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RESEARCH ARTICLE

Evaluating methods for identifying large mammal road crossing locations: black bears as a case study

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Abstract
Context Roads have several negative effects on large mammals including restricting movements, isolating populations, and mortality due to vehicle collisions. Where large mammals regularly cross roads, driver safety is also a concern. Wildlife road crossing structures are often proposed to mitigate the negative effects on wildlife and human safety. However, few studies have compared the efficacy of different methods in identifying wildlife road crossing and mitigation locations.
Objectives We examined five commonly used methods to identify road crossing locations for wildlife to determine which method best captured empirical crossing locations.
Methods We used GPS collar data on black bears in Massachusetts, USA, to estimate road crossing locations with a road crossing resource selection function, factorial least-cost paths, resistant kernels, Circuitscape, and an individual based movement model. We evaluated model performance on each road class and all road classes combined with a hold out road crossing data set.
Results All methods performed well, but Circuitscape consistently outperformed the other methods, both for each road class and all road classes combined.
Conclusions Road mitigation efforts for wildlife are often costly and have a long-term footprint on the landscape, therefore, it is important to select locations for these efforts that provide functional connectivity for wildlife. We are the first to compare different road crossing models for large mammals across a large study area and on different road types. Our results provide information to assist researchers and managers in selecting an analytical method for identifying potential road mitigation locations for large mammals.

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Introduction

Roads cover about 20% of the earth's surface and fragment natural areas into disjunct patches, only 7% of which are larger than 100 km^2 (Ibisch et al. 2016). Large mammals, due to their large home range requirements, must often cross roads to access critical resources and survive (Fahrig and Rytwinski 2009). Navigating the road and transportation network can cause direct mortality due to vehicle collisions (Seiler and Helldin 2006), but roads have also been shown to restrict movements, isolate populations, and reduce gene flow, which can all have indirect negative effects on survival (Forman et al. 2003; Balkenhol and Waits 2009; Gustafson et al. 2017). Large mammals crossing roads also pose risks to human safety. Annually, in the United States, there are over one million large mammal-vehicle collisions resulting in approximately 26,000 human injuries and 200 deaths (Huijser et al. 2008).

Road mitigation efforts are often proposed to alleviate the negative effects on wildlife and increase human safety. Mitigation measures may include warning signs, reduced speed limits, large animal detection systems, fencing, construction of crossing structures (e.g. wildlife overpasses or underpasses), or a combination of these measures (Clevenger and Huijser 2011). For example, combining fencing with crossing structures can reduce large mammal roadkill by 83% (Rytwinski et al. 2016). However, retrofitting existing road networks with mitigation measures like crossing structures can be costly, therefore, it is important to select locations along the roadway that will be the most successful at providing functional connectivity for wildlife.

Currently, there are myriad methods for identifying locations for road mitigation efforts. One method is to use wildlife-vehicle collision locations to create models of collision risk for a species or groups of species, and then identify mitigation locations from these results (Gunson et al. 2011). There are multiple methods based on animal tracking data (e.g. Schuster et al. 2013). Some studies use high-frequency GPS-telemetry data to identify consistent road crossing locations from collared individuals (e.g. Bastille-Rousseau et al. 2018). While others use road crossing locations identified by collar data to model road crossing probability across an entire road network (Lewis et al. 2011; Zeller et al. 2018b). There are also studies that identify probable crossing locations with connectivity models such as least-cost path (Adriaensen et al. 2003; Loro et al. 2015), factorial least-cost path (FLCP Cushman et al. 2009, 2013), resistant kernel (Compton et al. 2007; Cushman et al. 2014), or Circuitscape models (McRae et al. 2008, 2012). These connectivity models are typically run across a resistance surface derived from expert opinion, telemetry, or genetic data (Zeller et al. 2012) and sites along roadways with high connectivity values are considered for mitigation. Lastly, high-use road crossing locations can be identified with individual-based movement models (IBMMs; e.g. Quaglietta et al. 2019). With IBMMS, it is assumed a location that has a high frequency of crossings by simulated individuals would also have a high frequency of crossings by real animals and that these locations might be appropriate for mitigation efforts.

