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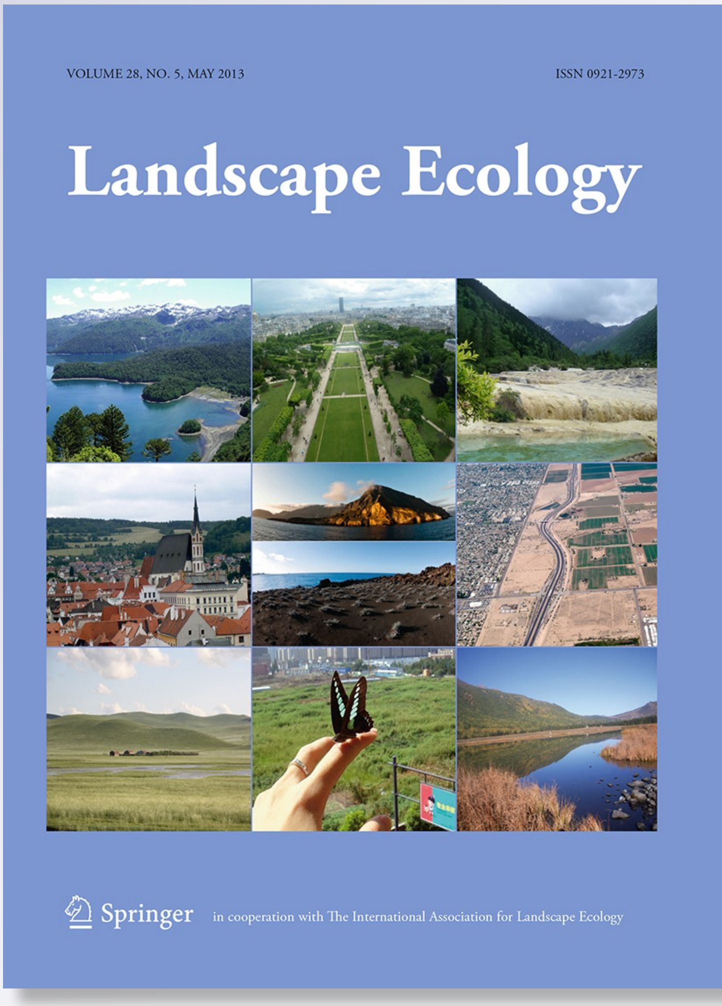
Landscape Ecology

ISSN 0921-2973
Volume 28
Number 5

Landscape Ecol (2013) 28:979-991
DOI 10.1007/s10980-013-9874-0



Springer

Landscape Ecol (2013) 28:979–991
DOI 10.1007/s10980-013-9874-0

RESEARCH ARTICLE

Modeling the indirect effects of road networks on the foraging activities of bats

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Received: 27 August 2011 / Accepted: 6 March 2013 / Published online: 17 March 2013

Abstract Negative impacts of road networks on wildlife are of global concern. While direct mortality of wildlife via roads has been well-documented, we know little about indirect effects of roads. Using a simulation model parameterized from empirical data, we explored how roads in proximity to maternity roosts influenced foraging activities of the endangered Indiana bat. First, we conducted manipulated landscape simulations to identify characteristics (such as traffic volume, foraging habitat availability, etc.) that influenced landscape permeability. We used a classification and regression tree procedure to assess which landscape and road-related variables, alone or in combination, influenced bat movement. We determined that roads did act as filters (>10 vehicles/5 min) or barriers (>200 vehicles/5 min) to movement. However, it is a combination of the proportion of foraging habitat accessible without crossing a road, and roost-to-road distance that dictated whether the barrier and filter effects of roads hindered the bats' foraging abilities. We then simulated movement patterns and foraging success of Indiana bats at 32 existing maternity roosts to identify conditions under which colonies currently persist. We established a foraging success threshold, above which Indiana bats currently persist. The value represents the time virtual bats spend in foraging habitat during the simulation period. Finally, simulations from these landscapes around known maternity roosts demonstrate that the road network and landscape configuration are critical to foraging success. This modeling approach and threshold value are beneficial to road developers and represent an invaluable tool in the ecological design of transportation infrastructures.

Keywords Accessible habitat · Anthropogenic disturbance · Disturbance-related behavior · Foraging success · Individual-based model · *Myotis sodalis* · Threshold

Electronic supplementary material The online version of this article (doi:10.1007/s10980-013-9874-0) contains supplementary material, which is available to authorized users.

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Introduction

Across five continents, negative impact of roads has been detailed for invertebrates (Yamada et al. 2009), amphibians (Elzanowski et al. 2009), reptiles (Steen et al. 2006), birds (Tremblay and St Clair 2009), and mammals (Kusak et al. 2009). Driven by public safety and economic repercussions, direct mortality of wildlife due to wildlife-vehicle-collisions has been well documented (Grilo et al. 2009; van Langevelde et al. 2009). Such studies have focused on (1) determining which species or groups of individuals are most vulnerable to road-related mortality (Litvaitis and Tash 2008) and (2) preventing or encouraging safe passage of wildlife across the road network (Ramp et al. 2005). However, less is known about the indirect effects of transportation corridors on wildlife (Rydell 1992; Balkenhol and Watts 2009). Beyond direct morality, roads can become barriers or filters to movement when animals perceive them as a risk. Deviations in the natural behavior of animals, such as avoidance, can lead to habitat loss, degradation, and fragmentation, as well as a reduction in habitat connectivity (Jaeger et al. 2005; Shepard et al. 2008). In turn, changes in landscape permeability can restrict movement, and thus, alter the distribution and abundance of wildlife (Roedenbeck and Voser 2008), which can have cascading effects on community and ecosystem dynamics (Trombulak and Frissell 2000).

