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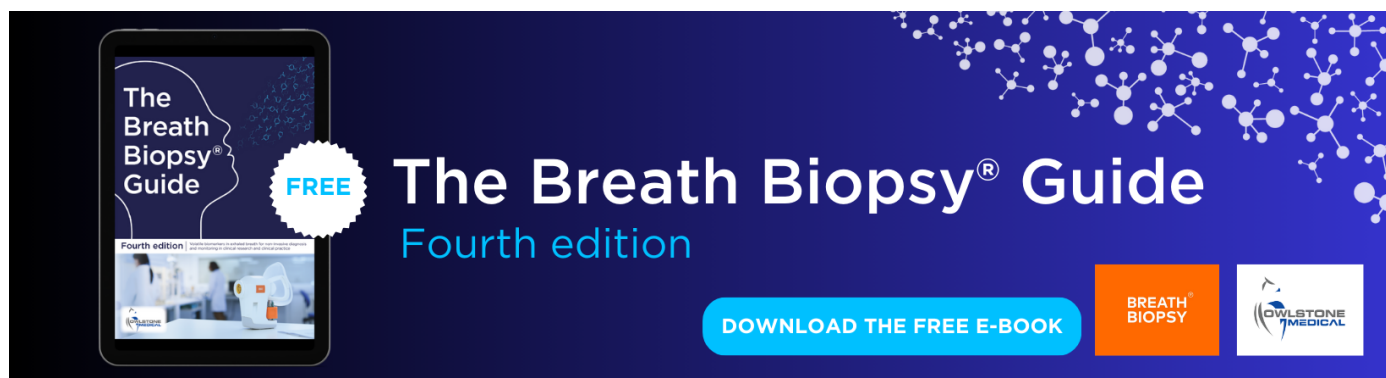
Human and animal movements combine with snow to increase moose-vehicle collisions in winter

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Supplementary material for this article is available [online](#)

Abstract

Wildlife-vehicle collisions imperil humans, wildlife, and property. Collisions with moose (*Alces alces*) are especially consequential and there are indications they may increase during severe winters. We tested hypotheses regarding the influence of moose movements and vehicular traffic patterns on collision risk. We first modeled daily snow depth and accumulation across 5.6 million km² of the North American Arctic-Boreal region. Next, we analyzed the movements and road use of 113 GPS-collared moose in response to snow depth. Finally, we examined the influence of these snow properties on vehicular traffic and 7680 moose-vehicle collisions. As winter progressed and the snowpack deepened in each study area, GPS-collared moose migrated to lower elevations, leading them into areas with shallower snow but higher road densities. This elevational migration corresponded with a higher probability of road-use by moose (by up to ten-fold) in winter than in summer. Corresponding to these patterns, moose-vehicle collisions were 2.4–5.7 times more frequent from December through February (compared to early summer). Collision risk was highest when and where snow depth was less than 120 cm, indicating that migration into areas with shallower snow increased collision risk in those areas. Most (82%) moose-vehicle collisions occurred after dark. This pattern was strongest during winter, when nighttime traffic volumes were eight times higher than summer due to longer nights. Overall, our findings suggest that concurrent seasonal changes in human and wildlife behavior increase the frequency of moose-vehicle collisions during winter. Snow depth influences collisions primarily through its impacts on moose movement, while strong seasonal changes in daylight hours cause an increase in nighttime traffic that further contributes to risk. This information may help predict times and places where risk of moose-vehicle collisions are highest and to develop seasonally dynamic mitigation strategies.

1. Introduction

Wildlife-vehicle collisions (WVCs) imperil wildlife, cause human deaths, and damage property. In the United States alone, two million collisions with ungulates kill ~ 440 people, injure $\sim 59\,000$ people, and cause more than US\$10 billion of economic losses annually (Huijser *et al* 2008, Conover 2019). Collisions also endanger wildlife populations, with vehicle strikes estimated as the second largest cause of anthropogenic mortality (Collins and Kays 2011). Expanding road networks, coupled with increasing wildlife populations, such as deer in North America and Europe (Côté *et al* 2004, Apollonio *et al* 2010), have caused steady growth in WVCs in recent decades (Huijser *et al* 2008, Hill *et al* 2019). A projected 60% expansion in the global road network by 2050 means the problem will likely continue to grow (Laurance *et al* 2014).

WVCs are the product of human and animal behavior, both of which respond to processes at various timescales. Seasonal movements associated with migration or reproduction are driven by environmental cues (Nelson 1995, Monteith *et al* 2011, Rivrud *et al* 2016, Pedersen *et al* 2021), whereas daily movements can follow both cyclical circadian patterns (Owen-Smith and Goodall 2014, Cunningham *et al* 2019) and/or be more dynamic, like avoiding areas with fresh, deep snow (Mahoney *et al* 2018). Human driving patterns also play a key role in WVCs, but unlike animal activity, which responds to solar time (Nouvellet *et al* 2012), the timing of human activity is largely determined by clock-time (Cunningham *et al* 2022). This means seasonal changes to day length can alter the amount of traffic at night, when animals are most difficult for drivers to see (Cunningham *et al* 2022). Understanding the mechanisms that increase collision risk could facilitate real-time predictions of WVC risk, with even modest mitigation improvements capable of providing large economic and social benefits (Raynor *et al* 2021).

