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Effects on New York State Roadways on Amphibians and Reptiles: A Research and Adaptive Mitigation Project

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16. Abstract

This report explains the impacts of transportation infrastructure on herpetile populations, the landscape, local habitat, and architectural attributes of effective herpetile crossing structures and employ's habitat analyses to identify "connectivity zones" where crossing structures would be most appropriately deployed along New York State roadways.

To conserve New York's herpetiles we must protect a diversity of habitats that they require as well as the connections between them. Roadways are a critical consideration because they frequently divide migration and dispersal routes of herpetiles.

Virtually all species of frogs, toads, and salamanders move each year from forests and fields, where they spend much of the year feeding, resting, and hibernating, to wetlands to breed. Snakes also roam widely in search of prey and mates, visiting both wetlands and uplands in their meanderings. This study can provide science-based guidance for mitigating the effects of road-mortality on herpetofauna, both in New York State and elsewhere in the northeastern United States. It is clear from studies that roads have the capacity to influence both local and regional population dynamics of amphibians and reptiles. The degree to which road mortality affects populations seems highly dependent on the life-history characteristics of species and the degree to which natural habitat has been altered (both by roads and in other ways), however. Road mortality is of particular concern to populations of species such as turtles (i.e., species with high adult survival under natural conditions, late sexual maturity, and relatively low fecundity compared to other species of herpetofauna). To address these objectives seven integrated studies were conducted in support of these objectives

Studies focusing on the design of crossing structures have tended to be based either on animals translocated to experimental arenas or monitoring the use of existing structures. The behavior of animals in the former approach may not represent that of animals under natural conditions. To test the effects of culvert attributes including length, diameter and substrate on choice, we applied a novel technique whereby experimental arrays were placed in the path of migrating spotted salamanders, allowing choice to occur under natural movement conditions. A higher abundance of spotted salamanders were found where flowing water was present on the upslope of the road. More American toads were found on sections of road without a wetland on the downslope side and where there was a culvert nearby. Spotted salamanders showed no clear preference for culverts with different attributes. Our results show that predicting where amphibians will be concentrated within crossing hotspots is possible, allowing effective placement of mitigation, but that these patterns are likely to differ between species. We found that spotted salamanders undergoing their natural movements appear to be more tolerant of differences between culverts when compared with studies in experimental arenas, and that a variety of different culverts will work as crossing structures..

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PROJECT C-04-02 EFFECTS OF NEW YORK STATE ROADWAYS ON AMPHIBIANS AND REPTILES: A RESEARCH AND ADAPTIVE MITIGATION PROGRAM.

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EXECUTIVE SUMMARY

BACKGROUND

New York State hosts 67 species of frogs, toads, turtles, snakes and lizards, collectively called "herpetiles." This group of small-bodied, generally slowly moving creatures is, somewhat paradoxically, an extremely mobile group of animals. Virtually all species of frogs, toads, and salamanders move each year from forests and fields, where they spend much of the year feeding, resting, and hibernating, to wetlands to breed. Many aquatic turtles do the reverse – females emerge each year from ponds, lakes, and other wetlands to dig holes in the uplands and lay their eggs. Snakes also roam widely in search of prey and mates, visiting both wetlands and uplands in their meanderings.

To conserve New York's herpetiles we must protect a diversity of habitats that they require as well as the connections between them. Roadways are thus a critical consideration because they frequently bisect migration and dispersal routes of herpetiles. Owing to the lack of information on the scope of the risks posed by road mortality to the viability of herpetile populations in New York State, in conjunction with the scarcity of guidance available on how to mitigate for the problem, we undertook an integrated research and adaptive mitigation program that addressed three primary objectives:

1. *Document the impacts of transportation infrastructure on herpetile populations*
2. *Determine the landscape, local habitat, and architectural attributes of effective herpetile crossing structures*
3. *Employ habitat analyses to identify "connectivity zones" where crossing structures would be most appropriately deployed along New York State roadways.*

To address these objectives we conducted seven integrated studies in support of these objectives, which addressed the project tasks outlined in RFP C-04-02. A cross-tabulation of study objectives and project tasks are listed at the conclusion of this summary. In Chapter 1, we synthesized available information on the effects of roads on herpetile populations and developed an agenda for future research in this arena. Chapters 2-4 focused on documenting the impacts of transportation infrastructure on herpetile populations: we sampled aquatic turtle populations across an urban-rural gradient for three years and documented the effects of roads on both local and landscape-scale populations (Chapter 2); we deployed a series of coverboards in old-fields at different distances from roads and forest edges to look at the effects of proximity to these interfaces on snake populations (Chapter 3); and we conducted an extensive survey of forest-plots at different distances from roads to separate the influence of roads and other habitat variables on amphibian abundance (Chapter 4). In Chapter 5, a comprehensive experimental approach was used to evaluate how differences in behavior determined the efficacy of crossing structures for different species of herpetofauna including both amphibians and turtles. Chapter 6 extended this analysis to examine the choice of crossing structures made by amphibians during their natural movements, as well as the attributes determining where amphibians cross roads within a known crossing hotspot. In Chapter 7, we integrated our existing knowledge of habitat associations of herpetofauna in New York State to develop spatially-explicit models of the likelihood of different species occurring on roads and thus identify crossing hotspots for possible accommodation during planning by the NYSDOT.

SUMMARY OF RESULTS

The literature analysis we conducted (Chapter 1) highlighted both the accumulated knowledge about the effects of roads on herpetofauna as well as where knowledge gaps still exist. It is clear from this review that the variation in life-history traits of different species clearly influences the vulnerability of populations to road-mortality. Long-lived species that reach sexual maturity late such as many turtle species are more likely to see reductions in viability then short-lived species that reproduce at an earlier age. Similarly, more vagile species are more prone to road-effects, as are sexes that move farther, for example female turtles. Our literature review indicated that a lack of information of basic population biology for many species, especially the vital rates needed to parameterize population models, represents one of the main barriers to predicting the likely effects of roads on herpetofauna.

Chapters 2-4 clearly demonstrate the complex effects of roads on herpetofauna. In Chapter 2, we found that roads influenced the local population structure of turtles, but little evidence to indicate that these effects translated into dramatic reductions in population viability. The proportion of female snapping turtles was related to the linear distance of roads within a 500m buffer of the pond ($P<0.05$), with a higher proportion of female turtles in ponds surrounded by fewer roads. The proportion of female painted turtles in populations was also best explained by the amount of roads within 500m of the pond, with more females in ponds surrounded by less road extent. When looking at the influence of roads at the landscape-scale, logistic regression coupled with AIC identified four models as the best predictors of movement by snapping turtles, with explanatory variables in these models including (1) the suitability of habitat between ponds, with fewer turtles dispersing through poorer quality habitat, (2) the size of local populations, with more turtles dispersing from larger populations, (3) and the distance between ponds, with the probability of dispersal decreasing as the distance between ponds increased. In Chapter 3, we found a strong increase in the number of adult common gartersnakes and DeKay's brown snakes farther from the forest edge. The distance from the nearest road edge was not, however an important driver of snake distributions. When examining the effects of proximity to road on amphibian abundance in forested plots (Chapter 4), many environmental factors contributed to determining the occurrence of amphibians but distance from roads was not one of them.

When assessing the attributes of culverts in experimental arenas (Chapter 5), we found that some species responded to certain attributes of culverts, but that a strong preference was not seen in all cases. In Experiment 1*: Aperture Diameter*, choice of pipe was significantly non-random for snapping turtles and painted turtles. Individuals of both snapping and painted turtles tended to use pipes of the mid-size diameters more frequently than pipes with the largest and smallest diameters. For Experiment 2: *Substrate Type,* we detected significant choice only for green frogs. Individuals of this species used soil and gravel-lined pipes more often than the concrete - and PVC-lined pipes. For Experiment 3: *Pipe Length*, only painted turtles showed preference for tube length, but their choice patterns were not readily interpretable as more animals choose the intermediate rather than longer or shorter tubes. For Experiment 4: *Light Permeability,* both green and northern leopard frogs showed non-random movement through the pipes, although the results for neither turtle species were significant. In both frog species, the pipe with the most permeable surface area received the greatest usage.

During our assessment of the choice of culverts by amphibians during their natural migrations at the Labrador Hollow Unique Area (Chapter 6), we captured 446 spotted salamanders during the 5 nights of sampling. Our analyses of the position treatment (where position within the array was the only factor), revealed no significant relationship between the number of salamanders and the diameter of culverts or types of substrate. We did, however, observe a statistically significant difference in the length array. When testing to see whether this difference related exclusively to either treatment or position, however, we found no significant differences, indicating that this result was likely to be an interaction between the two factors.

Several factors were found to influence where amphibians crossed a two-lane highway while moving from forested overwintering sites to breeding habitat within Labrador Hollow, a known hotspot (Chapter 6): A higher abundance of spotted salamanders were found where flowing water was present on the upslope of the road and where there was a culvert nearby. Of these two variables, however, the presence of flowing water explained much more of the variation than did the distance to the nearest culvert. More American toads were found on sections of road without a wetland on the downslope side and where there was a culvert nearby.

The spatially explicit hotspot models we developed for the location of herpetofauna on New York State roads (Chapter 7) showed that amphibians and reptiles were more likely to be found on roads closer to suitable aquatic habitat and in high-quality terrestrial habitat. The predicted occurrence of species on roads in New York State clearly differed, as did the occurrence of different life-history stages of the same amphibian species (juveniles *c.f.* adults). The range of aquatic habitats species used, estimated maximum movement distances, and their relative sensitivity to terrestrial habitat change caused these differences. The proportion of the total length of the road network in our study area that was encompassed by different prioritization metrics varied by species: Migrating adult wood frogs 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, with 8.7% of the road network being classified in the highest occurrence index quantile (top 20%). When using the length of continuous high-occurrence as a metric, 28.4% of the road network fell in the 'long' length category of >500 m continuous high occurrence. Snapping turtles, a habitat generalist with a maximum reported movement of 2020 m had at least some probability of occurrence on 97.6% of the road network, with 19.5% of the road network being classified in the highest occurrence index quantile. When using the length of continuous high-occurrence as a metric, 35% of the road network fell in the 'long' length category of >500 m continuous high occurrence. Of the three species for which field data was used to validate hotspot models, the observed distributions of spotted salamanders and green frogs differed significantly from the null hypothesis of a random pattern of occurrences in relation to both the overall occurrence index and the length of high occurrence areas, i.e., our models were able to accurately prioritize roads based on the occurrence of herpetofauna.

CONCLUSIONS

This study can provide science-based guidance for mitigating the effects of road-mortality on herpetofauna, both in New York State and elsewhere in the northeastern United States. It is clear from our studies that roads have the capacity to influence both local and regional population dynamics of amphibians and reptiles. The degree to which road mortality affects populations seems highly dependent on the life-history characteristics of species and the degree to which natural habitat has been altered (both by roads and in other ways), however. Road mortality is of particular concern to populations of "K-selected" species such as turtles (i.e., species with high adult survival under natural conditions, late sexual maturity, and relatively low fecundity compared to other species of herpetofauna).

The results of our experiments into the attributes of culverts that facilitate passage indicate strong evidence that differences in culvert design have the potential to influence choice, but our study of choice under natural conditions indicated that these differences might be muted when animals are motivated to move. When examining factors determining why animals cross in specific locations within known hotspots, we found clear differences between our two focal species, American toads and spotted salamanders, with these differences apparently related to variation in life-history strategies. The results of this study indicate that it is possible to predict where animals are likely to cross roads, but that these predictions should include consideration of the biology of individual species. Based on the habitat-associations of focal species, we were able to develop predictive hotspot maps for large areas of New York State. Our validation data indicated that the models we developed were good predictors of where animals were likely to occur on roads. We were also able to develop several metrics for prioritizing these hotspots for the purposes of mitigation. Together predictive models and the results of our combined studies can be used to improve institutional capacity to mitigate the effects of roads on herpetofauna in New York State.

Table 1
Project summary and relationships of chapters to initial project proposal tasks. Relationships between chapters and initial tasks are indicated "●"

	Task from initial proposal				
Final report chapter	1. *Literature review and synthesis*	2. *Effects of roadways on herpetile populations*	3. *Crossing structure assessment*	4. *Crossing location assessment*	5. *NY State herpetofauna hotspot models*
1. A synopsis and research agenda	●				
2. Freshwater turtle populations		●			
3. Snake occurrence in relation to roads		●			
4. Proximity to roads and amphibians		●			
5. Crossing structures and behavioral analysis			●		
6. Crossing behavior at Labrador Hollow			●	●	
7. Habitat resistance models	●			●	●

1. ROAD-KILLS, REPTILES AND AMPHIBIANS: A SYNOPSIS AND RESEARCH AGENDA

ABSTRACT

Road-kill is an ever-increasing source of wildlife mortality. Herpetofauna, including amphibians and reptiles is particularly prone to the effects of roads. Many species of herpetofauna are slow moving yet paradoxically mobile, making frequent movements between different habitats during their life-histories, and thus increasing the likely contact with roads. Translating road-effects to changes at the population level remains difficult, however.

By reviewing current knowledge of herpetofauna and roads, we demonstrate that differences in the life-histories of species determine the likely effects of roads on populations. Slow growing K-selected species are especially vulnerable, as are species that move longer distances, or between aquatic and terrestrial habitats. Future research should focus on understanding how roads affect vital rates of species with a diversity of life-history traits, and the effects of roads on spatial ecology. Targeted research is also needed if mitigation such as crossing structures is to be successful.

Road-kill is a massive problem for wildlife; vehicles cause the deaths of millions of vertebrate animals on roads each day in the United States (Forman and Alexander 1998). Amphibians and reptiles are particularly vulnerable because these low-slung, slow-moving organisms are paradoxically quite mobile, typically needing to access multiple habitats annually to complete their life cycles. Coupled with the immense biomass these exothermic animals constitute in many ecosystems (Burton and Likens 1975a, Regester et al. 2006), road mortality can be truly impressive. Anyone who drives a car is engaged in this destruction. Oddly, road mortality in amphibians and reptiles more often generates jokes than concern. But conserving herpetofauna is neither a laughing matter nor an easy task: Not only are we now confronting global amphibian and reptile declines (Gibbons et al. 2000, IUCN et al. 2006), but we are increasingly reliant on roads and the ever expanding transportation infrastructure for economic security.

Balancing continued development with conservation of biodiversity is one of the most difficult problems facing societies throughout the world. For example, as the economy of the United States has grown, so too has the transportation network needed to facilitate this growth. The 4,010,217 miles of roadways in the United States in 2005 covered 1% of the country's land area (Forman 2000). Traffic volume on these roads is increasing at a fast rate; in 1970 1,100 billion vehicle miles traveled were logged in the United States, with this figure more than doubling to 2,400 billion by 1995, an increase of 3.16% per year (Festin 1996). Thus, the extent of the roadway network is increasing while its permeability to migrating animals is decreasing rapidly.

We are frequently asked how road-crossing structures for herpetofauna could be included in road-engineering projects. Bearing in mind the sizable body of research that has recently been directed towards understanding "road ecology" (Forman et al. 2003), it is surprisingly difficult to provide simple directives. A large gulf exists between our understanding of the ecological effects of roads, and our ability to translate this knowledge into clear directives for solving problems in the field. We do not know, for example, when road-kill is an important issue at the population level for amphibians and reptiles. When it is, what forms of mitigation are most effective for dealing with it? At what spatial scale is mitigation most appropriate? Does "one shoe fit all" or are different approaches needed for different taxa?

Herein, we develop an agenda for better targeting ecological research for addressing the road-kill issue. We first summarize research relevant to understanding the likely effects of roads on populations of herpetofauna, including studies specifically focusing on the effects of roads, and studies that examine life-history traits and demographic sensitivity of the species and taxa in general. We conclude by identifying key knowledge gaps and recommending research efforts for the future.

WHY HERPETOFAUNA?

Herpetofauna, which includes amphibians, snakes, lizards, and turtles, are often reported as road-kill (Fahrig et al. 1995, Houlahan and Findlay 2003). There are several reasons why members of this group may be particularly prone to road mortality compared with other vertebrate taxa. First, many herpetofauna are relatively slow moving, thus raising their risk of mortality on road crossings. This can lead to extremely high rates of mortality (Hels and Buchwald 2001); for example, 100% of 343 turtles attempting to cross a 4-lane highway were killed (Aresco 2005). Second, herpetofauna also tend to require seasonal movements between different habitats, for example to track food resources, breed/nest, or over-winter (Haxton 2000, Roe et al. 2006, Semlitsch and Bodie 2003). Such movements increase the chances of contacting roads (Steen 2003). Third, herpetofauna can also be incredibly numerous (Burton and Likens 1975a, Davic and Welsh Jr. 2004). The high abundance of some herpetofauna is principally because being ectothermic allows a greater allocation of energy to growth and reproduction, rather than using the energy to stay warm. For example, it has been estimated that over 36 billion eastern red-backed salamanders may be found in New York State alone (Gibbs et al. 2007).

WHAT WE KNOW

Life-history strategies and interactions with road mortality

Understanding how differences in the life-histories of organisms relate to their relative susceptibility to changes in their environment is a cornerstone of conserving biodiversity. When we consider the effects of roads on populations of animals, it is important to consider which individuals are more affected. The extent to which the death of any one animal affects the likelihood of a population persisting is unlikely to be equal for all ages or life-history stages. In general, ecological theory suggests that those life-history stages that have the highest levels of variability in abundance in natural populations (relative to the species) are the stages least likely to be driving changes in the viability of populations (Pfister 1998). By focusing on differences in the life-history traits of different taxa and species, and identifying life-history stages that naturally show little variability, we can begin to understand which species and/or stages we may want to be more concerned about in terms of the likely effects of road mortality.

Amphibians exhibit a wide diversity of life-history strategies. For example, frogs and toads tend to be relatively short-lived with high fecundity and frequent breeding (typically every year). Because of the abundance of offspring produced, these species have been shown to have the potential for high density-dependent mortality both in aquatic (Altwegg 2003) and terrestrial (Harper and Semlitsch 2007) life history stages. The result is variable population levels, and susceptibility to environmental stochasticity, but also potential to rapidly recover from a reduction in population (Berven 1990). In contrast, many of the species of salamanders, especially so-called "mole" salamanders (Genus *Ambystoma),* live much longer, reach sexual maturity later, and have lower fecundity (both the number of eggs, and the frequency of breeding). Although their life-history strategy reduces the fluctuations seen in populations, and tends to lead to slower rates of population change, it also means that salamander populations tend to take longer to recover from reduced populations sizes. Research has shown that the differences in life-history traits when comparing between ranid frogs and salamanders lead to very different patterns of susceptibility to loss of terrestrial habitat (Harper and Semlitsch 2007) and that population viability of salamanders may be significantly reduced when annual adult mortality is increased only by 10 % (Gibbs and Shriver 2005).

The habitats used by different amphibian species also play a role in determining road effects. Unsurprisingly, most of the large numbers of amphibians reported killed on roads every year are abundant species that migrate between aquatic and terrestrial habitats, especially bufonid toads, ranid frogs, and ambystomatid salamanders (Ashley and Robinson 1996). Both roads and the wetlands most amphibians and reptiles haunt tend to lie in valley bottoms and often along lakeshores, thereby increasing the likelihood of interactions between roads and herpetofauna. Vagility may also factor in determining the likely effects of roads on amphibians. Studies have also shown that within migratory species of amphibian, those that range farther such as northern leopard frogs are more prone to the effects of roads (Carr and Fahrig 2001). Many amphibians also show intrasexual variability in movement. In general, female amphibians move farther than males (Faccio 2003, McDonough and Paton 2007), suggesting that females are more likely to contact roads and be prone to road-associated mortality.

The interaction between breeding biology and breeding habitat availability sometimes create conditions exacerbating the effects of road-kill on local populations. Pond-breeding amphibians with very short reproduction windows and limited egg-laying site availability will often congregate by the hundreds at the only local breeding pool. When that site is in close proximity to a road, very large numbers of breeding adults can fall victim to cars.

In summary, the susceptibility of amphibian populations to direct road mortality is likely to increase when moving from species with shorter life-spans to more long-lived species; with decreasing annual fecundity; as vagility increases; and for species reliant on both aquatic and terrestrial habitats. Bearing in mind these differences, we now know that populations of amphibians are most sensitive to change in the vital rates of terrestrial life-history stages (Biek et al. 2002, Vonesh and De la Cruz 2002), which are obviously the subject of direct road-mortality. Thus, although we can identify traits that are likely to increase the susceptibility of populations to road effects, we should be concerned about the effects of roads on all species of amphibians.

Turtles form a conspicuous component of the seasonal road-kill in many areas. Like amphibians, the majority of this mortality is among species that annually move between aquatic environments and terrestrial habitat (Ashley and Robinson 1996, McClure 1951), but unlike amphibians, many turtles affected spend most of the time in aquatic habitats, emerging primarily to nest, or to move between ponds. In some cases, the documentation of mortality has revealed some startling data. For example, 612 turtles were counted dead on a single 700 m stretch of road in Florida over the course of a 3 year study (Aresco 2005). The slow travel speed of many turtle species seems to make them especially prone to mortality when crossing highways, with 30% of snapping turtles (*Chelydra serpentina*) observed crossing a road being killed annually in one area (Haxton 2000).

Road mortality is likely a significant concern for many tortoises and freshwater turtles because of their demographic characteristics (Congdon 1993, Congdon et al. 1994). Delaying sexual maturation to a decade or more followed by decades of a low but steady level of egg production characterizes the demography of many turtles. Species such as snapping turtles and Blanding's turtles (*Emydoidea blandingii*), for example, start to reproduce at 10-18 years of age, resulting in susceptibility to as little as 2-3% additive mortality (Brooks et al. 1991, Doroff and Keith 1990, Gibbs and Shriver 2002), i.e., a much lower threshold than is seen for amphibians. In general, turtles are characterized by relatively low survival of early life-history stages such as eggs and hatchlings, and high adult survival (some species of turtle have been shown to live for over a century). Because of this, populations are far more sensitive to changes in adult survival rates than these earlier stages. For this reason turtles conservation efforts focusing on nests or hatchlings rather than juvenile and adult turtles are unlikely to halt population declines (Crouse et al. 1987, Heppell 1998). As road mortality primarily affects juveniles and adults, and may even disproportionately target egg-laying (i.e., reproductively mature) females that are drawn to the roadside margins for nesting (Steen et al. 2006), the effects on populations are likely exacerbated.