To address less obvious impacts of roads on wildlife, we need to understand and devise appropriate management (Woess et al. 2002). This is pertinent when species of concern are involved (Mech 1989; van der Ree 2006). Government agencies are required to demonstrate that actions (such as road construction) avoid or minimize negative impacts to such species prior to development (US Congress 2002). Furthermore, mitigation must adequately reduce any negative impacts proposed developments might have on a species of concern (Cain et al. 2003). Effective mitigation for road projects should therefore be based on (1) how animals respond to a road and/or its traffic (Clark et al. 2001), (2) specific characteristics that cause a response (e.g. road width, traffic volume, etc.; Mazerolle 2004), (3) level or type of response associated with each characteristic; alone or in combination (e.g. the distance from a vehicle an animal becomes alert; Andrews and Gibbons 2005; Jaeger et al. 2005) and (4) implications of these responses, such as fitness and reproductive consequences (St. Clair and Forrest 2009).

Several studies have explored one or more of these aspects, although, as Shepard et al. (2008) point out, few studies consider the cumulative implications of road-related disturbance on wildlife as the empirical studies required are often logistically complex. The application of simulation modeling is proving to be an effective way of reducing such logistical constraints (Jaeger et al. 2005; Finke et al. 2008). However, without appropriate empirical data, the insights generated from such simulations may be too broad. Mitigation then based on these insights may be ineffective and even detrimental. By combining a simulation modeling approach with empirical studies explicitly designed to parameterize the model, it is possible to improve the power of the simulations and still be more efficient than conventional empirical studies.

To explore this, we investigated the impact of road networks on the endangered Indiana bat (*Myotis sodalis*). Any form of anthropogenic disturbance in proximity to the maternity roosts and associated foraging habitat can have negative impacts, which must be addressed under the U.S. Endangered Species Act (Clawson 2002; USFWS 2007).

Using the aforementioned modeling approach, our objectives were to assess (1) whether roads influenced bat movement, (2) if any influence of roads affected the ability of bats to access critical foraging habitat (Kerth and Melber 2009), and (3) whether limited access to foraging habitat due to the presence of roads near a maternity roost rendered that roost unsuitable to bats (Duchamp and Swihart 2008; Hale et al. 2012). Thus in a series of simulation exercises, we first explored whether the presence of a road in proximity to a maternity roost restricted the movement and foraging success of the Indiana bat. We then simulated the foraging success of female Indiana bats at existing maternity roosts in Indiana, USA, to identify the range of conditions under which Indiana bat colonies currently persist. We discuss how such insights can inform road development decisions, how our approach can assist in the route planning process, and how such a model represents an essential tool in the ecological design of transportation infrastructures.

Materials and methods

Model overview

Simulation of Disturbance Activities (SODA) is an individual-based model designed specifically to simulate the movement patterns of wildlife individuals exposed to anthropogenic disturbance in a spatially explicit virtual environment (see Bennett et al. 2009, 2011). This environment can be built using GIS maps and a defined set of variables that characterize wildlife movement, anthropogenic activities and the responses (type and magnitude) of wildlife to those anthropogenic activities. The environment can represent an existing landscape, allowing the user to assess how permeable that landscape currently is for wildlife. Alternatively, the environment can be manipulated. By creating alternative conditions (hereafter referred to as scenarios), the user can explore the specific variables and/or features that influence wildlife movement and to what extent. In two separate simulation exercises, we use both approaches (manipulated and existing landscapes) to assess how roads may influence Indiana bat foraging activity. We used a manipulated landscape technique to first assess which characteristics of a road (i.e. speed, number of lanes and traffic volume), alone and in concert, restricted the movement and foraging success of Indiana bats. A total of 187 different scenarios were constructed and each was replicated five times using an alternative random number seed, resulting in a total of 935 simulation runs. We then used the existing landscape technique to explore the foraging success of female Indiana bats at 32 existing maternity roosts in Indiana, to identify the range of conditions under which Indiana bat colonies currently persist. Each of the 32 virtual landscapes was replicated five consecutive times using an alternative random number seed. A total of 160 simulation runs were conducted. Variables used to populate SODA for both simulation exercises are discussed below and given in Table 1. Figure 1 provides a flow diagram delineating how these two simulation processes inform each other. Please refer to Bennett et al. (2009) for a full ODD (Overview, Design concepts, and Details) protocol regarding SODA.

Manipulated landscape simulations

Virtual environment

Three GIS map layers were generated for each scenario. The first layer delineated foraging habitat. Extensive radio-telemetry studies indicate that Indiana bats' forage no further than 10 km from their roosts (Sparks et al. 2005b). We therefore based the extent of the habitat map layer on this maximum foraging range. To determine whether there was a correlation between foraging habitat availability and the implications of road avoidance on bats' foraging success, we created a series of alternate habitat map layers. For this exercise, we identified 30 potential locations within the state of Indiana which were within the Indiana bat's known range and contained large mature trees which we assumed indicated the presence of available roosting habitat (taken from the 2010 Indiana big tree register). From these sites, we systematically selected 11 locations where the proportion of suitable foraging habitat for Indiana bats varied at approximately 5 % increments from a low of 5 % foraging habitat to 56 %. This range represented the variation of available foraging habitat typically recorded within the Indiana bat's current range in Indiana (Clawson 2002; Whitaker and Sparks 2008). We used ArcGIS to clip an area of habitat within a 10 km buffer of a roost site from land cover maps provided by the Indiana GIS Atlas (http://inmap.indiana.edu). For each of the 11 habitat layers, foraging habitat was identified as mixed and hardwood woodlands, wooded wetlands and riparian habitat typically used by Indiana bats in Indiana (Menzel et al. 2005; Sparks et al. 2005a), while all other cover types were deemed non-foraging habitat.

A road layer was also required to generate a scenario. For manipulated landscapes we created a hypothetical road that extended across the habitat map layer (i.e. ca. 20 km). To explore whether the orientation of the road affected the foraging success of the bats, we created four alternative road map layers which varied the cardinal position of the road (north/south, east/west, northeast/southwest and northwest/southeast). This enabled us to assess how the proportion of available foraging habitat on the roost-side and opposite side of the road from the roost affected the movement dynamics of the bats. In addition, as a control, we created a road layer without a road.

The final map layer needed to build a scenario was a roost layer. Using Hawth's Analysis Tools for ArcGIS (Beyer 2004) we randomly generated a hypothetical primary maternity roost within a 2 km radius of the center of each habitat layer (Britzke et al. 2003; Whitaker and Sparks 2008).