Collisions with moose (*Alces alces*) are the most common and consequential form of ungulate-vehicle collisions in Alaska and western Canada. Compared to collisions with deer (*Odocoileus spp.*), moose-vehicle collisions are 13 times more likely to cause human death and are twice as expensive to repair ($\sim \$7500$ in 2022 US dollars; Huijser *et al* 2009). In Alaska and western Canada, moose are of high socio-ecological importance because they are a staple subsistence resource, particularly in rural and indigenous communities (Ballew *et al* 2006, Titus *et al* 2009). In some regions, moose-vehicle and moose-train collisions increase during winter (Gundersen *et al* 1998, Noordeloos 2016, McDonald *et al* 2019) and during years with deep snow (Rolandsen *et al* 2011). Like

most cold-adapted ungulates, moose are partially migratory, with some individuals migrating between summer and winter ranges, while others remain year-round residents (Singh *et al* 2012, White *et al* 2014). Migration of ungulates can occur across large distances (e.g. mean of ~ 40 km and max of 196 km for moose; Mauer 1998) or shorter-distance elevational gradients (John and Post 2021), with winter ranges usually at lower elevations below tree-line where snow is typically shallower. Travel between seasonal ranges can be especially dangerous. For example, migration corridors are the most likely locations for collisions with mule deer (*O. hemionus*) (Coe *et al* 2015). Understanding the key determinants of moose-vehicle collisions would potentially assist managers to develop mitigation strategies that target the processes that contribute most to increased risk.

We pose three non-exclusive hypotheses for how winter processes could shape moose-vehicle collision risk:

- (a) *Migration promotes road use*—as winter progresses, moose will migrate to lower elevations where snow is shallower and forage is more available (Joly *et al* 2015b). Because roads are usually more common in valleys and lowlands (Elsen *et al* 2020), migration to lower elevations in winter could place moose closer to roads and therefore increase collision risk.
- (b) *Plowed roads facilitate travel*—moose may prefer travelling on plowed roads during winter because movement through deep snow carries higher metabolic costs (Parker *et al* 1984), thereby increasing collision risk.
- (c) *Winter impairs driving*—snowfall impairs driving conditions by reducing visibility and making vehicles more difficult to control, leading to increased frequency of vehicle collisions during severe snow events (Khattak and Knapp 2001). In addition, less daylight in winter causes a higher proportion of traffic to occur at night when animals are harder for drivers to see (Cunningham *et al* 2022).

To address these hypotheses, we began by modeling snow properties over four decades across 5.6 million km² of the North American Arctic-Boreal region (Liston *et al* 2022). Next, we examined the effect of snow depth and daily snow accumulation on migration and road-use of 113 GPS-collared moose from five study sites in Alaska and western Canada. Finally, we modeled the influence of snow conditions on vehicular traffic volumes and moose-vehicle collision rates, aiming to characterize seasonal patterns in collisions and identify snow conditions that increase collision risk.

2. Materials and methods

2.1. Data sources

We used four independent data sources: GPS locations of moose, vehicular traffic volumes, incidents of moose-vehicle collisions, and simulated snow properties.

2.1.1. Moose locations

We collected data from 113 GPS-collared moose from five study areas across Alaska, the Yukon Territory, British Columbia, and Alberta (figure 1). These study sites spanned almost the entire latitudinal distribution of moose and represented a wide range of environmental and snow conditions (figure 1), from the flat boreal forest of northern Alberta to north of the Arctic Circle in Alaska. Data collection at each site spanned two to five years between 2001 and 2013, with location fix rates ranging from two to eight hours. Data were cleaned to remove obvious fix errors following protocols similar to Gupte *et al* (2022). See table 1 for a summary of the GPS data and references therein for methodological details.

2.1.2. Vehicular traffic volumes

The Alaska Department of Transportation collects data on traffic volumes (vehicles per hour) at ~130 permanent traffic stations spread across much of the Alaskan road network (Grimes *et al* 2020). We were provided with data from 104 stations from 2014–2018. Huijser *et al* (2008) report that ~90% of ungulate-vehicle collisions occur on two-lane rural roads. Thus, to characterize traffic patterns on roads most relevant to moose-vehicle collisions, we excluded traffic stations within the cities of Anchorage and Fairbanks. We further thinned the dataset to include only stations with >365 d of observations, leaving 3.1 million observations of hourly traffic volumes from 53 stations for our analysis (figure 1).

2.1.3. Moose-vehicle collisions

The governments of Alaska and British Columbia collect comparable datasets of WVCs, including the coordinates, date, and the species involved. The Alaska dataset also includes the time of each collision (in one-hour bins). The Alaska Department of Transportation provided WVC data from 2009–2017, totaling 5084 moose-vehicle collisions (figure 1). The British Columbia Department of Transportation provided moose-vehicle collision data from 2011–2020, but we excluded incidents from 2018 onwards because of a change in data collection protocol, leaving 2596 moose-vehicle collisions from 2011–2017 (figure 1).

2.1.4. Snow data

We simulated snow distribution and evolution using MicroMet (Liston and Elder 2006b) and SnowModel (Liston and Elder 2006a). SnowModel

incorporates first-order physics required to simulate snow evolution within each of the global snow classes (i.e. Ice, Tundra, Boreal Forest, Montane Forest, Prairie, Maritime, and Ephemeral; (Liston and Sturm 2021, Sturm and Liston 2021)). Processes simulated by SnowModel include snow precipitation, blowing-snow redistribution and sublimation, snow interception by forest canopy, unloading, sublimation, snow density evolution, and snowpack ripening and melt. These modeling tools have been widely used for climate, hydrology, remote sensing, wildlife, vegetation, avalanche, glacier and ice sheet mass balance (see Liston *et al* (2020) for a sample).

We produced a SnowModel simulation covering the NASA Arctic Boreal Vulnerability Experiment (ABOVE) Core Domain comprising 5.6 million km² of northern North America (figure S1). The simulation was performed on a 3 km × 3 km grid using a 3-hourly time step, for the period 1 September 1980 through 31 August 2020. Meteorological forcing was provided by data products from NASA's Modern Era Retrospective-Analysis for Research and Applications (MERRA-2; Gelaro *et al* 2017). For this study of moose, we used snow depth (cm) and snow accumulation (cm over 24, 48, and 72 h). However, daily outputs for 15 meteorological and snow-related variables (figure S1) are available at the NASA ABOVE Distributed Active Archive Center (Liston *et al* 2022).

2.2. Statistical analyses

Our analyses involved three main themes: (a) movements of GPS-collared moose, (b) seasonal changes in traffic patterns, and (c) timing and predictors of moose-vehicle collisions. All models were fit using the *mgcv* package (Wood 2011) in R v4.1.2 (R Core Team 2022).