When identifying locations for road mitigation measures, sometimes the choice of approach is limited to the data at hand, but often, one can implement a number of the methods outlined above. For example, if GPS-telemetry data are available, those data can be used to model road crossing locations across a road network. Or, GPS-telemetry data can be used to model resistance to movement for a study area, which can serve as the basis for running connectivity models or IBMMs. The direct modeling of wildlife vehicle collisions or road crossing locations is attractive because the analysis is localized to the road network and incorporates specific attributes along the roadway that may affect crossing behavior. However, the connectivity models are also appealing because they contextualize crossing locations in the larger landscape by modeling movement and flow not only at roadways, but also in areas leading up to and away from roadways. Therefore, these two different approaches represent two different scales for modeling road crossings and potential mitigation locations. The IBMM models might be considered a hybrid of these scales since they model movement across the landscape, but the result is ultimately an iterative process of fine scale movement decisions.

To our knowledge, there have been only a few studies comparing the efficacy of different road crossing identification methods for wildlife. Clevenger et al. (2002) compared local-scale approaches for black bears (*Ursus americanus*) in Banff National Park informed by expert opinion, literature, and empirical data and found the empirical data outperformed the other two methods at identifying highway crossing locations. Cushman et al. (2014), compared a local-scale approach and two landscape-scale approaches for black bears in Idaho. They assessed the ability of two resistance surfaces (one derived from genetic data and one from telemetry data) and two connectivity models (FLCPs and resistant kernels) to predict black bear highway crossing locations. They found that telemetry data outperformed genetic data for developing the resistance surface and that the FLCP method outperformed the resistant kernel method. Bastille-Rousseau et al. (2018) compared results of different samples of GPS data from African elephants (*Loxodonta*) in identifying intensity of use for siting road and rail crossing mitigation locations. Their methods were not predictive, but they did find biases may be introduced with different samples of individuals. All these studies focused on a single large transportation corridor and did not evaluate other road classes or other commonly-used road crossing models.

We expand upon these previous studies with a GPS-telemetry dataset on black bears in a high-density road network in Massachusetts, USA. We used GPS telemetry data to predict road crossing locations across the study area with (1) a resource selection model of road crossings, (2) FLCPs, (3) resistant kernels, (4) Circuitscape, and (5) IBMMs. To assess the predictive ability of these models, we sampled the model outputs at black bear crossing locations from a hold-out data set and compared these values with a random sample of crossing locations. We evaluated method performance for each of six road classes in the study area and all road classes combined. Identifying which method best captures empirical road crossing sites is an important first step to ensure the efficacy of road mitigation measures for large mammals.

Methods

Black bear and road data

The Massachusetts Division of Fisheries and Wildlife almost exclusively collars females due to the importance of females in driving black bear reproductive output and population trends. Therefore, we used data from GPS collared female black bears with established home ranges in the central and western parts of the Commonwealth of Massachusetts to develop and evaluate the performance of road crossing models (Fig. 1). The collar fix interval was either 15 or 45-min. Bear capture and handling procedures and GPS data post-processing methods are detailed in Zeller et al. (2018a, b).

Bears collared from 2012 to 2017 (36 individuals; 75 bear-years) were used in developing the road crossing models and bears collared in 2018 (17 individuals) were used in model evaluation. All females were over 2 years of age; 46% had newborns, 32% had yearlings, and 22% had no offspring at the time of collaring. We combined all reproductive states into a single data set because we were interested in the female population-level response to road crossings.

We used road data from the Massachusetts Conservation Assessment and Prioritization System (McGarigal et al. 2015). Roads were classified as follows: Class 1, interstates and major state highways; Class 2, other state highways; Class 3, major roads; Class 4, minor roads with an average daily traffic $>$ 200 vehicles / day; Class 5, minor roads with an average daily traffic $<$ 200 vehicles/day; Class 6, local roads with $<$ 10 vehicles/day. Paved roads accounted for 92% of roads while unpaved sections of roadway were found on some Class 4—6 roads throughout the study area.

Black bear road crossing models

All analyses were performed with R software (R Core Team 2019) unless otherwise noted.

