available statistics the changes seem to be rather small, e.g., during 1977–1999 the length of highways increased with approximate 6% (Statistics Norway, <http://www.ssb.no>). As we find it likely that this increase was more or less similar in all counties, the increase in road density should have no significant effects on our conclusions. We excluded private roads and forest roads because of their generally low traffic volume and because about 97% of road killed moose are recorded on public roads (C. M. Rolandsen, *unpublished data*). Traffic volume (million km) was defined as the total private car mileage within county and year. This was calculated as the annual number of private cars, recorded by Statistics Norway (<http://www.ssb.no>), multiplied with the annual average private car mileage. The mileage was estimated by Statistics Norway and the Institute of Transport Economics (<http://www.toi.no>) for the period 1970–2001 (range 11,800–14,200 km). For the period 2002–2007 we assumed the same average mileage as in 2001 (i.e., 13,600 km).

Weather data

Weather data were obtained from the Norwe-

gian Meteorological Institute (<http://met.no/>). The data included downscaled gridded daily maps of temperature and snow depth with 1 km horizontal resolution for the whole of Norway in the period 1977–2008 (Skaugen et al. 2003). We excluded data above the tree line and data on small islands off the coast. From the weather data we calculated mean monthly values for snow depth and temperature. Based on monthly mean values, we calculated the annual variation in mean snow depth (November–April), mean winter temperature (January–April) and mean summer temperature (June–August) within each county.

Statistical analysis

The dependent variable (MVC) was ln-transformed to reduce heteroscedasticity. Similarly, we ln-transformed harvest density, traffic volume and the total length of public roads, to test the extent to which MVC showed isometric scaling with the covariates over time or between counties. A slope parameter deviating from one would indicate that the ratio between MVC and the covariate changed with the size of the covariate (e.g., that the proportion of the moose population killed in traffic increased with increasing density).

Because covariates may differ in their effects within and between counties, we split them into mean (\bar{x}) and relative ($x - \bar{x}$) terms within county, where the new variables represent the spatial and temporal variation, respectively. We then tested their separate effects on the variation in (ln)MVC, as well as the interaction between the spatial and temporal terms (spatiotemporal interactions) for each variable (Singer 1998). Presence of such spatiotemporal interactions would indicate that the magnitude of temporal effect depends on the mean value in a county.

We tested the contributions of different explanatory variables on the variation in (ln)MVC by the use of linear mixed effect models (Bates and Maechler 2010). The (ln)total length of public roads, (ln)harvest density, (ln)traffic volume, snow depth, winter temperature and summer temperature were included as fixed factors. We included county as a random factor (random intercept) to account for the interdependence of data within counties (i.e., time series). Moreover, we also tested a model adding year as a random

factor to account for the possibility of unexplained variation caused by missing covariates (not measured), which may be represented as a year-effect (e.g., temporal autocorrelation).

We tested the global model and all possible nested models, but retained the respective main effects when entering interaction terms. The models were evaluated based on Akaike's information criteria (AIC) corrected for small sample size (AICc; Burnham and Anderson 2002).

We considered candidate models that differed by two or less in absolute value ($\Delta\text{AICc} \leq 2$) to be the set of models best supported by the data (Burnham and Anderson 2002). We fitted models with Restricted Maximum-Likelihood (REML) to compare models with different random effect structure (i.e., a model with only county compared to a model with both county and year as random effects). In the next step, models were fitted with Maximum Likelihood (ML) for the AICc-based model selection procedure, whereas REML was used to obtain un-biased parameter estimates (Pinheiro and Bates 2000). Confidence intervals (95% CI) from the mixed models were based on 10,000 resamplings from the posterior distribution of the parameters. All statistics were performed using R 2.9.1 (R Development Core Team 2008).

