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Response of female black bears to a high-density road network and identification of long-term road mitigation sites

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Abstract

Roads can result in negative effects on wildlife including habitat loss, behavioral avoidance, reduced survival, reproduction and gene flow. These road effects are especially pronounced for large mammals given their large home-range requirements and low reproductive rates. To counteract these negative effects, road mitigation measures, such as underpasses and overpasses, are promoted; however, future landscape changes are rarely considered when selecting mitigation locations. We used GPS telemetry data on female American black bears *Ursus americanus* to examine their response to roads in Massachusetts, US. We compared bear road crossing frequency with a null crossing model derived from a correlated random walk, estimated road crossing movement speeds, and fit a road-crossing resource selection function. We found that, though black bears crossed roads less than expected based on the null model, 10% of their observed steps, on average, crossed roads. We also found bears crossed roads at higher movement speeds than during other home-range behaviors, and that bears preferred to cross smaller, less trafficked roads in areas with lower speed limits, less human development and more forest. We used the resource selection model to identify road segments for potential mitigation efforts and then used future human development projections to forecast future changes in these segments. We found a decrease of 15% in the length of suitable mitigation segments from 2019 to 2050. Given the sizeable investment in wildlife crossing structures and their longevity on the landscape, we recommend incorporating future projections into crossing site selection to ensure the long-term viability of road mitigation efforts.

Introduction

Twenty per cent of the Earth's terrestrial surface is within 1 km of a road and, of the remaining roadless patches, 80% measure less than 5 km^2 in size (Ibisch *et al*., 2016). Roads can act as ecological traps and have other negative impacts on wildlife including collisions with vehicles, habitat loss and behavioral avoidance, which can all affect the reproductive success and survival of populations (Forman *et al*., 2003; Fahrig & Rytwinski, 2009; Morales-González *et al*., 2020). Roads can also be barriers to movement and result in the isolation of populations, reducing gene flow and genetic heterogeneity (Epps *et al*., 2005; Riley *et al*., 2006; Gustafson *et al*., 2017). These negative effects are especially prevalent in large mammals due to their larger home-range requirements and relatively low reproductive rates (Whittington, St. Clair & Mercer, 2005; Dodd *et al*., 2007; Fahrig & Rytwinski, 2009). Large mammals whose home ranges are intersected by roads typically need to cross roads to access resources, which can increase their probability of mortality from vehicle collisions (Fahrig & Rytwinski, 2009).

Mitigating the negative effects of roads for large mammals has primarily been focused on building wildlife crossing structures. Wildlife crossing structures, whether underpasses or overpasses, when paired with fencing, have been shown to facilitate the movement of wildlife across roads (Clevenger & Waltho, 2005), and to provide connectivity for substantial portions of wildlife populations (Sawaya, Clevenger & Kalinowski, 2013). Wildlife crossing structures have also been estimated to reduce wildlife-vehicle collisions by 83–87% (Huijser & McGowen, 2010; Huijser *et al*., 2016; Rytwinski *et al*., 2016). The human safety benefit of these crossing structures has enormous potential; annually, there are over one million vehicle collisions with large mammals in the US resulting in substantial risk to human safety and over a billion dollars in property damage (Conover *et al*., 1995; Huijser *et al*., 2008; Huijser *et al*., 2009).

Despite the advantages of wildlife crossing structures, their implementation is not widespread due to the enormous cost and effort involved with construction (Glista, DeVault & DeWoody, 2009). Crossing structure effectiveness for large mammals requires large structures and long stretches of fencing which, in North America, can cost hundreds of thousands to millions of dollars. Therefore, selecting sites that provide functional connectivity for species across roadways is imperative. Siting crossing structures has been based on multiple data types and analyses such as road crossings from monitored individuals (e.g. Dodd *et al*., 2007), wildlife-vehicle collision locations (e.g. Clevenger, Chruszcz & Gunson, 2003), or expert opinion (Clevenger *et al*., 2002). However, ecosystems are dynamic, and landscape change due to human development or climate change is rarely considered when selecting crossing structure locations. A wildlife crossing structure that may provide connectivity today may not be functional in the future if there are changes in the surrounding environment. Given the cost of building wildlife crossing structures for large mammals, their relative permanence on the landscape, and their importance in maintaining long-term movement and metapopulation processes, it is paramount that these structures provide functional connectivity into the future.

The American black bear *Ursus americanus*, a large mammal with large home-range requirements, has been shown to display a stress response when close to roads and when crossing roads (Ditmer *et al*., 2018*a*). Black bears have also been shown to change their diel patterns around roads (Barrueto, Ford & Clevenger, 2014; Zeller *et al*., 2019). Roads can be a source of direct mortality for bears through vehicle collisions (Baruch-Mordo *et al*., 2008; McCown *et al*., 2009), and in some areas, collisions with vehicles have been shown to be the largest source of mortality for black bear populations (Beckmann & Berger, 2003; Beckmann & Lackey, 2008; Wynn-Grant *et al*., 2018). Black bears in the vicinity of roadways can also experience increased mortality from other sources such as management removals and hunting (Wynn-Grant *et al*., 2018).

Black bears in the Commonwealth of Massachusetts may be especially prone to the negative effects of roads. As the third most densely populated state in the U.S. (US Census Bureau, 2010), Massachusetts has a high road density. Where bears currently range in the state, they experience road densities in their home ranges from 0.55 to 5.8 km/km^2 ($\bar{x}$ = 2.23 km/km^2, unpublished data). These road densities are some of the highest reported in studies on black bears in North America (Brody & Pelton, 1989; Beringer, Seibert & Pelton, 1990; Gold, 1997; Gantchoff & Belant, 2017; Loosen, Morehouse & Boyce, 2018). Across North America, black bears have been shown to use wildlife overpasses and underpasses (Allen, 2011; Sawaya *et al*., 2013; Healy & Gunson, 2014). Black bear use of crossing structures can provide connectivity for large portions of black bear populations (Sawaya *et al*., 2013). Therefore, there is precedent for the ability of crossing structures to alleviate the negative effect of roadways on black bears in Massachusetts, and research is needed to determine black bear response to roads, and for siting effective crossing structures.