Road-crossing resource selection function

Zeller et al. (*in press*) used black bear road crossing locations (identified as the intersection of the GPS paths and the road network) and random locations along the road network to create a multi-scale road

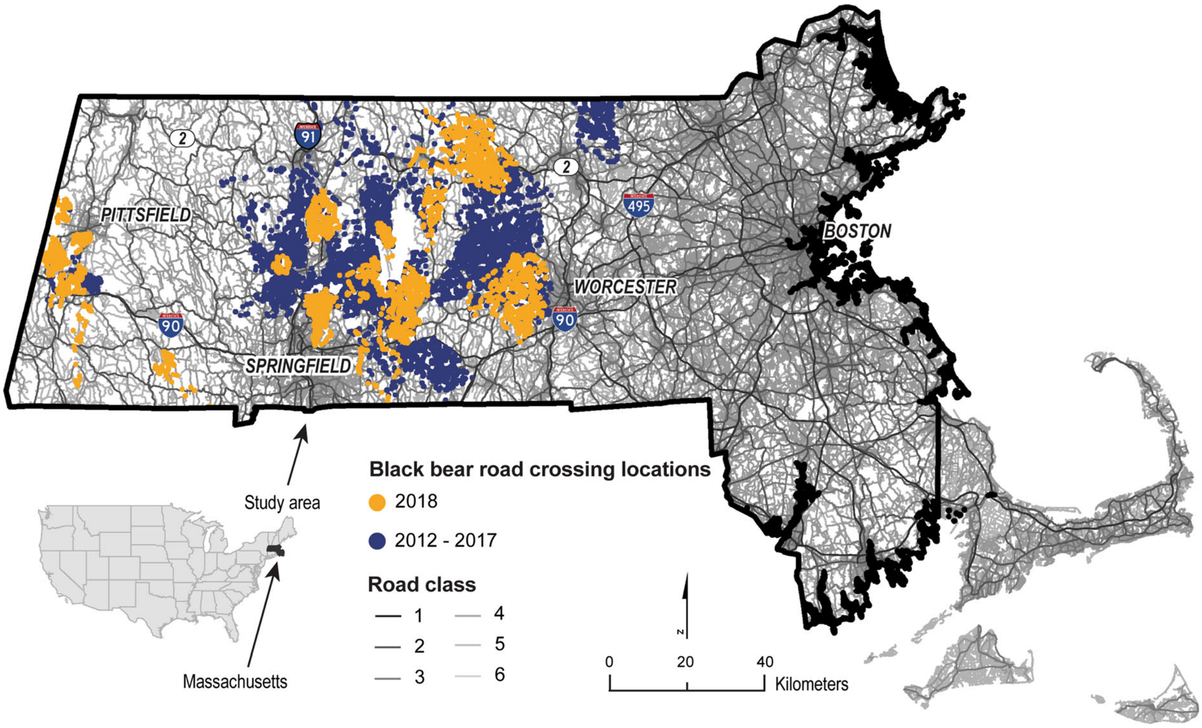

Fig. 1 The Commonwealth of Massachusetts shown with the analysis area (heavy black line), the road network, and black bear road crossing locations from 2012 to 2018

crossing resource selection function. They found that bears preferred to cross roads in areas with a high proportion of forest and forested wetland, high values of topographic position and ruggedness, and a low proportion of human development. They also found black bears preferred crossing roads on smaller roadways with lower speed limits and traffic volumes. The resource selection function was used to predict the probability of a black bear road crossing on the road network in the study area (Fig. 2a).

Resistance surfaces

The other four road crossing models—the resistant kernel, FLCPs, Circuitscape, and the IBMM—all require a resistance surface across which connectivity or movement is modeled. Black bears in the study area display different movement behaviors depending on season and time of day (Zeller et al. 2019), therefore, we wanted to preserve these differences by modeling connectivity across resistance surfaces that were derived for different seasonal and diel periods.

