The Journal of Wildlife Management 82(5):929–939; 2018; DOI: 10.1002/jwmg.21459

Research Article

Response of Moose to a High-Density Road Network

DAVID W. WATTLES, *Massachusetts Cooperative Fish and Wildlife Research Unit, University of Massachusetts, Amherst, MA 01003, USA*

KATHERINE A. ZELLER,[1] *Massachusetts Cooperative Fish and Wildlife Research Unit, University of Massachusetts, Amherst, MA 01003, USA*

STEPHEN DESTEFANO, *U.S. Geological Survey, Massachusetts Cooperative Fish and Wildlife Research Unit, University of Massachusetts, Amherst, MA 01003, USA*

ABSTRACT Road networks and the disturbance associated with vehicle traffic alter animal behavior, movements, and habitat selection. The response of moose (*Alces americanus*) to roads has been documented in relatively rural areas, but less is known about moose response to roads in more highly roaded landscapes. We examined road-crossing frequencies and habitat use of global positioning system (GPS)-collared moose in Massachusetts, USA, where moose home ranges have road densities approximately twice that of previous studies. We compared seasonal road-crossing frequencies of moose with a null movement model. We estimated moose travel speeds during road-crossing events and compared them with speeds during other home range movements. To estimate the extent of the road effect zone and determine how roads influenced moose habitat use, we fit a third-order resource selection function. With the exception of the lowest use road class (<10 vehicles/day), we found moose crossed roads less than expected based on the null movement model and frequency decreased with increasing road size and traffic. Moose crossed roads faster than they traveled during other times. This effect increased with increasing road use intensity. Overall, roads were a major factor determining what portions of Massachusetts moose used and how they moved among habitat patches. Our results suggest that moose in Massachusetts can adapt to a high-density road network, but the road effect is still strongly negative and, in some cases, is more pronounced than in study areas with lower road densities. Future road construction and the expansion of road networks may have a large effect on moose and other wildlife. Published 2018. This article is a U.S. Government work and is in the public domain in the USA.

KEY WORDS *Alces americanus*, correlated random walk, disturbance intensity, habitat fragmentation, Massachusetts, resource selection, road-crossing, road density.

Road networks and vehicle traffic can directly and indirectly affect wildlife populations. Direct effects include mortality from vehicle collisions (Seiler 2005, Fahrig and Rytwinski 2009) and fragmentation of habitat (Forman et al. 2002). Indirect effects include changes in behavior, resource use, and movements, which can reduce or prevent the use of otherwise suitable habitat (Dyer et al. 2002, Laurian et al. 2012). Wildlife may avoid roads because of vehicle traffic, human activity, noise, light, and other factors (Forman et al. 2002, Coffin 2007, Polfus et al. 2011). Roads may also isolate habitat patches and populations, affecting distribution and abundance (Fahrig and Rytwinski 2009). This can reduce gene flow and lower genetic diversity (Keller and Largiader 2003, Riley et al. 2006, Balkenhol and Waits 2009). Furthermore, roads can result in habitat degradation due to logging, development, or other human activities (Laurance et al. 2009) and increased hunting pressure (Frair et al. 2008).

Road effects on moose (*Alces americanus*) have been documented in a number of studies in North America. Most studies have reported moose alter their behavior to avoid roads. Dussault et al. (2007) reported moose avoided roads except when crossing a road was needed to access resources. At a broad-scale, Laurian et al. (2008) reported moose avoided roads within a 1-km buffer. At finer scales, Laurian et al. (2012) reported road avoidance was strongest in the 100–250 m nearest to roads; Shanley and Pyare (2011) reported this road effect to extend from 500 m to 1,000 m. Both studies reported effects of sex and season. Avoidance of roads has been reported to increase with road disturbance intensity (i.e., major roads, higher traffic volumes, day vs. night; Shanley and Pyare 2011, Laurian et al. 2012). Other studies reported moose favored areas with moderate road densities because of creation of forage along roadsides (Rempel et al. 1997, Bowman et al. 2010). Moose can also be attracted to roadsides by de-icing salts (Laurian et al. 2008) or to

Received: 31 May 2017; Accepted: 23 February 2018

---

[1] *E-mail: kathyzeller@gmail.com*

avoid predators (Yost and Wright 2001, Berger 2007). Beyer et al. (2013) argued that responses to roads are context- and scale-dependent and may vary with road density. These studies were conducted in areas with relatively low road densities (reported road densities in these studies were $<0.9\,\mathrm{km/km^2}$). However, a greater understanding of how moose respond to and potentially adapt to roads in heavily roaded areas is needed.

Massachusetts, a state in New England, has the third highest population density in the United States (336 people/km^2; U.S. Census Bureau 2010). Southern New England also has the southernmost population of moose in northeastern North America. Moose were extirpated from southern New England by the mid-to-late 1800s, primarily through unregulated hunting and clearing of forests for agriculture (Wattles and DeStefano 2011). Moose have since recolonized much of their historical range (Wattles and DeStefano 2011). The mean road density in moose home ranges in Massachusetts is 1.31 km/km^2, with road densities increasing to 3.99 km/km^2 in adjacent areas (Wattles 2015).

Our objective was to examine moose response to roads in Massachusetts, by comparing empirical road-crossing frequency with the expected road-crossing frequency derived from simulated moose movement under a null model of no road effect. We also fit resource selection functions to assess habitat selection and the zone of influence of the road effect. We predicted moose would be more tolerant of roads and show a higher functional response threshold to road density than previously documented in North America; moose would show some avoidance of roads and the strength of this avoidance would increase with larger roads or more traffic; when moose did cross roads, they would move faster than observed during other movements; and because of the greater presence of roads, we would observe a reduced road effect zone compared with other studies in North America. We also predicted differences among seasons because changes in vegetation could affect visibility and sound and based on previously documented differences in seasonal movement rates (Wattles and DeStefano 2013). We also expected diurnal versus nocturnal differences because of lower traffic at night.

STUDY AREA

We captured moose in 2 study areas in western Massachusetts: the Worcester Plateau (3,172 km^2) and the Berkshire Hills (3,483 km^2; Fig. 1). Elevations ranged from 100 m above sea level in the valleys to 425 m in the Worchester Plateau and 850 m in the Berkshire Hills. Topography was dominated by glaciated hills separated by small stream valleys, lakes, ponds, and palustrine wetlands. For the analysis, we specified 3 seasons based on differences in seasonal moose movement rates (Wattles and DeStefano 2013): summer (16 Apr–31 Aug), fall (1 Sep–31 Oct), and winter (1 Nov–15 Apr). July was the hottest month with mean high and low temperatures of 27.5°C and 13.5°C, respectively. January was the coldest month with mean highs and lows of −1°C and −12.5°C, respectively. The average date of last frost was 15 May; the average day of first frost was 21 September. Mean annual precipitation was 1,155 mm.