Here we examine the response of female black bears to roads in Massachusetts. We expected bears to respond to roads by (1) showing road avoidance when compared with a null movement model of no road effect, (2) having a higher movement speed during road crossing events and (3) crossing roads non-randomly. For this last expectation, we examined black bear crossing behavior by road type, speed, traffic volume, season and time of day, and developed a resource selection function to identify environmental variables associated with road crossing locations. From the resource selection function, we spatially projected the relative probability of black bear road crossings across our study area. Lastly, we incorporated future human development projections to identify changes in the probability of black bear road crossings. This approach allows the identification of crossing sites that are consistent across years, regardless of human development or landscape change. To our knowledge, we are the first to predict the long-term feasibility of crossing sites for mitigating the negative effects of roads on wildlife. Our goal was to increase our understanding of black bear response to roads in a high-density road network and provide information that can be used by wildlife and transportation managers.

Materials and methods

Black bear data

Female black bears were captured, collared and tracked in the central and western parts of Massachusetts (Fig. 1). Females were used in this study since they are the focus of the Massachusetts Division of Fisheries and Wildlife due to their role in driving reproductive output and population trends. We captured bears annually between 2012 and 2018 and fit individuals with either a Telonics Gen 3 or Gen 4 GPS collar. We used data from bears collared from 2012 to 2017 to develop our models and data from bears collared in 2018 to assess the predictive performance of our models. Bears captured from 2012 to 2017 were collared at a 15-min (n = 7) or 45-min (n = 69) fix interval, bears from 2018 were collared at a 45-min fix interval (n = 17).

The collar data from 2012 to 2017 represented 75 bear-years from 36 individuals. With the exception of four bears that were 2 years old at the time of collaring, all bears were three years old or more and were of reproductive age. Of the 75 bear-years, 33 females had newborns (44%), 26 had yearlings (35%) and 16 had no offspring (21%).

We captured bears with barrel traps, dart projectors and during winter den checks. We used 191 mg/mL Telazol R (Tiletamine HCl and Zolazepam HCl) to immobilize bears. A dosage of 5 mg/kg was used in summer, and 7 mg/kg in winter. All capture, handling and immobilization was in accordance with the University of Massachusetts, Amherst IACUC Protocols # 2011-0074, 2014-0074 and 2017-0066.

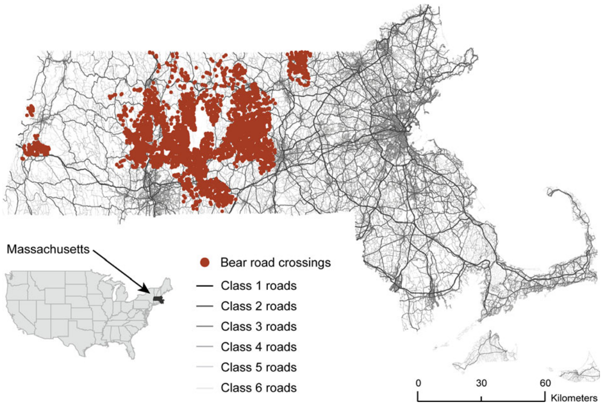

Figure 1 Black bear road crossing locations from GPS-collared individuals. The Massachusetts road network is also shown in the six road classes used in the analysis: class 1, interstates; class 2, state highways; class 3, major roads; class 4, minor roads with an average daily traffic of >200 vehicles/day; class 5, minor roads with an average daily traffic of <200 vehicles/day; class 6, local roads with <10 vehicles/day.

To minimize locational error, we removed fixes if they fell into one of the following categories: (1) unresolved fixes, (2) fixes classified as 2D or resolved QFP (uncertain) with a PDOP > 5, (3) fixes classified as 3D or resolved QFP (certain) with a PDOP > 20. Approximately 3.93% (SD = 2.67%) of the data points were removed in this process. For each bear-year, we visually examined the GPS points to identify when bear movement stopped and points clustered in a single location in the fall and when movement began in the spring. We used only GPS points outside of the denning period in our analyses.

Black bear road crossing locations and road crossing behavior

We identified female black bear road crossing locations by intersecting the bear paths with the road network. We explored black bear road crossing behavior in all females and for females with newborns or without newborns by assessing, (1) the annual number and proportion of bear steps that crossed roads, (2) the relationship between the density of roads in a bear home range and the proportion bear steps that crossed roads, (3) the frequency at which bears crossed roads of different classes, speeds and traffic volumes and (4) the speed at which bears crossed roads relative to movement speeds during other home-range behaviors.

We were also interested in temporal responses to roads. We expected female black bears to cross roads more in the summer than during other seasons and more during crepuscular periods than during other times of day because previous analyses have shown greater movement during these times (Zeller *et al*., 2019). We identified seasons using an ecologically based k-means approach that clustered step lengths, turning angles and time spent in different cover types into three distinct times of year; spring (den exit to June 14th), summer (June 15th to August 9th) and fall (August 10th to den entry; Basille *et al*., 2013; detailed in Zeller *et al*., 2019). We categorized times of day into four periods, dawn (sunrise + 1 h), dusk (sunset + 1 h), day (sunrise + 1 h to sunset – 1 h) and night (sunset + 1 h to sunrise – 1 h). We also examined the behavioral state of the road crossing steps and calculated the proportion of road crossing steps in each of three behavioral states; encamped, foraging and resting. These behavioral states were identified from the turning angle and step length distributions of each bear with a three-state hidden Markov model in the moveHMM R package (Michelot *et al*., 2016; Zeller *et al*., 2019).

We examined female black bear avoidance of roads by comparing empirical road crossings with a null model of black bear movement. We derived the null model by simulating 100 correlated random walks (CRWs) for each bear with the same number of steps as the empirical data in the R software environment (R Core Team, 2019). Simulated steps started from the first location of each collared bear and subsequent steps were drawn from the empirical distribution of step lengths and turning angles for each bear. Simulated movements were constrained to each bear's minimum convex polygon home range. For each CRW, we calculated the crossing rate (number of crossings per road class/kilometers of that road class in a bear's home range) for each road class. We compared the simulated crossing rate with the empirical rate. We also tested if road avoidance was significant compared with the null movement models. Avoidance of roads was significant when the empirical number of road crossings for a road class was less than or equal to the 5th quantile of the CRW road crossing distribution for each bear.