Bearing in mind these general life-history traits of turtles, variability between species in this taxa also plays a role in determining road-effects. Research has shown that large-bodied pond turtles and terrestrial turtles species are likely more susceptible to additive mortality than are small-bodied pond turtles such as painted turtles (Gibbs and Shriver 2002). This is partly due to the higher annual fecundity of the latter group (some painted turtles may lay multiple clutches of eggs per year), and the fact that these species reach sexual maturity earlier (e.g., 5-10 years in the case of painted turtles compared with 14-20 years for Blanding's turtle). As with amphibians, vagility can also alter the susceptibility of individuals to roads. Many terrestrial species of turtles make long journeys between isolated wetlands each year, increasing the chances that they will encounter roads. Female turtles are known to roam further than males, and studies have now shown that as roads increase in density and traffic volume, the sex ratio changes such that a higher proportion of males are found (Steen et al. 2006).

As with the other herpetofauna, snakes demonstrate a diversity of life-history strategies. Some species such as garter snakes (*Thamnophis* species) are sexually mature at two years of age and reproduce every year, whereas species such as black ratsnakes reach sexual maturity much later at 8 years of age and may breed less frequently (Row et al. 2007). Although no studies have made specific comparisons between species, less fecund species are likely to be more prone to the effects of roads: A study with black ratsnakes showed that even if only 9 snakes out of a population of 340 were killed by roads annually, the extinction probability for the population over 99 years would increase from 7.3% to 90% (Row et al. 2007).

Unlike the majority of turtles and amphibians, aquatic habitat is not a requirement for most snakes (although some species spend the majority of the time in the water). Snakes do make seasonal movements between habitats, for example to and from winter hibernacula, but in many cases these movements tend to be diffuse, rather than concentrated on specific pathways (Shine et al. 2001). Because of this, snake mortality can be less spatially predictable. Exceptions include species that live in variable environments, for example, species that inhabit wetlands that dry each year. In these cases, when the wetlands dry extremely high mortality has been reported on roads that border aquatic habitat (Bernadino Jr. and Dalrymple 1992). Snake mortality is often highest during periods of migration to and from hibernacula and during the period when snakes are looking for mates (Jochimsen 2005).

Many snakes do move long distances, covering large areas each year. For example female black ratsnakes (*Elaphe obsolete*), and timber rattlesnakes (*Crotalus horridus*) have been reported as moving over 4 km, and garter snakes over 8 km (Blouin-Demers and Weatherhead 2002, Macartney et al. 1988). As with other taxa, inter-specific differences in vagility are likely to influence the likelihood of road mortality, with species moving further being more vulnerable. For example, road mortality accounted for 14-21% of the annual mortality of copperbelly water snakes (*Nerodia erythrogaster neglecta*) (a relatively vagile species), compared to 3-5% of the annual mortality of the more sessile common water snake (*Nerodia sipedon*) (Roe et al. 2006).

Rare species

Quantifying the effects of road mortality on populations is more difficult for rare, long-lived species that may in fact be of greatest concern in relation to road-kill. For example, Row et al. (2007) demonstrated that even though only 3 black rat snakes were killed in 115 road crossings over an 8-year period, there could be significant effects on the long-term viability of the population. Such estimates of population-level effects are obviously prone to a large degree of uncertainty, increasing the need for accurate data relating to these rare mortality events. This problem is exacerbated when a species' life-history results in a relatively low chance of road-kill but the exposure to the risk occurs over long periods of time during each year. For example, turtles with more terrestrial life-history strategies such as box turtles (*Terrapene* spp.), Blanding's, and spotted turtles (*Clemmys guttata*) travel extensively during each year, tracking ephemeral resources such as amphibian egg-masses. During the course of this movement, they may cross roads on a number of occasions, but over a wide area.

Roads and animal behavior

Animal behavior also plays a critical role in determining the effects of roads on herpetofauna. This has been shown to vary depending on both the species, and the nature of the road itself. In cases where roads bisect critical habitat, for example between the aquatic breeding habitat and forested uplands needed by *Ambystoma* salamanders, animals have no choice but to cross the road (Gibbs and Shriver 2005). Where roads present a barrier that can be avoided, for example if a road bisects an area of forest but other terrestrial forested habitat is available, many species of amphibian avoid crossing roads leading to increasing population isolation (Vos and Chardon 1998). The barrier effect forest roads can have on salamanders (deMaynadier and Hunter 2000, Marsh et al. 2004) essentially leads to habitat fragmentation. Snakes have also been documented to avoid crossing roads (Andrews and Gibbons 2005, Shine et al. 2004).

Reduced movement can affect population genetics. Roads act as barriers to gene flow between populations of desert tortoises (*Gopherus agassizii*) in Arizona (Edwards et al. 2004), and lead to reduced polymorphism, lower heterozygosity, decreased fitness, and genetic differentiation among populations of the common frog (*Rana temporaria*) (Hitchings and Beebee 1997, Reh and Seitz 1990) and common toad (*Bufo bufo*) (Hitchings and Beebee 1998). Conversely, environmental factors can prompt large numbers of individuals to make mass movements across roads. When the drying of wetlands instigates snakes to find alternative foraging locations, they have been shown to cross roads *en masse*, resulting in extremely high mortality rates (Bernadino Jr. and Dalrymple 1992). Similar patterns have been observed with some turtles (Aresco 2005).

Behaviors specific to road crossings can also influence road mortality risk. For example, in one study all nine species of snakes tested showed a tendency to cross roads perpendicularly, thus reducing their exposure to vehicles (Andrews and Gibbons 2005). However, for at least three snake and five amphibian species, the risk was increased because they were likely to stop moving in response to a passing vehicle (Andrews and Gibbons 2005, Mazerolle et al. 2005). Data on road crossing frequency, crossing angle, and speed are needed for most amphibian and reptile species currently threatened by road mortality in order to understand how vulnerability varies among species.

Road-effects on regional/metapopulation dynamics

So-called road effects may extend beyond local populations. Many species of herpetofauna are likely to exist as metapopulations, where a group of spatially separated populations interact via inter-population movement. Reduced movement of individuals between populations (both due to avoidance of roads or direct mortality) has been shown to lead to a reduction in the probability of suitable aquatic habitat being occupied by amphibians (Vos and Chardon 1998), and to a reduction in gene flow (Vos et al. 2001). These effects in turn could reduce the overall viability of a metapopulation by decreasing the probability that a population will be "rescued" from extinction, and increasing deleterious effects of inbreeding at the local population level.

Beneficial effects of roads for herpetofauna

Interaction between roads herpetofauna can be positive. The construction of roads and associated roadside ditches/pools may create amphibian breeding or overwintering habitat (Lamoreux and Madison 1999). Similarly, road embankments often create attractive nesting habitat for many turtles. For many snakes, roadside margins provide hunting grounds with numerous insects and small mammals as prey. The roads themselves also can act as warm spots for snakes to bask and thermoregulate (Rosen and Lowe 1994). Many of these purported "advantages" are dubious, given that they are likely to draw animals onto the road surface, and thus increase mortality.

WHAT WE DON'T YET KNOW

Understanding population-level effects

Is road mortality a significant issue for population viability or simply an unfortunate but negligible component of overall mortality? Translating the effects of roads either via direct mortality, or via indirect effects such as habitat degradation, into an understanding of population-level effects is difficult. Previous research shows that population sensitivity to changes in the vital rates of different life-history stages of herpetofauna varies considerably between species and taxa. There is increasing evidence that this sensitivity is also likely to vary within a species depending on factors such as breeding and foraging habitat.

To understand the relative importance of road-mortality on population viability, we need to develop basic population models for species that exhibit a wide-variety of life-history traits. It is remarkable for how few amphibians or reptiles we have sufficient demographic data to even build a simple life table, which could then be used for sensitivity analyses to assess the relative importance of different life-history stages in determining population viability. Finally, comparisons of this sensitivity between species can be used to pinpoint general life-history traits that lead to patterns of susceptibility to road-effects.

Translating road-effects into changes in metapopulation viability may differ greatly from a local population perspective. In many amphibian species, juveniles are the dispersing life-history stage. Thus, although mortality of a juvenile may have less of an effect on local population viability than would loss of a mature adult, it may have a much greater effect on reducing the probability of successful dispersal between populations. To address this problem, metapopulation models can be developed for different species of herpetofauna, with sensitivity analyses used to examine at what point a reduction in dispersal events leads to a reduction in metapopulation viability.

Both local and metapopulation models offer valuable tools for answering specific management questions. For example, in the case of road mitigation, population models can be used to assess how many animals can be killed on a road before population viability is reduced below a specified threshold, or how many animals need to use a wildlife crossing structure for maintenance of metapopulation viability. Importantly, population projection can be used to look at trends in long-lived or rare species. These species may take a long time to respond to road effects, and by the time a decrease in abundance is seen in the field, it may be too late to reverse this trend.

How do we measure road-effects?

We have so far concentrated on the ways in which roads may affect the viability of both local and regional populations, identifying traits that change this level of risk. As discussed, some species (often those that are abundant, short-lived and have high annual fecundity) are less prone to road effects and may be able to withstand a much higher degree of annual additive mortality in the form of road-kill without reducing population viability. Using changes in population viability as a metric of road effects, these species would rank low down on the list of concern. There are, however, other measures of the effects of roads that may be more useful, for example, changes in abundance. These common species annually convey large amounts of biomass and associated nutrients from aquatic to terrestrial systems, and play an important role in nutrient cycling and ecosystem processes (Burton and Likens 1975b, Regester et al. 2006). By extension, a 10% increase in mortality of a large population of frogs may result in literally thousands of animals not arriving at their destination on forested uplands, with the corresponding decrease in availability of prey for species at higher trophic levels, and the resulting loss of ecosystem processes that these animals would have performed.

Changes in behavior in response to roads

One of the crucial aspects of understanding the effects of roads on populations is determining how individual animals respond to the presence of roads. For short-lived species, it is unlikely that many animals were familiar with the landscape before the construction of the road. Nevertheless, many models of road mortality assume that animals disperse equally away from aquatic habitats. As many amphibians have been shown to follow specific migratory pathways, animals that move in the direction of the road may be selected against, whereas those animals that head in a different direction are favored. It remains to be seen whether over time, amphibians may change directionality of migration away from roads in favor of lower risk paths, or if animals eventually migrate shorter distances to avoid crossing roads. For long-lived species such as turtles, many living individuals moved through the landscape before roads were built, especially in newly developed areas. Again, it is not clear whether turtles continue to follow the same pathways after road construction or if they avoid crossing roads when possible.

Effective road mitigation measures

With increased concerns about road mortality, mitigation measures have been developed and implemented particularly in Europe and to a lesser extent in North America. Methods applicable to reptiles and amphibians include fencing, underpasses, signage, traffic calming, and driver education. Unfortunately, relatively little research on the effectiveness of these methods has been conducted so far. To maximize the returns on our conservation investments, the location, components and design of mitigation projects should be chosen based on scientifically sound evaluations.

Given the wide spatial variability in roadkill occurrence, the appropriate location for mitigation measures first needs to be determined, usually through road surveys of live and dead individuals. Locations for mitigation projects have also been identified with the assistance of predictive models based on animal movement behavior, or on the presence of habitat characteristics correlated with high road crossing rates.

The choice of a mitigation project's elements should be based on their ability to meet the project's objectives. For example, what are the shape, dimensions, substrate, water flow, and light conditions that will favor tunnel use? What fence material and height will prevent turtles from trespassing onto a roadway, herding them instead towards a safe passage? Behavioral experiments could explore these questions at relatively little cost, and the results would have broad utility for managers. Once the methods have been chosen, projects should be implemented in the context of a study of their effects. One approach to test a mitigation project's ability to reduce roadkill is to compare changes in roadkill rates at the project site with the changes observed at control sites. Other metrics of success include changes in abundance, survival rate, or other population parameters. The essential final step of this process is to publish the results so that scientists and managers can build upon the knowledge of previous successes and failures. Research has been conducted to look at some of these issues (Aresco 2005, Woltz 2006), but we have only scratched the surface in terms of the data needed to effectively mitigate the effects of roads.

WHAT CAN WE TELL FROM WHAT WE KNOW ALREADY? WHAT DO WE DO NEXT?

Our review highlights a number of common themes with species life-history traits that help in understanding the likely effects of roads on populations of herpetofauna. In general, populations of K-selected species with late reproductive maturity and lower fecundity are more likely to be affected by roads than r-selected species. This holds true both when comparing between taxa (for example most turtles compared to most amphibians), and within taxa (for example the explosive breeding wood frog, compared to the spotted salamander). For amphibians, mortality of later life-history stages, especially adults are most likely to affect local population viability. Juveniles form the dispersing life-history stage for many species, however, and thus from a regional or metapopulation standpoint, ensuring that juveniles are able to cross between populations is vital. All of these statements are relative, however, and in no way are we suggesting that mortality of r-selected species is not of concern. It is also vital to note that many species vary greatly in terms of life-history traits when comparing across a species range, or under different conditions.

The concept of cumulative mortality risk is especially important when comparing differences in life-history traits and population dynamics. It is difficult not to compare the mass mortality seen during many amphibian breeding migrations with the relative scarcity of road-killed land turtles and conclude that the former group is more likely to be detrimentally affected by roads than the latter. Given that many species of amphibian are able to breed at 2 or 3 years of age, however, and many turtles don't breed until they are considerably older, one can see that by the time the turtles reach breeding maturity they have had to withstand many more years of possible mortality. It is the sum of the likelihood of road mortality at any one crossing event, multiplied by the number of crossing events that must be considered when assessing population level effects.

To assess the likely effects of roads on herpetofaunal populations, we advocate models based on a mechanistic understanding of the relationship between animals and their environment, rather than based on species or taxa-specific labels. By understanding this mechanistic link across a range of conditions, including species-specific differences, and intra-species variation, we can develop functional relationships between factors. For example, models could be used to assess the effects of roads on species with low egg and larval survival, high juvenile and adult survival, and limited dispersal ability. These models could be applied to any species in a specific study locale that conform to this suite of factors.

A research agenda

Based on our review, we offer a research agenda specific to herpetofauna to guide future road-effects studies to better understand the road-kill problem and clarify options for intervention (Table 3). We have focused on the types of information required for improving our understanding of the effects of roads on herpetofauna, and modeling approaches based on these data. Issues of experimental design relating to road effects studies have been addressed by (Roedenbeck et al. 2007). Together, refocusing research efforts on these topics could significantly improve our prospects for accommodating reptiles and amphibians in our transportation systems that increasingly pervade the landscape.

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Table 1.1. Estimates of road mortality of amphibians crossing Rt. 23 during the spring breeding season outside Oneonta, New York in 1984-1986 (derived from Wyman 1991).

Species	Number observed crossing road	Percent killed
Wood frog	551	34%
Pickerel frog	201	34%
Spring peeper	308	47%
American toad	53	28%
Eastern newt	277	56%
Spotted salamander	169	73%
Eastern red-backed salamander	4	100%
Total	1563	41%

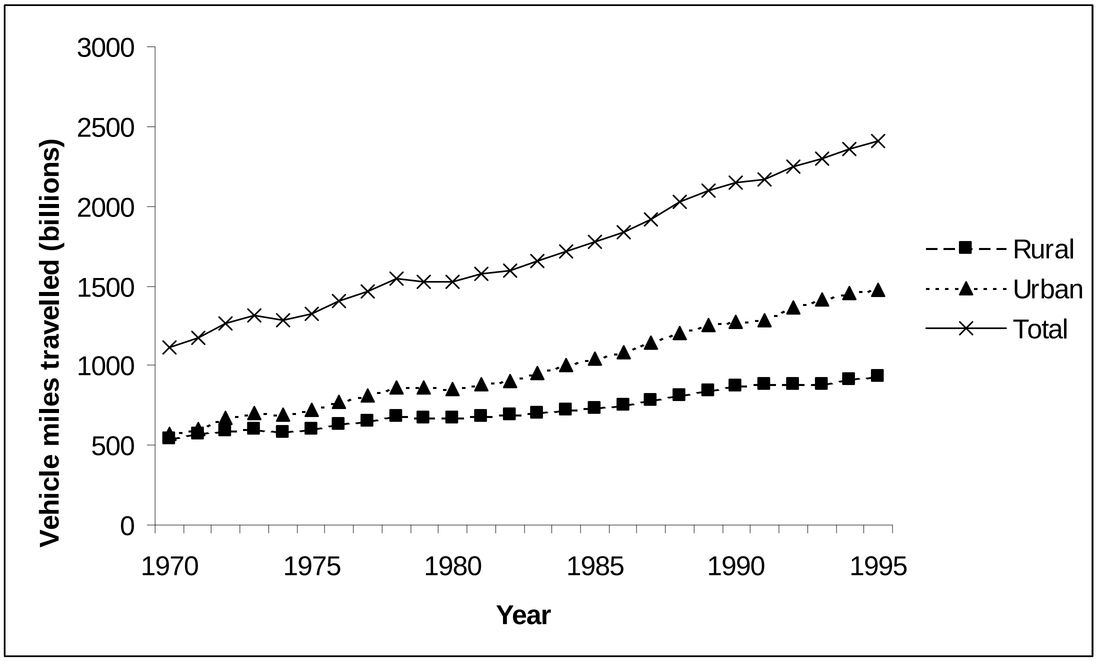
Table 1.2. Estimates of road mortality of reptiles on a 3.6 km stretch of Long-Point Causeway, Lake Erie during a 4-year study (1979-1980 and 1992-1993), adapted from Ashley and Robinson (1996).

Species	Number killed
Painted turtle	341
Spotted turtle	17
Common snapping turtle	272
Eastern garter snake	114
Northern water snake	8
Eastern milk snake	1
Total	743

Table 1.3. A research agenda to better understand the road-kill problem for herpetofauna and to clarify intervention options.

Task	Expected outcome
Field research that assesses the effects of roads on vital rates of life-history stages of different species	Provide input data for structured population models
Develop spatially explicit population models for species of herpetofauna with different life-history traits	Identifies characteristics of vulnerable species, allows the effects of management strategies to be evaluated
Sensitivity/perturbation analyses to develop functional relationships between changes in vital rates, changes in predictor variables (such as road-density, areas of suitable habitat), and trends in populations	Sets targets for management and thresholds for changes in population viability
Examine the response of species' to roads in terms of spatial ecology (habitat use, localized density etc.)	Allows more accurate population models to be developed, including incorporation of density-dependence
Behavior at the scale of road crossings, identifying behavioral traits affecting the roadkill risk (e.g. frequency, angle, and speed)	Allows road mortality to be more accurately included in models
Measure the effectiveness of a) mitigation structures, using behavioral experiments, and b) entire mitigation projects (e.g. whether a tunnel system reduced roadkill incidence)	Identifies the features of mitigation structures that are important for usage. Assesses if mitigation measures have been successful

Figure 1.1.
Trends in road traffic volume (billions of vehicle miles traveled) in the United States from 1970 to 1995 (adapted from Festin 1996)



2. POPULATION STRUCTURE AND MOVEMENTS OF FRESHWATER TURTLES ACROSS A ROAD-DENSITY GRADIENT

ABSTRACT

Understanding interactions between roadways and population structure and movements of wildlife is key to mitigating "road effects" on wildlife associated with increasing urbanization of the landscape. Aquatic turtles are a useful focal group because (1) population persistence is extremely sensitive to mortality of individuals upon roads; (2) turtles frequently move among wetlands and encounter roads, and (3) turtles are an important component of vertebrate biomass in aquatic ecosystems. From 2005-2007, we examined the effects of urbanization on local- and landscape-scale populations of turtles. To do so, we sampled and individually marked turtles in 15 ponds arranged along a sharp, urban-rural gradient in central New York State. We captured 494 turtles, representing 327 individuals, the majority of which were common snapping turtles *Chelydra serpentina* (n = 191) and eastern painted turtles *Chrysemys picta picta* (n = 122). At the local population (pond) scale, a higher proportion of female snapping turtles in ponds was associated with lower road densities within 500m of ponds. The mean size of snapping turtles increased in ponds with more forest, less urbanized area, and a lower density of roads within 100m. At the landscape-level, we observed fewer turtles dispersing through urbanized habitat than forested. Our study suggests that roads alter both local- and landscape-level turtle populations through a loss of female turtles, a decrease in size indicating either slower growth or mortality of older animals, and by reducing movement between ponds. By extension, the study targets key landscape features upon which to focus mitigation efforts.

INTRODUCTION

Transportation networks, especially roadway systems, underpin economic activity and ongoing expansion of urbanization around the world (McDonnell and Pickett 1990) yet roadways have detrimental effects on biodiversity. These effects include direct mortality of migrant individuals crossing roads (Lode 2000; Smith and Dodd 2003) as well as ecosystem degradation (Karraker 2007; Welsh Jr. and Ollivier 1998), loss and fragmentation (Trombulak and Frissell 2000). If a reduced area of habitat is also fragmented, species loss can be exacerbated because once continuous populations act as *de facto* meta-populations, with the survival of the landscape-level populations reliant on continued persistence and movement between local populations (Hanski 1999; Hanski and Gilpin 1991; Levins 1969). Determining how best to balance expanding transportation networks with conserving movements and the effective population sizes of wild species requires understanding the effects of roadways and associated urbanization at both the local and landscape/meta-population level.

Turtles are a taxon thought to be particularly vulnerable to the ecological effects of expanding roadway systems and urbanization. A principal reason for this is the high adult survival and late sexual maturity typical of most species and hence sensitivity of population growth to changes in adult mortality such as that associated with roadways (Congdon 1993; Congdon et al. 1994). Moreover, many turtle species are obligated to move between aquatic and terrestrial habitats each year, mainly to lay eggs and disperse to new areas. Roads established along the interface between these two habitat types (for example, along lake or river shores) are associated with substantial mortality to adult turtles (Aresco 2005b; Ashley and Robinson 1996; Smith and Dodd 2003).

Previous research suggests differential response by turtle species to roads. For example, populations of land turtles are predicted to be more likely to be affected than are small-bodied aquatic species (Gibbs and Shriver 2002). Similarly, female turtles are more prone to road mortality than males due to their tendency to move farther (Steen et al. 2006). This differential mortality between species and sexes could play an important role in determining the effect of roads on both local and regional population levels of turtles but these relationships remain poorly understood.