The study areas were >80% mixed deciduous, second- or multiple-growth forest, much of it resulting from regeneration of farm fields abandoned in the mid-to-late 1800s (Hall et al. 2002). There were 4 main forest types: spruce (*Picea* spp.)-fir-northern hardwood forest, northern hardwood-hemlock (*Tsuga canadensis*)-white pine (*Pinus strobus*) forest, transitional hardwoods-white pine-hemlock forest, and central hardwoods-hemlock-white pine forest. Transitions

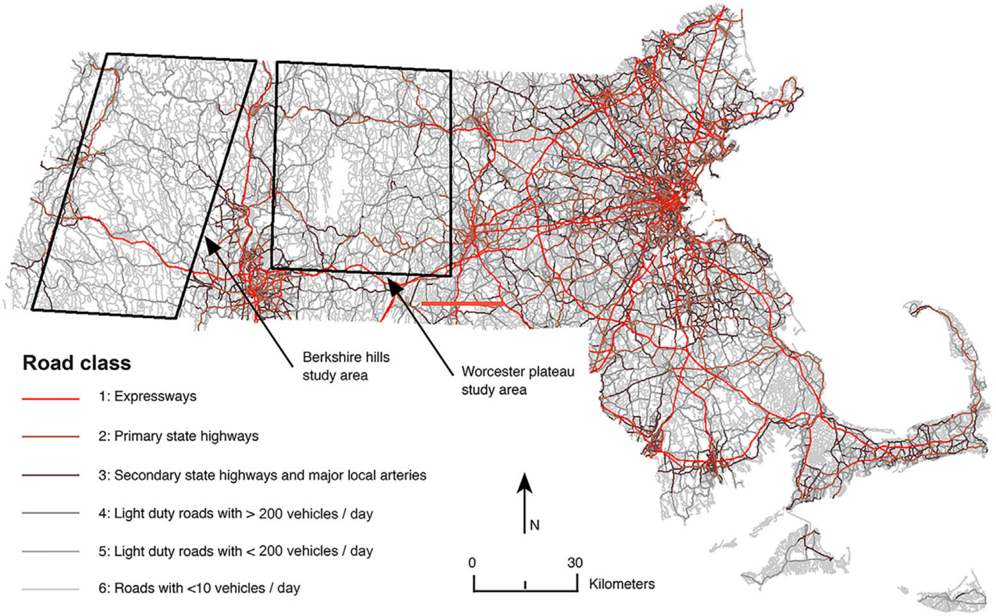

Figure 1. Massachusetts, USA, road network with the Worcester Plateau and Berkshire Hills capture areas, 2006–2009. Also depicted are the road classes used in the study along with the classification criteria.

between forest types were gradual or distinct depending on localized physiography, climate, bedrock, topography, and soil conditions, resulting in a patchwork of forest types and species groups (Westveldt et al. 1956, DeGraaf and Yamasaki 2001). In addition to moose, common fauna in the study areas included black bears (*Ursus americanus*), white-tailed deer (*Odocoileus virginianus*), coyotes (*Canis latrans*), bobcat (*Lynx rufus*), red fox (*Vulpes vulpes*), gray fox (*Urocyon cinereoargenteus*), and numerous smaller species.

We calculated mean road densities in the study areas, which were 1.95 km/km^2 in the Worcester Plateau and and 1.32 km/km^2 in the Berkshire Hills (Fig. 1). Road densities in the adjacent areas of the Connecticut River Valley and eastern Massachusetts were 3.99 and >5 km/km^2, respectively.

METHODS

Capture and Telemetry Data

We captured adult (>1 yr old) moose in the 2 study areas by darting them from the ground between March 2006 and November 2009. More information on our immobilization protocol was provided in Wattles and DeStefano (2013). We fit moose with either ATS G2000 series (Advanced Telemetry Systems, Isanti, MN, USA) or Telonics TWG-3790 global positioning system (GPS) collars (Telonics, Mesa, AZ, USA). Depending on the collar, a GPS fix was attempted every 45, 75, or 135 minutes. These different collar schedules were a result of our attempts to acquire a GPS fix as frequently as possible while allowing the battery life to extend for ≥1 year. The University of Massachusetts Institutional Animal Care and Use Committee approved our capture and handling procedures (protocol numbers 25-02-15, 28-02-16, and 211-02-01).

We deployed GPS collars on 21 adult moose (5 females and 16 males). We recaptured and recollared 9 moose to avoid GPS collar battery exhaustion. We obtained 127,408 locations of the 21 moose, with an overall fix rate of 85% and removed locations with obvious location errors. We pooled sexes in the analyses because of the low number of female moose in our sample.

Road Crossings and Correlated Random Walks

We processed all geospatial data with ArcGIS 10.1 software (Environmental Systems Research Institute [ESRI] 2011). We classified existing geographic information system (GIS) road data for Massachusetts (McGarigal et al. 2011) into 6 classes of road (Fig. 1): class 1 (expressways, which were roads with multiple lanes in each direction and an average daily traffic volume of >25,000 vehicles), class 2 (primary state highways with an average daily traffic volume of 10,000–25,000 vehicles), class 3 (secondary highways or major local arteries with an average daily traffic of 5,000–9,999 vehicles), class 4 (light duty roads with an average daily traffic of >200 vehicles), class 5 (light duty roads with an average daily traffic of ≤200 vehicles), and class 6 (forest roads and roads with an average daily traffic of <10 vehicles). Class 1 roads did not intersect with any moose home ranges and were not included in any analyses.

We analyzed road-crossing frequencies of GPS-collared moose by quantifying the intersection rate of their movement paths with the road network. We compared the empirical road-crossing frequencies with the expected road-crossing frequencies derived from simulated movement paths using correlated random walks (CRWs; Turchin 1998). We generated CRWs with the movement.simplecrw tool in the software package Geospatial Modelling Environment (Beyer 2012), which estimated moose road-crossing frequency under a null model of no road effect (Beyer et al. 2013). We initiated 100 CRWs for each moose-season using the first moose location for that season. We determined subsequent locations by randomly drawing a step length and turn angle from the seasonal distribution of step lengths and turn angles of that moose for that season, until the number of steps equaled the number taken by the moose. We spatially restricted the CRWs to the seasonal minimum convex polygon (MCP) home range of the moose plus a 1-km buffer. We used the buffered MCP home range rather than the MCP (Beyer et al. 2013) because roads outside the MCP could serve as boundaries to movement. Therefore, using only the MCP would exclude those roads from the analysis and prevent us from determining their effect. We selected 1 km as the buffer size because it was the lowest mean daily movement rate across our collared moose (Wattles 2015).

We estimated the road response index (following Beyer et al. 2013) for each moose for each season across road classes to determine if moose responses to roads varied with road density. The road response index is the position of the empirical number of road crossings in the distribution of the number of road crossings from the 100 CRWs for each individual, subtracted from 1. A road response index >0.5 indicates a lower road-crossing frequency than expected from the null model, an index <0.5 indicates a higher road-crossing frequency than expected, and a value of 0.5 indicates equivalent frequencies between the null and empirical crossings. We used Program R version 3.2.4 for all statistical analyses (R Development Core Team 2016). Following Beyer et al. (2013), we attempted to fit the non-linear Gompertz distribution to the data using the form $y = \beta_1 \exp(-\beta_2 \exp(-\beta_3 \mathrm{rd}))$, where y was the road response index, *rd* was the road density, and the β parameters were fit to the data using the nls function in R. Fitting such a distribution allows for the identification of a threshold effect of road density on moose road-crossing rates.