Environmental variables

We selected a suite of landscape variables that may affect female black bear road crossing behavior (Table 1). Given results of previous studies, we expected bears to cross smaller roads with less traffic and lower speed limits more than larger roads (Ditmer *et al*., 2018*a*,*b*; Evans *et al*., 2018; Zeller *et al*., 2019), to cross roads in areas with wetlands and forests away from human development (Evans *et al*., 2014; Tri *et al*., 2016; Zeller *et al*., 2019), and to cross roads in areas of higher elevations and steeper slopes (Powell & Mitchell, 1998; Cushman & Lewis, 2010; Tri *et al*., 2016). Raster variables were available at a 30 m pixel resolution and we rasterized vector data to match this resolution. We represented these variables at multiple spatial scales (360 m, 650 m, 837 m, 1007 m, 1288 m and 1523 m) that were determined by estimating the mean distance black bears moved over the following time periods: 45 min, 1.5 h, 2.25 h, 3 h, 4.5 h, 6 h. The scales were used as the standard deviation for a Gaussian kernel that was used to smooth each variable with the smoothie package in R (Gilleland, 2013). We also represented each variable in the models at the original 30 m resolution. Exploring multiple spatial scales allows for the identification of the appropriate scale of

Table 1 Environmental variables, descriptions and sources used in the black bear road crossing analyses

Variable	Description	Source
Roads		
Road class	Roadways represented as the following classes: 1. Interstates 2. State highways 3. Major roads 4. Minor roads with average daily traffic >200 vehicles/day 5. Minor roads with average daily traffic <200 vehicles/day 6. Local roads with <10 vehicles/day	McGarigal et al. (2015)
Road speed limit	Posted speed limit	Massachusetts Department of Transportation (2013)
Road traffic	Average vehicles/day	McGarigal *et al*. (2015)
Development		
Open space	Cemeteries, golf courses, recreation areas	Massachusetts Bureau of Geographic Information (2018)
Commercial/Industrial	Commercial, industrial, junkyard, urban public, institutional, waste disposal	Massachusetts Bureau of Geographic Information (2018)
High-density residential	Housing on <1/4 acre lots	Massachusetts Bureau of Geographic Information (2018)
Medium density residential	Housing on 1/4–1/2 acre lots	Massachusetts Bureau of Geographic Information (2018)
Low-density residential	Housing on 1/2–1 acre lots	Massachusetts Bureau of Geographic Information (2018)
Very low-density residential	Housing on >1 acre lots	Massachusetts Bureau of Geographic Information (2018)
Powerline corridors	Powerline corridors	Massachusetts Bureau of Geographic Information (2018)
Per cent impervious surface	Per cent of a pixel that has impervious surfaces	McGarigal *et al*. (2017)
Topography		
Per cent slope	Calculated from digital elevation model	Derived from USGS National Elevation Dataset
Aspect	Calculated from digital elevation model	Derived from USGS National Elevation Dataset
Topographic position index	Calculated from digital elevation model	Derived from USGS National Elevation Dataset
Canyons	Derived from topographic position index	
Ridges	Derived from topographic position index	
Slopes	Derived from topographic position index	
Ruggedness	Calculated from digital elevation model	Derived from National Elevation Dataset
Water and wetlands		
Emergent wetland		USFWS National Wetlands Inventory (2019)
Forested wetland		USFWS National Wetlands Inventory (2019)
Vegetation		
Coniferous forest		Pasquarella *et al*. (2018)
Deciduous forest		Pasquarella *et al*. (2018)
Mixed forest		Pasquarella *et al*. (2018)
Landscape configuration metrics		
Similarity	Ecological similarity of each pixel to surrounding pixels	McGarigal *et al*. (2015)

response for each variable and has been shown to result in models with higher predictive power than single-scale models (McGarigal *et al*., 2016).

Road crossing models

We modeled female black bear road crossings with a logistic regression model in a use: availability framework (Manly *et al*., 2007). To account for uncertainty in the exact location of the road crossings, we implemented Brownian Bridge Movement Models (BBMMs) with the BBMM package (Nielson, Sawyer & McDonald, 2013) in R to identify the width of the area across the road where each crossing may have occurred. We based the BBMMs on the three locations before and after each road crossing and measured the road segment captured by the 90% BBMM contour. The average width along the roadway at a crossing was 964 m. To avoid spatial autocorrelation in the data and account for locational uncertainty, we rarified the road crossing locations with a 500 m buffer, which resulted in 6,111 road-crossing locations for the analysis (Fig. 1). We counted the other road crossings within the 500 m buffer of each used point. We used that number to weight the road crossing points in the model so that road crossing locations with more crossings in the surrounding buffer were weighted more heavily than those that had fewer crossings in the surrounding buffer. We sampled available locations at 1000-m intervals along the road network in black bear minimum convex polygon home ranges 2019. We attempted to sample available locations at a 10:1 ratio with the used locations, but road length was limiting, therefore, we were only able to sample 11,378 available points. We calculated the mean of each environmental variable at each scale in a 500 m uniform buffer around each used and available location and z-score standardized the variables. We weighted the available points in the models to maintain a 1:1 ratio with the used points.

We ran two sets of models. We first used the *glmer* function from the lme4 package (Bates *et al*., 2019) in R to run univariate logistic regression models with a random effect for individual bear for each environmental variable at each scale. We used the model AICc values (Burnham & Anderson, 2002) to compare scales and determine the strongest scale of selection for each variable. We then ran correlations among the variables at their selected scales and removed variables with the higher AICc value from any pair with a correlation> |0.6|. We included all uncorrelated variables in a global logistic regression model with a random effect for individual and used the *dredge* function in the MuMIn package (Bartoń, 2019), to identify the candidate models. Models within two ΔAICc units of the highest performing model were averaged to obtain our final weighted parameter estimates.