From the best model we calculated a quantitative measure of the relative importance of moose density compared to the effects of traffic volume and climatic variables. Following Singer (1998), we calculated the proportion of variation explained by the fixed effects by omitting each of the variables from our best model. From the highest ranking model we omitted population density, traffic volume and climatic variables one by one, and then calculated how much variation was explained by the fixed effects. In each case both the spatial, temporal and spatiotemporal interaction of the variable of interest were removed. The proportion of variance explained by different models was calculated as $(\text{VC1} - \text{VC2})/\text{VC1}$, where VC1 and VC2 are the variance components in the baseline and the more complex model, respectively.

RESULTS

During the study period, we found large variation in MVC and harvest density between

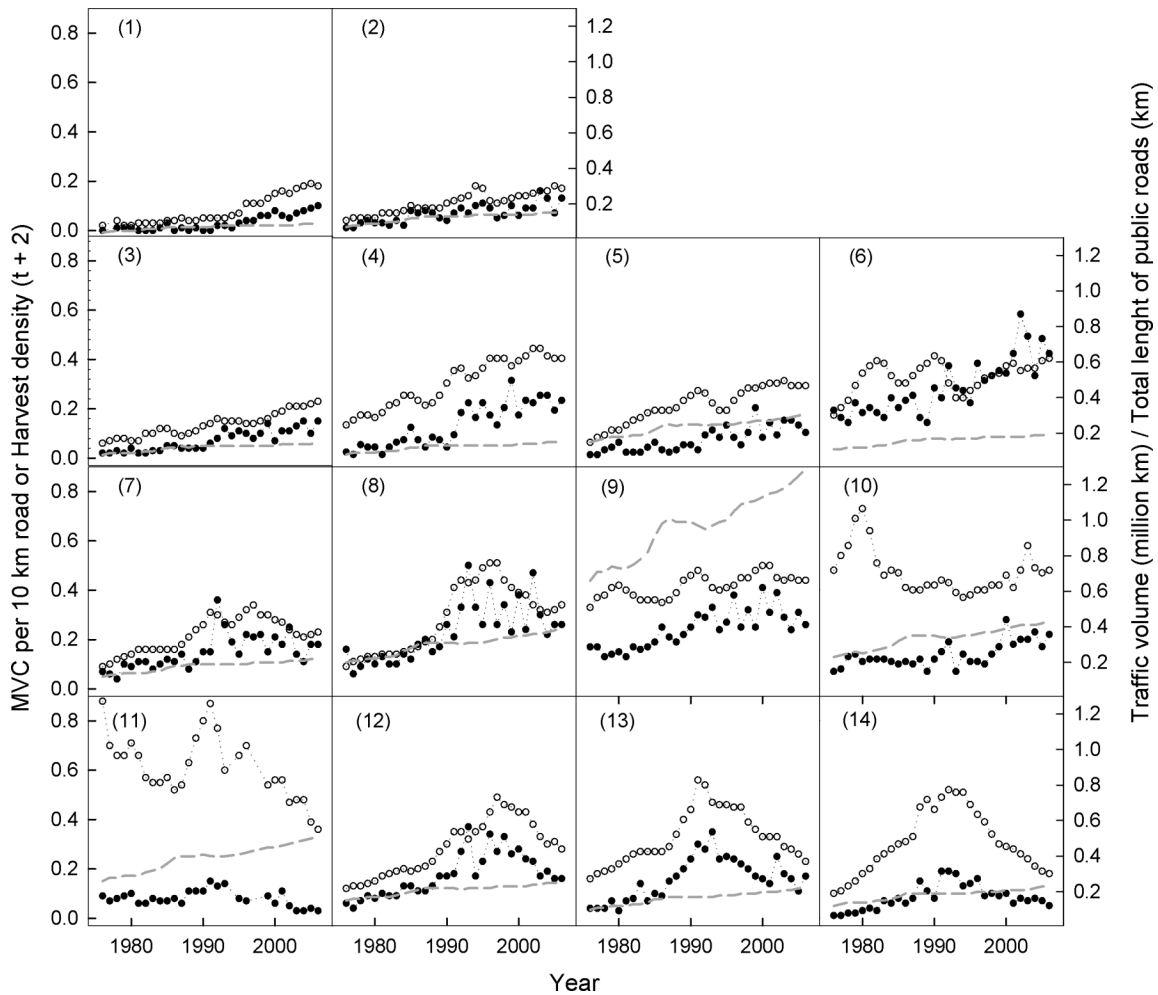


Fig. 2. Number of moose-vehicle collisions per 10 km public road (MVC/10 km, filled circles), and the number of harvested moose per km² (open circles) in the period 1976–2006. The counties are numbered in accordance with Fig. 1. Dashed grey lines indicate traffic volume divided by the total length of public roads within county.

and within counties (Fig. 2). Both variables decreased from south to north, and in most counties there were an increase in MVC and harvest density during the study period. In 1977, 456 moose were reported killed on Norwegian roads (0.07 moose per 10 km public road), increasing to 1309 moose in 2007 (0.19 moose per 10 km public road). The peak year was 2003, when 1568 moose were reported killed (0.23 moose per 10 km public road). Also the relative traffic volume (i.e., total car mileage divided by the total length of public roads) varied much between counties (Fig. 2), ranging from about 0.07 million km per km public road in Finnmark (county 1, Figs. 1 and 2) to 0.97 million km per

km public road in Oslo–Akershus (county 9, Figs. 1 and 2). In Norway as a whole, the traffic volume increased from 10,893 million km in 1977 to 21,186 million km in 2007.