Road-related variables

To assess which characteristics of a road influenced bat movement, such as number of lanes (Rico et al. 2007), traffic volume (van Langevelde and Jaarsma

Table 1 Variables used to parameterise 'Simulation of Disturbance Activities' model to explore the implications of roads and road networks on Indiana bats at Indiana, USA

Temporal scales		
Length of simulation e.g., maternity period	30 days	
User specified timestep length	5 min	
Spatial scale		
User specified unit	Meters	
Environmental variables		
Habitat patches		
Type	(a) foraging	
	(b) non-foraging	
Location	Varies between each habitat map layer (see Appendix A in Supplementary materials)	
Size	Varies between each habitat map layer (see Appendix A in Supplementary materials)	
Paths		
Manipulated: four road orientations		
(a) North/South		
(b) East/West		
(c) Northeast/Southwest		
(d) Northwest/Southeast		
(e) No road present (control)		
Existing: road network		
Represents the existing road network around each primary maternity roost.		
Road-related variables		
Class		
(1) County road (2 lanes)		
(2) State road (2 lanes)		
(3) State road (4 lanes)		
(4) Interstate (4 lanes)		
Speed		
Manipulated		
(1) 7,000 m/TS		
(2) 7,000 m/TS		
(3) 7,000 m/TS		
(4) 9,000 m/TS		
Existing		
Corresponds to existing road network. (data from INDOT)		
Traffic volume		
Manipulated		
(1) 1.5 vehicles/lane/TS		
(2) 15.5 vehicles/lane/TS		
(3) 52 vehicles/lane/TS		
(4) 17.5 vehicles/lane/TS		
Existing		
Corresponds to existing road network (data from INDOT)		
Wildlife-related variables		
Number of individuals	5	
Behavioral modes	Flight in foraging habitat	Flight in non-foraging habitat
Speed	800 m/TS	2,000 m/TS
Tortuosity	0.24	0.98
Foraging range		
Minimum	500 m	
Maximum	10,000 m	
Behavioral responses to disturbance		
Flight initiation distance	10 m	

2004) and speed (Andrews and Gibbons 2005), we created four road-related variables. These corresponded to the four primary road classes common in the Indiana road network [data provided by the Indiana Department of Transportation (INDOT) in the Indiana GIS Atlas], including, (1) county roads and (2) state roads, both comprising two lanes and a 55 mph (89 kph) speed limit, (3) state roads with four lanes and a 55 mph (89 kph) speed limit and (4) interstates comprising four lanes with a 70 mph (123 kph) speed limit. We also applied the state-wide average traffic volumes associated with each road class (provided by INDOT) to each of our four road-related variables (Table 1). We thereby created four different virtual roads with the specified number of virtual vehicles moving along them, which were incorporated in separate scenarios.

Wildlife-related variables

The variables described in this section define the wildlife individuals' natural behavior, movement patterns and responses to human activities. An extensive long-term study conducted at Indianapolis airport in Indiana provided a unique opportunity to effectively populate this parameter space (see Sparks et al. 2005a; Whitaker and Sparks 2008).

From 48 radio-tracked bats over 198 days, we determined that Indiana bats forage on average at speeds of 0.08 km/min and commute at an average of