We spatially predicted the relative probability of a female black bear road-crossing using the following formula: $w(x) = \exp\ (\beta_1 x_1 + \beta_2 x_2 + \beta_3 x_3 + \cdots + \beta_p x_p)$ (Johnson *et al*., 2006). We evaluated the predictive performance of the road crossing surface with the Boyce Index (Boyce *et al*., 2002; Hirzel *et al*., 2006). The Boyce Index compares the predicted values at the locations of validation data with the expected values across the study area and ranges from 0 to 1, with values closer to 1 indicating better predictive ability. For the validation points we combined two sets of data. The first dataset was the 2009–2017 bear road crossing locations that were held out of the model. The second dataset was all the road crossing locations from bears collared in 2018. We used 14 472 validation points from 2009 to 2017 and 4800 points from 2018 for a combined total of 19 272 validation points.

Future road crossing predictions

We used future human development predictions from the Designing Sustainable Landscapes project (DSL; McGarigal *et al*., 2017) to estimate the relative road crossing probabilities for black bears for the years 2020, 2030, 2040 and 2050. The DSL project developed an urban growth model to simulate development in the northeastern USat 10-year time steps (McGarigal *et al*., 2018). The DSL project provides three categories of development intensity, high, medium and low, as well as roads. Because percent impervious surface was the development category in our final road crossing model, we reclassified these development categories as 100%, 50% and 25% impervious surface for high, medium and low intensity development, respectively. We also reclassified all future paved roads as 100% impervious surface. We overlaid the current percent impervious surface layer with each of the four future development projections to add new areas of development. We then projected the road crossing model across the study area for the years 2020, 2030, 2040 and 2050.

We examined the relative probability of a black bear road crossing on class 1 and 2 roads across the state from 2019 to 2050 and calculated the per cent change in the length of these roadways that had a crossing probability greater than or equal to 0.7. We assumed all areas with a greater than 0.7 probability of crossing on class 1 and 2 roads might be considered for road mitigation efforts, since 75.5% of black bear-vehicle collisions from 2013 to 2018 occurred on these road types (Massachusetts Environmental Police, unpublished data). We also used a subset of the Berkshire Linkages Project Priority Road Segments (The Nature Conservancy, 2016) as a localized case study for siting road mitigation projects. The Berkshire Linkages Project is actively assessing these priority segments and working with the Massachusetts Department of Transportation to identify locations for road mitigation projects.

Results

Black bear road-crossing behavior

We identified 20 583 black bear road crossing locations from the GPS data. Annually, each black bear crossed roads an average of 285 times (range: 53–850, median: 257, standard deviation: 156). Females with newborns crossed roads an average of 255 times (range: 15–584, median: 237, standard deviation: 136) and females without newborns crossed an average of 296 times (range: 3–850, median: 265, standard deviation: 176). The average annual proportion of black bear steps that crossed a road was 0.10 (range: 0.02–0.27, median: 0.10, standard deviation: 0.05). The average annual proportion of road crossing steps by females with newborns was 0.09 (range: 0.02–0.18, median: 0.08, standard deviation: 0.04) and by females without newborns was 0.12 (range: 0.02–0.27, median: 0.11, standard deviation: 0.05). The relationship between the proportion of bear steps that crossed roads and road density within a bear home range was positive and significant ($P < 0.026$; Appendix S1).

Female black bears crossed smaller, less trafficked, lower-speed roads more frequently than other roads (Fig. 2, Appendix S2). Of the road crossings, 77% occurred when a bear was in a movement state compared with a foraging (0.16) or an encamped (0.08) state. Movement speeds when crossing roads were higher than mean movement speeds across all steps regardless of road class (Fig. 3,