We found harvest density in year $t + 2$ ($AICc = 403.0$) to better explain the variation in MVC than the harvest density in year t ($\Delta AICc = 51.4$) and $t + 1$ ($\Delta AICc = 16.1$). Thus, the variation in harvest density seems to be a time delayed reflection of the population density (see *Methods: Moose density*). The model with both county and year as random factors ($AICc = 403.5$) was selected compared to a model with only county as random factor ($\Delta AICc = 13.6$).

According to $AICc$, all main effects and

Table 1. The nine highest ranked models according to AICc explaining variation in ln(MVC) using linear mixed effect models with county and year as random factors. Explanatory variables included in the models are marked by an X, where X* denotes where the 95% confidence intervals did not include zero. The highest ranked model (Model 1) had an AICc value of 399.1. The global model also included a spatiotemporal interaction of summer temperature, but this variable did not enter any of the models within $\Delta AICc \leq 2$.

Explanatory variables	Rank								
	1	2	3	4	5	6	7	8	9
Spatial terms									
ln(Total length of public roads)	X*	X*	X*	X*	X*	X*	X*	X*	X*
Mean (ln)harvest density t + 2	X*	X*	X*	X*	X*	X*	X*	X*	X*
Mean (ln)traffic intensity	X*	X*	X*	X*	X*	X*	X	X*	X
Mean snow depth	X*	X*	X*	X*	X*	X*	X*	X*	X*
Mean winter temperature	X*	X*	X*	X*	X*	X*	X*	X*	X*
Mean summer temperature									X
Temporal terms									
Relative (ln)harvest density t + 2	X*	X*	X*	X*	X*	X*	X*	X*	X*
Relative (ln)traffic intensity	X	X	X	X	X	X	X*	X	X
Relative snow depth	X	X	X	X*	X	X*	X*	X*	X
Relative winter temperature	X	X	X	X*	X	X*	X	X*	X
Relative summer temperature		X		X	X				
Spatiotemporal interactions									
Mean (ln)harvest density t + 2 * Relative (ln)harvest density t + 2			X		X		X*	X	
Mean (ln)traffic volume * Relative (ln)traffic volume	X*	X*	X*	X*	X*	X*	X*	X*	X*
Mean snow depth * Relative snow depth	X*	X	X		X				X
Mean winter temperature * Relative winter temperature	X*	X*	X*	X*	X*	X*	X*	X*	X*
$\Delta AICc$	0	0.12	0.66	0.89	0.92	0.94	1.31	1.43	1.88