The resistance surfaces were developed with the black bear probability of movement surfaces from (Zeller et al. 2019). Zeller et al. (2019) modeled probability of movement for each of three seasons (spring, summer, and fall) and two times of day (day and night) with step selection functions (SSFs) derived from the 2012–2017 bear GPS collar data. SSFs for each season/diel period were generated for each bear and probability of movement was predicted across the study area. The individual probability surfaces for each season/diel period were weighted according to the distance from each bear's home range centroid and then combined. This spatial-weighting approach preserves spatial differences in bear movement and behavior across the study area (Osipova et al. 2019; Zeller et al. 2019). The probability of movement surfaces for each season/diel period were projected across the study area outlined in Fig. 1, plus a 10 km buffer to avoid any edge effects in subsequent modeling. The linear inverse of the probability surfaces was used to calculate resistance so that high probability of movement values resulted in low resistance and low probability of movement values,

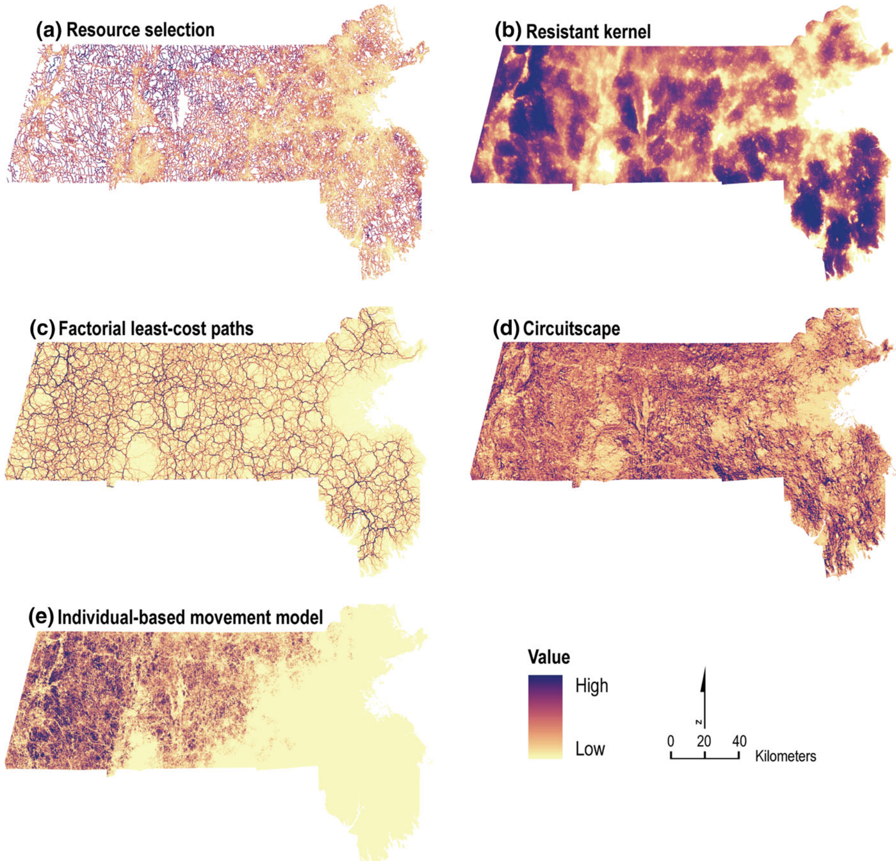

Fig. 2 Five road crossing methods examined in this study; (**a**) road crossing resource selection function, (**b**) resistant kernel connectivity model, (**c**) factorial least-cost path connectivity model (FLCP), (**d**) Circuitscape connectivity model, and (**e**) an individual-based movement model (IBMM). The darker blue colors indicate, for the resource selection model, a higher relative probability of a road crossing, for the resistant kernel, FLCP, and Circuitscape models, higher flow, and for the IBMM a higher number of simulated paths crossing a pixel

high resistance. These six resistance surfaces, spring day/night, summer day/night, and fall day/night, were rescaled to a range of 1–100 and used in the connectivity and IBMM models.