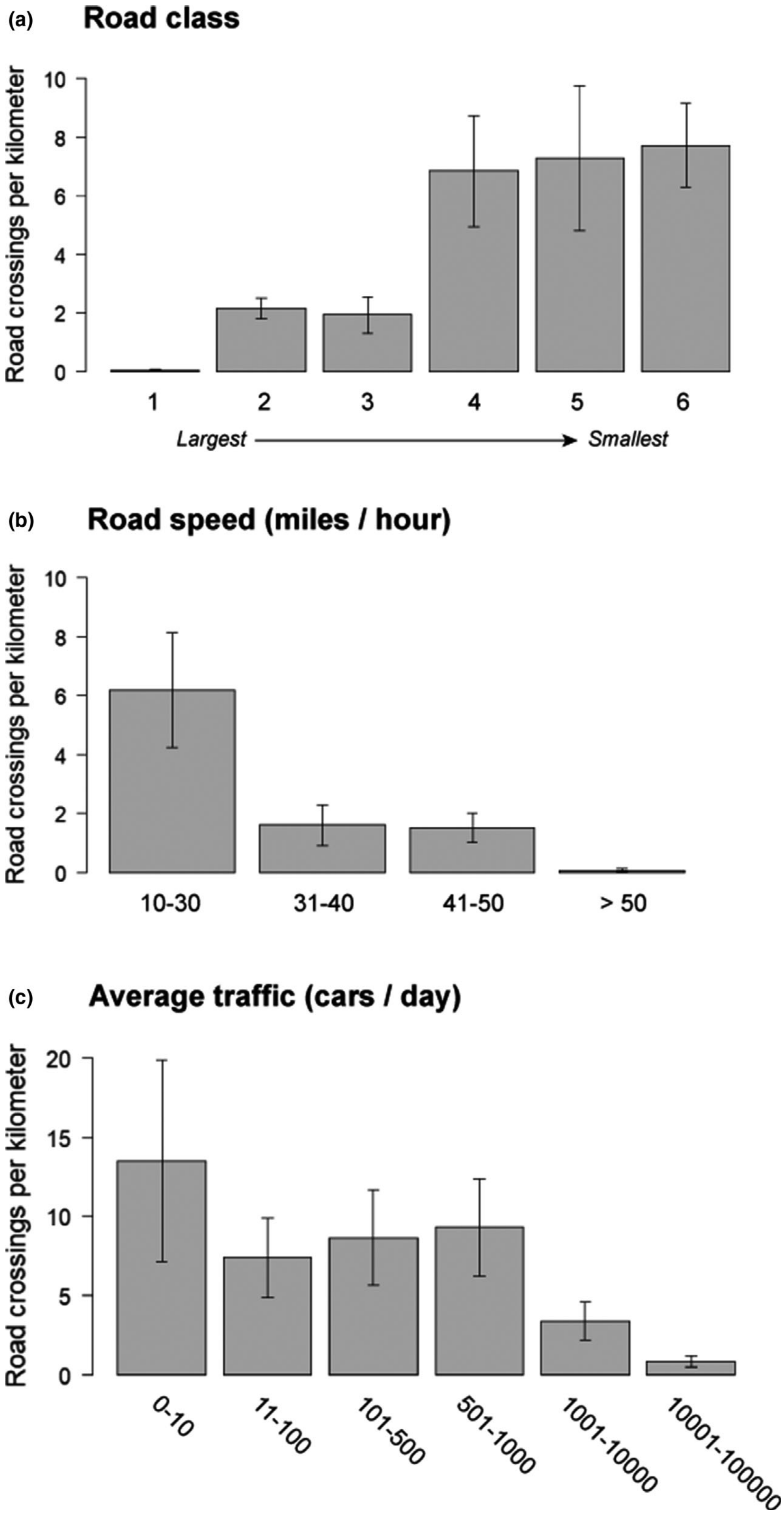

Figure 2 Mean frequency (number of crossings adjusted for the length of that road class in a female black bear home range) of crossing (a) roads of different class, (b) roads of different speeds, (c) roads of different average daily traffic.

Appendix S3). Road crossing frequencies peaked at dusk and were lowest during nighttime hours (Fig. 4a, Appendix S4a). Across all female bears, road crossing frequency peaked during the summer (Fig. 4b), whereas the lowest crossing frequency was observed in females with newborns during spring (Appendix S4b).

Female black bears crossed all road types 3.55 times less frequently than expected based on the null movement model. Specifically, black bears crossed class 1, 2, 3, 4, 5 and 6 roads, 13.23, 4.43, 4.61, 3.46, 3.77 and 2.97 times less often than expected based on the CRWs (Table 2).

Road crossing models

Percent impervious surface at the finest scale was the highest performing univariate model. The univariate models indicate bears selected for crossing sites with a low amount of human development and a high amount of forest (Table 3). Scales of selection for the geospatial layers were variable and no trends in scale were detected (Table 3). Black bears also selected for crossing locations on smaller roads with lower speed limits and traffic volumes.

The final averaged crossing model indicated bears crossed roads with lower speed limits, in forested areas away from intensive human development (Table 4). Bears crossed roads in areas along ridgelines, powerlines, and in areas that had higher heterogeneity (low similarity). Crossings were also associated with higher values of ruggedness, aspect and topographic position index. The crossing model had a Boyce Index value of 0.954.

The crossing model predicted relatively low crossing probability on most primary and secondary roads across the state as well as in large metropolitan areas (Fig. 5). However, there was variation along roadways and some segments of primary and secondary roads had slightly higher crossing probabilities. This indicates these roads may be semi-permeable to black bear movement (Fig. 5, inset). Crossing probabilities increased in more forested, mountainous and undeveloped parts of the state.

Projected future development across the state caused a decrease in the length of class 1 and 2 roads that had a crossing probability of at least 0.7 (Appendix S5; Fig. 6). We observed a 4% decadal decrease in the length of roadways with at least a 0.7 probability of crossing. This resulted