We also calculated the daily road-crossing rate for each moose for each season and road class, which we modeled as a function of road density. We used a mixed-effects linear model fit with the package lmerTest (Kuznetsova et al. 2014) to compare the empirical road-crossing rate with the mean of the 100 CRW paths. For each season and road class, we compared the full road-crossing rate model with reduced models using Akaike's Information Criterion (AIC) for small sample sizes (AIC$_c$; Burnham and Anderson 2004). The saturated model included the density of that class of road in the animal's buffered home range, a variable (moose) stating whether the crossing rate was associated with the real moose or the simulated moose, and an interaction between road density and moose. For all models, we included the

Table 1. Number and rates of crossing for each road class for real and simulated moose in Massachusetts, USA, 2006–2009. Road length is the total length of each road class in the study area. We calculated crossing rate as the number of crossings divided by the length of each road class in kilometers in each home range. For the simulated crossings, we report the mean across simulations.

Road class	Road length (km)	Real moose		Simulated moose	
		Number of crossings	Crossing rate	Number of crossings	Crossing rate
Class 2[a]	1,123	428	0.38	1,271	1.13
Class 3[b]	353	121	0.34	449	0.40
Class 4[c]	2,389	1,482	0.62	2,964	1.24
Class 5[d]	2,254	818	0.36	2,146	0.95
Class 6[e]	4,360	6,313	1.45	6,336	1.45

[a] Primary state highways.
[b] Secondary state highways and major roads.
[c] Light duty roads with >200 vehicles/day.
[d] Light duty roads with <200 vehicles/day.
[e] Roads with <10 vehicles/day.

effect of individual moose as a random intercept to pair the crossing rate of each moose with the associated crossing rate for its seasonal CRWs, and to account for repeated measures of an individual (Gillies et al. 2006). We assessed model fit using pseudo-R^2 after Nakagawa and Schielzeth (2013) and the package MuMin (Bartoń 2014). We averaged models within 2 AIC*c* units of the top model by averaging model coefficients (Burnham and Anderson 2004). Finally, we compared movement rates for steps where moose crossed roads (calculated as m/min) to the mean and 95th quantiles of all movement rates, including road crossings, to determine if moose altered their movement rates when crossing roads.

Habitat Selection

We estimated a within home range resource selection function (RSF; third order; Johnson 1980) in a use-availability framework to estimate moose habitat suitability (Manly et al. 2002). Used points were the moose GPS locations and available points were random locations drawn from each moose's buffered MCP. We created diurnal and nocturnal RSF models for each season. We differentiated daily and nocturnal periods based on times of sunrise and sunset.

To account for the high-density road network in our study area, we estimated the effect of the entire road network by first running roads-only models using a cumulative road effect layer. We assigned different weights to each road class and smoothed the road layer with a Gaussian kernel. We used different bandwidths of the Gaussian kernel to explore different road effect zones. This allowed us to represent the magnitude and scale of the road effect for all roads, not merely the closest road to a moose location. We fit mixed effects logistic regression models using multiple cumulative road effect layers created with various weights of each road class and scales of effect. We identified the weights and scale that resulted in the lowest AIC_c value for each season and time of day (Table S1, available online in Supporting Information). We fit the mixed effect logistic regression models in the lme4 package in R and included a random effect for individual (Bates et al. 2012). We carried forward the best performing weights and scales for each season and time of day into the multiple regression models.

In selecting the appropriate roads model for each road class, time of day, and season, we identified 2 individuals we considered outliers. These 2 moose had the most rural home ranges of all collared moose and had almost no encounters with roads. Because we were interested in analyzing the effect of heavily roaded areas on moose habitat use and behavior, we censored these 2 moose from the analysis.

In addition to the road variable, we used the following 7 land cover types as predictor variables: regeneration (logged areas <25 years old), mature deciduous forest, mature mixed coniferous-deciduous forest, mature coniferous forest, forested wetlands, open wetlands, and other (open and developed areas). Because available GIS land cover layers did not accurately identify forest structure and composition (e.g., deciduous vs. coniferous growth and age classes) in the study area, we manually assigned cover types to used and available points through visual examination of 1:5,000 orthophotos and other GIS layers (Wattles 2015).

We created a roads-only model with the 5 roads classes, a land cover-only model with the 7 land cover types, and 2 global models with roads and land cover. One global model

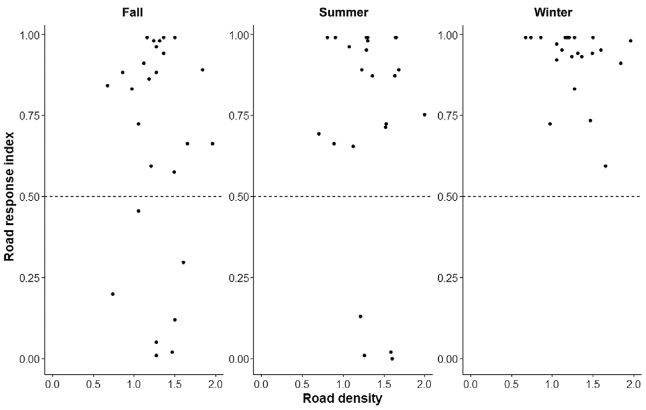

Figure 2. The road response index of moose in Massachusetts, USA, 2006–2009, plotted as a function of road density for winter, summer, and fall. We calculated the road response index by comparing the empirical road-crossing frequency with the frequency of moose simulated with a correlated random walk. The simulated moose represent moose movement in the absence of a road effect. A road response index >0.5 indicates moose cross roads less than expected based on the simulated distribution. A road response index <0.5 indicates moose cross roads more than expected based on the simulated distribution.

included an interaction between roads and each land cover type; the other global model did not include interaction terms. In addition to the random intercept for individual moose, the global models included a random slope for road class. We used a random intercept and random slope model, to account for repeated measures on an individual and for variation in the response to roads by individual moose (Gillies et al. 2006). We categorically represented all land cover types as dummy variables. We compared model fit among the 4 models using AIC$_c$. We also employed a 5-fold cross validation exercise to determine model predictive ability using the individual blocking approach described by Roberts et al. (2017). We used the Spearman's rank correlation coefficient (r_s) for evaluation. We predicted probability of use surfaces for each time of day and season across our study area using the exponential form of the RSF model following Manly et al. (2002): $w(x) = \exp(\beta_1 x_1 + \beta_2 x_2 + \ldots)$.

RESULTS

Road Crossings and Correlated Random Walks

Mean road densities across seasons in each moose home range were 1.31 km/km^2 (range = 0.86–1.70). We documented 9,162 empirical road crossings across 87 moose-seasons (number of moose × number of seasons) and 13,165 road crossings by simulated moose for the same number of moose-seasons (Table 1). Moose crossed all road classes less frequently than predicted by the CRWs. Specifically, moose crossed roads of class 2, 3, 4, 5, and 6, respectively, 0.34, 0.85, 0.50, 0.38, and 0.99 times as frequently as predicted by the CRWs.