Resistant kernel connectivity model

Resistant kernel connectivity is based on calculating cost and distance from source points distributed across a landscape (Compton et al. 2007). These cost distance kernels are then summed, resulting in a continuous surface of connectivity values representing the density of potential movements across the study area. Because black bear distribution in our study does not necessarily coincide with protected lands, we designed our connectivity models to model flow across the landscape irrespective of discrete source/destination patches (e.g. habitat cores or protected areas).

We distributed 2000 source points probabilistically across the study area according to the probability of movement surfaces described above for each season/diel period. Distributing the points in a probabilistic manner avoids the need to arbitrarily define population or habitat polygons and results in more realistic source points for our population of bears. We used UNICOR software (Landguth et al. 2012) to run resistant kernel models with the source points and resistance surfaces for each season and diel period. We set the edge distance parameter (the distance a bear could disperse in cost-distance units) to 100,000. A cost-distance unit is the sum of the resistance value of each pixel plus the distance across each pixel. Cost-distance accumulates as one moves away from a source point and stops when the cost-distance reaches 100,000. We averaged the resistant kernel models across seasons and times of day to obtain a single surface to be comparable with the other models (Fig. 2b).

Factorial least-cost path connectivity model

We used the same source points for the FLCPs as we did for the resistant kernel models. UNICOR software was used to calculate least cost paths between all pairs of source points for each season/diel period. All paths were summed to produce a surface representing the number of paths traversing a grid cell. We then averaged the FLCP outputs across seasons and times of day to obtain a single connectivity surface (Fig. 2c).

Circuitscape connectivity model

To create a Circuitscape connectivity model that allowed current to flow across the entirety of the study area without oversaturating current near the source points (Koen et al. 2014), we used a 'wall-to-wall' approach (Koen et al. 2014; Dickson et al. 2019). To implement this approach, we followed the recommendation of Koen et al. (2014) and buffered our study area by approximately 20% of its length, resulting in a buffer of 40 km. We then placed points every 2 km along the edge of this buffer and calculated connectivity between all pairs of points across the resistance surfaces for each season/diel period. We ran Circuitscape in Julia (Circuitscape.jl; v0.1.0 Anantharaman et al. 2019) and generated the cumulative current output. We clipped the resultant surface to our study area and then averaged the cumulative current output across seasons/diel periods to obtain a single surface (Fig. 2d).

Individual-based movement model

To simulate bear movement, we first estimated the step length of black bears collared at the 45-min fix interval for each season and time of day and fit a Pareto distribution to each distribution of step lengths. We then seeded the landscape with 3000 start points to simulate 3000 female bears. Our start locations were determined by sampling 2000 start points west of the Connecticut River and 1000 start points east of the Connecticut River probabilistically on the spring/day probability of movement surface within the known range of black bears in the state. The number of start points approximates the population of female black bears in the state and the east–west difference reflects the higher density of black bears west of the Connecticut River (MassWildlife unpublished data).

For each individual, we simulated 7296 steps (a detailed simulation procedure is described in Zeller et al. *in review*). This is the number of 45-min time steps from April 1st to November 15th each year (the average den emergence and entry for our GPS collared bear population). The start step for each individual was simulated on the spring/day resistance surface. We used the 'rawspread' function from the gridprocess R package (Plunkett 2019) paired with the Pareto distribution for each season and time of day to produce a kernel around the start point. The spread of this kernel was shaped by the Pareto distribution (how far a bear typically moves in each time step) and the resistance surface. Because the kernel accumulates cost and distance, the kernel spreads farther in areas of low resistance than in areas of high resistance. Each pixel in this kernel has a probability of movement value (with all probabilities summing to one). The next location for the individual was sampled from this probability surface with the 'strata' function of the sampling R package (Tillé and Matei 2016). The raw spread function was then performed on the new location and the process was repeated until 7296 steps were reached. During the simulation process, every 16-time steps the daytime resistance surface was swapped for the nighttime one and vice-versa. The spring resistance surface was swapped for the summer one at time step 2369, and the summer surface for the fall one at time step 4172.