2.2.1. Moose movement and road use

We modeled three aspects of moose movement: (a) selection of snow depth, (b) elevational migration, and (c) road use. To quantify selection for snow depth, we constructed a coarse-scale step selection function (SSF; Thurfjell *et al* 2014), but, rather than distributing available locations based on step length, we distributed five available locations for each used location across each animal's yearly home range (99% kernel density estimate) (AMT package; Signer *et al* 2019). This scale reflects third-order selection; that is, how a moose uses its home range (Johnson 1980, Thurfjell *et al* 2014). Because the aim was to investigate snow depth selection, we restricted the analysis to winter months (1 December to 31 March) and then extracted time-varying snow depth and vegetation class at each used and available location. Under the expectation that moose prefer deciduous vegetation in winter (Hundertmark *et al* 1990, Burkholder *et al* 2022), we aggregated land cover (30 m resolution; North American Land Change Monitoring

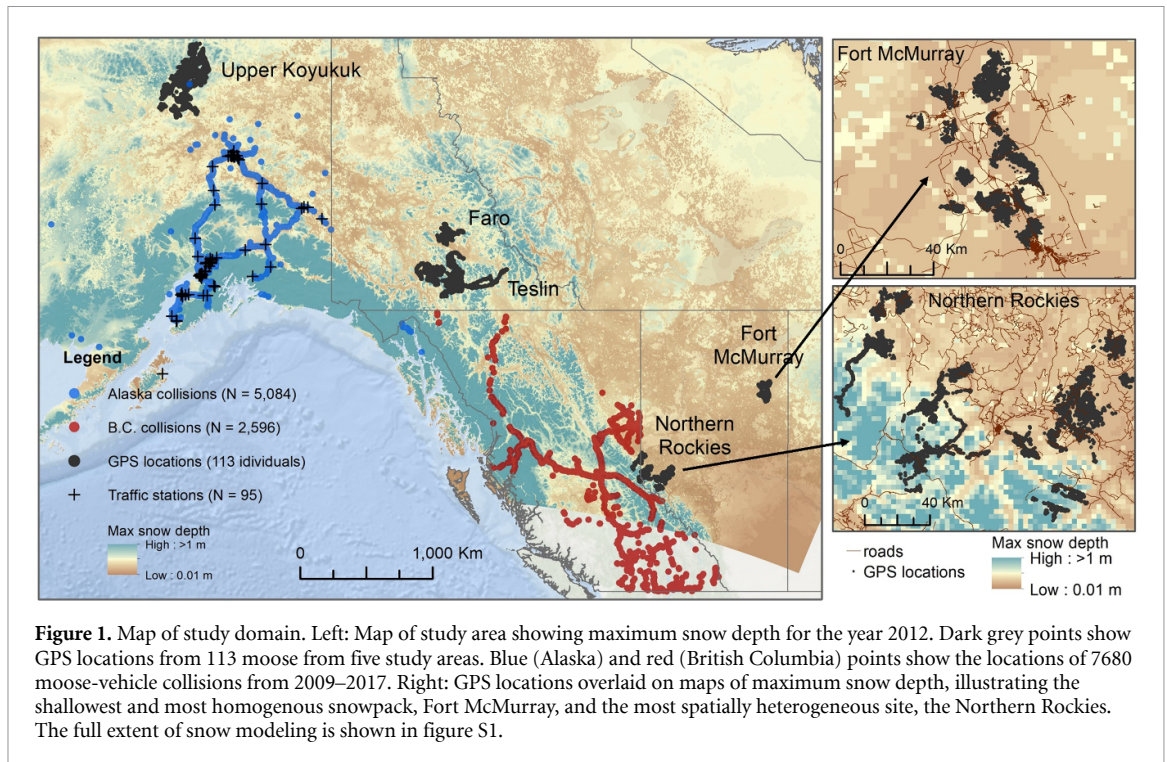


Table 1. Summary of GPS tracking data. We analyzed data from 113 moose from five study sites. Road density quantifies the density of roads within a minimum convex polygon surrounding all GPS locations at each study site. The references describe the methodological details for capturing and collaring moose.

Study location	N Moose	Years	N fixes	Fix rate (median; hours)	Road density (km km ⁻²)	References
Fort Mackay, AB	25	2010–2012	133 519	2	0.359	(Neilson 2017)
Northern Rockies, AB/BC	17	2008–2010	50 100	3	0.133	Peters <i>et al</i> (2013)
Faro, YT	13	2002–2005	4589	3.6	0.029	Yukon Government
Teslin, YT	23	2008–2010	73 570	4	0.016	Yukon Government
Upper Koyukuk, AK	35	2008–2013	71 675	8	0.041	Joly <i>et al</i> (2015a, 2015b)
Total	113	2001–2013	333 453			

System 2015) into four categories: coniferous forest, mixed forest, deciduous forests/shrubs, and other.

SSFs are usually fit using conditional logistic regression, which compares covariates at time-matched used and available locations. Conditional logistic regression is likelihood-equivalent to the Cox proportional hazards model with a strata for each used-available group (Signer *et al* 2019). We therefore used the Cox proportional hazards distribution and fit the model using a generalized additive mixed model (GAMM), allowing us to fit non-linear functions of covariates. The full model consisted of the binary used/available locations in response to a smooth function of snow depth that differed for each study site, vegetation class, and a stratum for each time-matched used-available group. We omitted Fort McMurray from the SSF because negligible variation

in snow depth (figure 1) provided little scope for moose to demonstrate preferences.

