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MULTI-SCALE HABITAT-RESISTANCE MODELS FOR PREDICTING ROAD MORTALITY "HOTSPOTS" FOR TURTLES AND AMPHIBIANS

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***Abstract.*—Roads represent a significant threat to biodiversity. If transportation managers are to reduce the effects of roads, they need large-scale data identifying where species are likely to occur ('hotspots'). In this project, ecologists and road-managers developed an approach to identify hotspots for 10 species of amphibians and reptiles on roads. We used the available literature to identify suitable aquatic habitats and to assign resistance values to terrestrial habitats, and then developed spatially explicit models that integrated habitat data at both the local and regional population level. We employed two approaches for prioritizing mitigation efforts, first by overlaying traffic intensity over predicted occurrences and second by selecting long stretches of road with continuously high predicted occurrences. We evaluated models using field data derived from road surveys. Our models showed clear differences in the predicted occurrence among habitat specialists and generalists, and between life-history stages. Wide-ranging habitat generalists were predicted to have at least some probability of occurrence on most roads. Conversely, species with limited movement ranges and specific aquatic and terrestrial habitat had more limited distributions. Validation data indicated that the models were effective for predicting occurrence of species with specialized habitat requirements, but that predictions for wide-ranging generalists were less accurate. These data also demonstrated that focusing on stretches of continuous hotspot and traffic intensity were effective parameters when identifying areas particularly in need of mitigation. Our modeling approach is an effective tool for identifying road-hotspots for herpetofaunal species with specific habitat requirements, allowing predictions to be made over large spatial extents, and with readily available data sources.**

Key Words.—cost-distance; occurrence modeling; road ecology; road mitigation; Spotted Salamander; Wood Frog

INTRODUCTION

Roads are vital to economic activity, but reduce the viability of animal populations and degrade surrounding ecosystems (Forman and Alexander 1998; Trombulak and Frissell 2000). To minimize the effects of roads on biodiversity, we need to be able to effectively integrate ecological knowledge into transportation planning. Transportation management agencies are where this integration occurs, but these organizations typically have limited resources and primary mandates focused on road construction and maintenance. For transportation planning agencies to be able to efficiently use resources in reducing the effects of roads on biodiversity, they need to have access to clear information to help them prioritize where to focus their efforts. For management agencies operating at large scales (e.g., state or national agencies), the information provided to them must also be broad-scale if it is to be of value for making decisions regarding resource allocation.

Herpetofauna represent an important target for modeling patterns of occurrence on roads as they are particularly vulnerable to road-effects (Fahrig et al. 1995; Gibbs and Shriver 2002). Many species undertake annual migrations between aquatic and terrestrial habitat and disperse among breeding sites, increasing the probability that an individual will encounter roads (Carr and Fahrig 2001). When crossing roads, the slow rates of locomotion of many species make them extremely susceptible to road-mortality (Ashley and Robinson 1996; Hels and Buchwald 2001). High road-mortality of herpetofauna during terrestrial movement is of particular concern as mortality rates of juveniles and adults are altered from those typically experienced by these life-history stages (Gibbs and Shriver 2002; Aresco 2005). Changes in survival of these stages, which typically have high survival relative to earlier life-history stages, are likely to drive overall population dynamics (Biek et al. 2002; Vonesh and De la Cruz 2002).

Approaches to predicting the distribution of organisms in relation to roads can be divided into two categories. Phenomenistic (or correlative) models relate data gathered in the field (e.g., road mortality locations) to potential explanatory factors. These models offer a valuable tool for predicting patterns in the same ecological system, but are likely to be less accurate when applied to novel circumstances (Guisan and Zimmermann 2000). Mechanistic models begin with a delineation of the relationships between organisms and their environment, using this information to predict patterns of distribution. Mechanistic models are more adaptable to changing conditions in habitat, and thus offer a valuable tool for use across wider spatial extents. Conversely, because they are unlikely to include every factor dictating the distribution of organisms, they may be less accurate than phenomenistic models at a local level. Furthermore, the data on which mechanistic models rely are often scarce.

In this paper, we present a novel adaptation of spatial modeling that combines mechanistic/computational and knowledge-based approaches to predict the occurrence of herpetofauna on roads. By knowledge-based, we mean studies that provide data relating to the fundamental relationships between our focal species and their environment (as compared with phenomenistic models that are not based on these fundamental relationships). Habitat suitability is incorporated in our models using resistance surfaces/friction modeling in Geographic Information Systems (GIS; Ricketts 2001). With this technique, each habitat type in a landscape is assigned a “friction” (or resistance) value based on the willingness of an animal to cross the habitat and the reduction in survival of the individual (Ray et al. 2002; Joly et al. 2003). These friction values are adapted for different species and life-history stages based on known movement ecology and behavior of each species. This hybrid approach weights the friction cost to movement by the Euclidean distance from the source of animals (e.g., a breeding pond), making it is more costly to move farther and through less suitable habitat, with the caveat that it assumes randomness in movement behavior, which is rarely true.

Our study goal was to use habitat-resistance modeling to identify herpetofaunal mortality hotspots on roads, with a particular focus on providing large-scale predictions for use in regional transportation planning. The spatial focus for our application was to predict mortality hotspots across a large part of New York State in the United States. Our objectives were: (1) to develop maps of predicted herpetofaunal occurrence in relation to roads at local and regional scales for species with a variety of life-history traits; (2) to develop means of prioritizing potential mortality hotspots for mitigation efforts; and (3) to develop a strong working collaboration with transportation management agencies, by building the capacity of both research scientists and managers, and ensuring that we provide the most useful and relevant information for mitigation efforts.

METHODS

Study area.—We developed models for 12 counties in New York State, USA: Cayuga, Cortland, Chenango, Onondaga, Madison, Oswego, Oneida, Delaware, Otsego, Schoharie, Albany, and Greene (Fig. 1). This approximately 67,450 km^2 area has a network of public

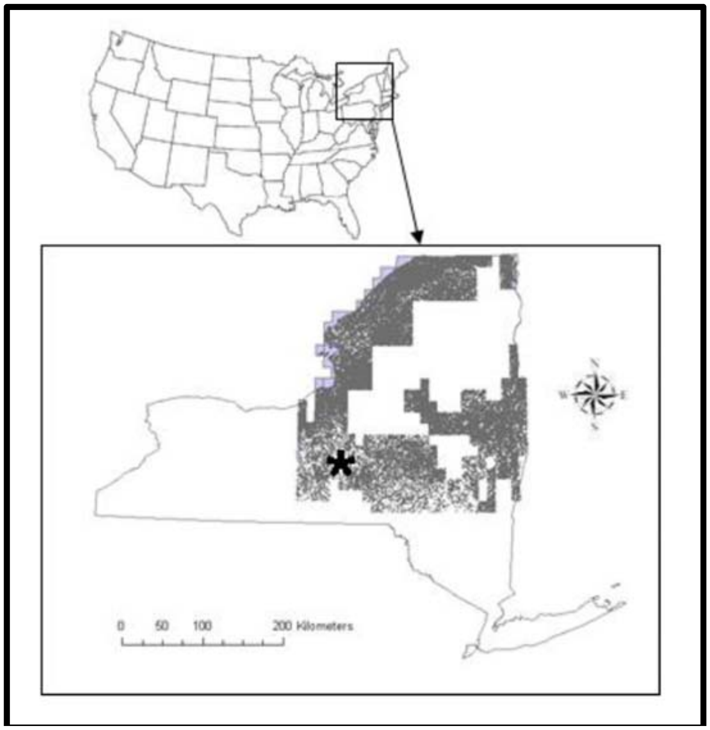


FIGURE 1. Location of the National Wetlands Inventory (NWI) data (shown in gray) used as the basis for assessing hotspots of herpetofaunal road-mortality for 10 species in New York State. The locations from which model validation data were gathered are indicated by the asterisk.

roads ca. 85,303 km in length, and encompasses gradient of urbanization and land cover (e.g., Syracuse and Albany metropolitan and surrounding rural areas) as well as diverse topography and ecosystem types (e.g., the alluvial plains south of Lake Ontario, ridge and valley systems of the northern terminus of the Appalachian Mountains, and the steep glacial valleys of the Adirondack Mountains). We chose this heterogeneous region specifically because it encompassed landscape variation broadly typical of the eastern United States and Canada and to increase the geographical applicability of the research. Areas within these counties were excluded if no National Wetlands Inventory (NWI) data were available.