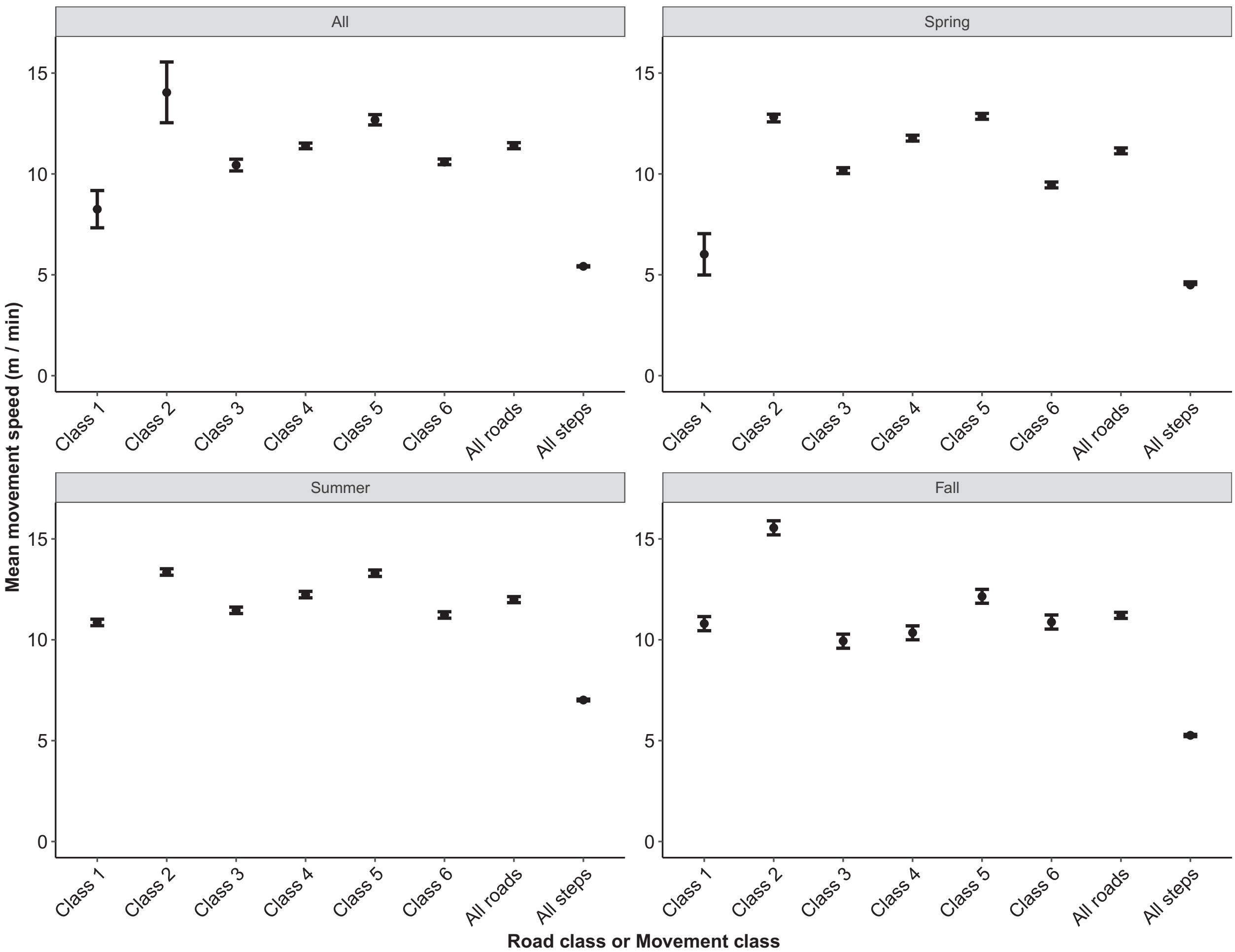

Figure 3 Mean rate (m/min) and standard error of movement steps by female black bears in Massachusetts, US when crossing roads of class 1 to 6 and all roads, compared with all movement steps.

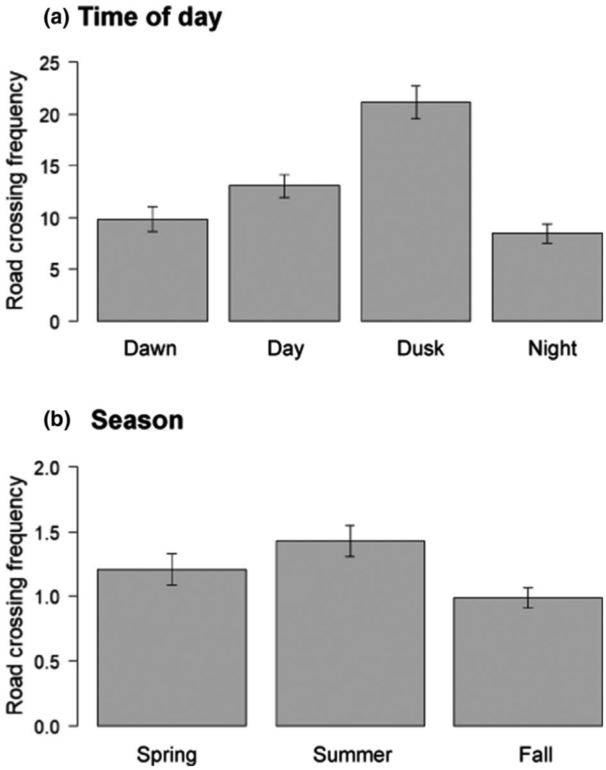

Figure 4 Road crossing frequency of female black bears in Massachusetts, USA, during (a) different times of day (mean number of crossings in that period/number of hours in that period), and (b) seasons (mean number of crossings in a season/number of days in that season).

in a total loss of approximately 15% of potential mitigation segments from 2019 to 2050. In the subset of areas identified as priority road segments for mitigation by the Berkshires Linkages Project, high probability road segments measured approximately 14.8-km long in 2019 and 10.4-km long in 2050, a 30% decrease in the length of road that might be considered for mitigation (Fig. 6).

Discussion

Female black bears in Massachusetts have relatively high road densities in their home ranges and we found that, on average, 10% of observed black bear steps crossed roads. However, black bears also displayed a negative response to roads in their home ranges. As anticipated, bears crossed all road types significantly less than expected based on a null model of no road effect. Bears also displayed higher movement rates when crossing roads compared with other home-range movements. Black bears selected for crossing locations non-randomly. Preferred crossing locations were in more rural forested areas and on roadways with low average daily traffic and low speed limits. When future development was incorporated into our spatial predictions, we found road segments with a high probability of black bear crossing to decline over time, potentially reducing road mitigation options.

Ten per cent of female black bear steps in Massachusetts crossed roads, which is slightly higher than the 9% found for males and females by Ditmer *et al*. (2018*a*,*b*) in Minnesota. This difference may be a result of the high road densities in the home ranges of black bears in our study area (Beringer *et al*., 1990). However, our study was based only on female black bears, and male black bears have larger home ranges and have been shown to cross roads more frequently than female bears (Karelus *et al*., 2017). Therefore, the road effect we found is likely biased low for all bears in the state.

We found black bears crossed smaller, lower trafficked roads with low speed limits more than other road types, which is consistent with other studies (Brody & Pelton, 1989; Beringer *et al*., 1990; Karelus *et al*., 2017; Ditmer *et al*., 2018*b*). Black bear movement speed during road crossing steps was significantly higher than other home-range movement steps. Karelus *et al*. (2017) and Ditmer *et al*. (2015) observed higher black bear movement speeds in areas of human development and Ditmer *et al*. (2018*a*,*b*) observed elevated heart rates when bears crossed roads, especially larger, more trafficked roads. These observations indicate black bears are stressed around roadways and may be moving

Table 2 Number and rates of road crossing events for each road class for real and simulated female black bears in Massachusetts, US. Road length is the sum total length of each road class in the study bears' minimum convex polygon home ranges

		Real bears		Simulated bears	
Road class	Road length (km)	Number of crossings	Crossing rate	Number of crossings	Crossing rate
All roads	12 132	20 583	1.70	72 093	5.94
Class 1	256	149	0.58	1974	7.71
Class 2	1373	1769	1.29	7732	5.63
Class 3	926	1331	1.44	6061	6.55
Class 4	4489	7051	1.57	23 934	5.33
Class 5	1834	2737	1.49	10 244	5.59
Class 6	3254	7546	2.32	22 147	6.81

Crossing rate was calculated as the number of crossings divided by the length of each road class in kilometers. For the simulated crossings, we report the mean across simulations. For all road classes, differences between the empirical number of crossings and the simulated crossings were significant.