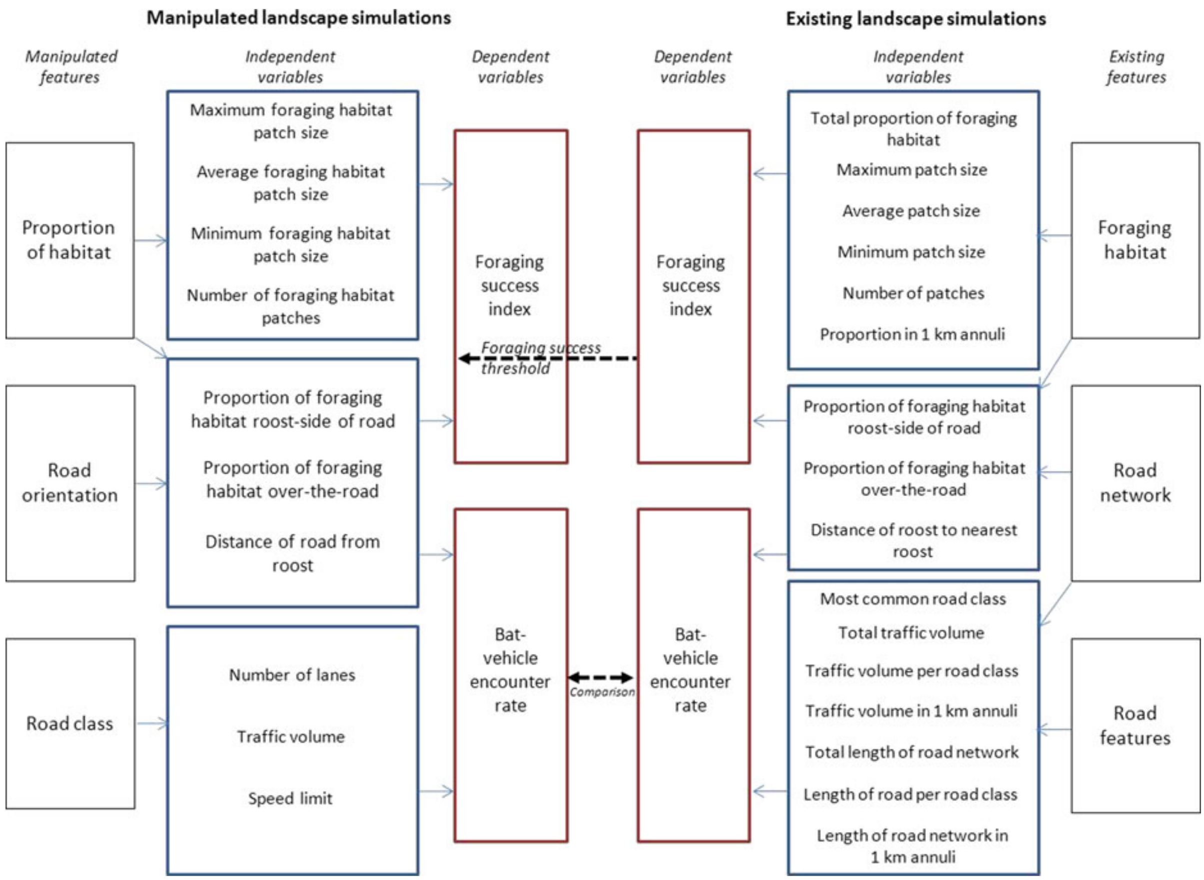

Fig. 1 Flow diagram delineating the two simulation modeling exercises (manipulated and existing) conducted in a study to explore the impact of roads on the foraging abilities of Indiana bats. The features used to test a series of alternative scenarios are provided, along with independent variables that define each scenario simulated and dependent variables generated from each simulation. The foraging success threshold represented the minimum time bats spend in foraging habitat in existing landscape simulations

0.26 km/min. These speeds appear to be comparable to those recorded for similar sized bat species (Hayward and Davis 1964; Kennedy and Best 1972; Zhang et al. 2007). We also calculated the tortuosity (the mean vector length of successive turning angles) of tracked bats using techniques described in Batschelet (1965). Thus commuting and foraging bats were estimated to have a tortuosity of 0.98 and 0.24, respectively. In each scenario built, we applied foraging flight variables to virtual bats in foraging habitat and commuting flight variables in non-foraging habitat (Table 1).

From targeted empirical studies, we know that foraging and commuting bats exhibit avoidance responses to vehicles travelling along roads (Schaub et al. 2008; Kerth and Melber 2009).We parameterized the responses of virtual bats to the virtual vehicles on roads using empirical data from behavioral studies that specifically investigated the responses of bats to vehicles on roads (Zurcher et al. 2010). These surveys revealed that on average bats within 10 m of a vehicle would turn around and fly back down their commuting path. We used this value to represent the flight initiation distance of virtual bats (Blumstein 2003).

Each simulation was run for 30 days representing the period of time females had dependent young in maternity roosts (Guthrie 1933; Whitaker and Sparks 2008). For each simulated day, the movement dynamics of five virtual bats were measured during the 3 h primary foraging period from 9.00 pm to 12.00 am via a series of timesteps (see Sparks et al. 2005a; Whitaker and Sparks 2008). Timesteps were set at 5 min intervals, and at the end of an interval [therefore one timestep (TS)] the location of each bat was recorded and whether the bat had responded to a vehicle.

From our simulation outputs, two dependent variables were produced. These included (1) bat-vehicle encounter rate (number of times a bat responded to a vehicle) and (2) an index of foraging success. We define 'foraging success' as the ability of a bat to access suitable foraging habitat. The index represented the number of timesteps virtual bats spent in foraging habitat.

Existing landscape simulations

For this exercise, each of the 32 scenarios created represented the location of an existing maternity roost in Indiana (courtesy of Environmental Solutions and Innovations, Inc), surrounding landscape and road network. We used ArcGIS to clip an area of habitat within a 10 km buffer of each roost location from land cover maps provided by the Indiana GIS Atlas (http://inmap.indiana.edu). Thus 32 different habitat layers were produced. As with manipulated landscapes, foraging habitat was identified as mixed and hardwood woodlands, wooded wetlands and riparian habitat typically used by Indiana bats in Indiana (Menzel et al. 2005; Sparks et al. 2005a), while all other cover types were deemed non-foraging habitat.

Using ArcGIS, we also produced 32 road layers by extracting the existing road network within a 10 km buffer of each existing roost from GIS maps provided by INDOT. Among these layers, we characterized each road by its class (i.e. county road, state road with two lanes, state road with four lanes and interstate), speed designation, and traffic volume equivalent to the existing road network (provided by INDOT; Table 1). We used average volume of traffic between 9 pm and 12 pm (i.e. the primary foraging period). The number of virtual vehicles in each existing landscape simulation was therefore set to reflect the actual traffic volumes.

As the 32 habitats and road networks extracted were each centered around an existing roost, we created a single roost layer with a roost positioned in the center of the layer. Finally, all wildlife parameters and response variables were kept the same as the manipulated landscape simulations (Table 1). Thus the movement patterns of a total of 800 virtual bats were simulated (i.e. 5 bats × 160 simulations, where each simulation represents one replicated virtual landscape).

Simulation outputs again included (1) bat-vehicle encounter rate and (2) an index of foraging success. We took the latter to represent the range in which the Indiana bat currently persists and assumed that below the minimum recorded index (a foraging success threshold) bats would not be able to persist. We then compared this foraging success threshold to the foraging success indexes recorded in the manipulated landscape scenarios to determine which road characteristics restricted the foraging activities of bats below the threshold.

Analysis

The extent to which virtual foraging bats were affected by roads in each scenario was analyzed using a Classification and Regression Tree (CART) procedure (Vayssiéres et al. 2000; Swihart et al. 2007). CART analysis stratifies response variables (bat-vehicle encounter rate and foraging success index) against the landscape and road conditions imposed, produces a tree diagram, and reports the percentage of scenarios that occur within a set of conditions. In manipulated landscape simulations, we identified the independent predictors as road class, distance of the road from the roost, total proportion of foraging habitat, proportion of foraging habitat on the roost-side of the road, proportion of foraging habitat on the opposite side of the road from the roost, total number of foraging habitat patches, average foraging habitat patch size, and minimum and maximum patch size. Landscape metrics for each habitat layer are provided in Appendix Tables A1 and A2.

In existing landscape simulations, we used the same independent predictors to those in manipulated simulations, except for road type (see Appendix Table A3). Instead we included total traffic volume of the road network, traffic volume for each road class, total length of road network, and length of each road class within the road network. We identified the most common road type, traffic volume, proportion of foraging habitat and length of road network in a series of zones (annuli) in 1 km increments extending out 5 km from the roost site (the average distance foraged by Indiana bats; Sparks et al. 2005b). Zone 'A' represented the annuli from a 1 to 2 km radius around the roost, zone 'B' a 2 to 3 km radius annuli, zone 'C' a 3 to 4 km radius annuli and zone 'D' a 4 to 5 km radius annuli. A zone between 0 and 1 km was not included as telemetry surveys revealed that Indiana bats do not forage within a 1 km radius of their roost site during their primary foraging bout (Sparks et al. 2005a; Whitaker and Sparks 2008).