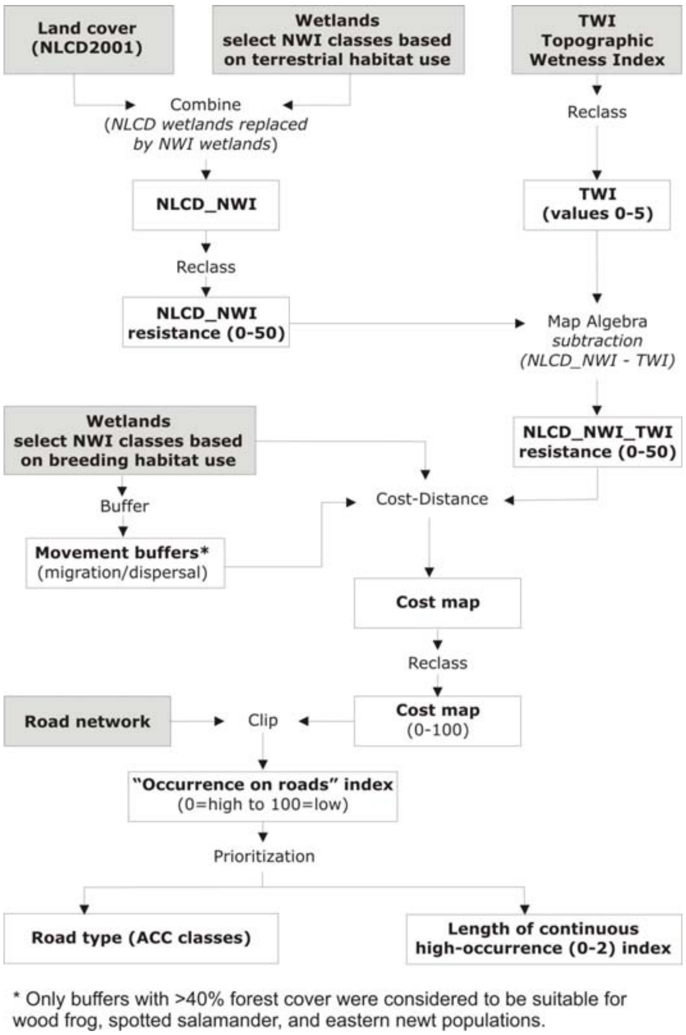
***Study species*.**—We chose the 10 study species based on incorporating a range of life-history traits, availability of literature data, and targeting species of specific conservation concern in New York State. The amphibian species included Green Frogs (*Lithobates clamitans*), Northern Leopard Frogs (*L. pipiens*), Wood Frogs (*L. sylvaticus*), American Toads (*Anaxyrus americanus*), Spotted Salamanders (*Ambystoma maculatum*), and Red-spotted Newts (*Notophthalmus viridescens*). The reptile species included Common Snapping Turtles (*Chelydra serpentina*), Eastern Painted Turtles (*Chrysemys picta picta*), Spotted Turtles (*Clemmys guttata*), and Wood Turtles (*Glyptemys insculpta*).

***Model development*.**—We used a suite of GIS datasets in our road-mortality hotspot models (details provided in Appendix A). All layers were set to a common coordinate system (Universal Transverse Mercator, Zone 18 North), and datum (North American Datum 1983). We rescaled data to a resolution of 30 m where necessary. We performed all analyses using ArcGIS 9.0 (ESRI, Redlands, California, USA). We used a seven-step process to create the friction models for herpetofauna (Fig. 2): (1) we initially determined potential suitable aquatic habitat for each species from which to initiate calculation of cumulative cost to movement; (2) we then assessed which of these aquatic sites has sufficient forest cover required by some amphibian species for population persistence and removed aquatic sites that did not meet these requirements; (3) we assigned literature-derived friction costs to each land-cover type in our study area for each species (and for migrating adults and dispersing juveniles separately in the case of amphibians); (4) we then created circular movement buffers around each of the potential aquatic sites for each species representing the maximum known movement distance (separated into migration and dispersal for amphibians); (5) we used the "Cost-Distance" procedure to calculate the cumulative cost-distance within these buffers; (6) we rescaled these cumulative costs to the probability of a species being present; and (7) we extracted the probability of presence on each of the roads in the existing road network.

We assigned the aquatic habitats for each of the species (the population centers from which animals moved and hence the starting point for calculation of resistance surfaces) based on literature data (Table 1). We grouped NWI wetland classes based on system and subsystem categories within Cowardin's wetland classification index (Cowardin et al. 1979). For the initial land-cover map (for which resistance values were assigned), we combined the National Land Cover Database 2001 (Homer et al. 2007) and NWI, replacing NLCD wetland categories with the more precise NWI classifications. Persistence of populations of three of our focal amphibian species (*L. sylvaticus*, *A. maculatum*, and *N. viridescens*) have been shown to be dependent on forest cover (Guerry and Hunter 2002; Homan et al. 2004; Herrmann et al. 2005). Estimates of the amount of forest cover needed by these species vary between

TABLE 1. Freshwater wetland types included in friction models (source: National Wetlands Inventory [NWI], Cowardin et al. 1979). Wetlands considered as focal habitats are indicated with an X. Study species are Green Frog (grfr), Northern Leopard Frog (nlfr), Wood Frog (wofr), American Toad (amto), Spotted Salamander (spsa), Red-spotted Newt (rsne), Painted Turtle (patu), Snapping Turtle (sntu), Spotted Turtle (sptu), and Wood Turtle (wotu).

				Study species nexus									
System	Subsystem	Class(es)	NWI label	wofr	grfr	nlfr	amto	spsa	rsne	sntu	sptu	patu	wotu
Lacustrine	Limnetic	(UB, AB, OW)	L1							X			
	Littoral	bed (UB, AB, EM, FL, OW)	L2 bed		X	X	X		X	X		X	
Riverine	Lower perennial	bed (AB, EM, OW, UB, RB)	R2 bed		X	X	X		X	X	X	X	X
Palustrine		Unconsolidated bottom (UB)	PUB		X	X	X		X	X		X	
		Aquatic bed (AB)	PAB		X	X	X		X	X	X	X	
		Emergent (EM)	PEM	X	X	X	X	X	X	X	X	X	X
		Scrub-shrub (SS)	PSS	X	X	X	X	X	X	X	X	X	X
		Forested (FO)	PFO	X	X	X	X	X	X	X	X	X	X
		Open water (OW)	POW	X	X	X	X	X	X	X	X	X	X



* Only buffers with >40% forest cover were considered to be suitable for wood frog, spotted salamander, and eastern newt populations.