Reduction in population viability and abundance of turtles is of concern for several reasons. In many aquatic systems, turtles play an important role in predation and scavenging (Steyermark et al. 2008). Turtles can also attain extremely high biomass. For example herbivorous turtles can maintain 583.5 kg/ha compared with 280 kg/ha for large mammals and 477 kg/ha for fish (Iverson 1982). Thus, ecological importance combined with vulnerability to increased adult mortality associated with roads make turtles a useful focus for efforts to seek a balance between ongoing urban development and maintenance the integrity of ecosystems and key biodiversity components.

In this study, we assessed the effects of roads on turtle populations across an abrupt, urban-rural gradient of road density in central New York State. The objectives of our research were: (1) to determine if two key attributes of local populations of turtles -- sex ratio and size/age-structure -- differed depending on the nature of disturbance, including roadway development of habitat surrounding their aquatic breeding ponds; and (2) to assess the effects of roadways on inter-population movement between ponds. To evaluate the role of interspecific variation in life-history traits on the effects of roads, we compared the responses of two species of aquatic turtles, one more sedentary than the other. We hypothesized that turtles occupying ponds surrounded by greater urban development would be younger and hence smaller, with the sex-ratio in these populations being male-skewed. We also predicted that turtles would avoid moving through more heavily roaded habitats, resulting in a reduction in the connectivity between ponds in more urbanized environments. When considering differences between the sedentary and more mobile turtle species, we predicted that the wider-ranging turtle would be more vulnerable to the effects of urban development and habitat change because of its increased likelihood of being exposed to roadways.

METHODS

Study area:

This study was conducted in a network of 15 ponds in Baldwinsville, New York (Fig. 1). The pond network spanned the Radisson Community, a suburban housing development, and the adjacent Three Rivers Wildlife Management Area, with all ponds were contained within a small (~7km^2) area. The location of the wildlife protection area, immediately adjacent to the housing development, minimized landscape heterogeneity while allowing us to concentrate on the variable of interest, that is, road density associated with urbanization. It also permitted us to track via mark-recapture methods movements of individual turtles in relation to location of roads, an approach that requires a network of adjacent ponds.

Focal species

We focused on two species with contrasting life histories: the common snapping turtle and the painted turtle. The common snapping turtle is an abundant, large-bodied species (sexual maturation not reached until 20 cm carapace length) that ranges from southern Quebec to Ecuador (Gibbs et al. 2007; Steyermark et al. 2008). Snapping turtles occupy almost all freshwater habitats including lakes, ponds, and slow-flowing rivers. Females emerge from the water to lay eggs in May-June, and may migrate over 2 km to nesting sites (Pettit et al. 1995).

The eastern painted turtle is also abundant but smaller than the snapping turtle (sexual reproduction reached at about 10 cm carapace length) and is found in almost all slow-moving freshwater aquatic habitats (Gibbs et al. 2007). The species is active from May to November in New York State, with nesting peaking in June, although females may produce multiple clutches of eggs per year (Gibbs et al. 2007). Overland movement of females is primarily related to nesting, whereas males may move between aquatic habitats in spring and early summer (Gibbs et al. 2007). Maximum reported overland movement distance for this species is 625m in Quebec (Christens and Bider 1987). Females typically reach maturity in 5-10 years (NatureServe 2006).

Turtle surveys:

Surveys were conducted from 12 July to 18 August 18 2005, 12 July 12 to 9 August 2006, and 25 June to 2 August 2007. During each of these years, 12 ponds were surveyed twice, with each sampling period lasting four trap nights. Three additional ponds were only surveyed in one or two of the years; inconsistent sampling effort in these ponds was caused by vandalism to traps (these data were excluded from some analyses as indicated below). During each sampling period, 4 to 6 hoop nets (~1m in diameter with 2.5cm net size) were baited with sardines and placed >10m apart at each pond. Each trap was checked daily, for a total of 1772 trap nights (32-40 trap nights/pond/year). All turtles captured were identified to species, and sexed using external secondary sexual characteristics (Gibbs et al. 2007). Measurements were also taken of straight-line carapace length (from the tips of the longest marginal scutes for snapping turtles). All turtles captured were individually marked using notching on the marginal scutes of the carapace.

Characteristics of ponds and surrounding terrestrial habitat:

Characteristics of breeding ponds and the surrounding terrestrial area were gathered from National Wetlands Inventory Freshwater data (NWI) and the National Land-Cover Database (NLCD 2001) (Homer et al. 2004). Information on roads was based on the New York State Office of Cyber Security and Critical Infrastructure Coordination (CSCIC) as part of the Accident Location Information System (ALIS). All layers were set to a common co-ordinate system (Universal Transverse Mercator Zone 18 North), and datum (North American Datum 1983). Land cover categories were grouped into developed land (developed open space, low intensity and medium intensity); forested land (deciduous, coniferous and mixed forest excluding forested wetlands); agriculture and recreational grasslands (pasture, cultivated crops and urban recreational grass); and wetlands (palustrine forested and palustrine shrub-scrub). To place our study site in the context of urbanization levels across the region, we randomly generated 1000, 500m-radius circles in upstate New York (an area encompassing urban areas such as Albany and Syracuse and rural areas such as the Tug Hill Plateau), and calculated the linear distance of roads and areas of forest and developed land within these samples (excluding samples where more than 50% of the area fell in open water).

Local populations (individual ponds):

To compare among the attributes of local turtle populations, namely proportion of females in the population and the size of individuals, we used data on individual turtles captured for the first time. The size of turtles was used as a relative index of turtle age as the size of turtles has been shown to increase reliably with age (Gibbons et al. 1981; Wilbur 1975). Ponds with total turtle captures <5 were excluded from analyses. To relate sex ratios and ages of turtles to the habitat surrounding each pond, we explored a suite of *a priori* models relating to the level of urbanization within 100 and 500m buffers. The closer distance (100m) was chosen to capture the effects of urbanization on the majority of turtle movements (observational data from the sites suggests that many turtles nest with a few meters of the pond margins). The larger buffer zone was chosen to include the effects of urbanization on longer-distance movements, for example, females that lay eggs further from the edge of ponds.

We used Program R version 2.4.1. (R Development Core Team 2006) for all statistical tests and Akaike's Information Criterion (AIC) to select models that provided the best fit to the data with the minimum number of parameters. To assess the role of urbanization on the sex ratio of turtles in each of the ponds, we compared the proportion of female turtles in each population to variables in each model using general linear models with binomial errors. To compare the size of turtles in each pond we used multiple regressions that related mean turtle size to associated habitat variables.

Landscape-level population:

To examine factors governing movement of turtles between local populations, we developed a series of *a priori* predictive models, with logistic regression used to relate the occurrence and absence of detected inter-pond movement between each pair of ponds to explanatory variables. AIC was then used to select the model that best explained the patterns observed. We excluded ponds not sampled each year of the study, allowing us to assume an equal probability of not detecting movement of turtles to each of the ponds (i.e., false absences). Because our data represent detections of movement only by marked turtles, they estimate relative probability of movement between ponds, rather than actual frequency of such movements per population.

As the terrestrial habitat between ponds represents an important factor potentially influencing movement, we converted terrestrial habitat surrounding ponds into a resistance surface (Ricketts 2001). With this technique, each habitat type in a landscape is assigned a "resistance" value based on the willingness of animals to cross the habitat type, the physiological cost incurred during this crossing, and the reduction in survival for the individual (Joly et al. 2003; Ray et al. 2002). The values and literature data on which these estimates were based for each species are shown in Table 1. The cost-distance function in ArcGIS version 9.0 was used to calculate the minimum cost-distance between each pair of ponds (based on the cumulative resistance values over the distance between the ponds), with this value used as the determinant variable, "habitat suitability," in models. In our model turtles could use wetlands to move between ponds without incurring "cost;" thus where riparian corridors were available, large distances could be covered with a low cost compared with much shorter distances overland. To incorporate the potential effects of roads as a source of disconnectivity among ponds, we calculated the number of roads occurring between each pair of ponds.

RESULTS

Summary of captures and urban-rural gradient:

Turtle captures totaled 494, representing 327 individuals. The majority of these were the common snapping turtle (n = 191) and eastern painted turtle (n = 122), but also sampled were 14 common musk turtles, *Sternotherus odoratus*, low numbers of which resulted in their exclusion from analyses. In comparing the urban-rural gradient found in our study area with New York State in general, the maximum length of road found within a 500m buffer surrounding our study ponds was in the 99th percentile compared with our random sample, the lowest forest cover was in the 24th percentile and the maximum amount of developed land coverage was in the 98th percentile.

Local populations:

Our samples of both species' were male-skewed: mean proportion males in the snapping turtle sample = 0.55 ± 0.17, range 0.25-0.83, number of ponds = 14; painted turtle 0.62 ± 0.08, 0.47-0.70, n = 8). The proportion of female snapping turtles was related to the linear distance of roads within a 500m buffer of the pond (Table 2, $P<0.05$), with a higher proportion of female turtles in ponds surrounded by fewer roads (Fig. 2). The proportion of female painted turtles in populations was also best explained by the amount of roads within 500m of the pond, with more females in ponds surrounded by less road extent (Table 3), although roads within 100m of the pond followed closely as a second-best model. None of the predictor variables were related (at $\alpha \leq 0.05$) to sex ratio variation in these models for either species.

Size of both snapping turtles (mean carapace length 27.4cm ± 2.5) and painted turtles (13.1cm ± 1.4) varied among ponds. For snapping turtles, this variation was best explained by the interaction between forest, developed, and road cover (*P*<0.01) within a 100m buffer (Table 4), with larger turtles occurring in ponds with more forest, less urban area, and a lower density of roads. For painted turtles, the best fitting model also included the proportion of forest and developed cover within 100m, although no individual variables were significant predictors (Table 5). For this species, turtles were smaller on average in ponds with more forest cover within 100m (*P*=0.055). The proportion of developed area contributed little to the model (*P*=0.700). Because of the smaller sample size of ponds with sufficient turtles for size-analyses, we were unable to assess models with 3-way interaction terms.

Landscape-level populations:
We recorded 29 inter-pond movements by snapping turtles, and 8 by painted turtles. These movements represented 22 individual snapping turtles and 8 individual painted turtles, i.e., 12% of marked snapping turtles moved and 7% of painted turtles. Of these movements, 24 snapping turtles moved between ponds that were sampled in every year of the survey and could be included in analyses, and 5 painted turtles. Because of the low sample size for the latter, we focused our analyses on snapping turtles. Logistic regression coupled with AIC identified four models as the best predictors of movement by snapping turtles (Table 6). Explanatory variables in these models included (1) the suitability of habitat between ponds, with fewer turtles dispersing through poorer quality habitat, (2) the size of local populations, with more turtles dispersing from larger populations, (3) and the distance between ponds, with the probability of dispersal decreasing as the distance between ponds increased.

DISCUSSION

Overall effects of urbanization on turtles:
Our results support the findings of previous research in showing that urbanization affects pond-turtle populations at both the local (Marchand and Litvaitis 2004) and landscape scale (Gibbs and Shriver 2002). Characteristics of terrestrial habitat including road-density, loss of forested habitat, and an overall decrease in habitat suitability were all related to demographic variables associated with the long-term viability of turtle populations, namely sex-ratios, size/age distributions and connectivity between ponds.

Local populations:
As expected from previous research, we found a higher proportion of female snapping and painted turtles in populations with lower road-densities (Aresco 2005a; Gibbs and Shriver 2002; Gibbs and Steen 2005; Marchand and Litvaitis 2004). It is important to note, however, that the overall male-bias in captures was likely to be at least partially a function of capture method used; hoop-nets preferentially sample males (Ream and Ream 1966). This said, road-mortality of pond-breeding turtles has been well-documented (Aresco 2005b; Haxton 2000), with females being more vulnerable due to both their longer movements during nesting and the suitability of many highway shoulders for nest sites (Aresco 2005a; Steen et al. 2006). In our study, forest and developed land cover as well as road-density surrounding ponds influenced mean size of turtles, although only the size of snapping turtles was significantly related to predictor variables. For this species, the mean size of turtle decreased as the number of roads and area of developed land surrounding the pond at 100m increased. This result could be indicative of either slower growth rates in these populations, or a higher proportion of younger (and therefore smaller) animals. Previous research supports the latter conclusion, with a higher proportion of adults compared with juveniles found in populations of both painted turtles (Marchand and Litvaitis 2004) and wood turtles (Saumure and Bider 1998) in less forested landscapes, and slower growth rates seen in turtle populations in deforested areas (Saumure and Bider 1998).

Differences between species:
Previous studies of the effects of habitat change on turtle populations have clearly demonstrated the role of variability in life-history traits in determining the relative vulnerability of different species (Gibbs and Shriver 2002; Rizkalla and Swihart 2006). We did not observe this pattern in our study, however: The two study species examined – snapping and painted turtles -- did not appear to differ in the scale at which they responded to habitat change, with the same factors predicting variation in sex-ratio and body size in our analyses. This finding is unexpected given differences in the relative vagility of the two species. Snapping turtles have been reported as moving up to 2.2 km overland (Brown and Brooks 1994), whereas the maximum movement distance reported for painted turtles is 621m, with most turtles moving much shorter distances (Christens and Bider 1987; Congdon and Gatten 1989). We did observe a higher proportion of our marked snapping turtles making inter-pond movement (12% of snapping turtles c.f. 7% of painted turtles), indicating that snapping turtles were the more vagile of the two species in our study area.

Landscape-level populations:
Our four competing models best explaining inter-pond movement included the quality of terrestrial habitat between ponds, straight-line distance, and the relative size of local populations. Bowne et al. (2006) found that the distance between ponds influenced the likelihood of movement of painted turtles, but that the quality of matrix habitat did not. The landscape in our own study area, i.e., a matrix of urban and forest, is likely much more heterogeneous in terms of habitat quality than the agricultural landscape in which Bowne et al. conducted their study. Notably, in contrast to Bowne et al. (2006) we also observed relatively lower frequencies of inter-pond movement (46% of painted turtles recaptured in the aforementioned study had moved between ponds, compared with 22% of marked snapping turtles and 28% of marked painted turtles in our own study). Pond turtles are known to move to track ephemeral resources including food and water, and when making nesting and overwintering movements (Bodie and Semlitsch 2000; Bowne et al. 2006; Gibbons et al. 1983; Joyal et al. 2001). None of the ponds in the study area dried during our research, thus removing one of the most pressing motivations for inter-pond movement.

Implications for conservation of pond-turtles in urbanizing landscapes:
It is important to note that the urban-rural gradient focused on in our study was pronounced and typical of the most heavily urbanized parts of the region in terms of road density and the developed-land coverage. There are many areas in the region, however, with more forest loss. Thus, the differences seen in turtle populations in our study are likely to typical of urbanized areas, at least in the northeastern United States

Although our results demonstrate that urbanization has the potential to reduce the long-term viability of turtle populations, whether the differences seen in vital rates across our study site are sufficiently pronounced to have actually caused such a reduction is less clear. Although we detected statistical differences in sex ratios and the size of turtles, these differences amount to a range in the proportion of male turtles in populations from 25% to 83% for snapping turtles and 47% to 70% for painted turtles. Similarly, the mean carapace length of snapping turtles from the population with the largest average size to that with the smallest decreased by 21.4% and painted turtle size declined by 27.0%. We suggest that spatially explicit population models incorporating both local and regional population dynamics would be an appropriate next step in evaluating the implications for these differences in vital rates on the viability of local and regional populations. Our study also demonstrates the synergistic effects that urbanization can have on populations of turtles. For example, the effects of habitat loss due to removal of forests may be exacerbated by increased mortality due to roads. These results suggest that the combined effects of urbanization may have more profound effects on both local and regional populations of turtles than might be expected based on focusing on a single component of habitat change.

Overall conservation of animal populations in urbanizing landscapes:
Our results contribute to a wider discussion of the effects of urbanization on animal populations. Research has shown that other taxa such as amphibians demonstrate similar responses to those observed in our turtle populations, including reduced abundance in urban compared with forested or agriculture areas (Gagne and Fahrig 2007), and reduced movement across roads (deMaynadier and Hunter 2000). The implications of these changes for population viability have also been demonstrated. For example, amphibian diversity and species occupancy has been shown to decrease in ponds in urban landscapes with reduced forest cover and an increase in road density (Gagne and Fahrig 2007; Houlahan and Findlay 2003; Vos and Chardon 1998), with some common species such as the American toad, *Bufo americanus* and spring peeper, *Pseudacris crucifer*, particularly sensitive to urban development (Gibbs et al. 2005).

Patterns observed in the responses of other taxa to urbanization differ from herpetofauna, however. For example, avian communities in large patches of undisturbed habitats are often characterized by a high diversity of low-abundance species, with urbanization leading to a reversal of this pattern, i.e., to a few, highly-abundant species (Crooks et al. 2004; Francois et al. 2008; Savard et al. 2000). The differences in the sensitivity of taxa to urbanization are reflective of variation in life-history traits, and particularly how these traits allow adaptation in the face of habitat change. For example, birds that have a narrow range of ecological tolerance are more prone to the effects of urbanization (Bonier et al. 2007). Understanding the relationships between life-history traits and the types of changes in habitat associated with urbanization can help conservation efforts, both by highlighting species and taxa that are likely to be particularly sensitive, and by suggesting avenues for development compatible with maintaining biological diversity such as maintaining large areas of undisturbed habitat and corridors for dispersal.

Table 2.1. Habitat resistance values assigned to each category of the National Land Cover Database 2001 for turtles. Based on available literature[1, 2] habitats for both species were assumed the same. Values range from 0 (most suitable) to 50 (least suitable). A value of 0 (i.e., no cost to movement) was used for the most suitable habitat, as it was considered to actually encourage movement.

NLCD class code and definition	Resistance value
11 Open water	5
21 Developed open space	10
22 Developed low intensity	15
23 Developed medium intensity	30
24 Developed high intensity	50
31 Barren lands	10
41 Deciduous forest	10
42 Evergreen forest	10
43 Mixed forest	10
52 Shrub/scrub	10
71 Grassland/herbaceous	10
81 Pasture/hay	10
82 Cultivated crops	10
90 Woody wetlands	5
95 Emergent herbaceous wetlands	5

[1] Resistance values for snapping turtles are based on the following resources: (Brown and Brooks 1994; Pettit et al. 1995; Steyermark et al. 2008; Ultsch 2006)
[2] Resistance values for snapping turtles are based on the following resources: (Baldwin et al. 2004; Christens and Bider 1987; Rowe 2003; Ultsch 2006)

Table 2.2. Results of candidate models developed using binomial general linear models for predicting the proportion of female snapping turtles in populations in the vicinity of Baldwinsville, central New York State. Models with multiple variables included all interactions. Variables included in models are total road length within buffer (“road”), proportion of buffer made up of developed land (“develop”), and the proportion forest (“forest)

Model	Variables[1]	Residual deviance	AIC	ΔAIC
Road within 500m	Road 500m *	12.031	54.820	0
Road within 100m	Road 100m	13.930	56.719	1.899
Land-cover within 100m	Develop 100m Forest 100m	10.263	57.052	2.232
Land-cover within 500m	Develop 500m Forest 500m	10.838	57.627	2.807
Urbanization within 100m	Road 100m Develop 100m Forest 100m	3.963	58.752	3.932
Urbanization within 500m	Road 500m Develop 500m Forest 500m	7.217	62.006	7.186

[1] Significance of variables is indicated as follows *** <0.001, **<0.01, *<0.05

Table 2.3. Results of candidate models developed using binomial general linear models for predicting the proportion of female painted turtles in populations in the vicinity of Baldwinsville, central New York State. Models with multiple variables included all interactions. Variables included in models are total road length within buffer ("road"), proportion of buffer made up of developed land ("develop"), and the proportion forest ("forest").

Model	Variables[1]	Residual deviance	AIC	ΔAIC
Road within 500m	Road 500m	0.994	26.22	0
Road within 100m	Road 100m	1.691	26.916	0.696
Land-cover within 100m	Develop 100m Forest 100m	1.165	30.39	4.170
Land-cover within 500m	Develop 500m Forest 500m	1.297	30.522	4.302
Urbanization within 100m	Road 100m Develop 100m Forest 100m	0.886	34.111	7.891
Urbanization within 500m	Road 500m Develop 500m Forest 500m	0.001	35.225	9.005

[1] Significance of variables is indicated as follows *** <0.001, **<0.01, *<0.05

Table 2.4. Results of candidate models developed using multiple regression for predicting the size of snapping turtles in populations in the vicinity of Baldwinsville, central New York State. Models with multiple variables included all interactions (indicated by ': '). Variables included in models are total road length within buffer ("road"), proportion of buffer made up of developed land ("develop"), and the proportion forest ("forest").

Model	Variables[1]	*F*-stat.	Adjusted R^2	AIC	ΔAIC
Urbanization within 100m	Road 100m* Develop 100m** Forest 100m Forest 100m:Develop 100m* Forest 100m:Roads 100m** Develop 100m:Roads 100m** Forest 100m: Develop 100m:Roads 100m**	8.399	0.799	102.28	0
Road within 100m	Road 100m	0.755	<0.001	122.73	20.45
Road within 500m	Road 500m	0.100	<0.001	123.47	21.19
Land-cover within 100m	Develop 100m Forest 100m Develop 100m:Forest 100m	0.536	<0.001	125.5	23.22
Land-cover within 500m	Develop 500m Forest 500m	0.118	<0.001	127.1	24.82
Urbanization within 500m	Road 500m Develop 500m Forest 500m Forest 500m:Road 500m	0.175	<0.001	132.99	30.71

[1] Significance of variables is indicated as follows *** <0.001, **<0.01, *<0.05

Table 2.5. Results of candidate models developed using multiple regression for predicting the size of painted turtles in populations in the vicinity of Baldwinsville, central New York State. Models with multiple variables included all interactions (indicated by ': '). Variables included in models are total road length within buffer ("road"), proportion of buffer made up of developed land ("develop"), and the proportion forest ("forest").