To optimally prune trees, we used receiver operating characteristic (ROC) curves and associated relative error value. The ROC provided an index that ranged between 0 and 1. The higher value the better a model was able to discriminate between the effects of the different predictor variables (Fielding and Bell 1997). The relative error value revealed relationships between classification errors and the number of nodes (i.e. tree size). It ranged from 0 to 1.0, where 0 indicated a perfect fit and 1 emphasized the model's inability to discriminate beyond chance. Finally, we incorporated a V-form cross validation in the CART analysis to validate the classification trees produced. For this, we used Cross Validation costs produced using 10 different 10 % subsets of our dataset to identify the 'minimum Cross Validation cost'. We then restricted the maximum tree size in the main CART analysis so that the relative cost of tree did not exceed the minimum Cross Validation cost.

Results

Manipulated landscape simulations

Bat-vehicle encounter rates for manipulated landscape simulations ranged from 0 to 15 encounters per bat across the simulation period (Fig. 2a). Virtual bats with encounter rates of 10 or more were not able to access foraging habitat on the opposite side of the road from the roost during the simulation (Fig. 2a). By stratifying response variables in CART, we found that bat-vehicle encounter rates were primarily influenced by road class (area under ROC curve = 0.53 with a relative error of 0.55; Fig. 3a). Road class represented an important overall variable in 100 % of the scenarios. Proportion of foraging habitat on the roost-side of the road represented the second most important variable in 25 % of scenarios, then foraging habitat on the opposite side of the road (13 %), distance of roost-to-road (10 %) and finally total proportion of foraging habitat (2 %).

The regression tree revealed significant difference in encounter rates between all four road classes (first and second split, left branch; Fig. 3a); county roads ($\bar{x} < 1$ encounter/simulation), 2-lane state roads ($\bar{x} = 2$ encounters/simulation), interstates ($\bar{x} = 4$ encounters/simulation) and 4-lane state roads ($\bar{x} > 4$ encounters/simulation). However, county roads were not significantly different from control scenarios ($\bar{x} < 1$ encounter/simulation). The regression tree also revealed that a combination of predictor variables influenced encounter rate in scenarios with 4-lane state roads. The closer the roost to a 4-lane state road the more vehicles bats encountered (third split) and this encounter rate significantly increased when the roost was <1 km from the road. In addition, encounter rates rose ($\bar{x} = 11$ encounters/simulation) when available foraging habitat on the roost-side of the road was lower (<13 km^2; fourth split). In contrast, when available roost-side foraging habitat was higher (>13 km^2) and foraging habitat on the opposite site of the road was lower (<10 km^2), encounter rates were higher than control scenarios, but on average these were lower than 2-lane state road scenarios ($\bar{x} = 1$ encounter/simulation). Finally, encounter rates significantly increased with a greater proportion of foraging habitat on the opposite site of the road (>10 km^2; $\bar{x} = 8$ encounters/simulation, fifth split).

Foraging success index for the manipulated landscape simulations ranged from 0 to 776 for each bat per simulation (Fig. 2c). By stratifying the response variables in CART, we found the proportion of foraging habitat on the roost-side of the road significantly influenced foraging success in 100 % of scenarios (area under ROC curve = 0.8 with a relative error of 0.4; Fig. 3b). The second most important variable was average foraging habitat patch size (85 %), then proportion of foraging habitat on the opposite side of the road to the roost (57 %), distance of roost-to-road (43 %) and number of foraging habitat patches (15 %). No other predictor variables could be discriminated beyond chance.

The regression tree revealed that when there was more roost-side foraging habitat, foraging success was significantly higher (>0.04 km^2; first split, left branch; Fig. 3b), unless the landscape was highly fragmented (second branch). In landscapes with smaller habitat patches (<34 m^2), foraging success was significantly lower ($\bar{x} = 29$ TS/simulation). Finally, foraging success was highest when there was less foraging habitat available on the opposite side of the road from the roost ($\leq$0.04 km^2; $\bar{x} = 674$ TS/simulation; third split).

In contrast, when roost-side habitat was lower ($\leq$0.04 km^2) foraging success was significantly lower overall (first split, right branch). However, foraging success was at its lowest when the roost was closest to the road ($\leq$0.2 km; $\bar{x} = 4$ TS/simulation; second