interactions, except for the two-way spatiotemporal interaction of summer temperature, were included in one or several of the nine highest ranked models ($\Delta AICc \leq 2$; Table 1). The highest ranked model included the spatial terms of total road length, harvest density in year t + 2, traffic volume, snow depth and winter temperature, as well as the temporal terms of harvest density in year t + 2, traffic volume, snow depth and winter temperature. In addition, the highest ranked

model included the two-way spatiotemporal interactions of traffic volume, snow depth and winter temperature (Tables 1 and 2).

In the highest ranked model, the slope of the spatial relationship between MVC and harvest density was not isometric (i.e., the log-log parameter estimate was larger than 1). This suggests that a relatively higher proportion of the moose population is killed in traffic in counties with high versus low population densi-

Table 2. Parameter estimates and test statistics for the highest ranked linear mixed effect model explaining variation in (ln)MVC (Table 1). Explanatory variables where the 95% confidence intervals did not include zero are in boldface.

Variables included	β	1 SE	95% confidence interval	
			Lower limit	Upper limit
ln(Total length of public roads)	1.4230	0.4726	0.8604	2.0214
Mean (ln)harvest density t + 2	1.5370	0.3937	1.0613	2.0199
Mean (ln)traffic volume	0.4207	0.3016	0.0499	0.7869
Mean snow depth	0.0225	0.0115	0.0085	0.0360
Mean winter temperature	-0.1509	0.0783	-0.2442	-0.0542
Relative (ln)harvest density t + 2	1.0770	0.0646	0.9566	1.2199
Relative (ln)traffic volume	0.1880	0.3005	-0.4044	0.7858
Relative snow depth	-0.0029	0.0059	-0.0143	0.0091
Relative winter temperature	0.0349	0.0233	-0.0118	0.0790
Mean (ln)traffic volume * Relative (ln)traffic volume	-0.5511	0.1601	-0.8836	-0.2273
Mean snow depth * Relative snow depth	0.0002	0.0001	0.0000	0.0004
Mean winter temperature * Relative winter temperature	0.0168	0.0044	0.0081	0.0260

ty. In contrast, the temporal relationship between MVC and harvest density was positive, but not significantly different from 1 (i.e., isometric relationship). Hence, over the full range of densities a similar proportion of the moose population seems to be killed in traffic accidents (Table 2).

The negative spatiotemporal interaction of traffic volume was due to a stronger positive effect of traffic volume in counties with low mean traffic volume, but weak or absent effects in counties with high mean traffic volume (Table 2).

The temporal relationship between MVC and snow-depth varied between counties (a positive spatiotemporal interaction). In counties with an overall low snow depth, the temporal relationship was negative or absent, whereas in counties with an overall high snow depth there was a positive relationship between snow depth and MVC (Table 2).

The temporal effect of winter temperature on MVC varied between counties (a positive spatiotemporal interaction). The relationship was negative in counties with on average low winter temperatures, and weakly positive or absent in counties with warmer winters (Table 2). Hence, the number of MVC seems to increase with decreasing winter temperature only in counties with generally cold winters.

Spatial and temporal effects of summer temperature on MVC did not enter the highest ranked model. However, the temporal effect was included as a positive term (not significant) in some of the lower ranked models (Table 1), indicating that the number of MVC may be higher in warm summers. Similarly, a negative two-way spatiotemporal interaction of harvest density entered some of the lower ranked models (Table 1).

The highest ranked model (Table 2) explained 72% (94.0%, 71.7% and 48.3% of the year, county and residual effect, respectively) of the explainable variation in the random intercept model. Removing, one at a time, population density, climate variables and traffic volume from the highest ranked model reduced the explained variation to 36.8%, 63.4% and 67.5%, respectively. This suggest that population density was the most influential variable explaining variation in MVC.