Simulated bear paths were compared with the average step lengths and home range sizes of collared individuals. We obtained a mean step length of 82.53 m (range 0–2249 m) in the simulated bears and 193.34 m (range 0–1998 m) in the collared bears and a mean home range size of 77.97 km^2 (range 6.85–228.44 km^2) in the simulated bears and 62.51 km^2 (range 5.47–260.55 km^2) in the collared bears. Because we did not include memory, territoriality, or interactions with other bears in our movement simulations, we would expect to obtain slightly smaller step lengths and larger home range sizes and therefore believe our simulations are a reasonable approximation of space use by black bears.

To create a connectivity surface from the 3000 individual movement paths, we rasterized and summed the paths so that the surface values reflected the number of simulated paths crossing each pixel (Fig. 2e).

Method performance

For the road crossing resource selection function, we assumed high probabilities would correspond to preferred road crossing locations, for the connectivity models we assumed high connectivity values on the road network would correspond to preferred road crossing locations, and for the IBMM, we assumed pixels with higher numbers of paths on the road network would correspond to preferred road crossing locations. We used data from 17 black bears from 2018 (5954 road crossing locations) to evaluate model performance of these five methods using a spatial permutation procedure.

We first extracted the values of the five road-crossing model surfaces at the 5954 empirical road crossing locations. Within the minimum convex polygon of each bear, we randomly sampled an equal number of points along the road network as the road crossing points for that bear, so that the population-wide random sample also had 5954 points. We repeated the random sampling procedure 1000 times so that we had 1000 random samples of the 5954 locations. We sampled the random points on each of the five road crossing model surfaces. We then took three approaches to compare the surfaces. In the first, we calculated the proportion of the 1000 random samples that had a mean value greater than the mean of the empirical road crossing values. This statistic tests the probability that the mean values on a surface at the empirical locations are different than the null distribution of mean values. The smaller the number, the better the surface performed.

In the second approach, we calculated an overlap statistic which measured the similarity or dissimilarity of two groups based on the distributions of their values (Pastore and Calcagní 2019). We used the overlapping R package and the 'overlap' function (Pastore 2018) to calculate the proportion of overlap between the empirical kernel density distribution and each random kernel density of distribution for each road-crossing model. The overlap function ranges from 0, where the distributions do not overlap at all, to 1 where the distributions are identical. In our data, the empirical distributions had consistently higher values than the random distributions. Therefore, the less these two distributions overlapped, the better the crossing model performed. We averaged the amount of overlap across all 1000 random samples to obtain a single value.

In the third approach, we calculated the difference in means between each of the 1000 random samples and the empirical values for a road crossing model using a right-sided Mann Whitney U test. We ran the test with the 'wilcox.test' function in the stats R package (R Core Team 2019). We then averaged the Mann Whitney test statistic and p values across all 1000 runs for each road crossing model.

We then repeated the above procedure for each road class separately with the exception of class 1 roads. We omitted class 1 roads because of a low sample size (n = 48) and because 90% of the points came from a single bear. Sample sizes of the empirical and 1000 random samples for the other road classes were as follows: class 2, 578; class 3, 343; class 4, 1464; class 5, 1041; class 6, 1326.

Results

For all roads, regardless of road class, all the road crossing models performed well (Table 1). Out of the 1000 random samples, none had a higher mean value than mean of the empirical road crossing locations for any road-crossing model, resulting in a zero for all models. The proportion of distributional overlap between the random samples and the empirical data ranged from 0.706 to 0.834 and the results of the Mann Whitney U test indicated that all the road crossing models significantly outperformed the random samples (Table 1). However, the Circuitscape model had, on average, the least amount of overlap with the random samples and the lowest p-value. This was followed by the FLCP model, the resistant kernel model, the resource selection function, and then the IBMM.

The Circuitscape model was also the best performing model for each road class (Online Appendix S1). The next best performing model depended on the road class, but was generally one of the other connectivity models, the FLCP or resistant kernel models. With the exception of class 5 roads, the IBMM was the worst performing road-crossing model.