To investigate elevational migration, we modeled seasonal changes in the elevation of moose at all study sites (m²; table 2). For the response variable, we extracted the elevation (meters) at each GPS location using a 30 m resolution digital elevation model (Abrams *et al* 2020). Using a GAMM with Gaussian distribution, we modeled elevation in response to a smooth function, differing by study site, of hydrological day of year (starting on October 1). Because day of year is a circular variable (i.e. 365 is next to 1), we fit this relationship using a circular cubic regression spline, forcing the ends to meet (Wood 2017). We also included a fixed effect for study site and a random intercept for individual ID, allowing each site and individual to have its own baseline elevation. We

Table 2. Description of statistical models. All models were fitted using either a generalized additive model (GAM) or a generalized additive mixed model (GAMM). ‘f’ denotes a smooth, non-linear function of a continuous predictor variable. We use ‘×’ to indicate various types of interactions (described in main text), including a by-factor interaction where a smooth function differs for each level of a categorical variable (e.g. m2), or for tensor product interactions between continuous variables (e.g. m7).

Analysis	Response	Predictors	Model type; distribution
<i>Moose movement</i>			
m1. Moose selection of snow	GPS locations (used/avail.)	$\sim f(\text{snow depth}) \times \text{site} + \text{veg} + (\text{random} = \text{individual})$	GAMM; step selection function
m2. Elevational migration	Elevation (GPS; continuous)	$\sim f(\text{day}) \times \text{site} + (\text{random} = \text{individual})$	GAMM; Gaussian
m3. Road use by moose	Road use (GPS; binary)	$\sim f(\text{day}) \times \text{site} + (\text{random} = \text{individual})$	GAMM; binomial
<i>Traffic volume</i>			
m4A. Daily traffic	24-hr traffic (count)	$\sim f(\text{day}) + (\text{random} = \text{station})$	GAMM; quasipoisson
m4B. Nighttime traffic	Nightly traffic (count)	$\sim f(\text{day}) + (\text{random} = \text{station})$	GAMM; quasipoisson
m5. Effect of snow on traffic	Winter traffic (count; scaled)	$\sim f(\text{snowfall}) \times \text{station} + (\text{random} = \text{station})$	GAMM; Gaussian
<i>Moose-vehicle collisions</i>			
m6. Timing of MVCs	MVCs (used/avail.)	$\sim f(\text{day} \times \text{time of collision})$	GAM; binomial
m7. Moose-vehicle collisions	MVCs (used/avail.)	$\sim f(\text{day} \times \text{snow depth} \times \text{region}) + f(\text{snowfall})$	GAM; conditional logistic

used a form of automatic model selection that allows for an effect to be penalized out of the model if it was not important (Marra and Wood 2011).

Finally, we modeled seasonal changes in road use by moose at all study sites. We defined road use as a binary variable depending on whether a GPS location fell within 100 m of a road, defined using shapefiles of roads and tracks from Open Street Maps (OpenStreetMap Contributors 2021). Using a GAMM with binomial distribution (m3; table 2), we modeled the probability of road use in response to the same explanatory variables as the model of elevational migration.

2.2.2. Traffic volume

We began by modeling seasonal changes in 24-hourly and nightly traffic volumes in Alaska. To categorize nightly traffic, we first calculated daily sunrise and sunset times for the coordinates of each traffic station using the ‘getSunlightTimes’ function of the *sun-calc* package (Benoit and Achraf 2019). We defined nighttime traffic as that which occurred between sunset and sunrise, but we acknowledge that twilight can persist for much of the night during summer at high latitudes. Separately for 24 h and nightly traffic (m4A and m4B; table 2), we fit a GAMM of traffic volume in response to (a) a smooth function of hydrological day of year and (b) a ‘factor smooth’ interaction between hydrological day of year and station ID, producing station-specific responses.

The factor smooth is analogous to a random slope in a generalized linear mixed model (Pedersen *et al* 2019). We fit the model using a quasi-Poisson distribution to account for overdispersion in the traffic counts (Ver Hoef and Boveng 2007). We fitted simpler combinations of the variables and selected the best-performing model using the generalized cross-validation score (GCV; Wood 2004), where smaller values indicate better model fit. To visualize the results of the best models, we predicted the mean traffic volume for each day of the year (i.e. excluding station-specific and random effects).

Next, we investigated the effect of 24 h snowfall on winter traffic volume (m5; table 2). To do this, we selected only winter traffic data (defined as between 1 November to 31 March). For each traffic station separately, we scaled traffic volume by centering and then dividing by a station’s mean, such that a one-unit change in scaled traffic volume reflects a change of one standard deviation from a station’s mean. Using a GAMM with Gaussian distribution, we modeled the scaled nighttime traffic volume in response to (a) a global smooth function of 24 h snow accumulation and (b) a ‘by-factor’ smooth effect of snow accumulation that differed for each traffic station. We *a priori* restricted all smooth functions to have a maximum of four knots because we did not expect complicated responses. We fit simpler combinations of the variables and selected the best-performing model using GCV.

2.2.3. Moose-vehicle collisions

We used a case-control framework to evaluate the effect of season and snow conditions on collision risk. We did this by comparing snow conditions associated with each collision against snow conditions at the same location on 20 random days in the 90 d leading up to each collision. We chose not to distribute available points on any days after a collision because we assumed those days were no longer available for a given moose-vehicle collision to occur on, as the vast majority of collisions result in the animal's death (Huijser *et al* 2008). Case-control data is usually analyzed with conditional logistic regression, which, for convenience, is usually fit with a Cox proportional hazards model. We therefore fit the model using a GAM with Cox proportional hazards distribution and a stratum for each case-control group.

We modeled the binary collision/non-collision data in response to (a) a tensor product interaction between hydrological *day of year* and *snow depth* (cm) differing by *region* (Alaska or British Columbia), (b) a smooth function of *snow accumulation* (cm) at three different temporal scales, and (c) a *stratum* for each used-available group. To select the most explanatory scale of *snow accumulation*, we first tested the full model to determine whether *snow accumulation* over the previous 24, 48, or 72 h performed best, under the expectation that snowstorms of longer durations and larger magnitudes may have stronger effects (Greaves *et al in prep*). Then, using the best-performing snowfall accumulation period, we fit simpler versions of the full model (*day of year* \times *snow depth* \times *region* + *snow accumulation*), totaling 15 models (table S5). We selected the best model using GCV.