FIGURE 2. Stages in development of the road-mortality hotspot models for 10 species of herpetofauna in New York State, USA.

studies, regions, and species. We set a minimum threshold for site occupancy by these species as 40% forest cover (deciduous, coniferous, and mixed forest, excluding the shrub/scrub category in the NLCD 2001 [Homer et al. 2007]) within the known migration or dispersal distance from the aquatic site. Although this figure does not take into consideration landscape configuration, it represents a best estimate based on the results from these previous studies. We removed any wetlands for the three focal species listed above that fell below this threshold from subsequent models. To assign friction values, we divided the available literature data into two groups: research that generally describes habitat suitability for study species (Appendix B) and research that specifically quantified the proportion of individuals using certain habitats when faced with a range of choices (Appendix C). The latter research affords a more accurate estimation of relative habitat resistance values, but was not available for all species or habitats. Additionally, two studies have previously reported friction values for amphibians: Popescu (2007) focused on Mink Frog, *L. septentrionalis*, in northern New York State and Compton et al. (2007) juvenile Marbled Salamanders, *A. opacum*, and adult *A. maculatum* in Massachusetts. We used these studies as qualitative benchmarks to compare our own estimates for anurans and *A. maculatum*, finding that our own estimates were similar to those of the other researchers. The friction values we estimated for each land-cover type are documented in Appendices D1 and D2 (for NLCD classifications), and Appendix E (for NWI classifications). Because there were no species for which habitat suitability or resistance to movement have been quantified across all of the available NLCD classifications, our translation of the available data into habitat resistance values can be seen as somewhat qualitative, representing a combination of empirical data and our own expert opinion. Our friction index ranged from zero (most suitable) to 50 (least suitable). A value of zero (i.e., no cost) was used for the most suitable habitat, as it was considered to provide no barrier to movement (Popescu 2007).

Because of the important role played by moisture in habitat selection by herpetofauna (Reagan 1974; Wyman 1988), we further adjusted friction values by a topographic wetness index (TWI). The TWI combines a measure of the upslope area and slope to predict the hydrology of a given location (Sorenson et al. 2005) and is defined as $\ln(a/\tan\beta)$, where a is the local upslope area draining through a specified point per unit contour length and $\tan\beta$ is the local slope. Initially the TWI was rescaled to range from 0–5 (dry-wet). We then used this index to alter resistance values, resulting in the wettest areas having a resistance value five points lower than the driest areas.

Following the development of the resistance values across the entire landscape, we then reduced this area for each species and life-history stage based on movement neighborhoods. Movement neighborhoods for amphibians were based on the maximum migration and dispersal distances reported for adults and juveniles (Appendix A). We were conservative in these estimates, discounting studies where movement was calculated based on displaced individuals, or where movement was inferred from unmarked individuals. We used the maximum distance reported in any study rather than mean values calculated across all studies as limited data for some species meant that mean distance was often much lower than the reported maximum.

Once friction landscapes had been generated for each species (and life-history stage in the case of amphibians), we used the cost-distance function to calculate a cumulative cost for each species as an individual moved away from suitable aquatic habitat. This represents a simple additive function whereby as an animal moves unit of distance away from a source it accumulates cost, with this cost being a function of the habitat resistance for that particular location; thus moving farther and through less suitable habitat is more costly. Following rescaling of cost-distance values for each species from 0–100, we extracted the cells that represented the locations of roads. The roads used in models were derived from the New York State Office of Cyber Security and Critical Infrastructure Coordination as part of the Accident Location Information System (ALIS). This provided us with a relative measure of the probability of an animal being found on each 30-m long section of road.

Output metrics and prioritizing hotspots.—We generated 15 initial models of the predicted occurrence index across the study area. These represented 10 focal species and included separate models for both migrating and dispersing individuals for all amphibians except Red-spotted Newts (adults of this species do not undergo terrestrial migration). We derived two methods of prioritizing these models. First, we selected occurrence index values in the range of 0–2 (i.e., the highest probability of occurrence) for each model and reclassified hotspots based on the length of continuous hotspot that remained within these occurrence index values. This method allowed identification of longer stretches of road where we predict large numbers of animals would be present (for example a road running along the edge of a wetland). As road mortality has been shown to increase with traffic intensity (Carr and Fahrig 2001; Gibbs and Shriver 2005), we also developed models wherein we classified roads/hotspots according to their Arterial Classification Code (ACC). This scale from 1–6 represents the relative importance of roads to the overall transportation network as measured by the volume of traffic carried, the capacity of the road to handle traffic (e.g., the number of lanes and the maximum speed on the road), and the purpose of the road. For example, ACC Class 1 represents the largest/longest highways connecting major cities with a maximum speed of 65+ mph (104+ km/h), whereas Class 6 represents one- or two-lane residential roads with a maximum speed of 15–25 mph (24–40 km/h). This method allowed identification of areas where we expected to see a large number of animal-vehicle collisions.

Model validation.—To validate the accuracy of our models, we selected two areas of road network within our study region that encompassed the same land-cover gradients as our full model within a small geographic region. The first area was in the vicinity of Labrador Hollow, approximately 30 km south of Syracuse, New York, hereafter called “Labrador Hollow”. This 32-km long road network included both busy roads (ACC Class 3) and low traffic volume rural roads (ACC Class 5). The entire network was sampled on four rainy nights from 31 March to 2 May 2008 between dusk and midnight. This period of time represents a period of peak migration for amphibians in the region, thus we were able to derive a large sample size for validating presence and absence. Our sampling consisted of driving slowly (< 48 km/h) along the road, and recording all live and dead animals, including details of age and sex where possible as well as the exact position of the animal using a global positioning system. A single route was established on which to sample all sites. We also conducted a more intensive sampling session on a second section of road within a region approximately 24 km south of Syracuse, New York, hereafter called the "Tully Valley." This 19-km long section of road was sampled on seven rainy nights from 27 May to 23 August 2007. This road section was ACC Class 3. Sampling was conducted using a bicycle riding at 13 km/h, ensuring that most animals on the road, including juveniles, were detected. Although sampling periods differed between the two validation sites, our focal species were actively migrating during both periods. However, to avoid any potential temporal issues with sampling time between the two sites, we only validated models with species that were abundant at a particular site. Although we used two different modes of transportation for collecting validation data, the adult amphibians we observed dead on roads were highly visible using both methods.

We used 30-m road segments (i.e., the minimum resolution of our hotspot model output) as our sampling unit for model validation and focused on predictions and field data for migrating adults of five species of amphibians: *A. maculatum*, *L. clamitans*, *L. sylvaticus*, *A. americanus*, and *N. viridescens*. One of these species, *A. americanus,* was sufficiently abundant during our sampling period on both survey routes to allow model validation. *Lithobates clamitans* were only observed in sufficient numbers on the Tully Valley route, and *A. maculatum*, *L. sylvaticus*, and *N. viridescens* on the Labrador Hollow route.

To compare the ability of our models to predict the locations of animals crossing roads, we compared the predicted occurrence index with the actual occurrences of amphibians on our survey routes. To avoid issues of spatial autocorrelation among adjacent road-segments for our most common species, *A. maculatum*, we initially stratified road segments based on either presence or absence, then randomly selected 75, 30-m sections in each category for validation analysis (random selection occurred across all habitat types). We then used negative binomial regression to compare the observed occurrences to the predicted occurrence index. For *L. clamitans*, *L. sylvaticus*, *A. americanus*, and *N. viridescens*, which were less abundant on roads and for which occurrences were not as aggregated, we used a logistic regression without random sampling.

RESULTS

Our model output provided us with maps identifying concentrations of amphibians and reptiles on roads proximate to suitable aquatic habitat and in high-quality terrestrial habitat; information that is vital for reducing the effects of roads on these taxa. The occurrence indices tended to be left-skewed for all species and life-history stages. This skew is a result of high-quality terrestrial habitats such as forested wetlands being assigned a resistance value of zero. Because of the abundance of wetlands in our study area, and as our models were designed to predict any probability of occurrence, no matter how slight, most road-segments had some probability of at least one of our study species being present.

Differences between species.—The predicted occurrence of reptile and amphibian species on roads in New York State clearly differed among taxa. The range of aquatic habitats species used, estimated maximum movement distances, and their relative sensitivity to terrestrial habitat change caused these differences. For example, wide-ranging generalist species such as the common snapping turtle are predicted to occur across a much greater proportion of the landscape than habitat specialists such as the spotted salamander (Fig. 3). The latter species has relatively specialized aquatic habitat requirements and high sensitivity to terrestrial habitat changes associated with development, urbanization and agriculture.