We were unsuccessful fitting the Gompertz function to the road response index. There were no clear relationships between the road response index and road density for each season, though most moose in summer and fall crossed roads

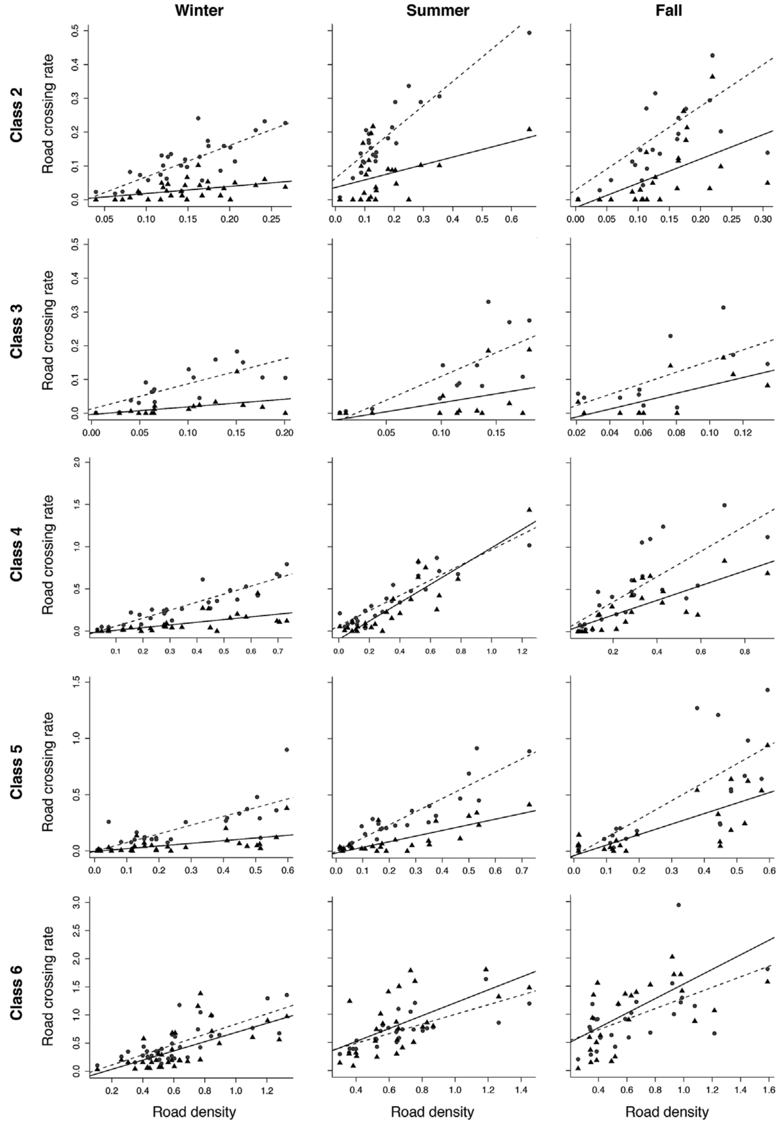

Figure 3. Road-crossing rates (number of crossings/day) of individual moose in Massachusetts, USA, 2006–2009, modeled as a function of road density (km/km^2) in each moose's winter, summer and fall home range. Real moose are represnted by the triangles and solid lines and simulated moose (based on correlated random walks) are represented by the circles and dashed lines.

Table 2. Comparison of candidate models predicting the road-crossing rate of class 2 to class 6 roads by real and simulated moose for all season-class combinations in Massachusetts, USA, 2006–2009. Model structure for m1 = road density + moose + density × moose, m2 = road density + moose, and m3 = road density; all models included a random intercept for individual. Included are the difference in Akaike's Information Criterion for small sample sizes (ΔAIC_c), AIC_c weight (w_i), and model rank. Top models are indicated by a rank of 1. We ran m1 and m2 for all seasons and road classes. If the full model (m1) was supported, we did not run m3. Therefore, some road classes and seasons have empty cells for m3.

	Class 2[a]			Class 3[b]			Class 4[c]			Class 5[d]			Class 6[e]		
Model	ΔAIC_c	w_i	Rank	ΔAIC_c	w_i	Rank	ΔAIC_c	w_i	Rank	ΔAIC_c	w_i	Rank	ΔAIC_c	w_i	Rank
Winter															
m1	0.0	1.00	1	0.0	0.72	1	0.0	1.00	1	0.0	1.00	1	4.6	0.05	3
m2	21.2	<0.01	2	1.9	0.28	2	23.3	<0.01	2	21.2	<0.01	2	0.0	0.48	1
m3													0.0	0.47	2
Summer															
m1	0.0	0.98	1	0.0	0.60	1	6.0	0.04	3	0.0	1.00	1	7.3	0.02	3
m2	8.2	0.02	2	0.8	0.40	2	2.0	0.26	2	21.0	<0.01	2	4.3	0.10	2
m3							0.0	0.71	1				0.0	0.87	1
Fall															
m1	1.6	0.31	2	9.0	0.01	3	0.0	0.92	1	0.0	0.92	1	7.0	0.03	3
m2	0.0	0.69	1	0.0	0.69	1	5.2	0.07	2	4.9	0.08	2	4.4	0.10	2
m3	13.0	0.01	3	1.7	0.30	2							0.0	0.88	1

[a] Primary state highways.

[b] Secondary state highways and major roads.

[c] Light duty roads with >200 vehicles/day.

[d] Light duty roads with <200 vehicles/day.

[e] Roads with <10 vehicles/day.

less than expected based on the null movement model (Fig. 2). In winter, all moose crossed roads less than expected based on the null model.

The null model for road-crossing rate was not supported; moose avoided roads of all types and avoidance increased as roads became larger and more heavily trafficked (Fig. 3; Tables 2 and 3). However, moose showed no avoidance of class 4 roads in summer and no avoidance of class 6 roads in summer and fall (Table 4, Fig. 3). The empirical and CRW movement models predicted an increase in the crossing rate of roads with increasing road density. The empirical crossing rate was, however, lower than the crossing rate obtained from the CRWs and increased at a lower rate (Fig. 3). Model selection supported the saturated models for most seasons (Tables 2 and 3). In these season-road combinations at low road density, the crossing rate by moose was low and similar to the null model, but as road density increased, the difference in crossing rate between the simulated and real moose increased. Pseudo-R^2 values for crossing rate models indicated strong explanatory power. Pseudo-R^2 for the fall class 6 roads model was 0.51, whereas the pseudo-R^2 for all other seasonal models ranged between 0.68 and 0.90.

Moose increased rates of movement when crossing roads; rates for road crossings were greater than the 95th quantile of movement rates during all seasons (Fig. 4). Movement rates were generally higher for roads with more traffic than for the smaller road classes (Fig. 4).

Habitat Selection

Univariate road model selection results indicated that roads with greater traffic and vehicle speeds had greater negative impacts on habitat selection adjacent to the roadway (Table 4). Models with variable weights that increased with road size and traffic volumes had more support than other weighting scenarios. Road weights were similar for all seasons and diel periods, with the most variation being for road class 6. There was no weighting (weight = 0) for class 6 roads in during the day in fall and at night in summer and fall (Table 4). The road effect zone varied with season and diel period. Model selection supported models that represented roads with smaller kernels in winter (500 m) for both day and night (Table 4), smaller kernels for summer in the daytime (500 m), and larger kernels for summer at night (1,500 m). In fall, across diel periods, a larger road effect occurred (1,000 m and 1,500 m for day and night, respectively; Table 4).