Next, we modeled changes in the timing of collisions across the entire year in Alaska, where collision times were recorded in one-hour bins. To distinguish periods where relative collision probably differed from uniform, we created a used-available dataset (similar to Borowik *et al* 2021). For the used dataset, we included all collisions, and for the available dataset, we distributed ten points for each collision randomly across the 8760 (365 d \times 24 h) hours in a year, resulting in an approximately uniform distribution of days and times at which collisions could have occurred. We fit the model using a GAM with binomial distribution, with the binary collision/non-collision data regressed against a tensor product interaction between time of day (1 h bins; 0–23) and the hydrological day of year (1–366). We fit simpler versions of this model and selected the best-performing model based on GCV.

3. Results

3.1. Moose movement

Moose preferred snow depths of ~ 30 cm on average (figure 2) in areas with deciduous vegetation and

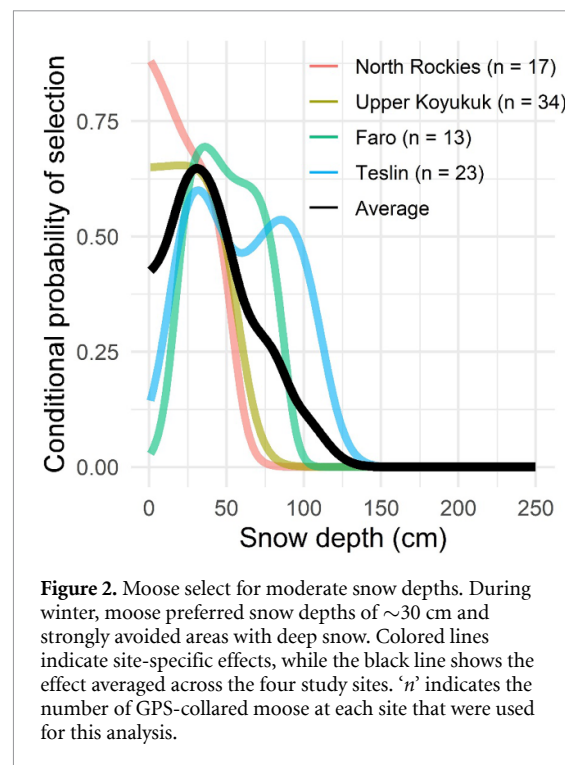


Figure 2. Moose select for moderate snow depths. During winter, moose preferred snow depths of ~ 30 cm and strongly avoided areas with deep snow. Colored lines indicate site-specific effects, while the black line shows the effect averaged across the four study sites. ‘*n*’ indicates the number of GPS-collared moose at each site that were used for this analysis.

mixed forests (table S1). Selection for snow depth differed across study sites, but in general, moose strongly selected against snow depths of more than 100 cm (figure 2; table S1). This selection against deep snow corresponded with elevational migration: as winter progressed and snow deepened (figure 3, top row), GPS-collared moose migrated several hundred meters lower in elevation (figure 3, middle row) where snow was shallower (figure S2). This migration commenced well before snow reached maximal depths. The exceptions to this were moose at the most homogenous study site, Fort McMurray, where there was little topographic variation for moose to seasonally exploit.

The best-performing model of road-use also contained strong, site-specific seasonal effects, revealing a marked increase in road-use that coincided with the period in which moose were at their lowest elevations. The probability of road use was generally low, but it increased by up to ten times during winter/spring compared to autumn (figure 3, bottom row). Even though moose at Fort McMurray were unable to migrate elevationally because of level topography (middle row, figure 3), their road use also increased substantially during winter (bottom row, figure 3).

3.2. Vehicular traffic

‘Rush hour’ consistently occurred at around ~ 5 pm across the year, irrespective of seasonal changes in day length (figure 4(B)). The best-performing models of daily and nightly traffic volumes (tables S2 and S3) showed that although 24 h traffic volume was 57% less in winter than summer, shorter day lengths in