Model	Variables[1]	*F*-stat.	Adjusted R^2	AIC	ΔAIC
Land-cover within 100m	Develop 100m Forest 100m	5.444	0.656	59.332	0
Land-cover within 500m	Develop 500m Forest 500m	3.895	0.554	61.408	2.076
Road within 500m	Road 500m	1.872	0.111	66.167	6.835
Road within 100m	Road 100m	0.626	<0.001	67.545	8.213

[1] Significance of variables is indicated as follows *** <0.001, **<0.01, *<0.05

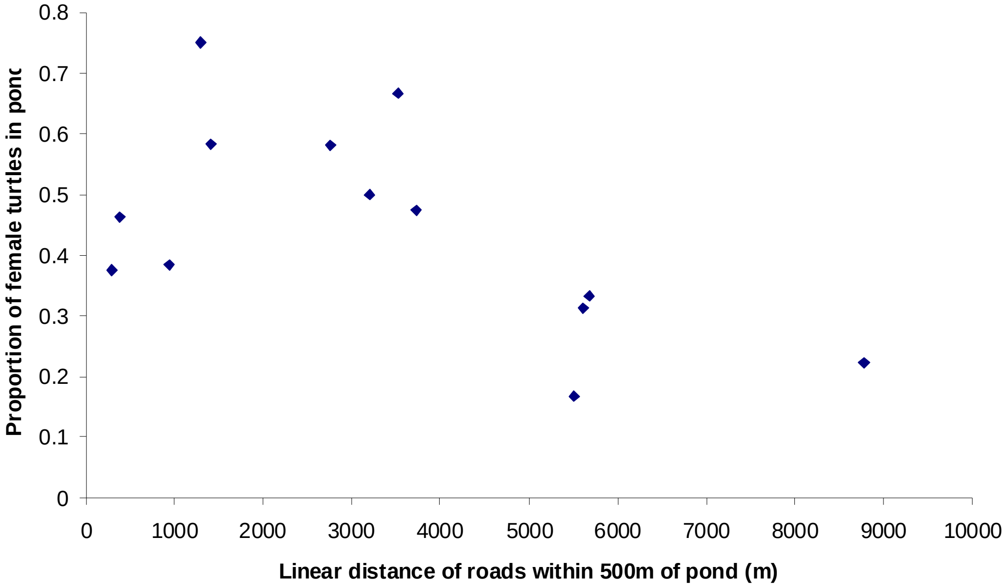
Table 2.6. Results of candidate models developed using binomial general linear models for predicting the likelihood of snapping turtles moving between ponds in the vicinity of Baldwinsville, central New York State. Models with multiple variables included all interactions except for inclusion of population size. The mean number of unmarked captures of each species per 100 trap-nights per year in the pond of origin was used as a relative measure of "Population size". "Distance" refers to the Euclidean distance between ponds; "Habitat suitability" is the cumulative cost-distance between ponds based on distance and habitat suitability; "Roads" the number of roads crossed by a straight line between each pair of ponds.

Model	Variables[1]	Residual deviance	AIC	ΔAIC
Habitat suitability	Habitat suitability*	127.27	131.27	0
Population size_distance	Population size Distance	124.37	132.37	1.1
Distance	Distance*	128.54	132.54	1.27
Population size_habitat suitability	Population size Habitat suitability	124.77	132.77	1.5
Roads	Roads	129.29	133.29	2.02
Population size	Population size*	129.38	133.38	2.11
Population size_roads	Population size Roads	125.87	133.87	2.6
Population size_urbanization	Population size Habitat suitability Roads	122.95	138.95	7.68

[1] Significance of variables is indicated as follows *** <0.001, **<0.01, *<0.05

Figure 2.1. Location of turtle study ponds (shown as gray circles) in the vicinity of Baldwinsville, central New York State. The Three Rivers Wildlife Management Area is located in the top left of the map, with the Radisson suburban development occupying the southern portion.

Figure 2.2. Trend in the proportion of female snapping turtles found in ponds in the vicinity of Baldwinsville, central New York State in relation to the linear distance of roads within a 500m buffer of each pond.



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3. SNAKE OCCURRENCES IN GRASSLAND ASSOCIATED WITH ROAD VERSUS FOREST EDGES

ABSTRACT

Roads cause direct mortality of animals but less is known about how this mortality translates into changes in populations. This is particularly true for snakes, which have been subject to little research at the population level compared to other taxa. We studied the effects of proximity to a heavily travelled road on snake populations in three old-field sites at Cicero Swamp Wildlife Management Area in Cicero, New York. We conducted 26 surveys of snakes from June to August 2006 on a regular grid of coverboards at different distances from the road and nearest forest edge and measured the microclimate at each coverboard. Adult Common Gartersnakes, *Thamnophis sirtalis*, and Northern Brown Snakes, *Storeria dekayi dekayi,* occurred independently of distance from the road but were more abundant farther from the forest edge. Lack of a 'road effect' could be due to either snakes avoiding crossing roads, or mortality events being rare whereas Increased abundance of snakes farther from the forest edge suggests that snakes prefer sites that receive direct sunlight for longer periods of the day.

INTRODUCTION

Roads have ecological effects on approximately one-fifth of the conterminous United States (Forman & Deblinger 2000). Although the consequences of roads for individual animals are well-documented, for example direct mortality (Ashley & Robinson 1996; Seibert & Conover 1991; Smith & Dodd 2003), less is known about how these effects translate into changes in populations. This is particularly true for snakes, which have been subject to relatively little research compared to other taxa (Bonnet et al. 2002) despite playing an important role in ecosystems as both predators and prey (Lind et al. 2005).

Road traffic has been shown to be a significant cause of mortality to snakes (Bernadino Jr. & Dalrymple 1992; Bonnet et al. 1999). This mortality may also reduce population viability. For example, Row et al. (2007) reported that if 9 out of population of 340 Black Ratsnakes, *Elaphe obsolete*, were killed annually by roads, the extinction probability over 500 years would increase from 7.3 to 90%. When considering the effects of roads on snake behavior, many species of snakes avoid crossing roads (Andrews & Gibbons 2005), and when they do so, they tend to cross in the most direct fashion possible (Shine et al. 2004). Interspecific variation in the responses of snakes to roads also represents an important factor when predicting the likely effects of roads on snake populations (Andrews & Gibbons 2005; Bonnet et al. 1999; Jochimsen 2005).

Our objective was to better understand potential population-level effects of roads on snake populations. To this end, we examined the spatial distribution of different members of a snake community occupying old fields (maintained grassland once used for agriculture). We predicted that there would be a reduced abundance of snakes close to the road edge, either due to behavioral avoidance of the road or an increased risk of mortality. We also predicted that the effects of roads on snakes might vary depending on differences in life-history strategy. To test this hypothesis, we contrasted relative abundance and probability of occurrence in relation to proximity to roads while controlling for variation in microhabitat. In addition to the influence of road-proximity in defining the spatial distribution of snakes, we were also interested in the potential role of a non-lethal edge, namely the forest-field interface. The habitat selection of snakes is known to vary in relation to forest edge due to both the need to thermoregulate (Row & Blouin-Demers 2006) and the potential for greater food availability along edges (Blouin-Demers & Weatherhead 2001).

Based on the increase shading close to the forest edge and the apparent abundance of potential prey throughout the old-field sites, we predicted that there would be a higher abundance of snakes farther from the forest edge.

MATERIALS AND METHODS:

Study site

Our research was conducted at three old-field sites in Cicero Swamp Wildlife Management Area in Cicero, New York (Lat. 43.151284° Long. -76.057558°). The sites were arrayed along Island Road, a two-lane paved rural road with a 45 mph average speed. The grasslands are mowed each year. Nearby fields were chosen (within 1 km of one another) to control for large-scale environmental heterogeneity among sites.

Sampling design

We sampled snake occurrence using metal road signs (0.7 X 0.7 m) as coverboards. Signs were arranged in a regular grid of rows (parallel to the forest edge) and columns (parallel to the road). The distance between columns farther from the road was increased to test for the possibility of road-effects at long distances. All coverboards on rows were spaced at 15 m intervals from one another, beginning within 10 m of the forest edge (the exact position varied as the forest-field boundary was slightly irregular). The distance of the closest column to the road varied slightly depending on the topography of the road-field interface at each site: At the northernmost field we placed 36 cover sheets in six columns, with the first column at 5 m from the road, and subsequent columns at 20, 35, 50, 65, and 105 m. At the middle field, we placed 50 coverboards in 10 columns with the first column at 6 m from the road's edge, and subsequent columns at 21, 36, 51, 66, 106, 206, 306, 406, and 506 m. At the southernmost field, we placed 52 coverboards in seven columns with the closest column at 10 m from the road, and subsequent columns at 25, 40, 55, 70, 110, 210, 310, 410, 510, and 610 m.

Snake Surveys

We conducted 26 surveys of all coverboards at each field from June 1, 2006 to August 27, 2006. Surveys were made between 0630 and 1200 with the order of fields and survey direction in each field (starting nearest versus furthest from the road) assigned at random each day to obviate the need to include sampling co-variates in our analyses. We recorded number of snakes of each species and estimated life stage (juvenile [≤ 20 cm in length and circumference ≤ that of a pencil] or adult).

Habitat Characterization

To assess the role of habitat on the distribution of snakes we recorded a suite of microhabitat parameters once at each coverboard, from September 14-16, 2006. Mean height density of vegetation was estimated using the height at which a PVC pipe placed upright in the vegetation at 1 m from each of the four corners of a coverboard was obscured (modified from Ribic & Sample 2001). Leaf litter accumulation was based on the mean of leaf litter depth at 0.5 m from each corner of each coverboard. Percent coverage of grass, forbs, and bare/sparse vegetation was estimated in a concentric square (2.1 X 2.1 m) surrounding each coverboard. Any patch of vegetation, grass or forbs with a height-at-density 20 cm or lower, was categorized as bare/sparse vegetation. To estimate soil moisture, we categorized each coverboard as covering mostly dry soil (no water produced when pressure applied), damp soil (water produced when pressure applied), mud (watery soil mix that failed to form aggregate), or standing water.

Statistical analyses

We developed four *a priori* candidate models to explain the distribution of snakes observed under coverboards. These models included the distance from the road, distance from forest edge, the combined effects of these two variables and microclimate. We only included microclimate in models with the principle variables of interest, namely forest and road edges, if it was initially found to be a significant factor. Akaike Information Criterion were used to select the models that best explained the data with a minimum number of parameters. For abundant snake species, negative binomial regressions were used to relate relative abundance of individuals (mean number of observations per 100 coverboard nights) at a coverboard to habitat factors. For rarely encountered snake species, logistic regression was used to compare patterns of presence/absence. All statistical analyses were conducted using Program R version 2.4.1. (R Development Core Team 2006).

RESULTS

A total of 1400 observations of four species of snake were made during the season (Table 1): Common Gartersnakes, *Thamnophis sirtalis*, (80.9% of observations), Northern Brown Snakes, *Storeria dekayi dekayi*, (18.1%), Eastern Milk Snakes, *Lampropeltis triangulum triangulum* (1.1%), and northern water snakes, *Nerodia sipedon sipedon*, (0.5%). Because juvenile snakes tended to be highly clustered under coverboards, counts were statistically dependent, thus we restricted our analyses to adult snakes. We also excluded eastern Milk Snakes and Northern Water Snakes from analyses due to the extremely low number of observations.

Adult Gartersnakes were encountered at all distances from both the road and the forest edges. Negative binomial regression indicated that the model with the best explanatory power included both the distance from the nearest forest and road edge, although only the forest term was significant (Table 2). Based on this model, there was a strong increase in the number of adult Gartersnakes found farther from the forest edge. Microclimate surrounding the coverboards was not related to the abundance of adult Gartersnakes. For adult Brown Snakes distance of coverboards from the nearest forest edge was the only significant explanatory variable (Table 3), with no relationship between the occurrence of this species and the distance from the nearest road edge, or the microclimate immediately surrounding the coverboard.

DISCUSSION

We found no evidence to support the hypothesis that the distance from the road influenced the spatial distribution of snakes in old fields. We did find more adult Gartersnakes and a higher probability of occurrence of Brown Snakes farther from the forest edge as predicted. The latter result supports the theory that increased shading at the forest edge results in a lower thermal quality for snakes (i.e., a larger difference between the environmental temperature and the optimal temperature for the animal), thus it is less costly energetically for snakes to thermoregulate in open habitat. This has been shown for other species including Eastern Milk Snakes (Row & Blouin-Demers 2006). However, research on Black Ratsnakes in Ontario, Canada, suggests that open areas present the least favorable thermal habitat, being too cold at night and too hot during the day, and that forest edges should be most favorable (Blouin-Demers & Weatherhead 2002). In addition to thermoregulation, snakes may also select habitat based on the abundance of prey (Madsen & Shine 1996) and avoidance of predation. All of these variables provide valid hypotheses for the distribution of snakes we observed, but were not addressed in this study.

The lack of a noticeable decrease in observations of Gartersnakes and presence of Brown Snakes closer to the road was unexpected given that previous studies have documented a relatively high frequency of road mortality of Gartersnakes compared to other species of snake (Ashley & Robinson 1996; McClure 1951) and at least some mortality of brown snake species (Gibson & Merkle 2004; Smith & Dodd 2003). The closest coverboards to the road were well within the reported home-range size of both species (Macartney et al. 1988), suggesting that individuals associated with coverboards were likely exposed to roads and traffic during typical movements and hence at risk of mortality.

The lack of road-effects in this study may be the result of very low snake road mortality on the stretches adjacent to the three study sites. Previous research has indicated that the probability of mortality is extremely low for an individual snake, for example, Black Ratsnakes (*Elaphe obsolete*) had a mortality rate of 0.0026 deaths per road crossing (Row et al. 2007). Thus, even if snakes closer to the road were more prone to mortality, it is unlikely that this would have translated into detectable differences when comparing between coverboards at different distances. For rarer species of snakes than our two study species, even a slight increase in mortality can cause a significant increase in the probability of population extinction (Row et al. 2007). Bearing in mind the high fecundity of Gartersnakes and Brown Snakes, and their high abundance at our sites, this decrease in population viability (assuming similar rates of mortality) seems less likely. If snakes are encountering the road (and presumably being killed in some cases), what seems more likely at our study sites is that snakes close to the road are more prone to mortality, but that these animals are quickly replaced by other animals moving in from farther from the road.

A further possibility as to why no effects of proximity to roads were observed on snake occurrence is that snakes may choose not to cross the roads, or have developed behaviors that minimize the risk of mortality. Although snakes may actively seek out roads for thermoregulatory reasons, thus increasing the risk of mortality (Ashley & Robinson 1996), road avoidance by snakes has been indicated in several studies, especially for smaller species such as the Gartersnake (Andrews & Gibbons 2005; Richardson et al. 2006; Shine et al. 2004). Understanding if snakes are choosing not to cross roads as well as the consequences of such behavior on snake metapopulation viability (e.g., Epps et al. 2005) , requires marking animals to allow examination of movement over roads as well as calculation of the probability of mortality during such events, the focus of future research efforts at the study site.

To conclude, proximity to road-edge does not appear to be a factor significantly affecting spatial distribution of snakes in old fields at our study site, whereas thermoregulation appears to be a more important mechanism in their spatial ecology. This raises the question as to why these local snake populations, which are clearly highly abundant, are apparently not affected by the road that borders their habitat. Is this due to behavioral avoidance of the road, or are the snakes encountering and being killed on roads? If the former hypothesis is true, roads may be acting as barriers to movement between populations. These questions could be asked by extending the study to populations on either side of the road, with mark-recapture used to assess inter-population movement.

Table 3.1. Total numbers of observations of snakes under coverboards at each of three old-field sites at Cicero Swamp in New York State. For each site, the total number of coverboard nights sampled is indicated next to the site name.

Snake species	Age class	N snakes per old-field site			Total
		Short (n = 932)	Ponds (n = 1292)	Long island (n =1327)	
Garter	Adult	187	267	225	679
	Juvenile	147	246	60	453
Brown	Adult	57	134	23	214
	Juvenile	14	18	0	32
Milk	Adult	5	9	1	15
Northern Water	Adult	1	4	2	7

Table 3.2. Results from negative binomial regression of the number of observations of adult Gartersnakes per 100 coverboard nights at Cicero Swamp, New York State. Candidate model variables include distance from the nearest road edge (road), distance from forest edge (forest), and moisture, height of vegetation, and leaf-litter depth around the coverboard. Interactions are indicated with a colon. Significance of variables is indicated as follows *** <0.001, **<0.01, *<0.05.

Model name	Variable	Residual deviance	AIC	Δ AIC
Road:Forest	Road Forest*** Road:Forest	166.92	1071.0	0
Forest	Forest***	166.51	1073.0	2.0
Microclimate	Moisture Height of vegetation Leaf-litter depth All interactions	167.43	1074.3	3.3
Road	Road	165.77	1089.1	18.1

Table 3.3. Results from logistic regression of the presence of adult Brown Snakes observed under coverboards at Cicero Swamp, New York State. Candidate model variables include distance from the nearest road edge (road), distance from forest edge (forest), and moisture, height of vegetation, and leaf-litter depth around the coverboard. Interactions are indicated with a colon. Significance of variables is indicated as follows *** <0.001, **<0.01, *<0.05.

Model name	Variable	Residual deviance	AIC	Δ AIC
Forest	Forest***	166.49	170.49	0
Road:Forest	Road Forest** Road:Forest	165.41	173.41	2.92
Road	Road	180.71	184.71	14.22
Microclimate	Moisture Height of vegetation Leaf-litter depth All interactions	171.90	187.9	17.41

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4. THE EFFECTS OF PROXIMITY TO ROADS ON HERPETOFAUNAL ABUNDANCE

INTRODUCTION

As the density of roads and volume of traffic on existing roads continues to increase in the United States, greater attention has been paid to understanding the likely effects on animal populations. Roads can affect these populations in two ways: (1) through direct mortality (Gibbs & Shriver 2005; Smith & Dodd 2003); and (2) indirectly through habitat loss, degradation and fragmentation (Forman & Deblinger 2000; Trombulak & Frissell 2000; Vos & Chardon 1998). The latter group of effects can include a number of factors such as alteration of natural habitat, increase light penetration into remaining areas of habitat with corresponding changes in micro-climate, increased run-off leading to sedimentation of aquatic habitats, and pollution from vehicle emissions and road-salt (Karraker 2007).

In this study, we examined the effects of roads on the distribution of amphibians while including the potential influence of roads on microhabitat. We hypothesized that amphibians would be more abundant farther from roads and where favorable microhabitats were found, for example closer to streams, in areas with few conifers and at lower elevations.

METHODS

Two groups of herpetofaunal surveys were conducted, the first July 16th to September 11th 2003 and the second from August 9th to September 11th 2006. Surveys were located in forested areas of six counties of Central New York, including Onondaga, Cortland, Cayuga, Madison, Oneida and Chenango. A total of 313, 50-m wide circular plots were sampled (213 in 2003 and 100 in 2006), with each plot searched for 10 minutes. Sampling included turning over obvious cover objects. All herpetofauna encountered were identified and recorded.

Sampling covariates including temperature and relative humidity were recorded at the time of sampling. Site covariates including % coniferous cover, slope, aspect and distance to the nearest road and distance to the nearest stream were gathered from remote sensing (GIS) data, specifically the National Land Cover data 2001.

All statistical analyses were conducted using Program R version 2.4.1. (R Development Core Team 2006). For abundant amphibian species, poisson regression was used to relate relative abundance of individuals to covariates. For rarely encountered species, logistic regression was used to compare patterns of presence/absence. We developed four candidate models based on factors that have been demonstrated to influence amphibian abundance in similar forested regions our own study. These included a sampling covariate model with temperature and relative humidity; a site covariate model with % coniferous cover, slope, elevation and distance to the nearest road and distance to the nearest stream; a road effects model with distance to the nearest road, distance to the nearest stream and % coniferous cover; and a model representing both sampling and site covariates including temperature, relative humidity, % coniferous cover, slope, elevation and distance to the nearest road and distance to the nearest stream. In these models, we only extended our analyses to two-way interactions (rather than up to the seven-way interactions possible in some models). This decision was made due to the difficulty of interpreting any results from more complex interactions. Models with AIC values within 2 AIC points were considered to be tied in ranks.

RESULTS

A total of 1312 amphibians and reptiles were observed, representing 13 species (Table 1). We excluded species with *N* <20 from further analyses due to insufficient statistical power, leaving 6 species of amphibians. Of these species, poisson regressions were conducted for dusky salamander, eastern red-spotted newt, red-backed salamander and two-lined salamander, and logistic regression for American toad and wood frog.

The results of our regression model analyses indicate a complex suite of co-variates influenced the distribution of amphibians in forest plots (Table 2). Some of our variables were correlated (although not to a sufficient degree to warrant removing terms from models). These general trends are provided here to help with understanding significant interaction terms for individual species: Higher temperatures tended to occur with lower humidity; coniferous cover tended to increase at higher elevations where there also tended to be lower temperatures; steeper slopes tended to be found at lower elevations (i.e., on the sides of valleys); steeper slopes tended to occur closer to roads as roads are typically found in the valley bottoms; higher elevation plots tended to be farther from streams; and plots far from roads also tended to be far from streams due to the location of both roads and streams in valley bottoms.

Two models best explained the relative abundance of red-backed salamanders: The site model, and the site and sampling model, with more individuals found where there was less coniferous cover (*P* = <0.001) on steeper slopes (*P* = <0.001) and farther from streams (*P* = 0.008). Significant interactions were seen between coniferous cover and elevation (*P* = <0.001) with more conifers and hence fewer salamanders at higher elevations; between slope and elevation (*P* = 0.024) with more salamanders at lower elevations, which tended to have steeper slopes; and between distance to road and both coniferous cover (*P* = 0.042) and slope (*P* = 0.008), with more salamanders on steeper slopes and in less coniferous cover and both these conditions tending to occur closer to roads. We also found significant interactions between distance to stream and both elevation (*P* = 0.050) and distance to road (*P* = 0.004).

The site and sampling model provided the best explanation of the variation seen in the relative abundance of dusky salamanders. More observations of this species were seen in plots with less coniferous cover (*P* = 0.029) and closer to streams (*P* = 0.036). Significant interactions were seen between temperature and humidity (*P* = 0.023) with more salamanders observed at higher temperatures and lower humidity; between humidity and coniferous cover (*P* = <0.001) with lower humidity tending to occur in higher elevations where there was an increase in coniferous cover and fewer salamanders; between temperature and slope (*P* = 0.010) with higher temperatures tending to be occur with a reduction in slope; between coniferous cover and slope (*P* = <0.001); between elevation and both humidity (*P* = 0.042) and slope (*P* = <0.001); between distance from road and both humidity (*P* = 0.021) and elevation (*P* = 0.003); between the distance from stream and humidity (*P* = <0.001), coniferous cover (*P* = <0.001), and slope (*P* = 0.009); and between the distance from road and distance from stream (*P* = 0.025).