Roads negatively influenced habitat selection by moose (Fig. 5). Global RSF models that included the interaction between land cover and roads were the best-supported models for all seasons and times of day (Tables 5 and 6). Some interactions, for example in fall models, indicated moose preferred regenerating forest, but as roads increased, avoidance of regenerating forest increased (Table 6). Additionally, multi-model inference indicated that there were seasonal and diel differences in the influence of roads and land cover in predicting habitat selection. Roads had a greater influence than cover type on diurnal habitat selection in summer and fall and both diurnal and nocturnal habitat selection in winter (Table 5). However, the influence of roads on nocturnal habitat selection in summer and fall was secondary to the influence of cover type. The roads-only and land cover-only models had less support than the models containing both roads and land cover (Table 5). K-fold cross validation showed acceptable model fit, with mean r_s values of 0.73, 0.94, 0.95, 0.97, 0.95, and 0.98 for summer day, summer night, fall day, fall night, winter day, and winter night, respectively.

Table 3. Model coefficients (β) and 95% confidence intervals (CI) for top models comparing the road-crossing rate of class 2 to class 6 roads in winter, summer, and fall, of real and simulated moose in Massachusetts, USA, 2006–2009. Road density is the density of each road class in each buffered moose home range. Moose is a categorical variable indicating whether the moose is real or simulated and density × moose is an interaction between road density and moose.

	Class 2[a]		Class 3[b]		Class 4[c]		Class 5[d]		Class 6[e]	
Parameter	**β**	**95% CI**	**β**	**95% CI**	**β**	**95% CI**	**β**	**95% CI**	**β**	**95% CI**
Winter										
Intercept	−0.02	−0.04 to −0.01	0.01^{f}	−0.01 to 0.03	−0.04	−0.07 to −0.01	0.02	−0.01 to 0.05	−0.01f	−0.11 to 0.09
Road density	0.87	0.76 to 0.98	0.73^{f}	0.59 to 0.87	0.94	0.89 to 1.01	0.68	0.60 to 0.76	0.77^{f}	0.63 to 0.91
Moose	0.02	0.01 to 0.04	−0.03^{f}	−0.05 to −0.01	0.02	−0.02 to − 0.06	0.00	−0.03 to 0.03	−0.06f	−0.08 to −0.04
Density × moose	−0.72	−0.83 to −0.61	−0.37^{f}	−0.53 to −0.21	−0.63	−0.72 to −0.54	−0.54	−0.61 to −0.47		
Summer										
Intercept	0.06	0.04 to 0.08	−0.01^{f}	−0.05 to 0.03	−0.05	−0.15 – 0.05	−0.01	−0.04 to 0.02	0.17	−0.29 to −0.05
Road density	0.72	0.64 to 0.80	1.19^{f}	0.85 to 1.53	0.78	0.64 – 0.92	1.18	1.09 to 1.27	0.87	0.69 to 1.05
Moose	−0.03	−0.06 to −0.01	0.04^{f}	0.01 to 0.08			−0.02	−0.05 to 0.01		
Density × moose	−0.49	−0.60 to −0.38	−0.53^{f}	−0.93 to −0.13			−0.67	−0.76 to −0.58		
Fall										
Intercept	0.07^{f}	0.02 to 0.12	−0.02^{f}	−0.06 to 0.02	0.03	−0.04 to 0.10	−0.05	−0.15 to 0.05	0.36	0.18 to 0.54
Road density	0.87^{f}	0.48 to 1.26	1.77^{f}	1.38 to 2.15	1.58	1.38 to 1.78	1.67	1.40 to 1.94	0.96	0.69 to 1.23
Moose	−0.10^{f}	−0.13 to −0.07	−0.04^{f}	−0.05 to −0.03	−0.03	−0.09 to 0.03	0.01	−0.05 to 0.07		
Density × moose	−0.16^{f}	−0.27 to −0.05			−0.62	−0.79 to −0.45	−0.70	−0.88 to −0.52		

[a] Primary state highways.
[b] Secondary state highways and major roads.
[c] Light duty roads with >200 vehicles/day.
[d] Light duty roads with <200 vehicles/day.
[e] Roads with <10 vehicles/day.
[f] Coefficients and standard error based on model averaging of top models.

Table 4. Final weights assigned to 5 roads classes and the scale (smoothing parameter – h [m]) used to create kernel density surfaces representing the road effect on seasonal day and night time moose habitat selection in Massachusetts, USA, 2006–2009.

	Day			**Night**		
	Summer	**Fall**	**Winter**	**Summer**	**Fall**	**Winter**
Scale (m)	500	1,000	500	1,500	1,500	500
Road weight						
Class 2[a]	100	100	100	100	100	100
Class 3[b]	85	85	80	85	85	80
Class 4[c]	65	60	60	60	60	60
Class 5[d]	40	40	40	40	40	40
Class 6[e]	5	0	20	0	0	20

[a] Primary state highways.
[b] Secondary state highways and major roads.
[c] Light duty roads with >200 vehicles/day.
[d] Light duty roads with <200 vehicles/day.
[e] Roads with <10 vehicles/day.

DISCUSSION

Our results clearly indicate that the high-density road network in Massachusetts had a negative influence on moose movements and habitat use. Expected road crossings within moose home ranges were lower than predicted by simulated movements and moose showed an avoidance of roads and areas adjacent to roadways. Avoidance was positively related to disturbance intensity. During the day, when the perceived safety risk associated with roads was greater, the road network was the main driver of moose habitat selection, determining what portions of the landscape moose would use. Within suitable areas, selection was driven by cover types that provided food, water, and shelter (e.g., mature and regenerating forests and wetlands). At night, constraints on habitat selection imposed by the road effects were fewer and cover type drove habitat selection, with roads a secondary effect. This is consistent with the risk-disturbance hypothesis articulated by Frid and Dill (2002). These results indicate that the road network is a strong determining factor of moose occurrence and moose movements at all scales.

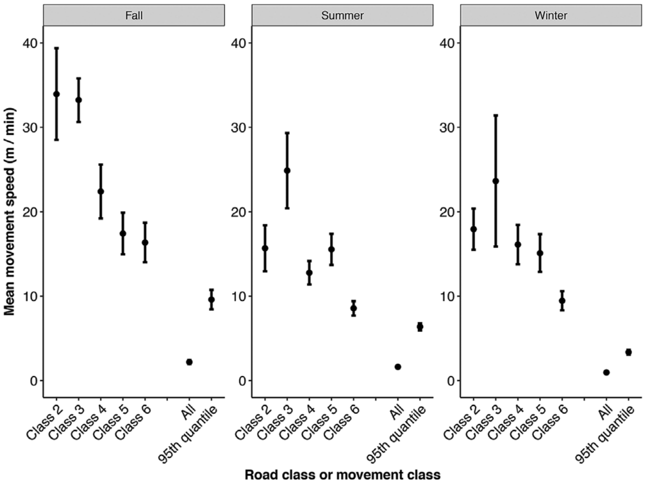

Figure 4. Mean (± SE) rate (m/min) of movement by moose in Massachusetts, USA, 2006–2009, when crossing roads of class 2 to class 6 compared with the mean and 95th quantile of all seasonal movements, including road crossings.

Our habitat selection analysis predicted the relative probability of selection of habitat patches. However, the predictions did not incorporate the likelihood of moose crossing roads to reach patches. It may be useful to model a step or path selection function to integrate road-crossing effects into the RSF models (Avgar et al. 2016, Zeller et al. 2016). Moose avoidance of roads at home range and patch scales is an indication that roads may affect moose fitness, but no studies have addressed this.