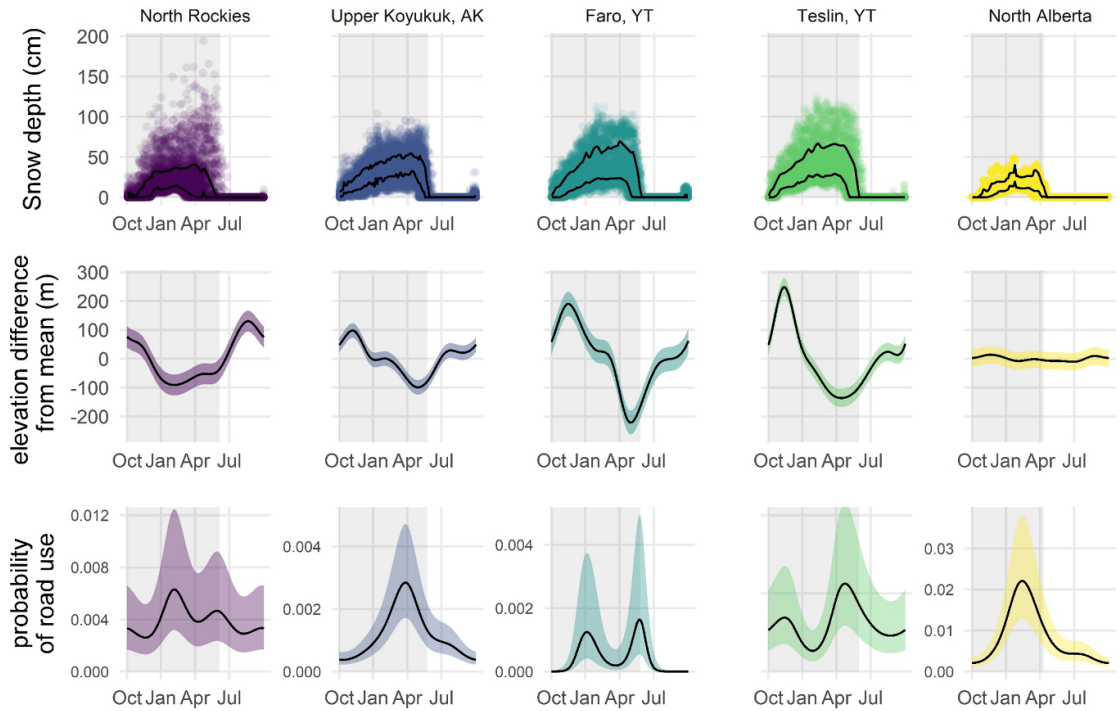


Figure 3. As the snowpack deepened, moose generally moved to lower elevations, increasing the probability of road use. Top row: a time-series of snow depth at 200 random locations at each study site, characterizing the yearly evolution of the snowpack. Black lines denote the 0.2th and 0.8th quantiles. Middle row: results of a generalized additive model of seasonal changes in the elevation of GPS-collared moose. The curves show the mean effects (i.e. excluding individual random effects). Bottom: seasonal changes in the probability of road use by moose. In general, the probability of road-use was highest in winter when moose were at their lowest elevations, but note the two peaks in road-use at Faro and Teslin. Because sites had different road densities and therefore different baseline probabilities of road use, we present each of the bottom panels on different *y*-axis scales for visual clarity. Gray boxes delineate the approximate snow season at each site.

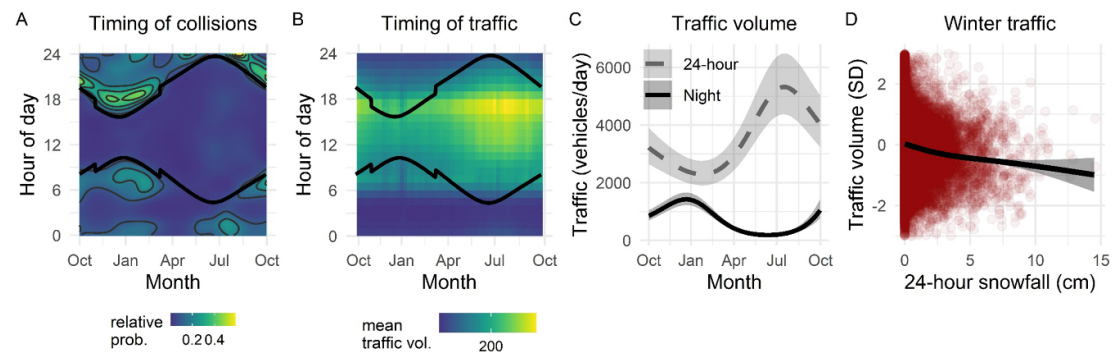
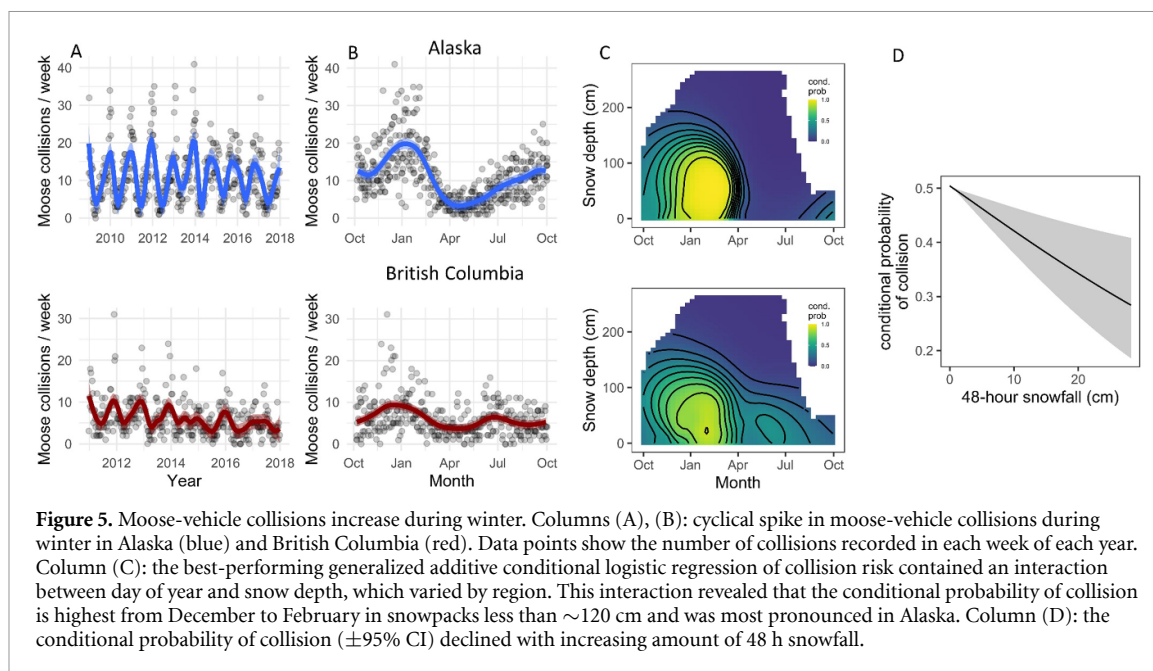


Figure 4. Seasonal changes in the timing of moose-vehicle collisions and of traffic volume in Alaska. (A) Moose-vehicle collisions were clustered in the hours before sunrise and after sunset. Contours and colors show model-estimated relative probabilities of collision risk, and the thick black lines denote sunrise and sunset in Anchorage, Alaska. (B) Seasonal shifts in the timing of sunrise and sunset cause changes in nighttime traffic, with ‘rush hour’ shifting to after sunset during winter. Pixel values represent hourly traffic volumes averaged across all stations. (C) Total daily traffic volume declined during winter, but because of shorter day lengths, there was an eight-fold increase in nighttime traffic. (D) Increasing 24 h snow accumulated was associated with a reduction in traffic volume. Traffic volumes in D were scaled for each site individually, such that a one-unit change in traffic volume represents a change of one standard deviation from a site’s mean. Confidence bands show the 95% confidence interval of the mean effect (i.e. excluding site-level random effects).

winter caused an eight-fold increase in total nighttime traffic (figure 4(C)). The best-performing model of winter traffic in response to snowfall (table S4) revealed a negative effect of 24 h snow accumulation, with a 10 cm snowfall causing traffic to decline by ~28% (figure 4(D)).