Differences between life-history stages: migration versus dispersal.—Models for migrating adults compared with dispersing juvenile amphibians differed depending on the maximum movement distance for the two life-history stages and the relative sensitivity to terrestrial habitat change. In general, juveniles tend to move much further during dispersal, but are relatively less tolerant of terrestrial habitat change than adults. Accordingly, where juveniles occur in areas of suitable habitat they tend to occur across a greater proportion of the landscape than adults (Fig. 4). With a reduction in habitat quality; however, the accumulated cost to movement means that juveniles may actually occur across less of the landscape then adults.

Prioritization.—The proportion of the total length of the road network in our study area that was encompassed by different prioritization metrics varied by species. For example, migrating adult *L. sylvaticus* with specific habitat requirements and a maximum movement range of 430 m were predicted to have at least some probability of occurrence on 43.3% of the road network. When using the length of continuous high-occurrence as a metric for the same species, 28.4% of the road network fell in the 'long' category of > 500 m continuous high occurrence index (Fig. 5). *Chelydra serpentina*, a habitat generalist with a maximum reported movement of 2,020 m (Pettit et al. 1995) had at least some probability of occurrence (i.e., > 0%) on 97.6% of the road network. When using the length of continuous high-occurrence as a metric for this species, 35% of the

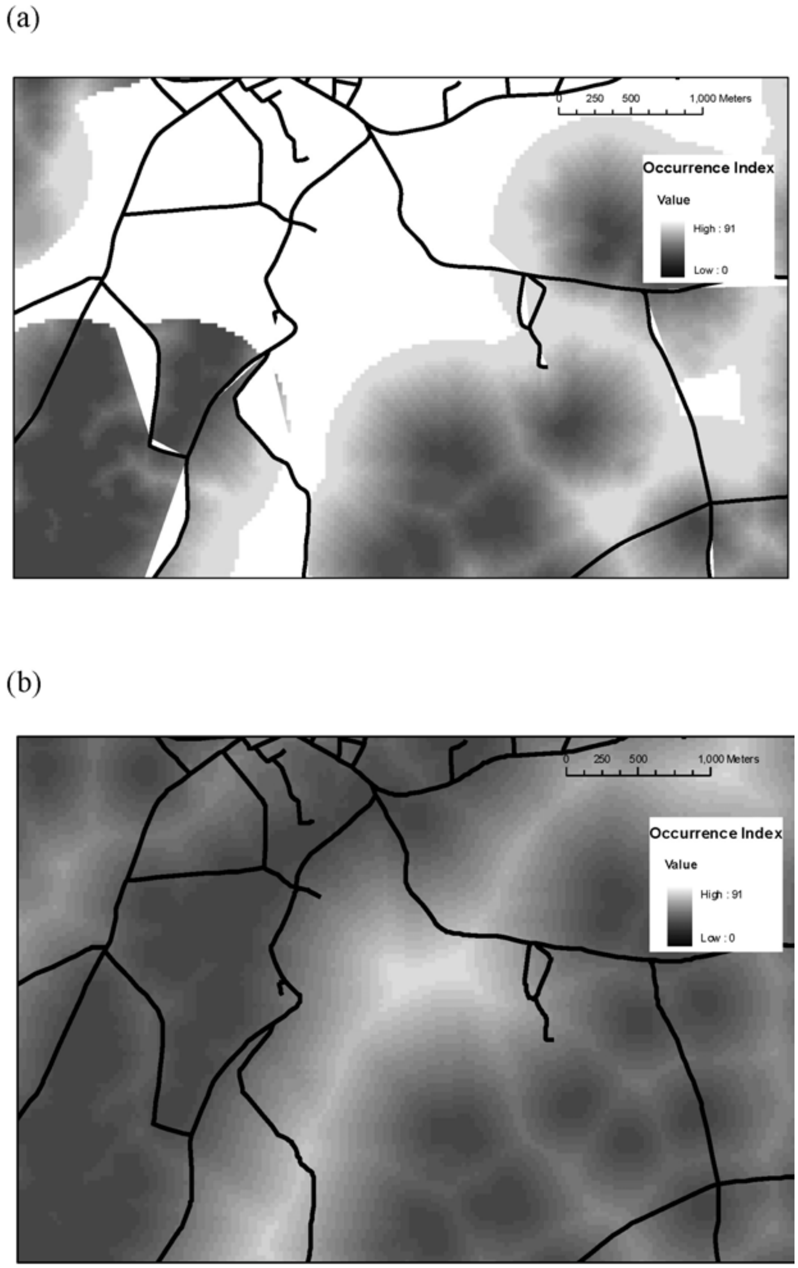


FIGURE 3. Example of the occurrence index output for all terrestrial habitat (rather than just roads), for (a) migrating Spotted Salamanders and (b) Common Snapping Turtles. Darker colors represent a higher probability of occurrence (i.e. a lower resistance/occurrence index). Roads are indicated as dark lines.

road network fell in the ‘long’ category of > 500 m continuous high occurrence.

Model validation.—We observed 330 animals (including both live and dead animals) on the 32-km stretch of road surveyed by car in the vicinity of Labrador Hollow, representing eight species. Four of these species were relatively abundant (*A. maculatum*, n = 206; *A. americanus*, n = 38; *L. sylvaticus*, n = 35; and *N. viridescens*, n = 40), with the remaining species being relatively rare (n < 8). We observed 260 animals on roads during our bicycle surveys of the agricultural Tully Valley, representing 10 species (two salamanders and eight anurans). These species can be loosely grouped into two categories: abundant species represented by *L. clamitans* (n = 138) and *A. americanus* (n = 91); and