Table 3 Best performing scales identified from the univariate female black bear road crossing models and associated standardized beta coefficients, and AIC*c* values. Variables are listed from lowest AICc value to highest

Variable	Scale (m)	Beta coefficient	Standard error	AICc
Per cent impervious surface	30	−0.69987	0.015109	66275.06
Commercial/Industrial	30	−0.46125	0.012437	67202.24
Low-density residential	1523	−0.47709	0.014136	67295.98
Mixed forest	650	0.472169	0.014755	67388.77
Housing density	650	−0.44611	0.014642	67576.37
Ridges	1523	0.423593	0.016992	67795.46
Open Space	1007	−0.31753	0.01242	67831.39
Conifer forest	1523	0.373698	0.015471	67832.91
Medium density residential	1523	−0.32088	0.012887	67876.6
Road speed	–	−0.04984	0.010569	67905.16
Deciduous forest	30	0.255518	0.011551	67932.66
Very low-density residential	1523	−0.27388	0.012164	67940.39
Slopes	1523	−0.38288	0.017575	67966.87
Ruggedness	1523	0.327248	0.016312	68008.44
High-density residential	30	−0.26942	0.012528	68009.7
Powerlines	1523	0.247728	0.012408	68026.02
Topographic position index	30	0.179364	0.01143	68196.66
Per cent slope	1523	0.267401	0.017711	68213.35
Similarity	1523	−0.21897	0.014617	68219.48
Canyons	1523	0.20192	0.015792	68282.24
Road traffic	–	−0.08271	0.010996	68358.77
Aspect	30	0.081675	0.011219	68393.85
Forested Wetland	30	0.077433	0.01176	68401.7
Road class	–	0.261634	0.011514	68424.89
Emergent wetland	30	−0.04522	0.010961	68430.16

more quickly across roadways to minimize exposure time during crossing. Another strategy for minimizing exposure to traffic and the presence of humans would be to cross roads at night, when traffic rates are typically lower. Though we did observe a strong peak in timing of road crossings at dusk, we did not observe a nocturnal peak, even when we accounted for different road classes (Appendix S6). However, black bears in Minnesota crossed high-traffic roads at night more often than lower-traffic roads (Ditmer *et al.* 2018*a*,*b*) and black bears in Florida crossed roads at night eight times more frequently than during the day (Guthrie, 2012). Beringer *et al.* (1990) found black bears in North Carolina crossed roads of all types more during the day than at night. These apparently confounding findings may be due to differences in study design, data collection method (VHF vs. GPS telemetry), parsing of the diel period into different classes (e.g. day/night vs. dawn/day/dusk/night) or real differences in bear populations, due to habituation or otherwise. Seasonally, black bears in Massachusetts crossed roads more frequently in the summer than during other times of year,

Table 4 Averaged standardized beta coefficients and standard errors for the final female black bear road crossing model

Variable	Beta coefficient	Standard error
Per cent impervious surface	−0.450	0.027
Mixed forest	0.172	0.027
Ridges	0.076	0.033
Deciduous forest	0.314	0.024
Similarity	−0.042	0.024
Coniferous forest	0.327	0.029
Powerlines	0.128	0.019
Road speed	−0.027	0.014
Emergent wetland	−0.031	0.018
Ruggedness	0.094	0.029
Forested wetland	0.106	0.017
Aspect	0.099	0.017
Topographic position index	0.064	0.022

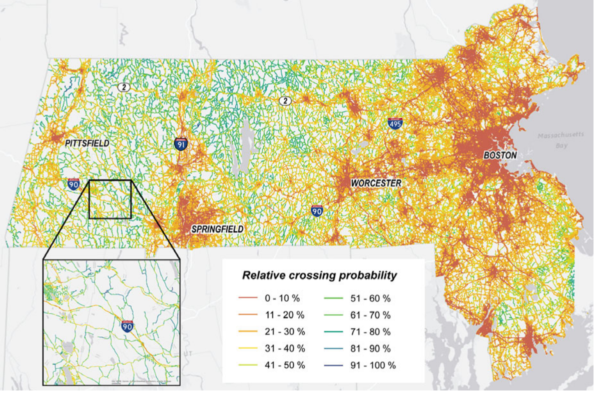

Figure 5 Relative probability of female black bear road crossings in the Commonwealth of Massachusetts, USA.