Our study moose avoided roads and the strength of this avoidance increased with larger and more heavily trafficked roads (Shanley and Pyare 2011, Laurian et al. 2012). The high density of roads and high levels of fragmentation of the landscape in Massachusetts may force moose to cross roads. State highways and high-traffic roads bisect the landscape at a coarse scale, creating large blocks of habitat (Fig. 1). Typical moose home ranges consist of several of these larger blocks, with local class 4 through-roads further fragmenting the larger blocks into smaller patches. To avoid higher-class roads, moose have no choice but to cross local through-roads. This may be the reason we observed no difference in the crossing rate of class 4 roads by real versus simulated moose during summer, and is an indication that the magnitude of disturbance influenced crossing rate and habitat selection. Moose also showed little to no aversion to class 6 roads with <10 vehicles/day. Though it has been reported moose may be attracted to roads because of increased forage (Dodd et al. 2007, Rea et al. 2010), availability of minerals (Laurian et al. 2008, Grosman et al. 2011), or to escape predators or insects (Berger 2007, Laurian et al. 2012), we do not believe these are the reasons we saw no avoidance with these road classes. There is little to no clearing of vegetation next to class 2–6 roadways in Massachusetts, de-icing salts are used in much lower quantities than in areas farther north, and there are no known roadside salt licks. Furthermore, moose in Massachusetts are free from selective pressures of predation by wolves (*Canis lupus*) and human hunters.

We found the road effect zone for moose in Massachusetts to be similar or larger than observed in other studies. Moose avoided areas within 500 m of roads during the day in summer and winter and during the night in winter. The road effect zone was 1,000 m for the fall during the day, and 1,500 m at night for summer and fall. Laurian et al. (2008) reported annual moose avoidance of roads up to 1,000 m from the roadway, whereas Laurian et al. (2012) reported avoidance of roads up to 100 m in spring and summer and up to 250 m in winter. Shanley and Pyare (2011) reported the effect zone to be 500–1,000 m.

We were unable to conclusively address our first prediction, that moose in a high-density road network would be more tolerant of roads and show a higher functional response threshold to roads than previously documented. We believe this was because road densities within moose seasonal home ranges were much higher than those presented in Beyer et al. (2013). Therefore, we could not identify a road density threshold at which moose started to cross roads less

Table 5. Comparison of candidate resource selection function models for moose in Massachusetts, USA, 2006–2009. Included are the difference in Akaike's Information Criterion corrected for small sample size (ΔAIC_c), AIC_c weight (w_i), and model rank. The land cover-only model included a random intercept for individual; all other models included a random intercept for individual and a random slope for road class.

	Summer			Fall			Winter		
Model	ΔAIC_c	w_i	Rank	ΔAIC_c	w_i	Rank	ΔAIC_c	w_i	Rank
Day									
Roads × land cover	0.0	1.00	1	0.0	1.00	1	0.0	1.00	1
Roads + land cover	144.2	<0.01	2	40.2	<0.01	2	57.4	<0.01	2
Roads	3,104.7	<0.01	3	1,915.5	<0.01	3	2,041.7	<0.01	3
Land cover	4,032.8	<0.01	4	3,065.5	<0.01	4	6,753.7	<0.01	4
Night									
Roads × land cover	0.0	1.00	1	0.0	1.00	1	0.0	1.00	1
Roads + land cover	72.4	<0.01	2	58.1	<0.01	2	52.6	<0.01	2
Roads	5,334.4	<0.01	4	4,435.9	<0.01	4	3,288.0	<0.01	3
Land cover	2,518.3	<0.01	3	3,084.5	<0.01	3	7,557.1	<0.01	4

frequently than expected. Beyer et al. (2013) observed a threshold at a road density of 0.2 km/km^2 in summer and 0.4 km/km^2 in winter. The lowest road density we observed in a seasonal moose home range was 0.5 km/km^2 and the average road density across seasons was 1.31 km/km^2. We may have detected a threshold if we had data from home ranges in areas of lower road densities.

Road-crossing rates indicated moose in Massachusetts crossed roads more often than in other study areas. In a study of moose in Quebec with a lower road density (~0.16 km/km^2), Laurian et al. (2008) estimated road crossings per day to be 0.01 for highways and 0.04 for forest roads. In a study of moose in Ontario, estimated mean road-crossing rates were 0.6 road crossings/day. We observed moose in Massachusetts crossing roads much more frequently: 1.1 crossings/day. We were unable to determine whether this higher crossing frequency was due to a developed tolerance for roads, or whether moose in Massachusetts have few options for existing outside the high-density road network and therefore have to cross roads frequently within their home ranges. However, because the road network is so dense in Massachusetts, we suspect that the latter was involved.

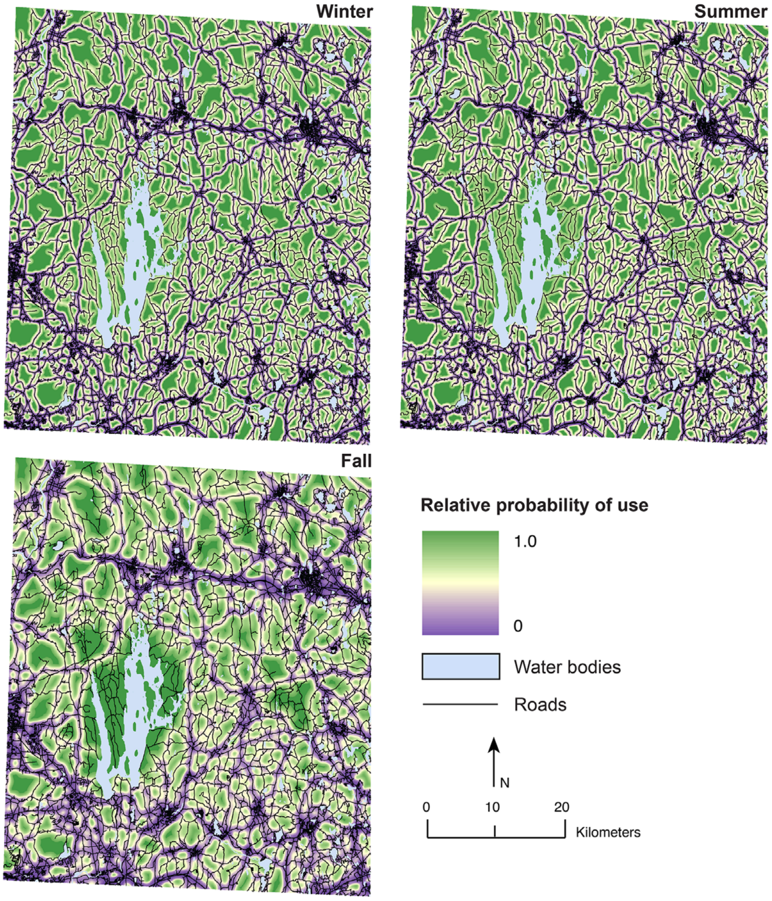

Figure 5. The relative probality of selection by moose from the top models in the Worcester Plateau area of Massachusetts, USA, 2006–2009 for winter, summer, and fall. We present resource selection function models from the daytime diel period.

Table 6. Model coefficients (β) and 95% confidence intervals (CI) for final resource selection functions for season and diel period for moose in Massachusetts, USA, 2006–2009. Categorical land cover paratemers included coniferous, mixed, and regenerating forest, open wetlands, forested wetlands, and other cover types representing open and developed areas. The roads parameter contained 5 classes of roads weighted and scaled according to season and time of day.