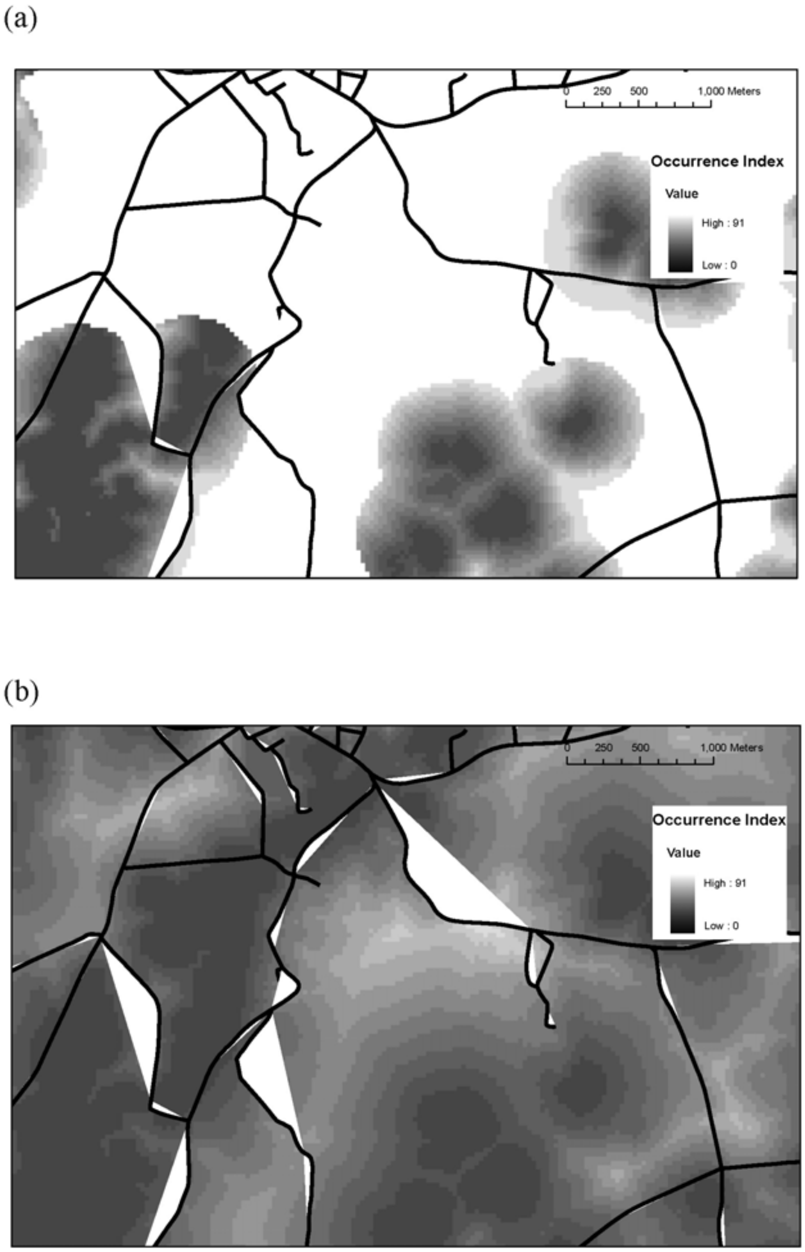


Figure 4. Example of the occurrence index output for all terrestrial habitat (rather than just roads), for (a) migrating adult Wood Frogs and (b) dispersing juvenile Wood Frogs. Darker colors represent a higher probability of occurrence (i.e. a lower resistance/occurrence index). Roads are indicated as dark lines.

rarely observed species (all other species, n < 7). Although bicycle surveys did help in locating small juvenile amphibians, these data were not used in analyses and thus predictions for juvenile organisms were not validated.

Disproportionately more *A. maculatum* were found along the Labrador Hollow route at road sections predicted as high-occurrence compared to low occurrence (Z = -3.377, df = 149, P = < 0.001; Fig. 6). Occurrence of both *L. sylvaticus* and *N. viridescens* was also found to be significantly related to model predictions, with a higher probability of occurrence in locations predicted as high-occurrence (*L. sylvaticus*, Z = -2.187, df = 592, P = 0.029 and *N. viridescens*, Z = -3.922, df = 782, P < 0.001). For *L. sylvaticus,* 84% of actual occurrences were correctly predicted by models, with 100% of *N. viridescens* occurrences correctly predicted by models. Occurrences of *L. clamitans* and

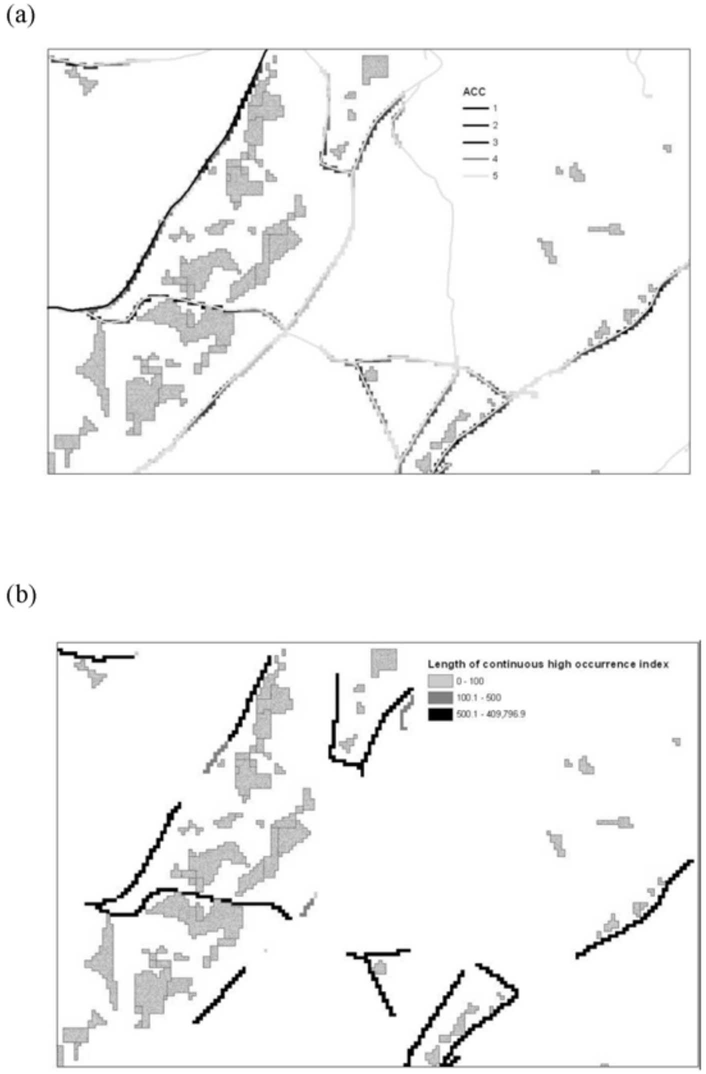


FIGURE 5. Illustration of two methods employed to prioritize hotspots of herpetofaunal occurrence on roads in New York State using migrating Wood Frogs as an example: (a) with the arterial classification code for roads overlaid (ACC); and (b) using the length of continuous high-occurrence rasters (divided into 3 categories based on length: short sections of road [length < 100 m]; medium sections [length 100–500 m]; and long sections [length > 500 m]). Aquatic habitats are shown in grey.

A. americanus in Tully Valley were not significantly related to their occurrence index (Z = 1.178, df = 656, P = 0.239 and Z = -0.015, df = 656, P = 0.988, respectively); however, nor were *A. americanus* at Labrador Hollow (Z = -1.303, df = 807, P = 0.930).

DISCUSSION

Our models predict a widespread occurrence of herpetofauna on roads in our study area with most sections of road having at least some probability of occurrence for at least one of our focal species. This phenomenon is likely a function of the abundance of wetlands found in this region, as well as our focus on a range of species that differ in their preference for aquatic and terrestrial habitats. This result also indicates the breadth of road impacts on herpetofauna in general. Similar to the results of other studies, particularly high concentrations of animals were found on roads that run adjacent to large wetland complexes, where breeding habitats for a variety of different species are found, and/or through areas of undisturbed terrestrial habitat (Compton et al. 2007; Langen et al. 2007). Despite the coarseness and broad assumptions of the study, the strength of our approach lies in the use of a large spatial extent, readily available datasets including national-coverage GIS layers and relatively simple prioritization methods, which can be easily replicated both in other

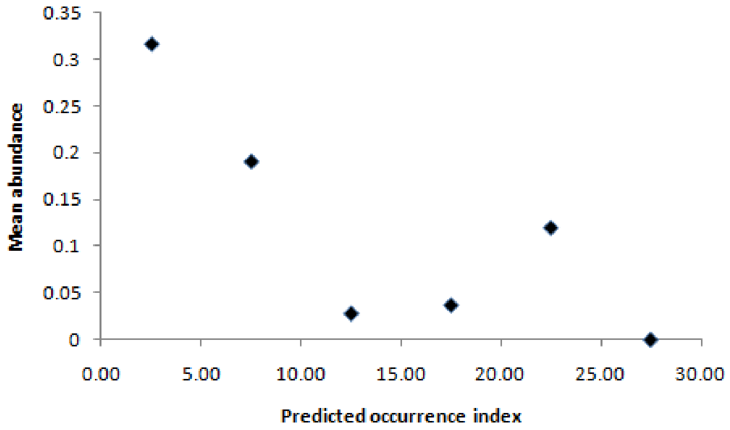


FIGURE 6. Relationship between the predicted occurrence index of Spotted Salamanders (*Ambystoma maculatum*), and actual abundances within 30-m road-sections along a 32-km long stretch of road in the vicinity of Labrador Hollow, Apulia, New York, USA. For visualization, data are presented as the mean number of occurrences within six categories of occurrence index, < 6, 6–10, 11–15, 16–20, 21–25, and 26–30. An occurrence index of zero represents the highest predicted probability of occurrence.

parts of the United States and in other countries where similar datasets are available.