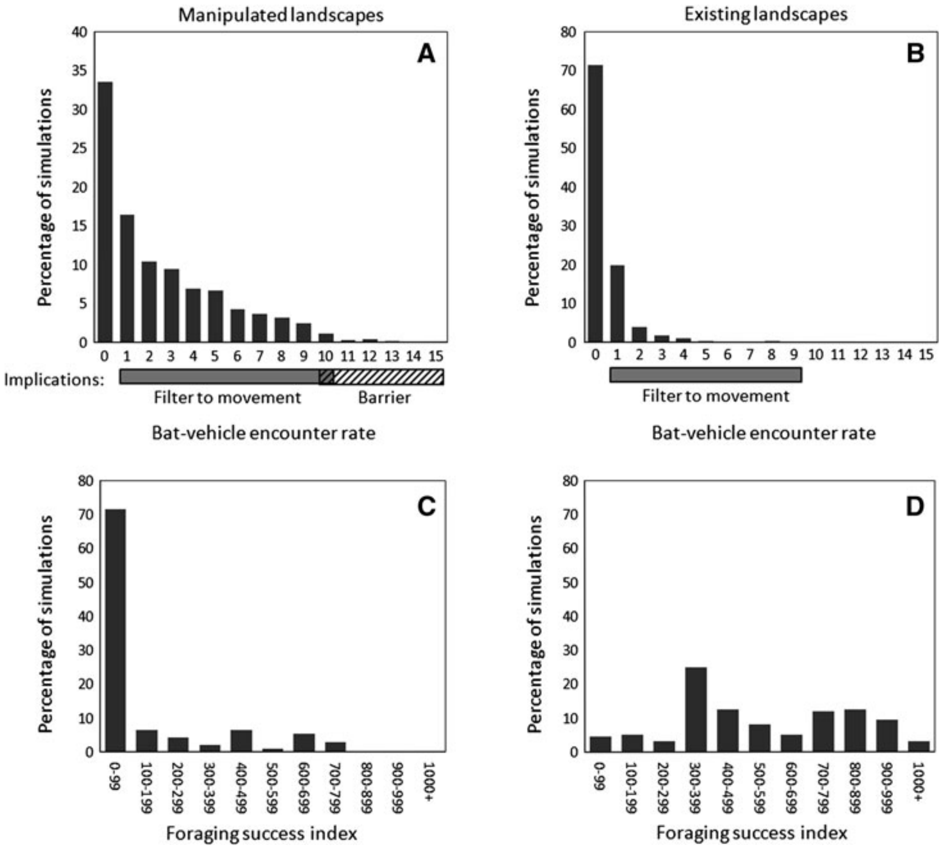

Fig. 2 Range of bat-vehicle encounter rates and foraging indexes generated from the two simulation exercises (manipulated and existing) conducted. Bar chart **a** shows the percentage of simulation runs associated with bat-vehicle encounter rates in manipulated landscape simulations, while **b** shows the rates for existing landscapes. A road becomes a filter to movement, when bat-vehicle encounters prevent bats from crossing a road. Roads then become a barrier to movement when bats are unable to cross any roads during the simulation period. Bar chart **c** presents the percentage of simulation runs that have foraging success index values that fall within intervals of 100, while **d** shows the indexes for existing landscape simulations

split). Habitat fragmentation also influenced foraging success. As the number of foraging habitat patches decreased (≤1,088; third split) and average habitat patch size increased (>34 m^2; fourth split), so did foraging success ($\bar{x}$ = 543 TS/simulation).

Existing landscape simulations

Bat-encounter rates for existing landscape simulations ranged from 0 to 9 encounters per bat across the simulation period (Fig. 2b). The maximum rate was two-thirds of the maximum recorded in manipulated landscapes. Furthermore, the majority of virtual bats (91 %) encountered a vehicle no more than once during a simulation run, 4 % encountered a vehicle twice and 3 % had four encounters. These encounter rates are equivalent to the lowest recorded rates in the manipulated landscapes. Encounter rates >4 occurred in one landscape in which the roost was situated in a tree-line 3 m from a 2-lane state road. The next shortest roost-to-road distance was approximately 50 m. We also noted that across all the existing landscapes, virtual bats were able to cross the majority of roads in the road network at least once during the simulation to successfully access foraging habitat on the other side (Fig. 2b).

The regression tree built in CART from bat-vehicle encounter rates in existing landscapes demonstrated that although the composition of each landscape was highly variable, encounter rates among existing landscapes were similar (area under ROC curve = 0.53 with an R squared value of 0.49; Fig. 4a). Roost-to-road distance represented the most important variable, occurring in 100 % of scenarios. Total length of 4-lane

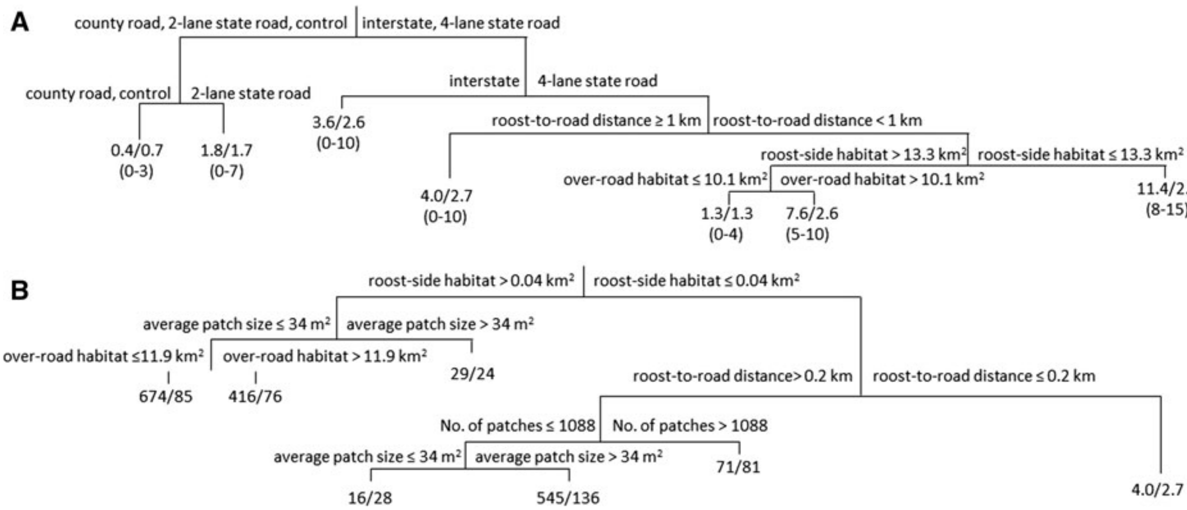

Fig. 3 Regression tree evaluating landscape and road characteristics on **a** the number of times bats encounter vehicles while moving across the landscape and **b** the time bats spent in foraging habitat in manipulated landscape simulations. Predictor variables defining a split are labeled at each branch split. Branch lengths are proportional to the number of scenarios represented. Below each terminal node the values represent (a) the average and (b) the standard deviation and (c) range of encounters in brackets (**a** only). County roads, 2-lane state roads, 4-lane state roads and interstates are defined road classes. Roost-side habitat and over-road habitat refer to the proportion of foraging habitat on the roost-side of the road and the opposite side of the road from the roost respectively

state roads in the road network (61 %) was the second most important variable, then major road class in zone 'B' (6 %), and finally total proportion of foraging habitat (2 %).