Table 1 Road crossing model performance. Percent overlap is the average percent overlap between each distribution of random road crossing values and the empirical road crossing values

Road crossing model	Proportion overlap	Test statistic	p value
Circuitscape	0.706	17,717,420	3.19e−86
FLCP[a]	0.717	16,586,049	1.44e−57
Resistant kernel	0.781	16,834,921	6.34e−51
RSF[b]	0.783	16,351,580	8.47e−31
IBMM[c]	0.834	16,041,988	6.87e−23

The test statistic and p value are the average of the Mann Whitney U tests between the empirical and random crossing values

[a]Factorial least-cost path

[b]Resource selection function

[c]Individual based movement model

Discussion

We evaluated the performance of five different road crossing models using data from female black bear movements in predicting an independent data set of crossings. We are the first to compare the performance of road crossing models for large mammals on multiple road types across a large study area. We found all the models performed well, but that the Circuitscape connectivity model outperformed the other models for each road class and for all road classes combined. Circuitscape can be considered a landscape-scale model—it models regional connectivity by incorporating landscape attributes not only at the roadway but also leading up to and away from it. The other two landscape-scale models, FLCPs and resistant kernels, also generally outperformed the more local-scale models. Though Cushman et al. (2014) did not evaluate Circuitscape, they also found that the FLCP and resistant kernel landscape-scale models outperformed the local-scale model. Therefore, analyzing road crossing locations within a wider landscape context may be preferable to other methods that focus solely on attributes adjacent to the roadway.

Circuitscape has been used to identify road crossing locations for grizzly bears (*Ursus arctos*; Proctor et al. 2015), pronghorn (*Antilocapra americana*; Poor et al. 2012), puma (*Puma concolor*; McClure et al. 2017), and to identify multispecies crossing locations (McRae et al. 2012; Meza-Joya et al. 2019). Due to the popularity of Circuitscape for modeling connectivity, easy-to-use software like LinkageMapper has been made available to run Circuitscape (McRae et al. 2014). Another advantage of Ciruitscape is that, compared with least-cost methods, it has been shown to be less sensitive to the data used for parameterizing resistance surfaces (Zeller et al. 2018a). Therefore, researchers may have a range of options for estimating resistance surfaces for use with Circuitscape, from occurrence data to tracking data, and may be able to use already-collected or archived data sources.

FLCPs and resistant kernels were the next top performing models and here our results agree with Cushman et al. (2014). The resource selection function based on crossing locations was the next best performing model followed by the IBMMs. A recent paper promoted the use of IBMMs for identifying road crossing locations (Quaglietta et al. 2019) due to advantages such as not relying on source and destination locations and simulating realistic movement over space and time. However, the authors did not compare the performance of their IBMMs, which were generated with the 'SiMRiv' R package (Quaglietta et al. 2019), against other road crossing models. Running IBMMs with different methods and software may produce different results and more research is needed to determine the efficacy of these different approaches and for using IBMMs in road crossing identification.

Our study was limited in that it only modeled road crossings for a single species using a single data type – GPS collar movement data. It would be useful to examine changes in the performance of these methods with resistance surfaces derived from different data types. Furthermore, we did not have vehicle collision data and therefore did not include a collision model among our methods. However, using wildlife vehicle collision data to identify crossing locations has been criticized since collision locations may have relatively low biological value for maintenance of populations and omit areas of safe passage for wildlife (Clevenger and Ford 2012; McClure and Ament 2014; Zimmermann Teixeira et al. 2017). Collision models are also a local-scale approach that may not perform as well as landscape-scale approaches. Nevertheless, the use of collision data could be informative if a site was both a high-value crossing location and a collision hotspot—indicating it is a site that may take priority for mitigation efforts (Zeller et al. 2018b). Our analysis could have been strengthened by using different numbers and configurations of source points for the connectivity surfaces; however, computational limitations prevented us from doing so. Lastly, due to our dataset, our analysis focused only on female bears, but including data from both sexes would provide results that could be extended to the entire population in our study area.

Some of the negative effects of roadways on wildlife can be mitigated with wildlife crossing structures. Crossing structures can provide passage and connect otherwise disjunct resource use areas or habitat patches and can increase human safety in areas with high rates of wildlife vehicle collisions. Given their cost and longevity on the landscape, it is important that siting and construction of these structures is done correctly, and our study provides information to help researchers and managers select an analytical method for identifying potential construction locations.

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