Differences between the predicted patterns of occurrence of species on roads have clear implications for mitigation. For species characterized by relatively limited vagility, specific aquatic habitat requirements, and high sensitivity to anthropogenic changes in terrestrial habitat (e.g., *A. maculatum* and *L. sylvaticus*), our models identified discrete locations in which mitigation can be focused. Many of our focal species are also considered 'explosive' migrants, with the majority of individuals crossing roads simultaneously at predictable points during the year (Paton and Crouch 2002). For such species, approaches to mitigation such as culverts, signage, and road closures may be valuable, and represent a feasible balance between transportation needs and biodiversity. Conversely, wide-ranging species such as *C. guttata*, characterized by low population densities and relatively continuous movement throughout the active season (Beaudry et al. 2008) may present a greater challenge to mitigation. These species have a relatively low probability of occurring on any one stretch of road; hence it is difficult to predict where they will cross. They do frequently cross roads, however, with their life-history strategy characterized by late reproductive maturity and high adult survival making populations extremely vulnerable to any increase in adult mortality. Thus, mitigation focused on single point locations (e.g., culverts) is unlikely to be sufficient to maintain the long-term viability of populations of such species. Broader-scale measures deployed at potential crossing hotspots (e.g., seasonally reduced speeds) and population-level measures (e.g., driver education) may be more appropriate (Beaudry et al. 2008).

The differences seen in model outputs for migrating versus dispersing amphibians are analogous to the inter-specific differences observed in other models. There are, however, important differences when considering mitigation. The fact that for many species of amphibians, juveniles are the dispersing life-history stage and range farther than migratory adults is reflected in our model outputs, where the predicted patterns of occurrences of juveniles cover a much greater area of the road network. Thus, juvenile amphibians can be considered to present similar issues for mitigation as the wide-ranging species discussed above, albeit with movement being closely associated with rainy nights (when they are almost impossible for motorists to spot and hence avoid). The role played by juveniles in the regional population dynamics is important to consider, because these individuals provide genetic connectivity between spatially separate populations. Maintenance of this connectivity has been demonstrated as vitally important to the long-term persistence of amphibian species such as *L. sylvaticus* (Harper et al. 2008).

Bearing in mind the widespread occurrence of many of our study species on roads in New York State and the limited resources available for mitigation along with a road network encompassing more than 228,000 km, there is a clear need for prioritizing efforts by transportation planners. The two methods we have highlighted (the length of continuous hotspot and classifying hotspots based on traffic intensity) represent useful metrics for transportation agencies. There are however a variety of ways of prioritizing hotspots that can be readily generated from our model output. These include identifying zones of connectivity between populations and identifying potential areas of high abundance of animals on roads (e.g., selecting contiguous areas of high occurrence). From a jurisdictional standpoint, there are many different agencies responsible for managing roads in New York State including the state, county, and municipal Departments of Transportation as well as New York Thruway Authority (responsible for the State's toll highways). These agencies vary in capacity for deploying mitigation as well as operating mandates and internal priorities. If we are to see the results of our models effectively implemented, understanding differences among agencies and providing information at a relevant spatial scale and technical level are vital.

Given the limited number of species, as well as the spatial and temporal scale over which validation occurred, the model validation we conducted demonstrates that our models are effective tools for predicting occurrences of species with limited movement ranges and relatively specific habitat requirements (e.g., *A. maculatum*, *L. sylvaticus*, and *N. viridescens*). Our models were less effective in predicting occurrences of generalist species with larger movement ranges such as *A. americanus* and *L. clamitans*. These results were expected and support the recommendations we have made for mitigation (i.e., that targeted mitigation, such as crossing structures, is only likely to be effective for habitat specialists). The routes we chose for model validation did not include any high-traffic intensity roads (e.g., four-lane highways) due to safety concerns. This is an important caveat given the likely effects such roads have on herpetofauna populations (Fahrig et al. 1995; Carr and Fahrig 2001).

Our models were designed to meet a specific purpose, i.e., to provide broad-scale data informing transportation managers as to where roads are most likely to detrimentally affect populations of herpetofauna. We believe that our models effectively meet this goal for habitat specialist species, especially given that prior to their development, the Department of Transportation had no large-scale data on which to base their decisions (Popescu and Gibbs 2009). As with all models, however, the reliability of the output is dependent on the quality and accuracy of the data used in development. For most of the focal species there are gaps in our understanding of their ecology, especially in the terrestrial environment. This is particularly true for the rare species that are often the focus of management efforts but do not lend themselves well to modeling or validation efforts. Documenting maximum dispersal distances is also extremely difficult given the scarcity of such events and the large area over which sampling must occur in order to detect these individuals (Trakhtenbrot et al. 2005). Given the focus of our modeling exercise on identifying potential mortality hotspots (high abundance across single or multiple species), underestimating dispersal distances is unlikely to change model predictions, however. Our models also assume that there is no behavioral avoidance of roads depending on traffic volume. Although behavioral avoidance has been demonstrated for other taxa (Andrews et al. 2007), to the best of our knowledge it has not been shown for amphibians. Models are also limited by the quality of remote sensing data. For example, small ephemeral wetlands that form important breeding sites for many amphibian species are often missed, particularly during times when these wetlands do not hold water. Our validation data are also limited both temporally and spatially. These limitations mean that we missed rare species and juveniles, and were not able to assess how well our models performed over a large spatial extent (a scale at which we would also expect to see intraspecific variation in life-history characteristics). A further caveat relates to the application of our models; because these tools are mechanistic there is inherent uncertainty in the predictions made at specific locations (i.e., although validation demonstrated our models were good predictors for key focal species, they were not 100% accurate). For small municipalities looking to implement a focused mitigation effort such as a single culvert or barrier fence, we suggest the use of direct observational data to determine suitable locations. However, it is important to recognize that a single culvert is unlikely to be suitable in many situations and barriers without passages are likely to lead to habitat fragmentation, including for non-target organisms.

Because of the large number of species and life-history stages included in this study, we were not able to conduct formal sensitivity analyses to assess how variation in estimates of life-history parameters would influence model results. Sensitivity analyses have been conducted in two previous articles using habitat resistance modeling for amphibians (Compton et al. 2007; Janin et al. 2009). Although neither of these studies was conducted at the scale of our research in terms of the number of species or area, the results showed no major effect of varying resistance values. As we used the most up-to-date knowledge of amphibian-habitat associations, our models are unlikely to differ in terms of sensitivity.

One of the principle challenges with existing approaches to predicting occurrence of road-mortality hotspots for amphibians is the reliance on direct observation. This is undoubtedly the most reliable way to locate individual hotspots, but the effort required to conduct these studies means that a limited spatial extent can be covered. Therefore, this approach is not suitable for large-scale decision making. Direct observation is also only suitable where populations are sufficiently abundant that animals can be detected on the road; this may not be the case if road mortality has already led to population declines (e.g., Fahrig et al. 1995), yet these populations may be of particular interest for conservation efforts. The approach we have documented in this study uses the best available data to allow transportation managers to make informed decisions at a statewide scale. Without the models we have produced, no information would be available to help in this decision-making process. Additionally, road surveys are limited in informing locations where road mortality may have already caused population declines and where mitigation may be particularly beneficial for population viability, abilities which are informed using the modeling process presented here. An important next step following the development of models such as ours is linking predicted occurrence of herpetofauna on roads to estimates of vehicle mortality to explore consequences of roads on abundance (Fahrig et al. 1995) and population viability (Gibbs and Shriver 2005). We speculate that the most vulnerable of all species will be those with low population sizes and scattered distributions for which a given level of road mortality may pose a greater population risk and hotspots are not easily identified, hence mitigation measures will be difficult to deploy effectively.