3.3. Moose-vehicle collisions

Moose-vehicle collisions showed a cyclical, annual spike during winter (figures 5(A) and (B)). Collisions were 5.7 and 2.4 times more frequent during winter than the low point in late spring in Alaska and British Columbia, respectively (figure 5(B)).



The best-performing case-control model (table S5) contained an interaction between day of year and snow depth. This interaction revealed that the conditional probability of collision was highest during December–February, but only when the surrounding snowpack was shallower than ~ 100 cm (figure 5(C)). Collisions were very unlikely when the surrounding snowpack was deeper than 120 cm (figure 5(C)). The low collision risk in very deep snow corresponds with our finding that moose strongly avoid snow depths greater than ~ 100 cm (figure 2), resulting in the highest collision risk in areas with shallow to moderate snow depths (figure 5(C)). The best-performing model also contained a negative effect of 48 h snow accumulation on collision risk (figure 5(D)).

In Alaska, 82% of collisions occurred during the night. The best-performing GAM of the timing of collisions contained an interaction between hour and day of year (table S6), revealing that collisions were tightly clustered in the hours before sunrise and after sunset (figure 4(A)). For example, in February relative collision probability was 16 times higher two hours after sunset than two hours before sunset. This crepuscular/nocturnal pattern of collisions tracked seasonal changes in day length but was most pronounced during autumn and winter (figure 3(A)), when traffic volumes were highest in the crepuscular period (figure 3(B)).

4. Discussion

Vehicle strikes have been estimated as the second largest anthropogenic cause of large vertebrate mortality (Collins and Kays 2011) and this threat is continuing to grow as human populations and road networks expand (Laurance *et al* 2014). Understanding the mechanisms that influence collision risk may

help managers tailor mitigation strategies to the most relevant processes. Our analyses show that moose-vehicle collisions in Alaska and British Columbia are most common during winter (December–February) but only in areas where the snowpack surrounding the road was shallower than ~ 100 cm. Multiple concurrent factors are implicated in this seasonal spike in collisions. First, moose strongly avoided snow depths >100 cm. This avoidance of deep snow corresponded with migration from higher to lower elevations where roads are more common, increasing the probability of road use and providing support for our hypothesis that *migration promotes road use*. Second, we found evidence (from the Fort McMurray region) of increased road-use by moose during winter that was unrelated to elevational migration. This suggests that moose might preferentially travel on roads to reduce energy expenditure, providing some support for the hypothesis that *plowed roads facilitate travel*. Third, collisions were tightly clustered in the hours before sunrise and after sunset, when it is darker and more difficult for drivers to see animals and when moose are usually more active (Borowik *et al* 2021). This pattern was strongest during winter when nighttime traffic volumes were highest due to shorter day lengths, providing support for the hypothesis that *winter impairs driving* conditions. Collectively, these results indicate that coarse-scale elevational migration, fine-scale movement, and seasonal changes in driving conditions act concurrently to culminate in a spike in moose-vehicle collisions after dark during winter.

Our *winter impairs driving* hypothesis posits that moose-vehicle collisions might increase during winter, as shorter day lengths cause more traffic to occur at night, and as snowstorms make it more difficult for drivers to see animals and control vehicles.

Two points of evidence indicate that nighttime traffic plays a key role in higher collision rates during winter. First, as day length shortened during winter, peak traffic volumes shifted from before sunset to after sunset (figure 4(B)). As in other regions, collisions were tightly clustered in the hours before sunrise and after sunset (Haikonen and Summala 2001, Huijser *et al* 2008, Borowik *et al* 2021, Cunningham *et al* 2022), particularly during winter (figure 4(A)). Second, winter day lengths are shorter in Alaska than British Columbia, suggesting Alaska has a higher proportion of nighttime traffic during winter. Consistent with this pattern, the magnitude of the increase in winter collisions was more than twice as large in Alaska than British Columbia (figure 5). While the larger magnitude of the peak during winter in Alaska could be caused by other factors (e.g. culture, driving laws, collision reporting rules), the concentration of collisions at night in both regions, coupled with longer night lengths in Alaska, suggests that seasonal changes in nighttime traffic play a key role in the observed increase in collision rates during winter. In contrast, we found no support for the second aspect of the *winter impairs driving* hypothesis, with collision risk decreasing in response to increasing 48 h snow accumulation (opposite to our prediction). This negative relationship could be caused partly by reduced traffic volumes during snowstorms (figure 4(D)), and possibly more cautious drivers. Collectively, our results strongly indicate that increased nighttime traffic in winter causes an increase in collision rates, but our results provide no support that collisions increase during winter as a direct result of snowstorms increasing driving difficulty.