For eastern red-spotted newts, the site and sampling model also provided the best explanation of relative abundance. More newts were observed with an increase in humidity (*P* = 0.013) and farther from roads (*P* = <0.001). Significant interactions between coniferous cover and temperature (*P* = <0.001) indicated that unlike red-backed and dusky salamanders, more newts were observed in cool coniferous areas. The decrease in humidity seen in coniferous areas also explains the significant interaction between these two variables (*P* = 0.043), with more newts in the more humid coniferous forests. Significant interactions were also seen between elevation and both humidity (*P* = 0.021) and slope (*P* = 0.012); and between the distance from road and temperature (*P* = 0.029), humidity (*P* = <0.001), and coniferous cover (*P* = 0.025); and between the distance from stream and humidity (*P* = 0.010).

For two-lined salamanders, the site and sampling model provided the best explanation of variation seen in patterns of occurrence. Two-lined salamanders were more likely to occur in areas with more coniferous cover (*P* = 0.009). There were also significant interactions between coniferous cover and humidity (*P* = 0.033), elevation and temperature (*P* = 0.045), humidity (*P* = 0.002) and distance from the nearest road (*P* = 0.001), humidity and the distance from the nearest road (*P* =0.026) and distance from the nearest road and stream (*P* = 0.009).

Unlike the other focal species, the occurrence of American toads was best explained by the road effects model. This model still provided a poor explanation of the variation seen in the data, however, with none of the individual variables or interactions being statistically significant.

The occurrence of wood frogs was best explained by the conditions during sampling, with a decreasing probability of occurrence with increased humidity (*P* = 0.039). The interaction between temperature and humidity was also significant (*P* = 0.048); higher temperatures tended to be accompanied by a decrease in humidity with a corresponding reduction in the probability of occurrence. The road effects model was ranked second by the AIC scores, with a significantly higher probability of occurrence of wood frogs at greater distances from roads (*P* = 0.016) and from the nearest stream (*P* = 0.29), and a significant interaction between these two variables (*P* = 0.008).

DISCUSSION

The results of our models demonstrate that a complex suite of interrelated variables drives the distribution of amphibians in the study plots. Although road proximity and the effects of road on microclimate may play a role in determining the distribution of some species, for example the American toad, it is clear that this is not the only factor in play. Previous research has shown that roads clearly have the potential to affect amphibian populations (Gibbs & Shriver 2005; Karraker 2007), raising the question as to why we did not observe a dominant effect of roads in our study.

One factor that may have influenced patterns of distribution is the topography of the study region. In this area of steep valleys bisecting upland plateaus, coniferous plantation forestry was typically located on the hill-tops, with roads in the valley bottoms. Many species of amphibian have been shown to select against coniferous forest, for example the red-backed salamander seen in our study. As deciduous forest plots were generally closer to roads, any effect of proximity to road on distribution may have been hidden.

Many of the differences we observed among species can be related to their life-history strategies. For example, the eft stage of the eastern red-spotted newt (the terrestrial life-history stage sampled in our plots) is extremely vagile and known to disperse a long way from aquatic breeding sites (Gill 1978), whereas all life-history stages of dusky salamanders are closely associated with streams and not often found in upland areas (Gibbs et al. 2007).

A further reason that we did not see a dominant road effect on the distribution of amphibians may be that we chose forested plots where conditions were likely to be highly suitable for our study species. The region of New York State in which the study was conducted falls well within the known range of all of our focal taxa (Gibbs et al. 2007). This makes it unlikely that any of the species are found close to physiological thresholds in temperature, moisture etc. Although we did observe clear variation in microhabitat among our plots, it may be that we did not encompass a sufficient range to detect any differences in distribution.

Table 4.1. Amphibians and reptiles observed in 313 50-m diameter circular plots in Central New York in 2003 and 2006.

Species	Total observed	Mean per plot ± SE
Red-backed salamander	724	2.313 ± 2.977
Dusky salamander (mountain and northern dusky)	258	0.824 ± 2.759
Eastern red-spotted newt	179	0.572 ± 1.483
Two-lined salamander	38	0.121 ± 0.535
Spotted salamander	12	0.038 ± 0.208
Jefferson's salamander	2	0.006 ± 0.080
Four-toed salamander	1	0.003 ± 0.057
American toad	29	0.092 ± 0.322
Wood frog	46	0.147 ± 0.405
Green frog	8	0.026 ± 0.309
Northern leopard frog	1	0.003 ± 0.057
Spring peeper	9	0.029 ± 0.186
Garter snake	5	0.016 ± 0.126
Total	1312	4.192 ± 4.750

Table 4.2. Akaike's information criterion (AIC) and model ranking for regression analyses of the relative abundance or occurrence of amphibians observed in 50-m diameter circular plots in Central New York in 2003 and 2006 (n both years combined = 313). Variables included in models are abbreviated as follows: Temperature (T), relative humidity (RH), % coniferous cover within plot (%Con), slope (Sl), elevation (Ele), distance to the nearest road (DRd), and distance to the nearest stream (DSt). AIC values are provided with model rank for each species indicated in bold text in parentheses (models with AIC values within 2 AIC points are considered to be tied in rank).

Species (and regression model)	AIC score for model and statistically significant covariates			
	Sampling (T, RH)	Site (%Con, Sl, Ele, DRd, DSt)	Road (DRd, Dst, %Con)	Sampling and site (T, RH, %Con, Sl, Ele, DRd, DSt)
Eastern red-backed salamander (poisson)	1593.2 (**4**)	1348.6 (**1.5**)	1478.1 (**3**)	1350.5 (**1.5**)
Dusky salamander (mountain and northern dusky) (poisson)	1236.0 (**4**)	955.17 (**2**)	1096.5 (**3**)	873.0 (**1**)
Eastern red-spotted newt (poisson)	781.53 (**4**)	659.92 (**2**)	726.03 (**3**)	632.85 (**1**)
Two-lined salamander (poisson)	259.67 (**4**)	227.66 (**2**)	234.94 (**3**)	208.42 (**1**)
American toad (logistic)	190.99 (**2**)	192.98 (**3**)	183.58 (**1**)	211.66 (**4**)
Wood frog (logistic)	234.41 (**1**)	252.85 (**3**)	242.51 (**2**)	257.45 (**4**)

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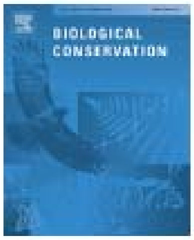

Road crossing structures for amphibians and reptiles: Informing design through behavioral analysis

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ABSTRACT

Road traffic causes significant amphibian and reptile mortality, which could be mitigated through the installation of road crossing structures that facilitate safe passage, but only if reptiles and amphibians are willing to use them. Through a series of behavioral choice experiments with frogs and turtles, we examined how aperture diameter, substrate type, length, and light permeability influenced individuals' preferences for specific attributes of crossing structures, and how individuals responded to various heights of barrier fences. Snapping turtles (*Chelydra serpentina*), green frogs (*Rana clamitans*), and leopard frogs (*Rana pipiens*) preferred larger diameter tunnels (>0.5 m) whereas painted turtles (*Chrysemys picta*) preferred tunnels of intermediate (0.5–0.6 m) diameter. Green frogs preferred soil- and gravel-lined tunnels to concrete- and PVC-lined tunnels. Painted turtles showed non-random choice of different lengths of tunnel, possibly indicating some avoidance of the longest tunnel (9.1 m); although no species preferred to exit via the longest tunnels (9.1 m), members of all four species used such tunnels. Green frogs preferred tunnels with the greatest light permeability. Fences 0.6 m in height were effective barriers to green frogs, leopard frogs, and snapping turtles, whereas 0.3 m fences excluded painted turtles. We conclude that tunnels > 0.5 m in diameter lined with soil or gravel and accompanied by 0.6–0.9 m high guide fencing would best facilitate road crossing for these and likely other frog and turtle species.

1. Introduction

Vehicles cause the deaths of millions of vertebrate animals on roads each day (Forman and Alexander, 1998). Roadways can also affect wildlife by obstructing movement patterns, and ultimately reducing and isolating populations (Spellerberg, 1998; Forman et al., 2003; Eigenbrod et al., 2008). Amphibians and reptiles may be particularly vulnerable to the effects of roads because they are slow-moving organisms that typically access multiple habitats seasonally to complete their life cycles (Hels and Buchwald, 2001; Steen et al., 2006; Roe and Georges, 2007). By increasing the permeability of roads through well-designed interventions, some detrimental impacts of roads could be alleviated (Yanes et al., 1995; Guyot and Clobert, 1997; Aresco, 2005). To this end, different types of crossing structures have been developed (Forman et al., 2003; Puky, 2003; Mata et al., 2008). The most successful structures for amphibians and reptiles appear to combine a system of guide fences and underpasses to funnel organisms beneath roadways (Dodd et al., 2004; Aresco, 2005). Despite

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the mitigation potential offered by road crossing structures, assessments completed to date suggest that nonfunctioning crossing structures are prevalent (Podloucky, 1989; Meinig, 1989). The failures of such structures appear to stem from inadequate considerations of placement, architectural design, and behavior of targeted organisms (Podloucky, 1989; Puky, 2003).

The costs of installing and maintaining road crossing structures are substantial (Mata et al., 2008), so more effort is warranted to determine the design attributes and placement strategies that maximize the return on the investment toward mitigation of road kill through deployment of such structures. In this study, we created a series of behavioral choice arenas to identify particular design attributes that might stimulate amphibians and reptiles to use road crossing structures. We built proto-typical crossing structures and evaluated preferences of individuals for crossing structure aperture, substrate, length, and light permeability. Concurrently, we evaluated the containment potential of various heights of guide fences. We examined individual behaviors of four species of amphibians and reptiles that are frequently killed on roadways in North America (Ashley and Robinson, 1996; Linck, 2000; Carr and Fahrig, 2001; Steen and Gibbs, 2004): green frogs (*Rana clamitans*), leopard frogs (*Rana pipiens*), painted turtles (*Chrysemys picta*), and snapping turtles (*Chelydra serpentina*). These species exhibit substantial terrestrial movement annually (e.g., Dole, 1968; Merrell, 1970; Quinn and Graves, 1998; Lamoureux and Madison, 1999), increasing their potential interaction with roadways (Paton and Crouch, 2002; Birchfield and Deters, 2005), which can impact their population sizes and structures (Fahrig et al., 1995; Carr and Fahrig, 2001; Steen and Gibbs, 2004; Steen et al., 2006). Although none of these species is considered threatened with extinction, the impacts of road mortality may be significant for specific populations (e.g., Steen and Gibbs, 2004; Rorabaugh, 2005).

2. Methods

We conducted experiments between 15 June–15 August, 2005 and 15 June–10 August, 2006 at the Three Rivers State Wildlife Management Area in Baldwinsville, New York, United States (43°N, 76°W) where we constructed a series of behavioral choice arenas to test animal responses to guide fences and crossing tunnels (Fig. 1). Crossing tunnel choice arenas were central, octagonal enclosures constructed of 3 mm thick, 1.2 m high, translucent corrugated plastic sheets, which allowed filtered light to penetrate the arenas while blocking all visual environmental cues. We constructed the arenas on level ground, and covered the top of each arena with a cotton drop cloth that blocked celestial cues, but allowed air and diffused light to penetrate the arena. Four different exit options radiated out from each arena as the only points of egress from the enclosures. Exit options were surrogate crossing structures formed from sections of corrugated black PVC (polyvinyl chloride) pipes, which are commonly used in road construction, and a readily available source material for crossing structures. To obscure views to the surroundings and establish an identical visual stimulus at each exit, we placed an opaque piece of plastic sheeting 0.6 m beyond the exit of each pipe.

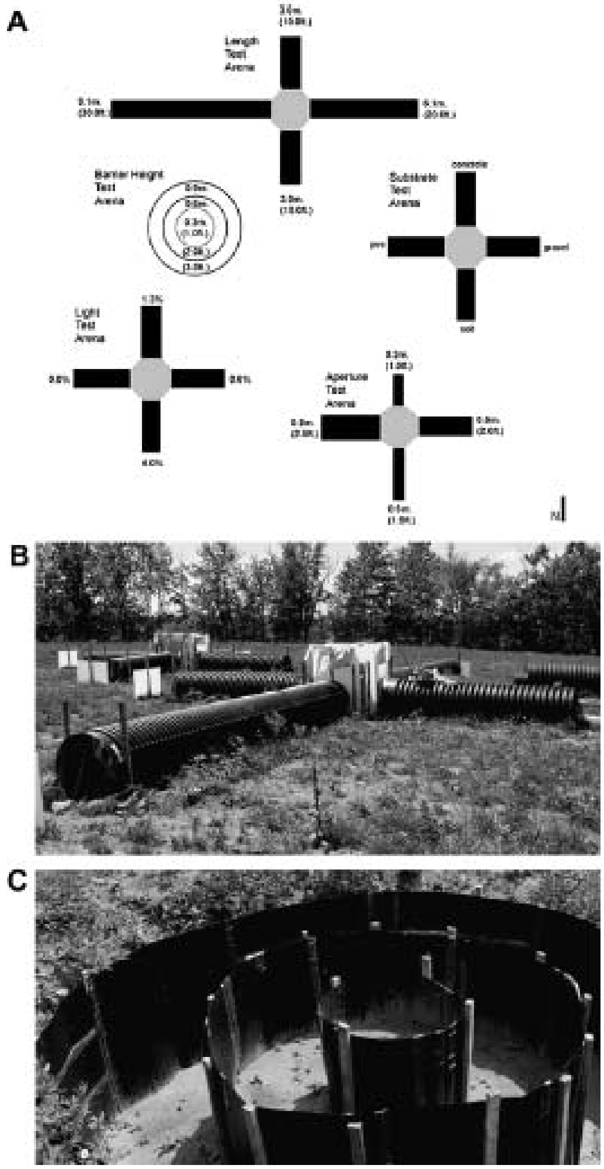

Fig. 1 – Behavioral choice arenas used in experimental evaluation of preference by frogs and turtles for variously designed road crossing structures, Three Rivers Wildlife Management Area, Baldwinsville, New York, 2005 and 2006: design schematic (A) and actual deployments of choice arenas for crossing structures (B) and barrier heights (C).

For both barrier and crossing structure tests, all test subjects (*C. serpentina*, $n = 62$; *C. picta*, $n = 74$; *R. clamitans*, $n = 135$; *R. pipiens*, $n = 187$) were gathered from wetlands, ponds and fields within a 10 km radius of the experimental site and promptly returned to their places of origin after trials (usually within 2 h). Test subjects were first placed within an acclimation chamber inside the central octagonal chamber to acclimate for 5 min. The acclimation chamber was constructed of a PVC ring 0.4 m high with a diameter of 0.6 m, and covered by a white cotton cloth. The observer then pulled a string attached to the acclimation chamber from an anchor point 1.5 m outside the arena to lift the ring and release the

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animal, thereby preventing direct visual contact between the test subject and the observer.

Experimental trials for individual test subjects extended for 15 min. At the terminus of each pipe, we installed a pitfall trap to collect released animals as they exited from their tunnel of choice. If an animal had not exited the arena after 15 min, a choice of no decision (a "balk") was recorded and the animal was transferred to another arena. To reduce the influence of repeated exposure to stimuli, and because experimental returns tend to diminish through repeated testing of subjects (Martin and Bateson, 1986), we tested individuals no more than once in each experiment. Turtles were tested individually whereas frogs were tested individually or in groups of 2–17 individuals.

- *Experiment 1: Aperture diameter* – We used 4, 3.0-m-long pipes of diameters 0.3 m, 0.5 m, 0.6 m, and 0.8 m, lined with an identical mixture of soil and sand gathered from the site.
- *Experiment 2: Substrate type* – We used four identical sections of 0.6 m diameter and 3.0-m-long pipe lined with concrete, soil, gravel, or bare PVC.
- *Experiment 3: Pipe length* – We used four, 0.6 m in diameter pipe sections two of which were 3.0 m, one 6.1 m, and one 9.1 m in length. All pipes were lined with an identical mixture of soil and sand gathered from the site.
- *Experiment 4: Light permeability* – We used four sections of 0.6 m diameter, 3.0-m-long pipe with overhead punctures of 0%, 0.65%, 1.3%, or 4.0% of the pipe's surface area, rendered by drilling 0.5 cm holes in the upper surface of pipes. Pipes were lined with an identical mixture of soil and sand gathered from the site.
- *Experiment 5: Barrier heights* – To test effective heights of barrier fences, we used opaque, corrugated plastic fences to construct three nested, circular enclosures with substrates of packed soil (Figs. 1 and 2) of heights 0.3 m, 0.6 m, and 0.9 m. Experimental subjects were placed in the center of each arena and allotted 15 min to attempt to scale the bounding fence. To motivate these desiccation-avoiding animals to leave the enclosures, we covered the ground of each arena with a dry sand substrate.

We tested the null hypothesis that choice of exit pipe was independent of design attribute by contrasting the observed frequency of choice against a null expectation of an equal number of individuals choosing each type of egress. All choice data were evaluated with the *G* statistic for the log-likelihood ratio goodness of fit test with Williams' correction for continuity (Sokal and Rohlf, 1995); we interpreted tests with probabilities <0.05.

It is well known that many species of amphibians and reptiles can use a variety of environmental cues to home toward particular locations (Russell et al., 2005), and that studies have examined the homing abilities of the particular species used in this study (e.g., Martof, 1953; Dole, 1968; DeRosa and Taylor, 1978; Quinn and Graves, 1998; Lamoureux and Madison, 1999). The design of our experimental apparatus allowed for the masking of some of the environmental cues, but not all. To address concerns that the compass orientation of the pipes might influence individual choices due to the homing instincts of the subjects, we analyzed the propensity of individuals to choose the same orientation in subsequent trials. To do so, we compiled choice sequences for individuals that were placed consecutively in each arena and we compared their propensity to choose an egress of the (1) same orientation as its previous choice and (2) same orientation as its initial choice. We calculated 95% confidence intervals about the estimate of the average propensity (% of choices) of individuals to track their earlier choices and determined if the confidence intervals included the null expectation of 25% chance of selecting the same orientation as the earlier choice (given four possible alternatives in each arena).

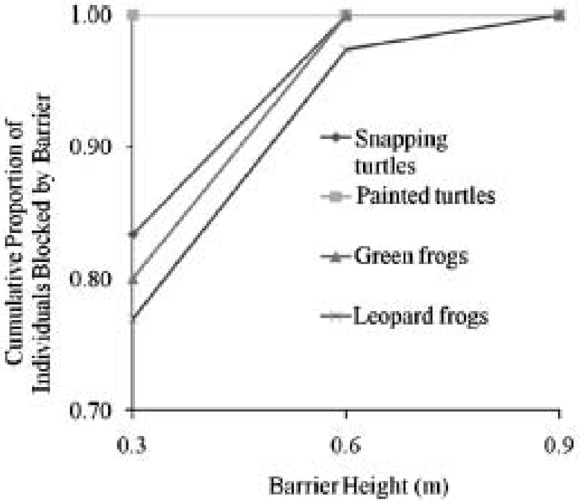

Fig. 2 – Barrier height efficacy for blocking passage by snapping turtles, painted turtles, green frogs and leopard frogs, Three Rivers Wildlife Management Area, Baldwinsville, New York, 2005 and 2006. Values represent the cumulative proportion of individuals released at the center of the barrier experimental set-up (see Fig. 1) blocked by barriers of successively greater heights.

3. Results

When placed in the arenas, most individuals being tested attempted to leave via one of the choices of egress (i.e., they did not "balk"): snapping turtles balked most frequently (56%), followed by green frogs (32%), leopard frogs (23%), and painted turtles (16%) (difference in balking propensity among species: G_{adj} 28.4, df 3, $P < 0.001$).

Among test subjects that did not balk, in *Experiment 1: Aperture diameter* choice of pipe was non-random for snapping turtles and painted turtles, and highly suggestive for leopard frogs (Table 1); individuals of both turtle species showed a tendency to use pipes of the mid-size diameters more frequently than pipes with the largest and smallest diameters. For *Experiment 2: Substrate type* we detected non-random choice only for green frogs (Table 1); individuals used soil- and gravel-lined pipes more often than the concrete- and PVC-lined pipes. For *Experiment 3: Pipe length* both leopard frogs and painted turtles showed some degree of avoidance of the longest pipes, although only the data for painted turtles were non-random. For *Experiment 4: Light permeability* both

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Table 1 – The crossing structure choices made by frogs and turtles as related to aperture diameter, substrate type, pipe length, and light permeability, Three Rivers Wildlife Management Area, Baldwinsville, New York, 2005 and 2006

Species	n(%)				G(adj.)	P
Aperture Diameter (m)	0.3	0.5	0.6	0.8		
Green frog	8(16)	13(27)	12(24)	16(33)	2.732	0.435
Leopard frog	16(25)	18(28)	24(12)	30(35)	7.729	0.052
Snapping turtle	2(6)	14(44)	10(31)	6(19)	10.852	0.013
Painted turtle	6(17)	14(39)	14(39)	2(6)	13.547	0.004
Substrate type	Concrete	Gravel	Soil	PVC		
Green frog	6(13)	17(38)	18(40)	4(9)	14.866	0.002
Leopard frog	18(29)	20(32)	12(19)	12(19)	3.250	0.355
Snapping turtle	6(19)	9(29)	8(26)	8(26)	0.620	0.892
Painted turtle	15(37)	10(24)	8(20)	8(20)	2.939	0.401
Pipe length (m)	3	3	6.1	9.1		
Green frog	12(26)	9(19)	11(23)	15(32)	1.553	0.670
Leopard frog	12(22)	13(24)	22(40)	8(15)	7.180	0.067
Snapping turtle	11(37)	6(20)	8(27)	5(17)	2.652	0.449
Painted turtle	12(30)	4(10)	18(45)	6(15)	11.829	0.008
Light permeability (%)	0	0.6	1.3	4		
Green frog	9(17)	14(26)	9(17)	22(41)	7.789	0.051
Leopard frog	12(24)	12(24)	7(14)	20(39)	6.989	0.072
Snapping turtle	9(31)	4(14)	7(24)	9(31)	2.464	0.482
Painted turtle	12(26)	11(23)	7(15)	17(36)	4.285	0.232

Shown are the numbers (percentages) of individuals using a particular pipe to exit the arenas, where *n* = number of non-balking individuals. All tests have 3 df.

frog species showed non-random movement through the pipes, although the results for neither turtle species were significant (Table 1); for both frog species, the pipe with the most permeable surface area received the greatest usage.