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No biography given for fourth author.

APPENDIX A. GIS data used in predicting hotspots of herpetofaunal road mortality in New York State, USA.

Dataset	Source	Format	Resolution	Projection	Datum
National Land Cover Database 2001	U.S. Geological Survey	Raster	30 m	Albers Conical Equal Area	NAD83
National Land Cover Database Zone 64 Tree Canopy Layer	U.S. Geological Survey	Raster	30 m	Albers Conical Equal Area	NAD83
National Wetlands Inventory Freshwater Wetlands	U.S. Fish & Wildlife Service	Vector		Transverse Mercator	NAD27
Topographic wetness index	State University of New York College of Environmental Science and Forestry	Raster	10 m	Transverse Mercator	
Road network	New York State Office of Cyber Security & Critical Infrastructure Coordination	Vector		Transverse Mercator	NAD83

APPENDIX B. Life-history characteristics of the focal study species in New York State, USA. In addition to the cited references, data were gathered from Natureserve Explorer (Natureserve. 2012. Natureserve Web Service. Available from http://www.natureserve.org/explorer [accessed 15 July 2010]), AmphibiaWeb (AmphibiaWeb. 2012. AmphibiaWeb: Information on Amphibian Biology and Conservation. Available from http://amphibiaweb.org/search/index.html [accessed 15 July 2010]), and Gibbs et al. (2007).

Species	Breeding habitat	Summer habitat	Winter habitat	Max. adult move. dist. (km)	Max. juvenile move. dist (km)	Types of movement	References
Wood Frog	Vernal pools, forested wetlands, beaver impoundments	Forested wetlands and moist forest	Forested uplands	0.43	2.53	Adult breeding, juvenile emigration, migration to summer foraging, and migration to overwintering sites	Heatwole 1961; Bellis 1965; Berven and Grudzien 1990; Baldwin et al. 2006; Patrick et al. 2006
Green Frog	Permanent wetlands	Pool/stream edge; juveniles will disperse into woods and meadows.	Underwater/ underground	1.26	4.80	Juvenile emigration, and adult movement to and from overwintering sites	Martof 1953, 1956; Schroeder 1976; Carr and Fahrig 2001; Guerry and Hunter 2002; Lamoureux et al. 2002; Livingston Birchfield 2002; Patrick et al. 2006
N. Leopard Frog	Permanent and vernal slow moving or nonflowing wetlands	Fields and meadows preferred to closed-canopy forest; juveniles may move to the edges of permanent water	Underwater	3.22	5.20	Adult breeding, juvenile emigration, migration to summer foraging, and migration to overwintering sites	Dole 1965, 1967, 1971; Merrell 1970; Seburn et al. 1997; Pope et al. 2000; Carr and Fahrig 2001
American Toad	Permanent and vernal slow moving or non-flowing wetlands typically without fish or wood frog tadpoles	Forest, agricultural lands, parks, and gardens	Underground	1.00	1.65	Juvenile emigration and adult breeding migrations.	Breden 1987; Petranka et al. 1994; Holomuzki 1995
Spotted Salamander	Vernal pools, forested wetlands, beaver impoundments	Underground in forests; adults will cross open areas	Underground in forests	0.76	0.15	Juvenile emigration, adult breeding migrations, and movement to overwintering sites	Douglas and Monroe 1981; Kleeberger and Werner 1983; Madison 1997; Guerry and Hunter 2002; Faccio 2003; McDonough and Paton 2007; Patrick et al. 2008
Red-spotted Newt	Ponds, lakes, and slow moving rivers	Adults are aquatic; efts in forests with strong edge avoidance		N/A	1.00	Juvenile/eft emigration	Hurlbert 1969; Gill 1978; Gibbs 1998
Snapping Turtle	Edges of lakes, ponds, and slow-moving rivers	Lakes, ponds, and slow moving rivers; nests close to water	Aquatic	2.02	N/A	Adult nesting, movement between ponds, juvenile emigration, and movement to hibernacula	Brown and Brooks 1994; Pettit et al. 1995; Ultsch 2006
Spotted Turtle	Several hundred yards into uplands	Vernal pools in spring, upland forests for dormancy; fields for egg laying	Wet meadows, forested swamps, or sphagnum bogs	1.03	N/A	Adult nesting, movement to upland estivation sites, and overwintering movements	Ernst 1976; Joyal et al. 2001; Milam and Melvin 2001; Ultsch 2006
Painted Turtle	Edges of aquatic habitat	Slow moving or still permanent freshwater wetlands; nest in open canopy uplands	Slow moving or still permanent freshwater wetlands	0.63	N/A	Adult nesting, juvenile emigration, and movement between ponds	Christens and Bider 1987; Rowe 2003; Baldwin et al. 2004; Ultsch 2006
Wood Turtle	Edges of aquatic habitat	River or streams with sand or gravel substrates bounded by woods; agricultural lands	Creeks	3.60	N/A	Adult nesting and juvenile emigration	Quinn and Tate 1991; Kaufmann 1992; Arvisais et al. 2002; Compton et al. 2002; Walde et al. 2003, 2007; Saumure et al. 2007

APPENDIX C. Studies examining habitat selection by focal species. Age classes were divided into juveniles (J; in the first year following metamorphosis), adults (A), and unspecified ages (U). Type of habitat use refers to the behavioral phase of the study animals (emigration refers to movement away from a natal site, breeding is the breeding site, feeding refers to all habitat use outside of emigration to and from breeding/natal sites with the exception of overwintering habitat).

Species	Age	Type of habitat use	Results of study	Reference
Wood Frog	U	Feeding	Preferred moist forest soils to drier forest soils	Wyman 1988
	J	Emigration and feeding	40% of captures were in forests, 31% in partial cut forests, and 14% in clearcut treatments	Patrick et al. 2006
	A	U	51% of captures were in forests, 26.5% in partial cut forests, and 11% in clearcut treatments	Patrick et al. 2006
	U	U	66% of captures were in closed canopy forests (> 20 m from edge) and remaining captures in edge of clearcuts	deMaynadier and Hunter 1998
	A	Feeding	75.3% of radio locations were in forested wetlands, even though these only made up 9.3% of the landscape	Baldwin et al. 2006
	U	U	Three times as many captures of wood frogs in forest interior compared to edges	Gibbs 1998
Green Frog	A	U	25% of captures were in forests, 17% in partial cut forests, and 26% in clearcuts	Patrick et al. 2006
	J	U	33% of captures were in forests, 27% in partial cut forests, and 20% in clearcuts	Patrick et al. 2006
N. Leopard Frog	A	U	30% of captures were in forests, 47% in partial cut forests, and 12% in clearcuts	Patrick et al. 2006
	J	U	33% of captures were in forests, 30% in partial cut forests, and 19% in clearcuts	Patrick et al. 2006
American Toad	U	Feeding	No difference seen in occurrence in moist compared to drier forest soils	Wyman 1988
	J	Emigration	Three animals entered old-fields and 44 entered forests when given the choice	Rothermel and Semlitsch 2002
	U	U	Approx.43% of captures were in closed canopy forests (> 20 m from edge) and remaining captures in edge of clearcuts	deMaynadier and Hunter 1998
Spotted Salamander	U	Feeding	Preferred moist forest soils to drier forest soils	Wyman 1988
	J	Emigration	Ten animals entered old-fields and 23 entered forest when given the choice	Rothermel and Semlitsch 2002
	A	U	37% of captures were in forests, 29% in partial cut forests, and 17% in clearcuts	Patrick et al. 2006
	J	Emigration	62% of captures were in forests, 20% in partial cut forests, and 9% in clearcuts	Patrick et al. 2006
	U	U	59% of captures were in closed canopy forests (> 20 m from edge) and remaining captures in edge of clearcuts	deMaynadier and Hunter 1998
Red-spotted Newt	J	U	Strong avoidance of forest edges (mean of 0.3 captures per drift fence on edge, compared with 3.1 in uplands). Approx. three times more captures in drier uplands than in stream beds.	Gibbs 1998
Spotted Turtle	A	All	Spent most of the active period in pools and emergent wetlands. Avoided shrub-scrub wetlands. Nested in open upland habitats (fields)	Milam and Melvin 2001
	A	All	Radio-tracked turtles in Maine spent 77% of the time in upland forested habitat	Joyal et al. 2001
Wood Turtle	A	U	When in the terrestrial environment, animals preferred an area of alder, herbaceous cover, and a cornfield. Forests and swamp represented only 14% of terrestrial habitat use, but occupied 54% of the terrestrial habitat.	Kaufmann 1992
	A	U	Lentic and lotic habitats combined accounted for 16% of use, shrub-scrub habitat 21%, emergent marsh and meadows 17%, fen/bog 17%, and forest 22%. Females during nesting were excluded.	Compton et al. 2002