The regression tree revealed that bat-vehicle encounter rate was significantly higher when roosts were closer to roads (<27 m; $\bar{x} = 4$ TS/simulation; first split; Fig. 4a). Structure and composition of the road network was then shown to influence the movement of virtual bats. Encounter rates were significantly higher when more 4-lane state roads comprised the road network (>35 km; $\bar{x} = 3$ TS/simulation; second split). In contrast, when county roads were the major road class specifically in zone 'B', encounter rates were significantly lower ($\bar{x} < 1$ TS/simulation; third split). However, encounter rates generated when other road classes dominated zone 'B' were kept to a minimum when the total proportion of foraging habitat was higher (>50 m^2; $\bar{x} < 1$ TS/simulation; fourth split).

Foraging success for existing landscape simulations ranged from 44 to 2,700 for each bat per simulation (Fig. 2d). In comparison to manipulated landscape simulations, in which 83 % of these values were under 300, 85 % were above 300 in existing landscapes (Fig. 2c, d). We noted that among the three existing landscapes with foraging success values <300, roost sites were all within riparian zones and these habitat strips comprised the majority of available foraging habitat. In contrast, the one existing landscape to produce foraging success values nearing 2,700 (approximately 50 % greater than all other simulations), was located in a national forest and thus consisted almost entirely of foraging habitat.

In CART analysis, we found foraging success was primarily influenced by the proportion of foraging habitat in zone 'A', occurring in 100 % of the scenarios (area under ROC curve = 0.93 with a relative error value of 0.1). The total length of 2-lane state roads in the road network (33 %) was the second most important variable and finally proportion of foraging habitat in zone 'B' (7 %).

The regression tree revealed that as the proportion of foraging habitat in zone 'A' decreased so did foraging success (<45 m^2; $\bar{x} = 194$ TS/simulation; first split, left branch; Fig. 4b). The highest foraging success index was recorded among scenarios with the greatest proportion of foraging habitat in zone 'A' and a less extensive road network ($\bar{x} = 2{,}089$ TS/simulation; fourth split; second split). In contrast, the foraging success index where lowest among landscapes with more developed road networks,

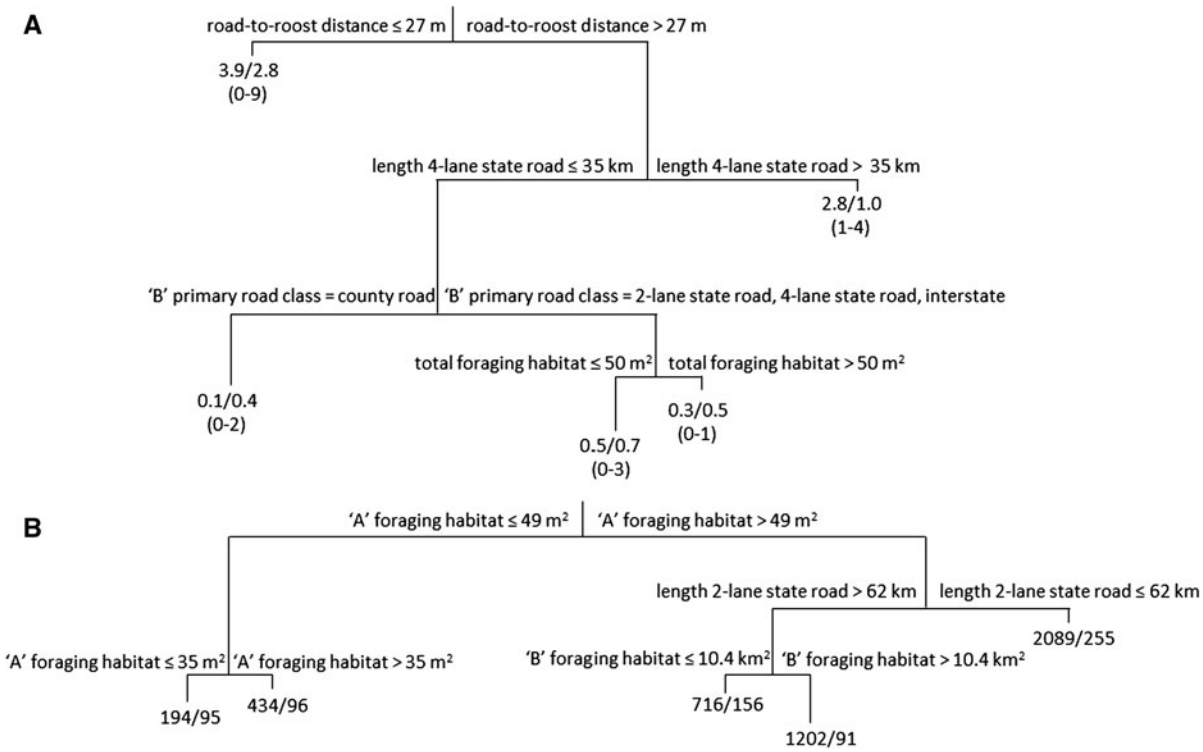

Fig. 4 Regression tree evaluating landscape and road variables that influence **a** the number of times bats encounter vehicles while moving across the landscape and **b** the time bats spent in foraging habitat in existing landscape simulations. Predictor variables defining a split are labeled at each branch split. Branch lengths are proportional to the number of scenarios represented. Below each terminal node the values represent (a) the average, (b) the standard deviation, and (c) range of encounters in brackets (**a** only). Roost-side habitat and over-road habitat refer to the proportion of foraging habitat on the roost-side of the road and the opposite side of the road from the roost respectively. Variables A to D refer to annuli that extend from the roost at intervals of 1 km

particularly those with >62 km of 2-lane state roads. However, under these same conditions the index increased when available foraging habitat increased in zone 'B' (>104 m^2; $\bar{x} = 1{,}202$ TS/simulation; fourth split; third split).