Across all trials, no species indicated a preference for a particular compass direction. Confidence intervals (95%) about the observed percentage of individuals both repeating the compass direction taken in their first trial and repeating the direction of each previous trial included the null expectation of 25%. More specifically, the tendency to orient in the same compass orientation as initial choice was as follows (average % of choices made by individuals followed by 95% lower and upper confidence levels and *n* individuals): green frog 21.6% (7.3, 35.8 [17]), leopard frog 29.0% (13.0, 44.9 [23]), snapping turtle 30.6% (21.6, 39.5 [51]) and painted turtle 31.1% (20.1, 42.1 [37]). Similarly, the tendency to orient in the same compass orientation as previous choice was as follows: green frog 17.6% (3.0, 32.3 [17]), leopard frog 28.3% (12.6, 44.0 [23]), snapping turtle 30.6% (21.5, 39.7 [51]), and painted turtle 28.4% (17.7, 39.1 [37]).

Evaluation of effectiveness of various barrier heights, *Experiment 5* (Fig. 2), indicated that painted turtles could not cross barriers of heights 0.3 m, but most other species could. This stated, 0.6 m high barriers excluded most individuals and 0.9 m virtually all: of 93 organisms tested, only a single leopard frog traversed the 0.9-m-high barrier.

4. Discussion

Our analysis indicates that although turtles and frogs will traverse crossing structures of widely varying features, certain attributes of these structures do influence the patterns of usage. Tunnel aperture diameter was evidently important; three of the four species tested indicated avoidance of the 0.3 m diameter tunnels. Although other studies have suggested that some amphibians and reptiles will use larger culverts (e.g., Yanes et al., 1995; Aresco, 2005), we are unaware of studies that indicate usage or avoidance of such narrow tunnels. In addition to simply excluding access by larger turtles, the narrow sides and low roofs of these tunnels may make it impossible for anurans to use their characteristic saltatory locomotion while traversing the tunnels.

In trials testing for the acceptability of particular substrates within the tunnels, only green frogs showed significantly non-random choice. The skin of amphibians is more prone to desiccation than that of many other vertebrate animals and dehydration rates of green frogs is correlated with substrate type (Mazerolle and Desrochers, 2005). Green frogs were the more aquatic frog of the two species that we tested (Martof, 1953; Merrell, 1970), and perhaps desiccation risk influenced their preference against concrete and PVC. Similarly, a previous study found that agile frogs (*Rana dalmatina*) and water frogs (*Rana esculenta*) were more likely than common toads (*Bufo bufo*) to choose a tunnel lined with soil over a substrate of bare concrete (Lesbarreres et al., 2004).

In relation to tunnel length, it is important to note that although no species evidently preferred it, all of the species used the 9.1 m pipe as a means of egress. From a designer's perspective, this result is encouraging because road crossing structures typically need to be this long or longer to traverse the full length of roadways, which are often >18.3 m wide (a distance we were unable to evaluate due to material limitations). The slight avoidance of our longest tunnels by painted turtles, and possibly leopard frogs, may indicate that these species might avoid even longer lengths of pipe. Future tests of length and choice could offer insights into the maximum length of pipes these species are able to navigate.

Within the limited literature on road crossing structures, the importance of light availability is unresolved. For example, Jackson and Tyning (1989) observed that when spotted salamanders (*Ambystoma maculatum*) move through tunnels with greater light penetration their speed is increased. In our study, leopard frogs and green frogs preferred the pipe with the greatest density of openings on the upper surface. The reasons for these preferences remain unclear, and warrant further investigation. Whatever the case, light availability may be among the least tenable attribute of road crossing structures because such structures are generally buried under roadways and largely impermeable to light. This said, light reflected from external sources (e.g., moonlight) and or emanating from internal sources (solar-powered bulbs) could be used to illuminate to varying degree the interior of such structures.

Our results indicate that barriers between 0.6 m and 0.9 m in height could prevent most individuals of the species we examined from accessing road surfaces as well as effectively guide them into crossing structures. Some caution in interpreting these results may be warranted because test subjects may have become fatigued crossing each successive barrier of successively greater height, rendering choices not independent of one another. However, observations in the field indicated that animals repeatedly bounded to (frogs) or reached to (turtles) predictable heights limited more by the saltatory ability imposed by morphology than physiological state. Effective heights could likely be increased by employing "lips" at the tops of barriers and, for climbing species, constructing barriers of materials with slick surfaces to prevent toe holds. Barriers of relatively modest height thus appear to provide an effective and economical means of both excluding frogs and turtles from roads, and guiding them toward road crossing structures.

Although we attempted to isolate behavioral responses to specific attributes of road crossing structures in a rigorous experimental design, our study nevertheless had limitations. First, many individuals, particularly of snapping turtles, simply did not make choices. It is unclear whether similar balking rates would be exhibited if study subjects had encountered crossing structures while in a truly migratory behavioral state (Guyot and Clobert, 1997; Birchfield and Deters, 2005; Aresco, 2005). Trial subjects were in various motivational states when tested, having been removed from their habitats when likely engaged in a variety of behaviors not necessarily associated with migration. Because the life cycles of snapping turtles, painted turtles, green frogs, and leopard frogs involve varying degrees of seasonal mobility (Obbard and Brooks, 1980; Carr and Fahrig, 2001; Steen and Gibbs, 2004), an organism tested during a period of migration could exhibit different preferences than an organism tested outside of a period of seasonal movement. The impact of seasonal movement and migratory patterns, and their potential influence on patterns of choice should be considered further and are the focus of ongoing studies (J.P. Gibbs, unpublished data). Balking rates are relative because due to the constraints of the weather, time, and trials of other individuals it was not possible to leave study subjects in the arenas without a time limitation. We suspect that balking rates would diminish, and patterns of selectivity become more resolved, if animals were provided with more extended trial periods within which to make a choice.

A further, potential limitation was that we deployed frogs in batches during some trials but do not know the extent to which one individual's choice was independent of another. Given the rapidity of most frogs' departures we saw no obvious indication of a "follow the leader" effect; nevertheless, the extent to which both amphibians and reptiles use pheromonal and visual cues to mediate their behaviors should be explored and could easily be done in an experiment such as this employing substrates imbued or not with skin secretions (pheromone cues) or supporting physical models (visual cues). Although many studies have indicated that amphibians use a variety of cues during migration, no studies to our knowledge have documented frogs using other migrating frogs as guides (Russell et al., 2005).

Despite its limitations, our study represents an experimental approach to resolving preference for attributes of road crossing structures by amphibians and reptiles. Our results provide general guidelines that can contribute to the design of more behaviorally palatable crossing structures. More specifically, we conclude that effective crossing structures can be constructed out of round PVC pipe, that these structures should be at least 0.5 m in diameter, that they should be lined with soil or gravel, and that they should be installed in tandem with a 0.6 m–0.9 m high guide fence.

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6. ROAD-CROSSING BEHAVIOR OF AMPHIBIANS: A CASE STUDY FROM LABRADOR HOLLOW, NEW YORK STATE.

ABSTRACT

The effective use of culverts to mitigate the effects of roads on amphibians and reptiles is reliant on knowledge of where animals cross and what structures they will travel through. To date, research has primarily focused on locating crossing 'hotspots', with less attention paid to where animals are concentrated on roads within these locations. This information is necessary when placing crossing structures. Studies focusing on the design of crossing structures have tended to be based either on animals translocated to experimental arenas or monitoring the use of existing structures. The behavior of animals in the former approach may not represent that of animals under natural conditions. Conversely, it can be difficult to isolate the large number of variables potentially influencing choice at existing structures. In this study, we assessed the abundance of spotted salamanders, *Ambystoma maculatum*, and American toad, *Bufo americanus* along a 700-m transect within a known crossing hotspot, and related these distributions to habitat variables within the site. To test the effects of culvert attributes including length, diameter and substrate on choice, we applied a novel technique whereby experimental arrays were placed in the path of migrating spotted salamanders, allowing choice to occur under natural movement conditions. A higher abundance of spotted salamanders were found where flowing water was present on the upslope of the road. More American toads were found on sections of road without a wetland on the downslope side and where there was a culvert nearby. Spotted salamanders showed no clear preference for culverts with different attributes. Our results show that predicting where amphibians will be concentrated within crossing hotspots is possible, allowing effective placement of mitigation, but that these patterns are likely to differ between species. We found that spotted salamanders undergoing their natural movements appear to be more tolerant of differences between culverts when compared with studies in experimental arenas, and that a variety of different culverts will work as crossing structures.

INTRODUCTION

Road-traffic kills or injures considerable numbers of amphibians and reptiles (herpetofauna) each year (Aresco 2005; Ashley & Robinson 1996; Langen et al. 2009). In addition to mortality of individuals, road-kill can reduce population viability and lead to extirpation of local populations (Fahrig et al. 1995; Gibbs & Shriver 2002). Because of the effects of roads on populations and the safety issues associated with drivers encountering animals, reducing animal-vehicle interactions has been the focus of a great deal of research. This research includes studies focusing on understanding where animals are likely to occur on roads and studies looking at reducing the number of animals on roads at these locations.

Research focusing on predicting occurrence of herpetofauna on roads has revealed both spatial and temporal predictors. In general, amphibians and reptiles are more likely to occur on roads in close proximity to wetlands (Langen et al. 2009), especially where suitable terrestrial habitat is found on the aquatic-terrestrial interface (Compton et al. 2007). For species that range more widely, for example Blanding's, *Emydoidea blandingii*, and spotted turtle, *Clemmys guttata*, animals are more likely to occur where roads bisect routes traveled during annual migration (Beaudry et al. 2008). For aquatic species of turtle such as common snapping, *Chelydra serpentina*, and painted turtles, *Chrysemys picta,* occurrence on roads has also been linked to the location of suitable nesting sites (often the roadside margins). Temporal patterns of occurrence are clearly linked to species' biology: For amphibians such as the spotted salamander, *Ambystoma* *maculatum*, explosive breeding migrations mean that the majority of adults are found on roads in a few nights in early spring (Gibbs & Shriver 2005). Conversely, terrestrial turtle species may have several periods of movement activity (and subsequent exposure to roads) during the year as they migrate to access food resources, to aestivate, or to nest (Beaudry 2007).

Based on this research, we are now able to predict likely locations of 'hotspots' of herpetofaunal occurrence on roads, albeit with some degree of uncertainty and not for all species or regions. When predicting where herpetofauna will be most concentrated *within* a hotspot, however, less information is available. Understanding occurrence at this scale is particularly pertinent to deciding where to place mitigation such as barrier fences and crossing structures. Site-specific studies, for example those conducted at Lake Jackson in Florida (Aresco 2005), have used data on road-crossing locations to place barriers and culverts. These studies do not offer the type of information needed to predict where animals will be found at unstudied sites, however.

In addition to predicting patterns of occurrence, attention has also been paid to constructing effective mitigation structures including fences and culverts. Studies focusing on this topic include those involving experimental approaches and those where the efficacy of existing structures for wildlife-crossings has been monitored. Both of these approaches have yielded important information: For example, experimental research has shown species-specific preferences for culverts depending on diameter and substrate (Woltz et al. 2008), with field research indicating that the vegetation at a crossing structure can also influence choice (Yanes et al. 1995). There are inherent drawbacks with the inferences drawn from research to date, however: Because of the need for replication, experimental research has tended to employ animals captured in the field and placed within enclosures, the concern being that choice is not the same as would be seen under natural conditions. Conversely, research based on monitoring existing crossing structures affords a view of animals under 'natural' conditions, but does not allow control of site-specific variables, thus it is hard to identify the specific mechanisms that determine the efficacy of a given crossing structure.

Our study had two related goals: (1) To determine factors predicting where concentrations of herpetofauna will occur within a hotspot; and (2) to evaluate how undisturbed animals in active migration mode respond to differences in the characteristics of culverts, specifically length, substrate and diameter. To address these questions, we used data gathered from an abundant population of spotted salamanders, *Ambystoma maculatum*, and American toads, *Bufo americanus*, found at Labrador Hollow, NY. We predicted that patterns of occurrence within this hotspot would relate to the location of both suitable upland habitat for overwintering and suitable breeding habitat, with higher abundances in closer proximity to these features. We did not expect microhabitat features such as the presence of streams or seeps to determine abundance as movement invariably occurs when it is raining and the ground is saturated and often still covered by snow in the study region (Patrick, *pers. obs.*). Furthermore, we predicted that animals would prefer to cross through wider and shorter culverts and avoid crossing over concrete.

METHODS

Study area

The study was conducted along Route 91, at Labrador Hollow Unique Area, Apulia, New York State from March 2007 to June 2008. Labrador Hollow is a glacial ribbon lake, bordered by forested wetlands with numerous small pools. It is in these pools that the spotted salamanders and American toads primarily breed. Route 91 is a two-lane highway to the east of the lake. A drainage channel on the upslope side borders the road, with culverts under the road allowing the flow of run-off into the wetlands. Steep wooded slopes extend from the road's edge up, forming a classic post-glacial U-shaped valley.

Predicting patterns of occurrence

A team of volunteers sampled amphibians crossing Route 91 along a 700-m transect divided into 10 m sections. Transects were patrolled for 4 nights, from 26th March to 27th April 2007. All species of herpetofauna seen crossing the road were collected in buckets, measured, sexed, and then released on the opposite side of the road. We also recorded where along the transect the animal was encountered.

We quantified microhabitat on route 91 on May 06, 2007. For each 10 m section of road, the microhabitat was divided into upslope and downslope (i.e., both sides of the road). Roadside vegetation, forest cover and the presence of a drainage ditch remained consistent along the transect and were therefore not included as covariates. We measured the presence of or distance to nearest culvert (m); and whether either a stream or a seep was present (grouped into one variable representing flowing water). The latter variable was only included on the upslope side of the road due to close correlation with the presence of a culvert on the downside slope of the road. We also assessed if any wetlands were found within 15 m of the road's edge as indicated by the presence of hydrophytic vegetation and standing water.

Culvert characteristics

We conducted experiments from March 19th to April 27th 2008. Experimental arrays were situated on the forested upslope adjacent to Route 91, i.e., animals migrating to breed encountered arrays before crossing the highway. We constructed four arrays, each of which consisted of two 9-m long wing fences (1-m high silt fencing buried ~5cm into the ground) arranged at a slight angle to the downslope direction of migration (see Fig. 1). Animals were funneled into a bay, also constructed of silt fencing, where they were then confronted with three choices of culverts. All culverts consisted of the corrugated black PVC (polyvinyl chloride) pipes often employed in road construction for drainage. At the terminal end of each of the culverts, a 5-gallon/19-liter bucket was placed as a pitfall trap to capture migrating animals. Plastic sheeting and 0.5 m wooden stakes were used to connect the end of the culvert to the rim of the bucket to ensure that all animals were sampled. Traps were opened before nightfall when conditions were suitable for salamander movement (either rain or high humidity and temperatures >35f). Animals were collected at daybreak the next morning and released into their breeding habitat.

Due to limitations in the number of culverts available, each of our four arrays consisted of a different treatment. To ensure independence between each nightly sample, we moved each of the treatments within an array to give us 5 unique combinations. The arrays we tested were as follows:

- Experiment 1: Position – Three 3-m long culverts, each 0.6m in diameter
- Experiment 2: Substrate – Three 3-m long culverts, each 0.6m in diameter. One pipe remained bare; one contained fine sand/gravel (typically <1cm in diameter) gathered from a streambed within 500m of the study site and placed throughout the base of the culverts to a depth of 5cm; and one contained a 5-cm deep layer of set quick-drying concrete.

- Experiment 3: Length – Three culverts, each 0.6m in diameter. One consisted of a single 3-m pipe; the second 2 pipes joined to form a 6-m length; and the third 3 pipes joined to form a 9-m length.
- Experiment 4: Aperture diameter – Three 3-m long culverts, one 0.3m in diameter, one 0.6m, and one 0.8m.

Predicting patterns of occurrence

Our analyses focused on our two most commonly captured amphibians, spotted salamanders and American toads. We applied models with a poisson distribution of errors, with the response variable being the number of animals of each species crossing within each 10-m section of the transect. We used Akaike's Information Criterion (AIC) to choose models that best explained the variation in the data.

Culvert characteristics

We applied contingency table analyses using chi-squared tests with the number of spotted salamanders captured per trap night as our response variable (this was the only species with a sufficiently large sample size). Expected frequencies captured at each culvert per night were calculated as a third of the total captures at the array on that night. We applied chi-square rather than a log-likelihood or G-test as our average expected frequencies were >5 (Zar 1999). Our experimental design was reliant on sampling salamanders during their annual migration: As an explosive breeder, the majority of adult salamanders migrate during a few rainy nights in early spring. This resulted in an insufficient number of nights to allow us to test all possible combinations of treatment and position.

We initially tested whether position of the culvert within the array influenced choice by salamanders in the 'position' array. As no changes were made in this array between each sample night, we compared the observed versus expected distributions of captures between culverts summing over all nights to avoid pseudoreplication.

We then tested the remaining arrays (length, diameter, and substrate) separately, using the treatments within each array as 'columns' and the three nights with sufficient sample sizes as 'rows' (i.e., a 3x3 contingency table for each test). As we moved the treatments within each array each night producing a unique combination, sample nights are independent of one another and represent the possible effect of position and treatment on choice. Because we do not have a fully balanced design (where each treatment was tested in each position on a different night), however, we are unable to detect an interaction between position and treatment. For arrays where a statistically significant difference between observed and expected choice was observed, we then tested the effects of treatment only by summing captures in the same treatment across all of the sample nights and position only by summing captures in the same position across all nights.

All statistical analyses were conducted using Program R version 2.4.1. (R Development Core Team 2006).

RESULTS

Predicting patterns of occurrence

During the 4 sample nights, we captured 551 spotted salamanders and 92 American toads crossing within the 700-m transect. Several of the covariates initially assessed in the field were closely correlated. Before running models, we removed the presence of culverts from models due to close correlation with the presence of downslope wetlands; wherever a culvert was present, there was also a downslope wetland, but not vice versa.

A higher abundance of spotted salamanders were found where flowing water was present on the upslope of the road and where there was a culvert nearby (Table 1). Of these two variables, however, the presence of flowing water explained much more of the variation than did the distance to the nearest culvert. For American toads, three competing models best explaining patterns of abundance (Table 2). More toads were found on sections of road without a wetland on the downslope side and where there was a culvert nearby.

Culvert characteristics

We captured 446 spotted salamanders during the 5 nights of sampling, although only 3 nights yielded sufficiently large samples for analyses. Our analyses of the position treatment (where position within the array was the only factor), revealed no significant relationship between the number of salamanders and the location of the culvert within the array ($X^2_2 = 5.022$, $0.1<P<0.05$). No statistically significant differences were seen between observed and expected frequencies of captures in the diameter ($X^2_{3,3} = 2.791$, $0.25<P<0.1$) or substrate arrays ($X^2_{3,3} = 8.765$, $0.1< P <0.05$). We did, however, observe a statistically significant difference in the length array ($X^2_{3,3} = 45.412$, $P<0.001$). When testing treatment within the length array individually (summing all captures per treatment over the sample nights), no significant difference between observed and expected captures was seen ($X^2_2 = 0.737$, $0.75>P<0.5$). Similarly, no significant difference was seen when assessing the role of position independent of treatment ($X^2_2 = 5.156$, $0.1>P<0.05$).

DISCUSSION

Predicting patterns of occurrence

Differences in the variables that best explained the abundances of our two focal species crossing Route 91 likely reflect variation in life-history traits. Ambystomatid salamanders have been shown to be susceptible to water-loss (Rothermel & Luhring 2005; Rothermel & Semlitsch 2002) and to prefer to move through moist habitats such as seeps. Although little is known about their fossorial ecology, underground moisture may also play a role in determining patterns of occupancy outside of the breeding season. Conversely, anurans such as American toads are relatively tolerant of desiccation (Duellman & Trueb 1986). The inverse relationship between toad abundance and the presence of wetlands downslope of the road is likely to be a function of their choice of overwintering habitat, rather than their avoiding these wetlands: We know from observations at the site that the toads do breed in these wetlands. Our data suggest that toads are choosing to overwinter in drier areas, and that there is a lower likelihood of their being a wetland directly adjacent to these types of overwintering sites.

Culvert characteristics

The results of our experiments with different culverts provide strong evidence that the different lengths, substrates, and diameters we tested did not affect the choices made by spotted salamanders during active migration. Our results also confirmed existing studies with spotted salamanders showing that they will readily move through culverts (Jackson & Tyning 1989), and that for amphibians in general, a combination of drift fences and culverts is an effective approach to mitigation (Aresco 2005; Dodd et al. 2004).

For the length array, the significant difference between observed and expected captures is most likely a function of a slight difference between this and the other arrays: Whereas with the other arrays we aligned the drift fences and bays exactly parallel to the slope, in the case of the length array the difficulty of incorporating the longest treatment forced us to change this alignment such that the drift fences and bay were at a slight angle to the slope (with the southernmost culvert entrance slightly downslope). Although position was not statistically significant at the length array, we captured 26% fewer animals than expected at the northernmost trap (where the culvert entrance was furthest upslope), 16% fewer in the middle trap, and 42% more at the southern trap.

It is important to recognize that our study does not show that the attributes of culverts have no effect on choice, but that the specific treatments we tested with a single focal species at a single site did not significantly which culverts were selected. There are several ways in which our study culverts differ from those typically placed under roads by management agencies: Our longest treatment of 9m is still shorter than many of the culverts under roads, and it may be that we did not reach some length threshold at which an effect on choice is seen. The substrate treatments we tested were also relatively benign, especially in relation to the desiccation risk presented by concrete and gravel in long dry tunnels. We know that amphibians are extremely prone to water loss (Mazerolle & Desrochers 2005; Rittenhouse et al. in press), and an animal moving long distances over a dry surface is likely to be more affected than one traveling over a moist surface.