Movement through snow carries an exponential metabolic cost as snow becomes deeper (Parker *et al* 1984), significantly impeding ungulate movement when it reaches 50%–70% of chest height (Kelsall 1969, Fancy and White 1987). With chest heights of 78–85 cm, the preferential selection of snow depths of ~30 cm indicates that moose select habitat where movement is relatively energetically efficient during winter. This preference corresponds remarkably well with earlier work showing that moose travel freely through snow depths of 44 cm (Kelsall 1969) and fits with an earlier management definition that a ‘severe winter’ for moose is one in which snow depths exceed 80 cm (Coady 1974). The avoidance of deep snow during winter, involving downhill migration, corresponds with our finding that collisions were rare in areas with very deep snow. This alignment between two independent data sources—GPS-collared moose and moose-vehicle collisions—reinforces the strong effect of snow on animal movement (Mahoney *et al* 2018, Boelman *et al* 2019, Davidson *et al* 2020) and highlights that snow properties can also mediate human-wildlife conflict. These effects of snow

are likely to change into the future, as high latitudes, especially the Arctic, continue to warm at rates far higher than the global average (Rantanen *et al* 2022). This warming will likely lead to regionally variable changes in snow properties; for example, our 40 yr SnowModel simulations showed that very cold regions have likely experienced small increases in annual snowfall (e.g. the Brooks Range; figure S3(C)), whereas warmer coastal regions have experienced substantial reductions in snowfall (figure S3(C)). Snow onset is generally becoming later (figure S3(G) and Liston and Hiemstra 2011) and snow-free duration is increasing in most regions (figure S3(H) and Liston and Hiemstra 2011), leading us to speculatively suggest that moose migrations in autumn may get pushed later in the year, which could in turn affect when moose are most concentrated around roads.

Our analysis of moose-vehicle collisions reveals an annual cycle in which collisions predictably peak each winter. Collisions follow predictable patterns for other species and populations too. White-tailed deer (*O. virginianus*), for example, have a defined peak in collisions during the 2–3 week breeding season in October/November (Huijser *et al* 2008, Cunningham *et al* 2022). In Norway, snow-rich counties experienced substantial increases in moose-vehicle collisions in years with deep snow, which was attributed to migration causing an increase in moose density near roadways (Rolandsen *et al* 2011). In contrast, in snow-poor counties of Norway, moose-vehicle collisions were unrelated to snowfall (Rolandsen *et al* 2011), indicating that other environmental processes play a more dominant role. Likewise, moose-vehicle collisions peaked in summer or autumn in other regions where snow is typically shallower than our sites, such as Maine (Danks and Porter 2010), Newfoundland (Joyce and Mahoney 2001), and Poland (Borowik *et al* 2021). Snow is a dominant seasonal feature of our five study sites, and our findings demonstrate that it significantly affects moose movement and therefore the locations in which moose-vehicle collisions are most likely. These findings can be used to infer seasonal changes in collision risk in other areas of the species’ geographic range, especially mountainous areas of western North America and northern Europe where deep seasonal snowpacks are common.

While the controls over collision risk vary by species and region because environmental context dictates the controls on animal movement (Peters *et al* 2019, Jennewein *et al* 2020, Spitz *et al* 2020), the temporal dynamics within a system are often predictable. This predictability suggests that seasonal speed limits, or even dynamic speed limits, could be effective at reducing collisions. In California, dynamic daily speed reductions for ships, based on daily maps of the probability of whale presence in shipping lanes, are more cost-effective than fixed seasonal speed limits

(Hausner *et al* 2021). While mitigation infrastructure (e.g. wildlife overpasses/underpasses) can be highly effective at reducing collisions in specific locations (Glista *et al* 2009, Huijser *et al* 2009), the strong seasonal patterns revealed here suggest that mitigation measures that address the temporal dimension of collisions could produce additional benefits. In the case of moose in Alaska and Canada, reduced nighttime speed limits from December–February, could reduce collision risk, especially if coupled with driver education and lighting improvements (of roadways or vehicles). As with most regulations, the key challenge would lie in compliance: recent research shows that seasonal speed limits are often ignored by drivers (Riginos *et al* 2022), suggesting future studies could investigate whether additional concurrent strategies (e.g. enforcement and education) could improve compliance.

While it is common for ungulates to migrate to lower elevations during winter and follow green waves back uphill in spring (Aikens *et al* 2017, Merkle *et al* 2016), some moose in the Arctic and subarctic instead migrate to higher elevations in winter, where forage availability differs and where it can be warmer because of temperature inversions (Mauer 1998, Cooley *et al* 2020). However, we generally expect that our movement analyses are broadly representative of the species' typical seasonal movements because our sample of moose spanned much of the species' latitudinal range, including diverse environments from the flat boreal forest of Alberta to above the Arctic Circle in Alaska. In order to analyze moose-vehicle collisions and moose movements across such a large area, the scale of our snow modeling (3 km resolution) was coarse compared to the daily movements of moose. As a result, our movement models were also coarse in scale. Future research could derive snow properties at finer spatial scales, which might reveal additional effects of fine-scale selection for snow properties. For instance, other research has shown fine-scale interactions between snow depth and snow density, with Dall's sheep (*Ovis dalli dalli*) preferring shallow snow when it is soft but responding less to snow depth when it is firm (Mahoney *et al* 2018). In this paper, we focus on snow depth and snow accumulation, but we note that the snow simulations produced a total of 15 variables (Liston *et al* 2022); figure S1) that may be of use for other ecological applications.

WVCs are a leading anthropogenic cause of wildlife mortality (Forman and Alexander 1998, Hill *et al* 2019) and the threat is growing globally as human populations and road networks continue to expand (Laurance *et al* 2014). Our findings show that snow, daylight, wildlife movement, and traffic patterns play important roles in seasonal spikes in moose-vehicle collisions across Alaska and western Canada. Our results also reinforce the dominant effect of snow on animal movement (Mahoney *et al* 2018, Boelman *et al*

2019, Davidson *et al* 2020), with deep snow shifting moose from higher to lower elevations where roads are more common. This seasonal downhill migration occurs at the time of year when nighttime traffic volumes are highest and therefore when animals are most vulnerable to collision. While the exact moment of a collision is impossible to predict, our results indicate that the general trend is predictable. This predictability suggests that seasonal or dynamic mitigation strategies could have substantial benefits for reducing WVCs (if accompanied by compliance measures), in turn preventing avoidable human and animal injury or death.

Data availability statement

The GPS and collision data generated and/or analysed during the current study are not publicly available for legal/ethical reasons but are available from the corresponding author on reasonable request. The snow simulation products can be found at the NASA ABoVE Distributed Active Archive Center (Liston *et al* 2022).

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