Discussion

From our simulation exercises parameterized by empirical data, we have established that roads can change the permeability of the landscape for foraging Indiana bats in maternity roosts in Indiana. We found this permeability to be governed primarily by road class, or more specifically the characteristics associated with road class, such as traffic volume and number of lanes. As these two characteristics increased so did the incidence of bats exhibiting road-related avoidance behaviors. Roads with very few vehicles on them and only two lanes, such as county roads (<10 vehicles/timestep), had little or no effect on bat movement. At the other extreme, 4-lane state roads (>200 vehicles/timestep), commonly associated with urban areas, had such high levels of traffic that bats would encounter vehicles consistently while attempting to cross the road. Subsequently, these bats were unable to access critical foraging habitat and in 37 % of simulations (17 of 44 scenarios), the road restricted bats from accessing foraging habitat for the entire simulation period. In these instances, the road became a barrier to movement (Fig. 2a). Among scenarios in which bats crossed a road at least once during the simulation period, these roads (to varying degrees) acted as filters to movement.

However, it is the quality, quantity and configuration of available foraging opportunities that dictate whether the barrier and filter effects of roads impact the bats' foraging success. Among the manipulated landscape simulations, foraging success was driven by the amount of suitable habitat that bats could access without crossing a road. We observed a similar trend among our existing landscape simulations. For example, in all existing landscapes there was at least 5 km^2 of foraging habitat available to bats without crossing a road. Furthermore, both manipulated and existing landscape simulations showed that the closer a roost was to a road the greater the impact on foraging success. For example, in 30 of the 32 existing landscapes, there were no roads within 2 km of an existing roost. This suggests that roost sites close to roads are generally not suitable for Indiana bats.

Our modeling approach also demonstrated that we cannot simply consider the implications of a single road on the foraging dynamics of bats. We must take into account the cumulative impact of the entire road network within the bats' foraging range. In the existing landscape simulations, those aspects of the road network associated with urban developments, such as high densities of 4-lane state roads and interstates with high traffic volumes, had the greatest influence on the foraging success of virtual bats. In contrast, road networks predominantly comprising county roads had the least impact. Between these two extremes, it was the overall configuration of the road network and foraging habitat availability that dictated landscape permeability, or more specifically, habitat accessibility. A study on anurans by Eigenbrod et al. (2008) established that the amount of accessible habitat (defined as habitat that could be reached from, for example, a roost site without crossing a road) best predicted the effects of habitat loss and roads among those species for which roads were major barriers to movement. Our study takes this concept one step further by identifying that the frequency at which animals can access habitat (i.e. the filter effects of roads) can also have deleterious implications.

As habitat accessibility is therefore associated with a diverse site-specific set of interacting conditions, we cannot provide universal criteria for road developers to follow. However, by using SODA during the planning process, we can evaluate the potential impact of a proposed road development on the permeability of the landscape for bats and by manipulating route design, we can assess whether alternative route options are more suitable.

From the existing landscape simulations, we have established a range of foraging conditions (foraging success index) in which the Indiana bat currently persists. Below the minimum recorded index (a foraging success threshold), we can assume that the foraging abilities of bats would be too restricted for them to persist. Thus any proposed developments that produce foraging success indexes below this threshold have the potential to negatively impact an existing Indiana bat roost.

In all but three existing landscape simulations, we established that Indiana bats at existing roosts in Indiana had index values above 300. The three landscapes below 300 were along riparian corridors. As parameterized in this study, SODA forced virtual bats to travel from their roost site in random directions in search of suitable foraging habitat, rather than concentrating their foraging efforts along these riparian corridors as actual bats would (Sierro 1999; Duchamp et al. 2004). Subsequently, the foraging success indexes simulated for these riparian landscapes are likely to be underestimates. However, this does not mean that SODA cannot be used to simulate roosts in this type of habitat. It is possible to populate the model parameter space with wildlife movement variables that are specific to certain habitat types, such as riparian corridors and edges of dense forests. Our modeling exercise simply highlights that roosts in these types of habitat should be parameterised with such site-specific variables.

By removing the three outliers (riparian landscapes) from the data, the minimum foraging success threshold reached within our 30 day simulation period came to 313. Foraging success values below this threshold therefore represent unsuitable foraging conditions. Note that 153 of the 178 scenarios tested in the manipulated landscape simulations had foraging success indexes below 313. Based on our findings this may be because all the roosts in these scenarios were within 2 km of the road and as a result >50 % of the landscape on the roost side of the road needed to be foraging habitat.

We must stress that as it stands, the threshold is a broad approximation of minimum requirements of Indiana bats in maternity roosts associated with an Indiana landscape. Caution should therefore be used when applying the model and threshold. Restricting the foraging ability of bats to a minimum does not guarantee that a roost site will persist. There will be other factors that impact foraging success, such as foraging habitat quality, or more specifically the quality, diversity and availability of insect prey

(Fukui et al. 2006). There are also other ecological factors that can influence site suitability, including colony size and additional foraging preferences (such as woodland edges). Incorporating these factors would certainly develop the model further for real-world application. SODA can also be adapted for other landscapes in which Indiana bats or other species persist. In such instances, a virtual environment equivalent to existing landscape and transportation infrastructure would need to be constructed and parameters modified to reflect species-specific habitat preferences and foraging dynamics.

Nevertheless, in its current form, SODA has demonstrated that roads can act as barriers and filters to the movement of Indiana bats and road networks do reduce landscape permeability. Incorporating a simulation modeling approach into project design is of great value to landscape architects and planners. As a decision-making tool, simulation models can be used strategically to explore proposed developments and associated mitigation in a virtual environment without risk to the target species (Dunkin et al. 2009). Essentially, they can address complex and uncertain circumstances that would be difficult to replicate and test empirically. Thus, we conceive that this approach will have inherent advantages in the ecological design of the transportation infrastructure (Peterson et al. 2003; Hostetler and Drake 2009).

Acknowledgments Thanks to Arthur Zurcher and Molly Maguire at Indiana State University for collecting data on the responses of bats to road traffic; Dr. Virgil Brack and the team at Environmental Solutions and Innovations, Inc for providing Indiana bat maternity roost locations; Andrew King (USFWS), Dr. Joe Duchamp, Dr. Inaki Rodriguez Prieto and Diana Raper for providing feedback on manuscript drafts and Ben Pauli for providing a movement analysis program.

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