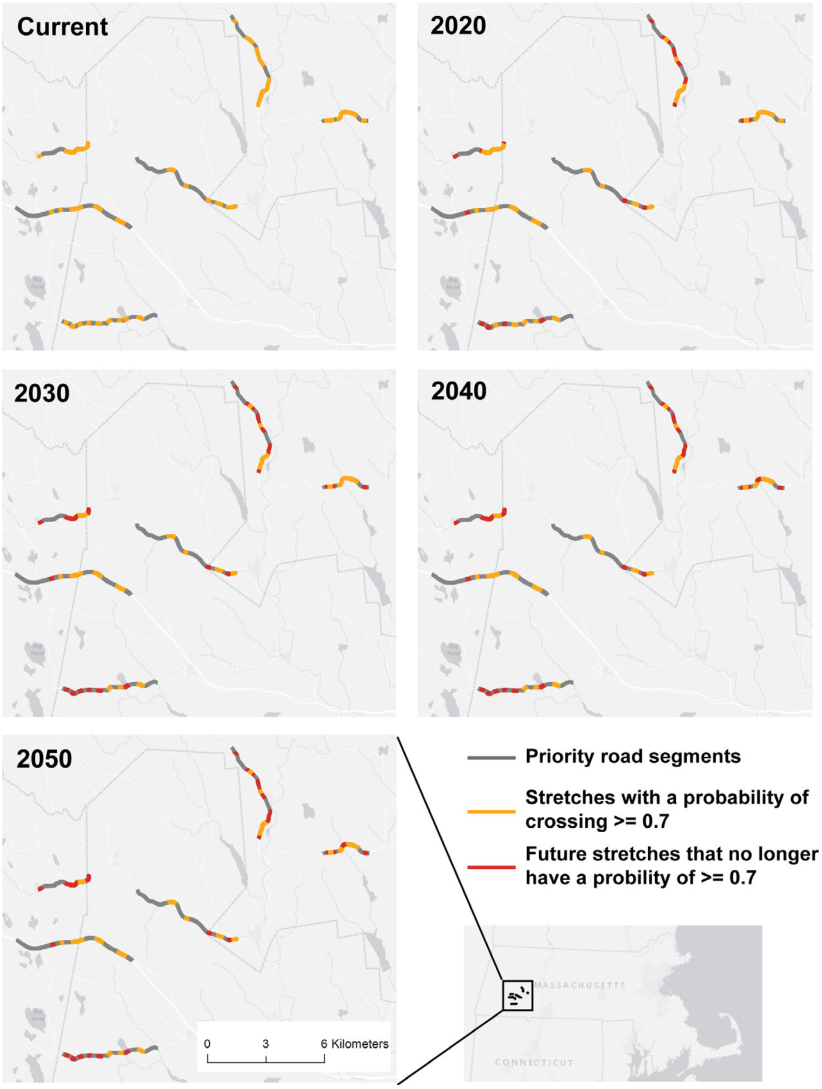

Figure 6 Six priority road segments for mitigation as identified by the Berkshires Wildlife Linkages project (dark gray) with areas that had a >70% probability of a black bear crossing (orange) in the current time step and in future time steps. Segments whose crossing probability fell below 0.7 in future time steps are highlighted in red.

likely due to higher movement rates during this season compared with spring and fall (Zeller *et al*., 2019). This result echoes that of Guthrie (2012) who found black bears in Florida also crossed roads more frequently during summer months.

Similar to other studies, we found black bears selected for road crossing locations non-randomly with respect to surrounding environmental features (McCown & Eason, 2001; Lewis *et al*., 2011; Guthrie, 2012). Black bears preferred to cross roads outside of heavily developed areas in any type of forest, while also preferring locations with a higher topographic position and broad scale landscape heterogeneity. Two of our most important predictor variables were human development and forest, which were also found to be the most important road crossing predictor variables for black bears in Idaho (Lewis *et al*., 2011). Bear preference for crossing roads in certain areas allowed us to spatially predict the relative probability of black bear road crossings in a study area which can aid in targeting sites for mitigation.

A novel approach used in our study was to incorporate future landscape change into our predictions of black bear road crossings and potential mitigation sites. By incorporating future landscape dynamics like land use and climate change, road segments that maintain consistently high crossing probabilities can be identified and prioritized over sites that may experience a drop in crossing potential over time. Because of the sizeable investment in wildlife crossing structures, and their longevity on the landscape, future projections for siting are recommended (Huijser *et al*., 2008), but to our knowledge, these projections are not typically implemented.

We found differences in black bear road crossing probabilities over time as a result of increasing human development across the state of Massachusetts and were able to identify road segments where high probabilities of crossing were stable into the future. Improvements to our approach would be to incorporate data from male black bears as well as other landscape dynamics like land cover change as a result of climatic shifts, however, we did not have access to such data. Railways are increasingly being recognized as barriers or sources of mortality for wildlife (Popp & Boyle, 2017), therefore, including railways would also be a welcome addition to studies such as this. Lastly, creating models at different hierarchical levels of analysis would capture the multi-dimensional processes of crossing site selection. For example deriving one model at the local level to capture important site characteristics at the roadway could be combined with a landscape model that captures landscape-level characteristics that may lead an individual bear to a particular crossing zone. In our current model, both levels are combined in a single model by using an array of spatial scales. Though our model had a high predictive ability, more information on hierarchical processes of crossing site selection might be gleaned from the separation of these two levels.

Our study found black bears to have consistent negative responses to all road types; however, 10% of bear steps, on average, crossed roads. This relatively high road crossing rate indicates black bears in Massachusetts must cross roads frequently to move about their home ranges, which can result in increased mortality from vehicle collisions (Fahrig & Rytwinski, 2009), and may affect black bear survival and population dynamics (Beckmann & Berger, 2003; Beckmann & Lackey, 2008; Wynn-Grant *et al*., 2018). To mitigate the effects of roads on black bears, wildlife crossing structures and fencing can be constructed (Clevenger & Waltho, 2005; Rytwinski *et al*., 2016). To this end, we predicted the relative probability of black bear road crossings into the future to account for expanding human development and identified road segments with consistently high road crossing probabilities to the year 2050. This approach can be expanded to include land use change due to climate and can be easily implemented in other study areas and species to ensure limited road mitigation resources are used to promote viable long-term corridors for populations of species.

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Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. Relationship between female black bear home range road density and the proportion of female black bear steps that crossed a road in Massachusetts, USA.

Appendix S2. Mean frequency (number of crossings adjusted for the length of that road class in a black bear home range) of females with and without newborns crossing (a) roads of different class, (b) roads of different speeds, and (c) roads of different average daily traffic, in Massachusetts, USA.

Appendix S3. Mean rate (m/min) and standard error of movement steps by female black bears with and without newborns in Massachusetts, USA when crossing roads of class 1 to 6 and all roads, compared with all movement steps. Class 1 roads are interstates, Class 2 roads are state highways, Class 3 roads are other major roads, Class 4 roads are minor roads with an average daily traffic >200 vehicles/day, Class 5 roads are minor roads with an average daily traffic of <200 vehicles/day, and Class 6 roads are local roads with <10 vehicles/day.

Appendix S4. Road crossing frequency of female black bears with and without newborns in Massachusetts, USA, during (a) different times of day (mean number of crossings in that period/number of hours in that period), and (b) seasons (mean number of crossings in a season/number of days in that season).

Appendix S5. Massachusetts statewide projections of relative road crossing probabilities for female black bears on class 1 and 2 roads (Interstates and State Highways). Probabilities and associated length of roadways greater than or equal to 0.7 are shown.

Appendix S6. Female black bear road crossing frequency (crossings per kilometer of road) with time of day on roads of Class 1 – Class 6 in Massachusetts, USA.