	Summer		Fall		Winter	
Parameter	**β**	**95% CI**	**β**	**95% CI**	**β**	**95% CI**
Day						
Intercept	−0.22	−0.30 to −0.14	−0.91	−0.98 to −0.84	−0.01	−0.08 to 0.06
Coniferous	0.16	0.14 to 0.18	−0.01	−0.04 to 0.02	0.72	0.70 to 0.74
Mixed	−0.27	−0.29 to −0.25	−0.40	−4.03 to −3.97	0.46	0.44 to 0.48
Other	−1.86	−1.98 to −1.74	−1.60	−1.80 to −1.40	−1.64	−1.77 to −1.51
Regeneration	0.61	−0.59 to 0.63	0.71	0.69 to 0.74	0.83	0.81 to 0.85
Open wetlands	−0.10	−0.13 to −0.07	−0.08	−0.12 to −0.04	−0.94	−0.98 to −0.90
Forested wetlands	1.26	1.24 to 1.28	1.33	1.30 to 1.36	0.81	0.79 to 0.83
Roads	−24.73	−27.04 to −22.41	−28.06	−30.55 to −25.57	−24.34	−26.13 to −22.55
Coniferous × roads	0.53	0.03 to 1.03	2.71	1.90 to 3.52	−0.57	−1.06 to −0.08
Mixed × roads	1.62	1.15 to 2.09	2.17	1.36 to 2.98	−0.87	−1.34 to −0.40
Other × roads	−2.12	−2.92 to −1.32	−7.61	−10.32 to −4.90	−2.70	−3.71 to −1.69
Regeneration × roads	5.65	5.21 to 6.09	−1.18	−1.91 to −0.45	3.75	3.31 to 4.21
Open wetlands × roads	9.54	8.97 to 10.11	9.14	8.24 to 10.04	2.96	2.21 to 3.71
Forested wetlands × roads	2.67	2.18 to 3.16	1.95	1.18 to 2.72	0.92	0.39 to 1.45
Night						
Intercept	−0.80	−0.89 to −0.71	−1.26	−1.35 to −1.17	0.13	0.06 to 0.20
Coniferous	−0.51	−0.54 to −0.48	−0.44	−0.48 to −0.40	0.72	0.70 to 0.74
Mixed	−0.65	−0.68 to −0.62	−0.63	−0.67 to −0.59	0.52	−0.54 to 0.50
Other	0.38	0.30 to 0.46	0.78	0.68 to 0.88	−0.86	−0.95 to −0.77
Regeneration	1.33	1.31 to 1.35	1.79	1.76 to 1.82	1.24	1.22 to 1.26
Open wetlands	0.81	0.77 to 0.85	1.10	1.06 to 1.14	−0.72	−0.75 to −0.69
Forested wetlands	0.87	0.84 to 0.90	1.22	1.18 to 1.26	0.65	0.64 to 0.68
Roads	−19.07	−21.64 to −16.50	−24.77	−27.38 to −22.16	−25.63	−28.64 to −22.62
Coniferous × roads	1.95	1.22 to 2.68	2.16	1.17 to 3.15	−0.90	−1.37 to −0.43
Mixed × roads	1.84	1.14 to 2.54	0.30	−0.68 to 1.28	0.79	0.36 to 1.22
Other × roads	−5.73	−6.66 to −4.80	−11.62	−13.01 to −10.23	−2.00	−2.74 – −1.26
Regeneration × roads	5.69	5.11 to 6.27	−4.15	−4.90 to −3.40	3.63	3.20 to 4.06
Open wetlands × roads	5.04	4.29 to 5.79	4.99	4.05 to 5.93	2.03	1.31 to 2.75
Forested wetlands × roads	0.08	−0.64 to 0.80	−1.27	−2.17 to −0.37	0.11	−0.41 to 0.63

MANAGEMENT IMPLICATIONS

Our results suggest that mitigation efforts may be needed to reduce the effect of roads on moose in Massachusetts. Mitigation efforts may include traffic control and land use planning to concentrate future development and reduce the need for new roadways, protecting existing tracts of roadless areas, and constructing wildlife crossing structures or implementing other roadway mitigation measures. These types of conservation efforts are dependent on collaborations between wildlife managers, conservation organizations, and the transportation agencies responsible for the construction and maintenance of transportation infrastructure. Our study of moose in southern New England has shown that a viable population can exist in the most highly developed region of moose range in North America, and our findings on movements in relation to a dense road network will assist in understanding and managing large mammal populations in increasingly urbanized environments throughout North America.

ACKNOWLEDGMENTS

Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government. Thanks to J. T. Finn and N. D. Rayl for statistical assistance. We also thank T. K. Fuller and T. L. Millette for their careful review and comments on drafts of this manuscript. The Massachusetts Division of Fisheries and Wildlife has provided long-term funding for moose research in Massachusetts through the Federal Aid in Wildlife Restoration program (W-35-R). The Massachusetts Department of Conservation and Recreation, United States Geological Survey, University of Massachusetts-Amherst, Massachusetts Department of Transportation Highway Division, and Safari Club International have also provided funding and logistical support.

LITERATURE CITED

Avgar, T., J. R. Potts, M. A. Lewis, and M. S. Boyce. 2016. Integrated step selection analysis: bridging the gap between resource selection and animal movement. Methods in Ecology and Evolution 7:619–630.

Balkenhol, N., and L. P. Waits. 2009. Molecular road ecology: exploring the potential of genetics for investigating transportation impacts on wildlife. Molecular Ecology 18:4151–4164.

Bartoń, K. 2014. MuMIn: model selection and model averaging based on information criteria (AICc and alike). <http://cran.r-project.org/web/packages/MuMIn/index.html>. Accessed Sep 2014.

Bates, D., M. Maechler, and B. Bolker. 2012. lme4: Linear mixed effects models using S4 classes. <http://lme4.r-forge.r-project.org/>. Accessed 22 Nov 2013.

Berger, J. 2007. Fear, human shields and the redistribution of prey and predators in protected areas. Biology Letters 3:620–623.

Beyer, H. L. 2012. Geospatial Modelling Environment (version 0.7.2.1). <http://www.spatialecology.com/gme>. Accessed 31 May 2013.

Beyer, H. L., R. Ung, D. L. Murray, and M.-J. Fortin. 2013. Functional responses, seasonal variation and threshold in behavioral responses of moose to road density. Journal of Applied Ecology 50:286–294.

Bowman, J., J. C. Ray, A. J. Magoun, D. S. Johnson, and F. N. Dawson. 2010. Roads, logging, and the large-mammal community of an eastern Canadian boreal forest. Canadian Journal of Zoology, 88:454–467.

Burnham, K. P., and D. R. Anderson. 2004. Model selection and multimodel inference: a practical information-theoretic approach. Second edition. Springer, New York, New York, USA.

Coffin, A. W. 2007. From roadkill to road ecology: a review of the ecological effects of roads. Journal of Transportation Geography 15:396–406.

DeGraaf, R. M., and M. Yamasaki. 2001. New England wildlife: habitat, natural history, and distribution. University Press of New England, Hanover, New Hampshire, USA.

Dodd, N. L., J. W. Gagnon, S. Boe, and R. E. Schweinsburg. 2007. Assessment of elk highway permeability by using global positioning system telemetry. Journal of Wildlife Management 71:1107–1117.