DISCUSSION

Based on 31 year long time-series from 14 Norwegian counties, we were able to explain a large proportion of the spatial (between county) and temporal (within county) variation in number of MVC. Our highest ranked model indicated a strong effect of population density, supporting our hypothesis that the number of MVC increases with increasing density. In addition, the number of MVC increased with increasing traffic volume and snow depth and with decreasing winter temperature, but depending on the average values within county. The effects of temporal variation in traffic volume and winter temperature were higher in counties with low average traffic and winter temperature, respectively, whereas the effect of varying snow depth was only present in counties with on average deep snow. Our hypothesized higher frequency of MVCs in years and counties of low summer temperatures were not supported.

Our results support a number of previous studies showing that the number of UVC's are positively related to population density and traffic volume, and that weather influence the number of UVC (McCaffery 1973, Lavsund and Sandegren 1991, Mysterud 2004, Seiler 2004, Dussault et al. 2006, Farrell and Tappe 2007). However, the temporal effects varied between areas, where the effect sizes were close to zero in several counties. For instance, the positive relationship between traffic volume and MVC was stronger in counties with low versus high average traffic volume. This may be the result of roads and moose being heterogeneously distributed across the landscape, leaving increasing traffic to have a stronger effect in counties where the overlap in distribution of moose and roads are high. Another likely explanation is that the risk of MVC is not linearly related to the frequency of vehicles. If increasing traffic volume led to the establishment of efficient mitigating measures, the number of MVC may not necessarily increase with increasing traffic volume. Wildlife fences are now increasingly established along roads in counties with high traffic volume in Norway, and have been shown to effectively reduce the number of UVCs in other countries (Clevenger et al. 2001, Hedlund et al. 2004). Likewise, high traffic may itself act as a barrier

for moose crossing roads. In Sweden, Seiler (2005) found the number of MVC to increase on roads with increasing traffic volume up to about 4000 vehicles per day, but to decrease as the traffic volume further increased (see also, Dussault et al. 2006). Hence, the negative spatiotemporal interaction of traffic volume in our study can have been the result of traffic acting relatively more as a barrier in counties with high compared to low traffic volume.

Interestingly, we also found some indications that a higher proportion of the moose population was killed on roads in counties with high versus low moose density. This can reflect a tendency for relatively more moose to aggregate in areas of high road density in moose dense areas, e.g., that because the primary productivity is usually higher in such areas (low altitude) and therefore can support more moose. However, as we have no data on the moose density relative to carrying capacity within county, the effect of food limitation on moose distribution may be independent of moose density. Moreover, no density dependent effects on MVC were observed over time within counties, making this explanation unlikely. An alternative explanation is that the variation in density simply reflects other aspects related to the risk of MVC. For instance, counties with the highest densities (e.g., counties 9–11; Fig. 1) are typically also characterized by low altitude, less broken topography, and with roads distributed more evenly throughout the moose range. Hence, although moose tend to have smaller home ranges (Bjørneraas et al. 2011) and show less seasonal movements in more productive areas (Hjeljord 2001), proportionally more moose are likely to live close to a road in Southeast Norway than in the low density counties further north. We are currently using GPS-collared moose to explore such interactions between moose behavior and landscape characteristics on the risk of MVC.

The negative effect of winter temperature is in accordance with similar results reported for moose-train collisions (Andersen et al. 1991, Gundersen and Andreassen 1998). Possibly, this is because moose are able to maintain higher levels of activity at lower temperatures, and thus is more likely to cross roads or rails (Andersen et al. 1991). Being physiologically adapted to cold environments (e.g., Geist 1999) moose increase

their heart rate, respiratory rate and metabolic rate when ambient temperatures rise above -5°C in winter and 14°C in summer (Renecker and Hudson 1986, Dussault et al. 2004), thresholds that are often exceeded in Norway. However, the number of vehicle collisions involving roe deer is also found to be higher in cold winters and warm summers (Solberg et al. 2009), despite roe deer being a much smaller species and presumably less disposed to heat stress under boreal conditions. Moreover, we found rather a tendency for more moose being killed in years of warm summers, not cold. This was not expected and does suggest that moose are not necessarily less active in warmer periods (Schwartz and Renecker 1998). Lack of behavioral response in moose to high temperatures was also reported by Lowe, Patterson and Schaefer (2010).