APPENDIX D1. Migrants. Habitat resistance values assigned to each category of National Land Cover Database 2001 (Homer et al. 2007) for migrating individuals of each of the 10 focal species. For amphibians, adults were considered the migrating individuals (i.e., resistance values are for adult amphibians). Values range from zero (most suitable) to 50 (least suitable). A value of zero (i.e., no cost to movement) was used for the most suitable habitat, as it was considered to actually encourage movement (Popescu 2007). Study species are Green Frog (grfr), Northern Leopard Frog (nlfr), Wood Frog (wofr), American Toad (amto), Spotted Salamander (spsa), Red-spotted Newt (rsne), Painted Turtle (patu), Snapping Turtle (sntu), Spotted Turtle (sptu), and Wood Turtle (wotu)..

	Species									
NLCD class code and Definition	wofr	grfr	nlfr	amto	spsa	rsne	sntu	sptu	patu	wotu
11 Open water	5	5	5	5	5	5	5	5	5	5
21 Developed open space	20	15	15	15	20	40	10	20	10	20
22 Developed low intensity	30	20	20	20	30	45	15	30	15	30
23 Developed medium intensity	40	30	35	30	40	50	30	40	30	40
24 Developed high intensity	50	50	50	50	50	50	50	50	50	50
31 Barren lands	30	20	20	20	30	40	10	30	10	10
41 Deciduous forest	10	15	15	15	10	30	10	10	10	10
42 Evergreen forest	10	15	15	15	10	30	10	10	10	10
43 Mixed forest	10	15	15	15	10	30	10	10	10	10
52 Shrub/scrub	12	12	12	12	12	35	10	10	10	10
71 Grassland/herbaceous	15	10	10	10	15	40	10	10	10	10
81 Pasture/hay	15	10	10	10	15	40	10	10	10	10
82 Cultivated crops	20	15	15	15	20	40	10	15	10	15
90 Woody wetlands	0	0	0	0	0	10	5	5	5	5
95 Emergent herbaceous wetlands	0	0	0	0	0	10	5	5	5	5

APPENDIX D2. Dispersers. Habitat resistance values assigned to each category of National Land Cover Database 2001 (Homer et al. 2007) for dispersing individuals of each of the 10 focal species. For amphibians, juveniles were considered dispersing individuals (i.e., resistance values are for juveniles). Values range from zero (most suitable) to 50 (least suitable). For turtles, very little information was available to differentiate between migrating and dispersing individuals; therefore we used the same resistance values for both. A value of zero (i.e., no cost to movement) was used for the most suitable habitat, as it was considered to actually encourage movement (Popescu 2007). Study species are Green Frog (grfr), Northern Leopard Frog (nlfr), Wood Frog (wofr), American Toad (amto), Spotted Salamander (spsa), Red-spotted Newt (rsne), Painted Turtle (patu), Snapping Turtle (sntu), Spotted Turtle (sptu), and Wood Turtle (wotu).

	Species									
NLCD class code and definition	wofr	grfr	nlfr	amto	spsa	rsne	sntu	sptu	patu	wotu
11 Open water	5	5	5	5	5	5	5	5	5	5
21 Developed open space	25	15	15	20	30	30	10	20	10	15
22 Developed low intensity	35	30	30	30	40	40	15	30	15	25
23 Developed medium intensity	45	40	40	40	50	50	30	40	30	35
24 Developed high intensity	50	50	50	50	50	50	50	50	50	50
31 Barren lands	30	20	20	30	30	30	10	30	10	10
41 Deciduous forest	10	10	10	10	10	5	10	10	10	10
42 Evergreen forest	10	10	10	10	10	5	10	10	10	10
43 Mixed forest	10	10	10	10	10	5	10	10	10	10
52 Shrub/scrub	15	12	12	15	20	20	10	10	10	10
71 Grassland/herbaceous	20	15	15	20	30	30	10	10	10	10
81 Pasture/hay	20	15	15	20	30	30	10	10	10	10
82 Cultivated crops	20	15	15	20	30	30	10	15	10	15
90 Woody wetlands	0	0	0	0	0	10	5	5	5	5
95 Emergent herbaceous wetlands	0	0	0	0	0	10	5	5	5	5

APPENDIX E. Resistance values given to freshwater wetland types included in road-mortality hotspot models (source: National Wetlands Inventory [NWI], Cowardin et al., 1979; United States Fish and Wildlife Service, 2006). Classes include: Aquatic Bed (AB), Rock Bottom (RB), Emergent (EM), Farmed (F), Forested (FO), Open Water (OW), Rocky Shore (RS), Scrub-shrub (SS), Unconsolidated Bottom (UB), Unconsolidated Shore (US). Equivalent NWI labels for system, subsystem and classes are also provided. Study species are Green Frog (grfr), Northern Leopard Frog (nlfr), Wood Frog (wofr), American Toad (amto), Spotted Salamander (spsa), Red-spotted Newt (rsne), Painted Turtle (patu), Snapping Turtle (sntu), Spotted Turtle (sptu), and Wood Turtle (wotu).

			NWI	Study species resistance values									
System	Subsystem	Class(es)	label	wofr	grfr	nlfr	amto	spsa	rsne	sntu	sptu	patu	wotu
Lacustrine	Limnetic (1)	(UB, AB, OW)	L1	20	20	20	20	20	20	0	20	20	20
	Littoral (2)	Shore (RB, RS, US)	L2 shore	0	0	0	0	0	0	0	0	0	0
	Littoral (2)	Bed (UB, AB, EM, FL, OW)	L2 bed	0	0	0	0	0	0	0	0	0	0
Riverine	Tidal (1)		R1	50	50	50	50	50	50	20	50	50	50
	Lower perennial (2)	Shore (RB, RS, US)	R2 shore	0	0	0	0	0	0	0	0	0	0
	Lower perennial (2)	Bed (AB, EM, OW, UB, RB)	R2 bed	0	0	0	0	0	0	0	0	0	0
	Upper perennial (3)		R3	5	5	5	5	5	5	0	0	0	0
	Intermittent (4)		R4	0	0	0	0	0	0	0	0	0	0
Palustrine		Farmed (f)	Pf	0	0	0	0	0	0	0	0	0	0
		Unconsolidated bottom (UB)	PUB	0	0	0	0	0	0	0	0	0	0
		Aquatic bed (AB)	PAB	0	0	0	0	0	0	0	0	0	0
		Unconsolidated shore (US)	PUS	0	0	0	0	0	0	0	0	0	0
		Emergent (EM)	PEM	0	0	0	0	0	0	0	0	0	0
		Scrub-shrub (SS)	PSS	0	0	0	0	0	0	0	0	0	0
		Forested (FO)	PFO	0	0	0	0	0	0	0	0	0	0
		Open water (OW)	POW	0	0	0	0	0	0	0	0	0	0