Dussault, C., J.-P. Ouellet, C. Laurian, R. Courtois, M. Poulin, and L. Breton. 2007. Moose movement rates along highways and crossing probability models. Journal of Wildlife Management 71:2338–2345.

Dyer, S. J., J. P. O'Neill, S. M. Wasel, and S. Boutin. 2002. Quantifying barrier effects of roads and seismic lines on movements of female woodland caribou in northeastern Alberta. Canadian Journal of Zoology 80:839–845.

Environmental Systems Research Institute [ESRI]. 2011. ArcGIS 10.1. ESRI, Redlands, California, USA.

Fahrig, L., and T. Rytwinski. 2009. Effects of roads on animal abundance: an empirical review and synthesis. Ecology and Society 14:21.

Forman, R. T. T., D. A. Sperling, J. A. Bissonette, A. P. Clevenger, C. D. Cutshall, V. H. Dale, L. Fahrig, R. L. France, C. R. Goldman, K. Heanue, J. Jones, F. Swanson, T. Turrentine, and T. C. Winter, editors. 2002. Road ecology: science and solutions. Island Press, Washington, D. C., USA.

Frair, J. L., E. H. Merrill, H. L. Beyer, and J. M. Morales. 2008. Thresholds in landscape connectivity and mortality risks in response to growing road networks. Journal of Applied Ecology 45:1504–1513.

Frid, A., and L. Dill. 2002. Human-caused disturbance stimuli as a form of predation risk. Conservation Ecology 6:11.

Gillies, C. S., M. Hebblewhite, S. E. Nielsen, M. A. Krawchuk, J. L. Friar, D. J. Saher, C. E. Stevens, and C. L. Jerde. 2006. Application of random effects to the study of resource selection by animals. Journal of Animal Ecology 75:887–898.

Grosman, P. D., J. A. G. Jaeger, P. M. Biron, C. Dussault, and J.-P. Ouellet. 2011. Trade-off between road avoidance and attraction by roadside salt pools in moose: an agent-based model to assess measures for reducing moose-vehicle collisions. Ecological Modeling 222:1423–1435.

Hall, B., G. Motzkin, D. R. Foster, M. Syfert, and J. Burk. 2002. Three hundred years of forest and land-use in Massachusetts, USA. Journal of Biogeography 29:1319–1335.

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65–71.

Keller, I., and C. Largiader. 2003. Recent habitat fragmentation caused by major roads leads to reduction of gene flow and loss of genetic variability in ground beetles. Proceedings of the Royal Society of London Series B-Biological Sciences, 270:417–423.

Kuznetsova, A., P. B. Brockhoff, and R. H. B. Christensen. 2014. lmerTest: tests for random and fixed effects for linear mixed effect models (lmer objects of lme4 package). <http://cran.r-project.org/web/packages/lmerTest/index.html>. Accessed Sep 2014.

Laurance, W. F., M. Goosem, and S. G. W. Laurance. 2009. Impacts of roads and linear clearings on tropical forests. Trends in Ecology & Evolution 24:659–669.

Laurian, C., C. Dussault, J.-P. Ouellet, R. Courtois, and M. Poulin. 2012. Interactions between a large herbivore and a road network. Ecoscience 19:69–79.

Laurian, C., C. Dussault, J.-P. Ouellet, R. Courtois, M. Poulin, and L. Breton. 2008. Behavioural adaptations of moose to roadside salt pools. Journal of Wildlife Management 72:1094–1100.

Manly, B. F. J., L. L. McDonald, D. L. Thomas, T. L. McDonald, and W. P. Erickson. 2002. Resource selection by animals: statistical analysis and design for field studies. Second edition. Kluwer, Boston, Massachusetts, USA.

McGarigal, K., B. W. Compton, S. D. Jackson, E. Plunkett, K. Rolih, T. Portante, and E. Ene. 2011. Conservation Assessment and Prioritization System (CAPS) Statewide Massachusetts Assessment: November 2011. <http://www.masscaps.org>. Accessed Oct 2013.

Nakagawa, S., and H. Schielzeth. 2013. A general and simple method for obtaining R2 from generalized linear mixed-effects models. Methods in Ecology and Evolution 4:113–142.

Polfus, J. L., M. Hebblewhite, and K. Heinemeyer. 2011. Identifying indirect habitat loss and avoidance of human infrastructure by northern mountain woodland caribou. Biological Conservation 144: 2637–2646.

R Development Core Team. 2016. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rea R. V., K. N. Child, D. P. Spata, and D. MacDonald. 2010. Road and rail side vegetation management implications of habitat use by moose relative to brush cutting season. Environmental Management 46:101–109.

Rempel, R., P. Elkie, A. Rodgers, and M. Gluck. 1997. Timber-management and natural-disturbance effects on moose habitat: landscape evaluation. Journal of Wildlife Management 61:517–524.

Riley, S. R., J. P. Pollinger, R. M. Sauvajot, E. C. York, C. Bromley, T. K. Fuller, and R. K. Wayne. 2006. A southern California freeway is a physical and social barrier to gene flow in carnivores. Molecular Ecology 15: 1733–1741.

Roberts, D. R., V. Bahn, S. Cuiti, M. S. Boyce, J. Elith, G. Guillera-Arroita, S. Hauenstein, J. J. Lahoz-Monfort, B. Schroder, W. Thuiller, D. I. Warton, B. A. Wintle, F. Harting, and C. F. Dormann. 2017. Cross-validation strategies for data with temporal, spatial, hierarchical, or phylogenetic structure. Ecography 40:913–929.

Seiler, A. 2005. Predicting locations of moose-vehicle collisions in Sweden. Journal of Applied Ecology 42:371–382.

Shanley, C. S., and S. Pyare. 2011. Evaluating the road-effect zone on wildlife distribution in a rural landscape. Ecosphere 2:1–16.

Turchin, P. 1998. Quantitative analysis of movement: measuring and modeling population redistribution in plants and animals. Sinauer Associates, Sunderland, Massachusetts, USA.

U.S. Census Bureau. 2010. Census 2010. Resident population data: population density <http://www.census.gov/2010census/data/apportionment-dens-text.php>. Accessed Feb 2013.

Wattles, D. W. 2015. The effect of thermoregulation and roads on the movements and habitat selection of moose in Massachusetts. Dissertation, University of Massachusetts, Amherst, USA.

Wattles, D. W., and S. DeStefano. 2011. Status and management of moose in the northeastern United States. Alces 47:53–68.

Wattles, D. W., and S. DeStefano. 2013. Space use and movements of moose in Massachusetts: implications for conservation of large mammals in a fragmented environment. Alces 49:65–81.

Westveldt, M. R., R. I. Ashman, H. I. Baldwin, R. P. Holdsworth, R. S. Johnson, J. H. Lambert, H. J. Lutz, L. Swain, and M. Standish. 1956. Natural forest vegetation zones of New England. Journal of Forestry 54:332–338.

Yost, A. C., and R. G. Wright. 2001. Moose, caribou, and grizzly bear distribution in relation to road traffic in Denali National Park, Alaska. Arctic 54:41–48.

Zeller, K. A., K. McGarigal, S. A. Cushman, P. Beier, T. W. Vickers, and W. M. Boyce. 2016. Using step and path selection functions for estimating resistance to movement: pumas as a case study. Landscape Ecology 31:1319–1335.

Associate Editor: Scott McCorquodale.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's website.