These results call for a better understanding of how moose behave during periods of high and low temperature and how this is related to traffic accidents. For instance, besides affecting the general activity level, temperature might affect the circadian activity pattern of moose relative to the daily distribution of traffic (Rolandsen et al. 2010). The frequency of vehicles on the road varies extensively during the day in Norway, being at its maximum in late afternoon and minimum in the middle of the night (Rolandsen et al. 2010). In contrast, the moose road crossing frequency tend to peak in early morning and in the evening (Rolandsen et al. 2010), indicating that even small changes in the timing of the main activity period can lead to substantially higher accident rate. In Canada, Dussault et al. (2006) found more moose to be killed on roads in warm summer days and speculated that moose under such conditions compensated by being more active during the night time when temperatures were lower, but the driving conditions less good (Dussault et al. 2004). The traffic volume may also be related to temperature, e.g., more people may be travelling in years of warm summers. However, given our crude estimate of traffic volume (see *Methods: Length of public roads and traffic volume*), such relations are not possible to examine in this study.

Snow depth is perhaps the most important weather variable affecting the number of MVC in Norway, but only in counties with on average deep snow (mean snow depth $> 50\text{--}70$ cm). In

snow rich counties, we observed a doubling in the number of MVCs between years of minimum and maximum snow depth. In accordance with earlier studies (Andersen et al. 1991, Lavsund and Sandegren 1991, Modafferi 1991, Gundersen and Andreassen 1998), we believe the effect of snow depth is mainly due to an increase in the local moose density close to roads in winter, and thus higher moose crossing frequency. Several studies have shown that moose are moving to lower altitude areas when snow is accumulating in surrounding hills (e.g., Gundersen and Andreassen 1998, Bunnefeld et al. 2011), and where the road density and traffic intensity is higher (public road density in areas of forest and bog relative to meter above sea level in Norway: Spearman's $\rho = -0.95$, $n = 1199$, $p < 0.001$, C. M. Rolandsen, *unpublished data*). No such migration is normally seen in areas that receive little snow during winter (Hjeljord 2001), explaining the absence of effect in counties with on average low snow depth. Possibly, deep snow can also affect other elements of MVC, e.g., moose behavior during road crossings. Anecdotal reports indicate that moose in snow rich areas are more inclined to run in the roadway when taken by surprise, possibly because of the obstructing effect of the snow banks along the roads. High snow banks may also reduce the detection probability of crossing moose and snow on roads is generally reducing maneuverability of the vehicles.

Our study highlights the varying importance of the underlying factors between areas. A notable exception is the effect of varying moose density over time, which seems to be scaled isometric to the variation in MVC. Thus, a given percentage decrease in moose density is likely to return a similar percentage decrease in MVC. On a national scale, the harvest to road kill ratio is about 17:1, but substantially lower in areas with most MVCs (Solberg et al. 2009). To successfully use population reduction to mitigate MVC it is important to increase the harvest pressure over the entire range of a population (Hedlund et al. 2004), e.g., because of migration. However, both from a harvesting and conservation point of view, population reduction alone may not be a welcomed solution. Other mitigating actions such as wildlife fences combined with safe wildlife passages and forest clearing on road

shoulders may be alternative solutions (Hedlund et al. 2004). Our results are also relevant for studies evaluating the efficiency of such mitigation measures. For instance, because of the strong temporal effect of varying snow depth and moose density on MVC, it is paramount that such variables are controlled for when evaluating the effects of preventive measures.

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