Bearing in mind these caveats, our results do suggest that spotted salamanders in active migration mode will move through a variety of structures. These findings differ from other experimental research where choice has been shown to be more dependant on the attributes of culverts. For example, Woltz et al., found that the diameter of culverts, substrate type and culvert length influenced choice for at least some of the focal species (green frog, *Rana clamitans*, northern leopard frog, *R. pipiens*, common snapping turtle, *Chelydra serpentina*, and eastern painted turtle*, Chrysemys picta picta*) (Woltz et al., 2008). The differences seen between this study and our own may well represent inherent differences in the species tested, but there is also the potential that animals translocated into experimental arenas may not behave in the same way as those undergoing natural movements. Differences in patterns of habitat selection by amphibians depending on life-history mode (i.e., dispersing compared with settled phases) have been seen in wood frogs, *R. sylvatica*, (Patrick et al. 2008). The weakness of the statistical analyses we were able to conduct with our study design clearly highlights the value of conducting experiments that can be readily replicated, however. Our suggestion is that wherever possible, studies based on experimental manipulation of animals should be accompanied by field studies looking at the same organisms during their natural movements. Even if the latter studies do not have sufficient statistical power in themselves, they can help provide support for results garnered from controlled experiments.

CONCLUSIONS

The results of our research at Labrador Hollow provide valuable information when mitigating the effects of roads on amphibians. For spotted salamanders, our study results indicate that culverts are likely to be best placed where seeps descend from upland overwintering areas. Choices regarding culvert diameter within the range from 0.3 to 0.8m, culvert length, and substrate may not be as important as other factors; we recommend choosing a substrate material that holds moisture, and locating the pipe such that at peak water flow, there is a continuous area along the bottom of the culvert without flowing water. The latter recommendation is important as it means that culverts used for amphibian crossing are unlikely to be suitable for drainage. Observations at Labrador Hollow suggest that animals are not choosing to use existing culverts for under-road passage as the water volume and velocity is extremely high during their period of migration. This finding has also been supported by previous research with spotted salamanders (Jackson & Tyning 1989).

Our data for American toads show that a one size fits all policy for culvert placement is unlikely to be effective. This places transportation managers in a difficult position given limited resources for mitigation. There are, however, groups of species with similar patterns of occurrence for example spotted salamanders and wood frogs. Culverts placed as passageways for one of these species are therefore likely to serve for others.

There is clearly need for further research into the placement of culverts. One intriguing result from our study was the increase in captures of animals in the southernmost/downslope trap of the length array. Bearing in mind that this array was still close to parallel to the direction of migration, it suggests that funneling salamanders in a specific direction (for example towards a passageway) may be relatively easy. This theory could be readily tested with a simple experimental design.

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Table 6.1. Results from poisson regression of the number of spotted salamander observed crossing Route 91 at Labrador Hollow, Apulia, NY. Variables in candidate models include distance to the nearest culvert ('Dist_culvert'); the presence of flowing water on the upslope ('Water'), and the presence of a wetland within 15m on the downslope of the road (Wetland). All interactions were included in models, but only significant interactions are shown (indicated by a colon).

Model name	Variable	Residual deviance	AIC	Δ AIC
	Dist_culvert* Water*** Dist_culvert:Water*	461.25	691.06	0
	Water***	468.69	694.50	3.44
Global	Water*** Dist_culvert Wetland Water:Dist_culvert*	460.76	694.58	3.52
	Water*** Wetland	467.61	695.42	4.36
	Dist_culvert Wetland***	520.37	750.18	59.12
	Wetland***	527.64	753.43	62.37
	Dist_culvert	539.49	765.3	74.24

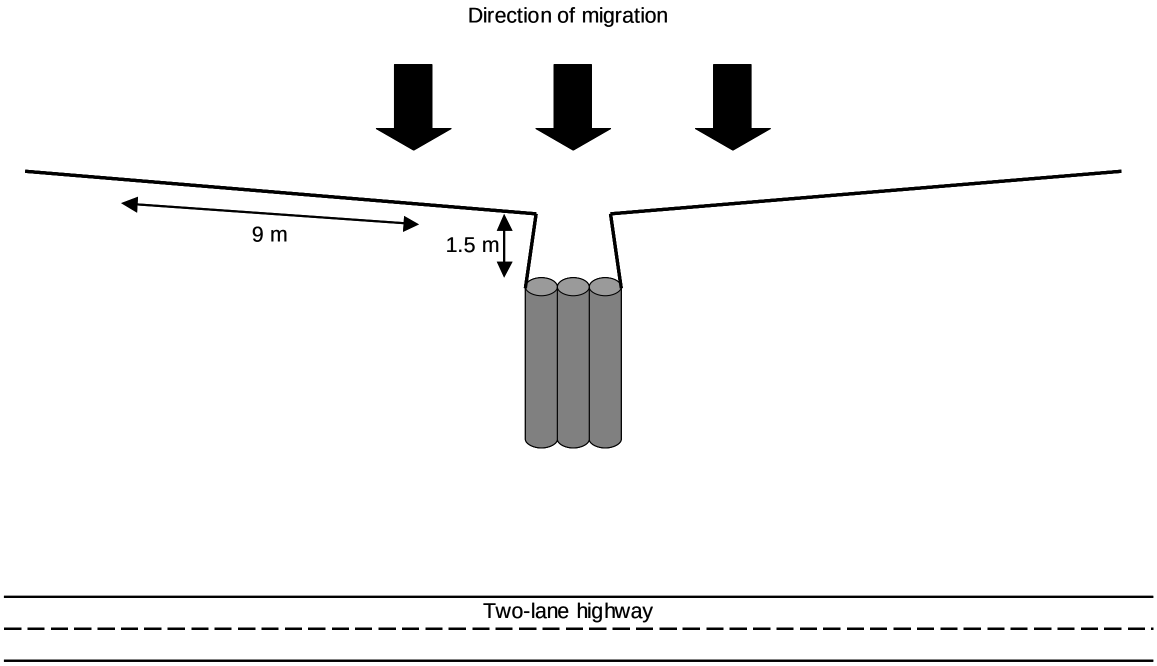
[1] Significance of variables is indicated as follows *** <0.001, **<0.01, *<0.05

Table 6.2. Results from poisson regression of the number of American toad observed crossing Route 91 at Labrador Hollow, Apulia, NY. Variables in candidate models include distance to the nearest culvert ('Dist_culvert'); the presence of flowing water on the upslope ('Water'), and the presence of a wetland within 15m on the downslope of the road (Wetland). All interactions were included in models, but only significant interactions are shown (indicated by a colon).

Model name	Variable	Residual deviance	AIC	Δ AIC
	Dist_culvert Wetland Dist_culvert:Wetland*	75.410	204.71	0
	Wetland***	79.994	205.30	0.59
Global	Water Dist_culvert Wetland Dist_culvert:Wetland*	73.256	206.56	1.85
	Water Wetland***	79.448	206.75	2.04
	Water	92.518	217.82	13.11
	Dist_culvert Water	89.896	219.2	14.49
	Dist_culvert	95.569	220.87	16.16

[1] Significance of variables is indicated as follows *** <0.001, **<0.01, *<0.05

Figure 6.1. Example of one of the four arrays used to test the influence of culvert attributes on selection by migrating adult spotted salamanders at Labrador Hollow, New York. The example shown is for the position array (where all culverts were the same). Culverts are shown as gray tubes, drift fences as solid black lines.



7. MULTI-SCALE HABITAT-RESISTANCE MODELS FOR PREDICTING ROAD MORTALITY "HOTSPOTS" FOR REPTILES AND AMPHIBIANS

ABSTRACT

As road networks and traffic volumes increase, road-effects on animal populations are becoming more prevalent. Our goal was to identify herpetofaunal crossing hotspots on roads and to use this information to prioritize deployment of mitigation efforts. Our focus was New York State where in a collaborative effort between ecologists and the New York State Department of Transportation we synthesized available literature to predict patterns of habitat use by 10 species of herpetofauna. A geographic information system was then used to develop habitat resistance-based models to predict hotspots of herpetofaunal abundance on roads. We developed three approaches for prioritizing model output for transportation planners: (1) Categorizing occurrence indices based on five quantiles; (2) overlaying the arterial classification code (a measure of traffic intensity) over model outputs, and (3) using the contiguous length of road remaining within specified high occurrence index values. Models were evaluated using field data derived from road surveys. Our models showed clear differences in the predicted occurrence of species of herpetofauna on roads depending on life-history strategies. Wide-ranging habitat generalists were predicted to have at least some probability of occurrence on most roads in the study area, for example the common snapping turtle, *Chelydra serpentina*, was predicted to occur on 98% of roads. Conversely, species with limited movement ranges and specific aquatic and terrestrial habitat had more limited distributions, for example the wood frog, *Rana sylcatica*, was predicted to occur on 43% of roads. Validation data indicated that models were effective tools for predicting occurrence of species with specialized habitat requirements, but that predictions for wide-ranging generalists were less accurate. These data also demonstrated that the use of quantiles and the length of continuous hotspot were effective approaches to prioritizing the deployment of mitigation for habitat specialists, with higher densities of animals occurring where there was a higher occurrence index and in longer sections of continuous high occurrence. Our modeling approach is an effective tool for identifying road-hotspots for herpetofauna, allowing predictions to be made over large spatial extents and with readily available data sources. Our results suggest that effective mitigation for movement-limited habitat specialists may include spatially and/or temporally targeted approaches such as road-underpasses or temporary signage. For widespread generalist species it is extremely difficult to determine exact locations for mitigation, thus broader-scale approaches such as driver education are likely to be more effective.

INTRODUCTION

A wealth of research has shown that roads can affect animal populations, both through direct mortality (Smith & Dodd 2003), and through habitat fragmentation, degradation and loss (Forman & Deblinger 2000; Trombulak & Frissell 2000; Vos & Chardon 1998). As road-networks and traffic volumes increase, agencies managing roads have an increasingly challenging task: how to build and maintain a system that facilitates the flow of people and commerce, while minimizing the effects on biodiversity. Balancing these objectives can be greatly enabled by understanding where roads are of most concern to animal populations. By identifying these "hotspots" of road-effects, transportation managers can prioritize mitigation efforts when re-engineering existing roads and minimize the likely effects of new roads.

Herpetofauna represent an important target for modeling hotspots as they are particularly vulnerable to road-effects. Many species of amphibians and reptiles make annual migrations between aquatic and terrestrial habitat, increasing the probability that an individual will encounter roads. When crossing roads, the slow rates of movement of many species of herpetofauna make them extremely susceptible to road-mortality (Ashley & Robinson 1996; Hels & Buchwald 2001). High road-mortality of herpetofauna during terrestrial movement is of particular concern as these individuals are members of later life-history stages (juveniles and adults) (Aresco 2005; Gibbs & Shriver 2002). Changes in survival of these stages, which typically have high survival relative to earlier life-history stages in undisturbed populations, are likely to drive overall population dynamics (Biek et al. 2002; Vonesh & De la Cruz 2002).

Because many species of herpetofauna rely on aquatic habitats, have high adult philopatry (Berven & Grudzien 1990) and limited terrestrial vagility (Patrick et al. 2006; Smith & Green 2005), populations tend to be spatially structured. Depending on the composition of wetlands, local populations may be centered around single or small groups of wetlands, with rare dispersal events connecting these local populations in regional or meta-populations (Marsh & Trenham 2001; Sjogren Gulve 1994). Maintaining the viability of herpetofaunal populations is therefore reliant on conservation efforts that focus on maintaining both local and regional viability (Semlitsch 2008). Road-effects can influence population dynamics at both these scales; at the local level, primarily by influencing survival of adults and philopatric juveniles that migrate to and from the same aquatic sites; and at the regional population levels by altering the frequency of juvenile dispersal between local populations.

To predict hotspots of road-effects for herpetofauna we must first be able to predict the distribution of animals in the landscape. A number of approaches have been used to model patterns of spatial distribution. Dispersal kernels represent one of the simplest forms, where the distribution of individuals away from a source (for example a pond) is typically calculated from empirical data (Worton 1989). This approach, however, fails to consider the role of habitat heterogeneity in determining habitat use (Ricketts 2001). The application of resistance surfaces/friction modeling in Geographic Information Systems (GIS) offers a means to include variation in habitat suitability. With this technique, each habitat type in a landscape is assigned a "friction" value based on the willingness of animals to cross the habitat type, the physiological cost incurred during this crossing, and the reduction in survival for the individual (Joly et al. 2003; Ray et al. 2002). Research has now combined friction modeling with information on the movement behavior of different species (Compton et al. 2007; Popescu 2007). These hybrid approaches weight 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. This provides a more realistic assessment of the probability of an individual being present at any point in the landscape.

This newly developed approach to predicting patterns of spatial distribution provides a valuable tool for modeling likely hotspots of road-effects for herpetofauna. Specifically, by using a mechanistic understanding of species-habitat relationships based on readily-available data to derive hotspot models, we are able to offer a valuable addition to current modeling efforts that are primarily phenomenistic (Langen et al. 2009). This information is of particular benefit when recommending how to reduce the effects of newly constructed roads on herpetofauna and for making predictions over wide geographic areas. Under these circumstances, hotspot modeling based solely on empirical studies is difficult; one cannot sample a road that does not exist yet and predictions based on observations in a limited suite of field-conditions are often inaccurate when applied to novel circumstances.

The goal of this study was to pilot the use of habitat-resistance modeling to map hotspots of herpetofaunal road mortality in New York State. Our objectives were: (1) To develop maps of predicted herpetofaunal occurrence for species with a variety of life-history traits; (2) to develop means of prioritizing these hotspots for mitigation efforts; (3) to validate models using empirical data; and (4) to develop a strong working collaboration with transportation management agencies, to build the capacity of both research scientists and managers, and to ensure that we provide the most useful and relevant information for mitigation efforts. To meet these objectives, this applied modeling project was developed in concert with transportation managers. We modeled 10 species with a variety of life-history traits allowing us to extend our results to additional species. We also looked at the effects of roads at multiple scales by developing separate hotspot models for local and regional populations of amphibian species (the only herpetofaunal taxa for which sufficient data were available). We validated our models *post hoc* by sampling herpetofauna on roads in a select area of New York State.

METHODS

We developed models for twelve counties in New York State: Cayuga, Cortland, Chenango, Onondaga, Madison, Oswego, Oneida, Delaware, Otsego, Schoharie, Albany, and Greene (Fig. 1). This ~67450 km^2 area has a network of public roads ~85303 km in length and encompasses gradients from rural-urban and agriculture-forest as well as including a variety of topography from the alluvial plains on the south of Lake Ontario to the steep glacial valleys of the Allegheny Plateau. Areas within these counties were excluded if no National Wetlands Inventory (NWI) data were available.

Study species were chosen based on incorporating a range of life-history traits, availability of literature data, and targeting species of specific conservation concern in New York State. Amphibian species included three ranids: the wood frog, *Rana sylvatica*, green frog, *R. clamitans*, and northern leopard frog, *R. pipiens*; one bufonid, the american toad, *Bufo americanus*, one ambystomatid salamander: the spotted salamander, *Ambystoma maculatum,* and one true salamander, the eastern red-spotted newt, *Notophthalmus viridescens*. Reptile species included four turtle species: snapping turtle, *Chelydra serpentina*, spotted turtle, *Clemmys guttata*, eastern painted turtle, *Chrysemys pictus pictus*, and wood turtle, *Glyptemys inscuplta*.

A suite of GIS datasets were used in our road-mortality hotspot models (Table 3). All layers were set to a common coordinate system (Universal Transverse Mercator Zone 18 North), and datum (North American Datum 1983). All analyses were performed using ArcGIS 9.0 (ESRI, Redlands, CA). Creating the friction models for herpetofauna involved a 7-step process illustrated in Figure 2: (1) Determine potential suitable aquatic habitat for each species from which to initiate calculation of cumulative cost to movement; (2) Assess which of these aquatic sites has sufficient forest cover required by some amphibian species for population persistence and remove aquatic sites that do not meet these requirements; (3) Assign 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) Create 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) Use the "Cost-Distance" procedure in ArcGIS 9.0 to calculate the cumulative cost distance within these movement buffers; (6) Rescale these cumulative costs to the probability of a species being present; and (7) Extract the probability of presence for the existing road network in the study area.

We assigned the aquatic habitats for each of the species (the loci on which resistance surfaces were centered) based on literature data (Table 1). NWI wetland classes were grouped based on system and subsystem categories within Cowardin's wetland classification index (Cowardin et al. 1979) (Table 4). For the initial land-cover map (for which resistance values were assigned), we combined the National Land Cover Database (NLCD 2001) and NWI, replacing NLCD wetland categories with the more precise NWI classifications. Friction costs assigned to each land-cover type for each species were based on literature data rather than expert knowledge. Our friction index ranged from 0 (most suitable) to 50 (least suitable). A value of 0 (i.e., no cost) was used for the most suitable habitat, as it was considered to actually facilitate movement (Popescu 2007).

Persistence of populations of three of our focal amphibian species, the wood frog, spotted salamander, and eastern newt have been shown to be dependent on forest cover (Guerry & Hunter Jr. 2002; Herrmann et al. 2005; Homan et al. 2004). Estimates of the amount of forest cover needed by these species vary between studies, regions, and species. We set a minimum threshold for site occupancy by these species as 40% forest cover (deciduous and coniferous but excluding the shrub/scrub category in the NLCD [2001]) 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.

To assign friction values, we divided the available literature data into two groups: Table 1 documents research that generally describes habitat suitability for study species. Table 2 represents research that specifically quantified the proportion of individuals choosing certain habitats when faced with a range of choices. 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, *Rana septentrionalis*, in northern New York State, and Compton et al. (2007) juvenile marbled salamanders, *A. opacum*, and adult spotted salamanders in Massachusetts. We used these studies as benchmarks to compare our own estimates for anurans and spotted salamanders respectively. The friction values we estimated for each land-cover type are shown in Tables 5a and b (for NLCD classifications), and 6 (for NWI classifications).

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). This index was then used to alter resistance values, resulting in the wettest areas having a resistance value 5 points lower than the driest areas.

Movement buffers for amphibians were based on the maximum migration and dispersal distances reported for adults and juveniles (Table 1). 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 as limited data for some species meant that mean distances were often much lower than maximums.

Once resistance surfaces had been generated for each species (and life stage in case of amphibians), 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 (CSCIC) as part of the Accident Location Information System (ALIS). This provided us with a relative measure of the probability of an animal crossing each 30 m long section of road. As road mortality has been shown to increase with traffic intensity (Carr & Fahrig 2001; Gibbs & Shriver 2005), we also developed models where 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 (for example 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, whereas class 6 represents residential roads with either one or two lanes and a maximum speed of 15-25 mph (http://www.nysgis.state.ny.us/gisdata/inventories/details.cfm?DSID=932).

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 both migrating and dispersing individuals for all amphibians except red-spotted newts.

We derived three means of prioritizing hotspots. In the first, we classified occurrence indices based on quantiles in ArcView using 5 divisions. We chose this method rather than an equal interval approach as the distribution of the occurrence index for each model tended to be highly left-skewed (i.e., many more occurrence rasters with a high rather than low predicted probability of occurrence). In the second approach, we initially selected occurrence index values in the range of 0-2 for each model (i.e., the highest probability of occurrence) then reclassified hotspots based on the length of continuous hotspot that remained within these occurrence index values. For the third approach to prioritization, we overlaid the ACC for roads over our occurrence indices, allowing hotspots to be identified based on traffic intensity.

Model validation

To validate the accuracy of our models, we selected an area of road network within our study region (in the vicinity of Labrador Hollow State Unique Area, approximately 20 miles south of Syracuse, New York, hereafter call "Labrador Hollow") that encompassed the same land-cover gradients as our full model within a small geographic region. This 20 mile-long road network was sampled in its entirety on rainy nights from 31st March to 2nd May 2008 between dusk and 12 pm. Sampling consisted of driving slowly (<30 mph) along the road and recording all live and dead animals, including details of age and sex where possible and 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 shorter section of road within an agricultural region approximately 15 miles south of Syracuse New York, hereafter called the "Tully Valley." This 12 mile-long section of road was sampled seven times on rainy nights from May 27- August 23 2007. Sampling was conducted using a bicycle riding at 8 mph, ensuring that most animals on the road including juveniles were detected.

We used 30m road segments as our sampling unit for model validation (i.e., the minimum resolution of our hotspot model output) and focused on predictions and field-data for migrating adults of three species of amphibians; the spotted salamander, green frog, and American toad. One of these species, the American toad was sufficiently abundant on both survey routes to allow model validation. Green frogs were only observed in sufficient numbers on the Tully Valley route and spotted salamanders on the Labrador Hollow route.

To compare the ability of our models to predict the locations of animals crossing roads in general, we examined whether more observations of animals were made in high occurrence index rasters, with a null hypothesis that observations occurred randomly and thus in the same proportions as the proportions of each occurrence index value. We reclassified rasters based on the occurrence index into 4 categories: (1) Rasters on the route that were predicted as non-occurrence; and rasters with an occurrence index of (2) 0-5; (3) 6-10; and (4) >10. Chi square tests were used to compare the observed distribution of occurrences with a null hypothesis of animals being randomly distributed along the route.

To compare the use of the length of contiguous high occurrence index values (i.e., 0-2), we assessed the number of observations per 30-m raster in 4 length categories: (1) Rasters on the route that were either non-occurrence or had an occurrence index of >2; (2) short sections of road [length <100m]; (3) medium [length 100-500m]; and (4) long [length >500m]. For these analyses, we compared the observed distribution of occurrences within rasters of these length classifications to that expected under a null hypothesis of a random pattern of occurrences.

RESULTS

As expected, our models predicted that amphibians and reptiles were more likely to be found on roads closer to suitable aquatic habitat and in high-quality terrestrial habitat. The occurrence indices tended to be left-skewed. This skew is a result of high-quality terrestrial habitats such as forested wetlands being assigned a resistance value of 0. 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 species on roads in New York State clearly differed. The range of aquatic habitats species used, estimated maximum movement distances, and their relative sensitivity to terrestrial habitat change caused these differences. Figure 3 illustrates the occurrence index model outputs (for all terrestrial habitat rather than just roads) for a wide-ranging generalist species, the common snapping turtle, compared with migrating spotted salamander, a species with 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. For example, Figure 4 documents differences between migrating adult wood frogs, which tend to remain closer to aquatic sites but are relatively more tolerant of terrestrial habitat change, and the wide ranging but relatively sensitive juvenile dispersers.

Prioritization

Figure 5 illustrates typical output for our target species (using migrating wood frogs as an example) based on the three methods of prioritization we developed: (1) classifying the occurrence index values based on 5 quantiles; (2) using the arterial classification code (ACC);

and (3) using the length of continuous high-occurrence rasters. The proportion of the total length of the road network in our study area that was encompassed by different prioritization metrics varied by species: Migrating adult wood frogs 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, with 8.7% of the road network being classified in the highest occurrence index quantile (top 20%). When using the length of continuous high-occurrence as a metric, 28.4% of the road network fell in the 'long' length category of >500 m continuous high occurrence. Snapping turtles, a habitat generalist with a maximum reported movement of 2020 m had at least some probability of occurrence on 97.6% of the road network, with 19.5% of the road network being classified in the highest occurrence index quantile. When using the length of continuous high-occurrence as a metric, 35% of the road network fell in the 'long' length category of >500 m continuous high occurrence.

Model validation

We observed 330 animals on the 20-mile stretch of road surveyed by car in the vicinity of Labrador Hollow, representing 8 species. Four of these species were relatively abundant (spotted salamander, n = 206; American toad, n = 38; wood frog, n = 35; and eastern red-spotted newt, 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 14 species (3 snake species, 2 salamander, and 8 anuran). These species can be loosely grouped into two categories; abundant species represented by green frogs (n = 138) and American toads (n = 91), and rarely observed species (all other species, n < 7).

Of the three species we used for model validation, the observed distributions of spotted salamanders and green frogs differed significantly from the null hypothesis of a random pattern of occurrences in relation to both the overall occurrence index (Table 7) and the length of high occurrence areas (Table 8). In the case of spotted salamanders, the null hypothesis predicted that 9.4% of observations should occur in non-occurrence rasters, with 2.5% of actual observations seen in these locations. For the highest occurrence index category (occurrence indices from 0-5), 53.5% of observations were predicted, with an actual occurrence of 84.2%. For the two lower occurrence index categories (6-10 and >10), fewer animals were observed than predicted. When comparing observed versus expected observations of spotted salamanders per 30-m section of road in relation to road length, more animals were observed on road sections in the longest length category, >500m, than expected under the null hypothesis (14.1% expected, 26.6% observed), with fewer observations than expected in the other categories (shorter lengths of road and those predicted as either non-occurring or with an occurrence index of >2).

Because of the large movement distances of green frogs, no sections of road were predicted as non-occurrence, i.e., we were not able to evaluate the commission error of our models. When comparing observed versus expected occurrences for this species, model performance was poor; in the highest occurrence index category (0-5), 67.9% of occurrences were predicted with 61.6% observed. Similar patterns were seen in the medium occurrence index category (30.8% predicted with 31.9% observed). In the lowest occurrence index category (>10), more animals were observed than predicted (1.2% predicted with 6.5% observed). The latter result drove the statistically significant difference in the overall comparison of observed versus expected. When comparing observed versus expected distributions of this species in relation to the length of predicted hotspot, models also performed poorly, with more animals observed in the short and medium length categories than expected (for roads <100m, 0.9% expected and 3.6% observed;

for roads 100-500m, 11.7% expected and 16.5% observed), and fewer animals on the longest hotspots (11.6% expected and 3.6% observed). Observed versus expected observations in areas predicted as either non-occurring or with an occurrence index of >2 were similar (75.8% expected, 76.3% observed).

Although no overall significant difference was seen when comparing the observed versus expected distributions of American toads, more animals occurred in the highest occurrence index category at Labrador Hollow (61.9% expected and 77% observed) with fewer observations than expected in all other categories. The same trend was seen on the Tully Valley route, although with less of a pronounced difference between observed and expected (for the highest occurrence index category, 59.6% expected, 61.8% observed). When comparing observed versus expected in relation to the length of hotspot, more animals were observed in the longest length category at Labrador Hollow (30.9% expected, 37.1% observed) with fewer in all other categories. In Tully Valley, however, fewer animals were observed in the longest length category (8.3% expected, 5.5% observed, with more observations in the medium (7.4% expected, 10.0% observed) and either non-occurring or with an occurrence index of >2 category (82.4% expected, 84.4% observed).

DISCUSSION

Our models predict a widespread occurrence of herpetofauna on roads in New York State 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. Similar to the results of other studies, particularly high concentrations of animals are found on roads that run adjacent to large wetland complexes (where breeding habitat 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, and relatively simple prioritization methods, which can be easily replicated in other parts of the state.

Differences between species

Differences between the predicted patterns of occurrence of species on roads have clear implications for mitigation. For species such as the spotted salamander or wood frog characterized by relatively limited terrestrial vagility, specific aquatic habitat requirements, and high sensitivity to anthropogenic changes in terrestrial habitat, our models identify discrete locations in which mitigation can be focused. Many of these species are also considered ‘explosive’ migrators, with the majority of individuals crossing roads simultaneously at predictable points during the year (for example the spring migration of adult amphibians into ponds to breed Paton & Crouch 2002). For species that have this type of life-history strategy, approaches to mitigation such as culverts, signage and potentially road-closures may be valuable and represent a feasible balance between the needs of road-users and biodiversity. Conversely, wide-ranging species such as spotted turtle characterized by low population densities and relatively continuous movement throughout the active season (although see (Beaudry 2007) may present a greater challenge to mitigation. Although these species have a relatively low probability of occurring on any one stretch of road and thus being vulnerable to road-mortality, their life-history strategy characterized by late reproductive maturity and high adult survival under natural conditions makes populations extremely vulnerable to any increase in adult mortality. Bearing this in mind, mitigation focused on single point locations, for example culverts, is unlikely to be enough to maintain the long-term viability of populations of species such as this. Broader-scale measures deployed at crossing hotspots, for example seasonally reduced speeds, and population-level measures such as driver education may be more appropriate (Beaudry 2007), with the best strategy for long-term conservation of these species likely to be maintaining contiguous areas with low road and traffic densities of sufficient size to maintain viable populations.

Differences between life-history stages: migration versus dispersal

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. The role played by juveniles in population dynamics is important to consider, however, with these individuals providing 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 the wood frog (Harper et al. 2008).

Prioritization

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 three methods we have highlighted — the use of quantiles in the data to identify where animals are most likely to occur on roads, the length of continuous hotspot, and classifying occurrence based on traffic intensity — represent useful metrics for transportation agencies. There are however a variety of different ways of prioritizing hotspots that can be readily generated from our model output. These include identifying zones of connectivity between populations and identifying likely areas of high abundance of animals on roads (for example selecting contiguous areas of high occurrence). From a jurisdictional standpoint, there are a number of different agencies responsible for managing roads in New York State including the State Department of Transportation, County Departments of Transportation and local town and villages as well as New York Thruway Authority (responsible for the State's main toll highway). Each of these agencies varies in terms of their capacity for deploying mitigation and the mandates given to them by their constituents. If we are to see the results of our models effectively implemented, understanding these differences and providing information at a relevant spatial scale and technical level is vital.

Model validation

Bearing in mind the limited number of species and spatial and temporal scale over which validation occurred, the model validation we conducted demonstrated that our models are effective tools for predicting occurrences of species with limited movement ranges and relatively specific habitat requirements, for example the spotted salamander. Our models were less effective in predicting occurrences of generalist species with larger movement ranges such as the American toad and green frog. 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. Our validation data also show that the use of the length of contiguous hotspot is a good indicator of the likely abundance of these habitat specialists on roads, and that if reducing the abundance of mortality on roads is the goal of mitigation, targeting these locations may be an effective approach.

Use of models in transportation planning and mitigation
Our models were designed to meet a specific purpose, i.e., to inform transportation managers as to where roads in the New York State are most likely to detrimentally affect populations of amphibians and reptiles. We believe that our models effectively meet this goal, especially given that before their development, the Department of Transportation had no large-scale data on which to base their decisions. There are a number of important caveats when applying our models to mitigation, however. As with all models, the reliability of the output is dependent on the quality and accuracy of the data used in development. There are three principle sources of error in our model development. The first is knowledge of the ecology of our focal species: For most species of herpetofauna there are large gaps in our understanding of their ecology, especially in the terrestrial environment. Although we used sufficient literature data as one of the criterion when selecting species, inevitably some of our estimates of habitat suitability, movement distances etc., were based on limited data, or from studies conducted outside of our region.

The second potential source of error is the remote sensing data we used. The categorical NLCD and NWI data miss some of the finer scale differences within each category of habitat. For species that are sensitive to change in aquatic or terrestrial habitat, this variation can be the difference between occurrence and non-occurrence. Similarly, certain habitat features are omitted from these data. An important example is the smaller ephemeral wetlands used by some of our study species such as the wood frog and spotted salamander. Lastly, landscapes are dynamic and as time progresses since the NLCD and NWI were assessed there is an increasing chance that habitat will no longer be the same.

The third potential source of error is that models were based on the presumption that populations would be located wherever suitable aquatic habitat and sufficient terrestrial habitat for certain species were found. This certainly led to an overestimation of the occurrence of some species on New York roads. In areas with high traffic intensity/road densities, the resulting mortality may have already led to the extirpation of these local populations.

Bearing in mind these caveats, the results of our models can be used to generate a number of specific recommendations for mitigating the effects of existing roads and constructing new roads with the minimum effect on animal movement: (1) The highest abundance of animals is likely to be found where roads run in close proximity to large wetland complexes. In these locations, a combination of directional fences and crossing structures is likely to be effective (Aresco 2005); (2) transportation managers should avoid constructing roads that run in close proximity to wetlands, especially where the road is likely to create a division between two critical habitat types, for example aquatic sites and nesting habitat for turtles and aquatic breeding sites and terrestrial foraging areas for amphibians; (3) for species with specific habitat requirements and predictable seasonal movement patterns, mitigation efforts focused on specific points in space and time are likely to be effective, whereas for species with more generalized habitat use and patterns of movement, mitigation also needs to include broader strategies such as traffic calming, reduced speed limits, and driver education; (4) the use of field-surveys to ground-truth model predictions is more likely to be an effective tool for species for which mortality is predictably concentrated in space and time; and (5) in limited circumstances, where animals are crossing a road to access a vital resource and sustaining high mortality in the process, moving the habitat rather than the road (for example constructing artificial nesting habitat or regenerating woodland), coupled with the use of a roadside barrier to movement may be appropriate. This last approach should not be viewed as a panacea, or as a proactive approach to issues with future road construction but may be an effective option for existing roads.

Table 7.1. Life-history characteristics of the focal study species. In addition to the cited references, data were gathered from natureserve explorer (http://www.natureserve.org/explorer/), AmphibiaWeb (http://amphibiaweb.org/search/index.html), and Gibbs et al. (2007). Where insufficient data were available for a species, data were gathered from similar species (indicated by *).

Species	Breeding habitat	Summer habitat	Winter habitat	Max. adult movement distance (km)	Max. juvenile movement distance (km)	Types of movement	References
Wood frog	Vernal pools, forested wetlands, beaver impoundments	Forested wetlands, moist forest	Forested uplands	0.43	2.53	Adult breeding, juvenile emigration, migration to summer foraging, migration to overwintering sites	(Baldwin et al. 2006; Bellis 1965; Berven & Grudzien 1990; Heatwole 1961; Patrick et al. 2006)
Green frog	Permanent wetlands	Pool/stream edge. Juveniles will disperse into woods and meadows.	Underwater/ underground	1.26	4.8	Juvenile emigration, adult movement to and from overwintering sites	(Carr & Fahrig 2001; Guerry & Hunter Jr. 2002; Lamoureux et al. 2002; Livingston Birchfield 2002; Martof 1953, 1956; Patrick et al. 2006; Schroeder 1976)
N. leopard frog	Permanent and vernal slow moving or nonflowing wetlands	Fields and meadows preferred to close-canopy forest. Juveniles may move to the edges of permanent water	Underwater	3.218	5.2	Adult breeding, juvenile emigration, migration to summer foraging, migration to overwintering sites	(Carr & Fahrig 2001; Dole 1965, 1967, 1971; Merrell 1970; Pope 2000; Seburn et al. 1997)
American toad	Permanent and vernal slow moving or nonflowing wetlands typically without fish or wood frog tadpoles	Forest, agricultural lands, parks, gardens	Underground	1.0	*1.650	Juvenile emigration, adult breeding migrations.	(Breden 1987; Holomuzki 1995; Petranka et al. 1994)
Spotted salamander	Vernal pools, forested wetlands, beaver impoundements	Underground in forest, adults will cross open areas	Underground in forest	0.756	0.150	Juvenile emigration, adult breeding migrations, movement to overwintering sites	(Douglas 1981; Faccio 2003; Guerry & Hunter Jr. 2002; Kleeberger & Werner 1983; Madison 1997; McDonough & Paton 2007; Patrick et al. 2008)
E. spotted newt	Ponds, lakes, and slow moving rivers	Adults are aquatic, efts in forest with strong edge avoidance		Na	1.0	Juvenile/eft emigration	(Gibbs 1998; Gill 1978; Hurlbert 1969)
Snapping turtle	Edges of lakes, ponds, and slow-moving rivers	Lakes, ponds, and slow moving rivers, nests close to water	Aquatic	2.020	na	Adult nesting, movement between ponds, juvenile emigration, movement to hibernacula	(Brown & Brooks 1994; Pettit et al. 1995; Ultsch 2006)
Spotted turtle	Several hundred yards into uplands	Vernal pools in spring, upland forest for dormancy, fields for egg laying	Wet meadows, forested swamps or	1.025	na	Adult nesting, movement to upland estivation sites, overwintering movements	(Ernst 1976; Joyal et al. 2001; Milam & Melvin 2001; Ultsch 2006)

			sphagnum bogs				
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	0.625	na	Adult nesting, juvenile emigration, movement between ponds	(Baldwin et al. 2004; Christens & Bider 1987; Rowe 2003; Ultsch 2006)
Wood turtle	Edge of aquatic habitat	River or streams with sand or gravel substrates bounded by woods, agricultural lands	Creeks	3.6	na	Adult nesting, juvenile emigration	(Arvisais et al. 2002; Compton et al. 2002; Kaufmann 1992; Quinn & Tate 1991; Saumure et al. 2007; Walde et al. 2003; Walde et al. 2007)

Table 7.2. 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 forest, 31 % in partial cut forest, and 14% in clearcut treatments	(Patrick et al. 2006)
	A	U	51% of captures were in forest, 26.5% in partial cut forest, and 11% in clearcut treatments	(Patrick et al. 2006)
	U	U	66% of captures were in closed canopy forest (>20 m from edge), remaining captures in edge of clearcut	(deMaynadier & 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 edge	(Gibbs 1998)
Green frog	A	U	25% of captures were in forest, 17% in partial cut forest, and 26% in clearcuts	(Patrick et al. 2006)
	J	U	33% of captures were in forest, 27% in partial cut forest, and 20% in clearcuts	(Patrick et al. 2006)
N. leopard frog	A	U	30% of captures were in forest, 47% in partial cut forest, and 12% in clearcuts	(Patrick et al. 2006)
	J	U	33% of captures were in forest, 30% in partial cut forest, 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, 44 entered forest when given the choice	(Rothermel & Semlitsch 2002)
	U	U	~43% of captures were in closed canopy forest (>20 m from edge), remaining captures in edge of clearcut	(deMaynadier & Hunter 1998)
Spotted salamander	U	Feeding	Preferred moist forest soils to drier forest soils	(Wyman 1988)
	J	Emigration	Ten animals entered old-fields, 23 entered forest when given the choice	(Rothermel & Semlitsch 2002)
	A	U	37% of captures were in forest, 29% in partial cut forest, and 17% in clearcuts	(Patrick et al. 2006)
	J	Emigration	62% of captures were in forest, 20% in partial cut forest, and 9% in clearcuts	(Patrick et al. 2006)
	U	U	59% of captures were in closed canopy forest (>20 m from edge), remaining captures in edge of clearcut[1]	(deMaynadier & Hunter 1998)
E. spotted newt	J	U	Strong avoidance of forest edge (mean of 0.3 captures per drift fence on edge, compared with 3.1 in uplands). Approximately 3 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 & 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 terestial 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)
N. water snake	A	U	Habitat use almost entirely confined to water (~40% of habitat use) and cattails on margins of the water (25% of use)	(Tiebout & Cary 1987)

[1] Did not distinguish between spotted and blue-spotted/Jefferson's salamanders (*A. laterale* / *jeffersonium*)

Table 7.3. GIS data used in predicting hotspots of herpetofaunal road mortality in New York State.

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

Table 7.4. Freshwater wetland types included in models (source: National Wetlands Inventory, Cowardin et al., 1979). Wetlands considered as focal nexuses for each of the study species are indicated with an X.

System	Subsystem	Class(es)	NWI label	Study species[1] nexus									
				Rasy	racl	rapi	buam	amma	novi	chse	clgu	chpi	glin
Lacustrine (L)	Limnetic (1)	(UB, AB, OW)	L1							X			
	Littoral (2)	shore (BB, RS, US)	L2 shore										
	Littoral (2)	bed (UB, AB, EM, FL, OW)	L2 bed		X	X	X		X	X		X	
Riverine (R)	Tidal (1)		R1										
	Lower perennial (2)	shore (BB, RS, US)	R2 shore										
	Lower perennial (2)	bed (AB, EM, OW, UB, RB)	R2 bed		X	X	X		X	X	x	X	X
	Upper perennial (3)		R3										
	Intermittent (4)		R4										
Palustrine (P)		Farmed (f)	Pf										
		Unconsolidated bottom (UB)	PUB		X	X	X		X	X		X	
		Aquatic bed (AB)	PAB		X	X	X		X	X	x	X	
		Unconsolidated shore (US)	PUS										
		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

[1] Abbreviations for study species (shown in parentheses) are as follows: Wood frog (rasy), green frog (racl), northern leopard frog (rapi), american toad (buam), spotted salamander (amma), eastern spotted newt (novi), snapping turtle (chse), spotted turtle (clgu), painted turtle (chpi), and wood turtle (glin)

Table 7.5a. Habitat resistance values assigned to each category of National Land Cover Database 2001 **for migrating individuals** of each of the 13 focal species. For amphibians, adults were considered the migrating individuals (i.e., resistance values are for adult amphibians). Values range from 0 (most suitable) to 50 (least suitable). A value of 0 (i.e., no cost to movement) was used for the most suitable habitat, as it was considered to actually encourage movement (Popescu 2007).

*Habitat resistance values refer to adults during nesting migrations

[1] Abbreviations for study species (shown in parentheses) are as follows: Wood frog (rasy), green frog (racl), northern leopard frog (rapi), american toad (buam), spotted salamander (amma), eastern spotted newt (novi), snapping turtle (chse), spotted turtle (clgu), painted turtle (chpi), and wood turtle (glin)

NLCD class code and Definition	Species[1]									
	rasy	racl	rapi	buam	amma	novi	chse	clgu	Chpi	glin
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

Table 7.5b. Habitat resistance values assigned to each category of National Land Cover Database 2001 **for dispersing individuals** of each of the 13 focal species. For amphibians, juveniles were considered dispersing individuals (i.e., resistance values are for juveniles). Values range from 0 (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 0 (i.e., no cost to movement) was used for the most suitable habitat, as it was considered to actually encourage movement (Popescu 2007).

[1] Abbreviations for study species (shown in parentheses) are as follows: Wood frog (rasy), green frog (racl), northern leopard frog (rapi), american toad (buam), spotted salamander (amma), eastern spotted newt (novi), snapping turtle (chse), spotted turtle (clgu), painted turtle (chpi), and wood turtle (glin).

NLCD class code and Definition	Species[1]									
	Rasy	racl	rapi	buam	amma	Novi	chse	clgu	chpi	glin
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

Table 7.6. Resistance values given to freshwater wetland types included in models (source: National Wetlands Inventory, Cowardin et al., 1979).

System	Subsystem	Class(es)	NWI label	Study species[1] resistance values									
				rasy	racl	rapi	Buam	amma	novi	chse	Clgu	chpi	glin
Lacustrine (L)	Limnetic (1)	(UB, AB, OW)	L1	20	20	20	20	20	20	0	20	20	20
	Littoral (2)	shore (BB, 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 (R)	Tidal (1)		R1	50	50	50	50	50	50	20	50	50	50
	Lower perennial (2)	shore (BB, 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 (P)		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

[1] Abbreviations for study species (shown in parentheses) are as follows: Wood frog (rasy), green frog (racl), northern leopard frog (rapi), american toad (buam), spotted salamander (amma), eastern spotted newt (novi), snapping turtle (chse), spotted turtle (clgu), painted turtle (chpi), and wood turtle (glin)

Table 7.7. Comparison of the observed occurrences of individuals of focal species along road-validation survey routes in central New York (Labrador Hollow and Tully Valley) with locations grouped according to the occurrence indices in which they occurred [n = 4 groups: (1) Rasters on the route that were predicted as non-occurrence; and rasters with an occurrence index of (2) 0-5; (3) 6-10; and (4) >10]. Chi square tests were used to compare the observed distribution of occurrences with a null hypothesis of animals being randomly distributed along the route.

Survey route	Species	Chi-square statistic	*P*-value
Labrador Hollow	Spotted salamander	75.599	0.001<*P*
Labrador Hollow	American toad	3.594	0.5<*P*<0.25
Tully Valley	American toad	0.195	0.99<*P*<0.975
Tully Valley	Green frog	32.819	0.001<*P*

Table 7.8. Comparison of the observed occurrences of individuals of focal species along road-validation survey routes in central New York (Labrador Hollow and Tully Valley) with locations grouped according to the length of contiguous high occurrence road in which they occurred [n = 4 groups: (1) Rasters on the route that were either non-occurrence or had an occurrence index of >2; (2) short sections of road with a length <100m; (3) medium with a length 100-500m; and (4) long with a length >500m] in relation to the expected distribution of individuals under a null hypothesis of individuals being randomly distributed.

Survey route	Species	Chi-square statistic	*P*-value
Labrador Hollow	Spotted salamander	26.539	0.001<*P*
Labrador Hollow	American toad	2.227	0.75<P<0.5
Tully Valley	American toad	3.320	0.5<P<0.25
Tully Valley	Green frog	21.395	0.001<*P*

Figure 7.1. Location of the National Wetlands Inventory (NWI) data (shown in gray) used as the basis for assessing hotspots of herpetofaunal road-mortality for 11 species in New York State.

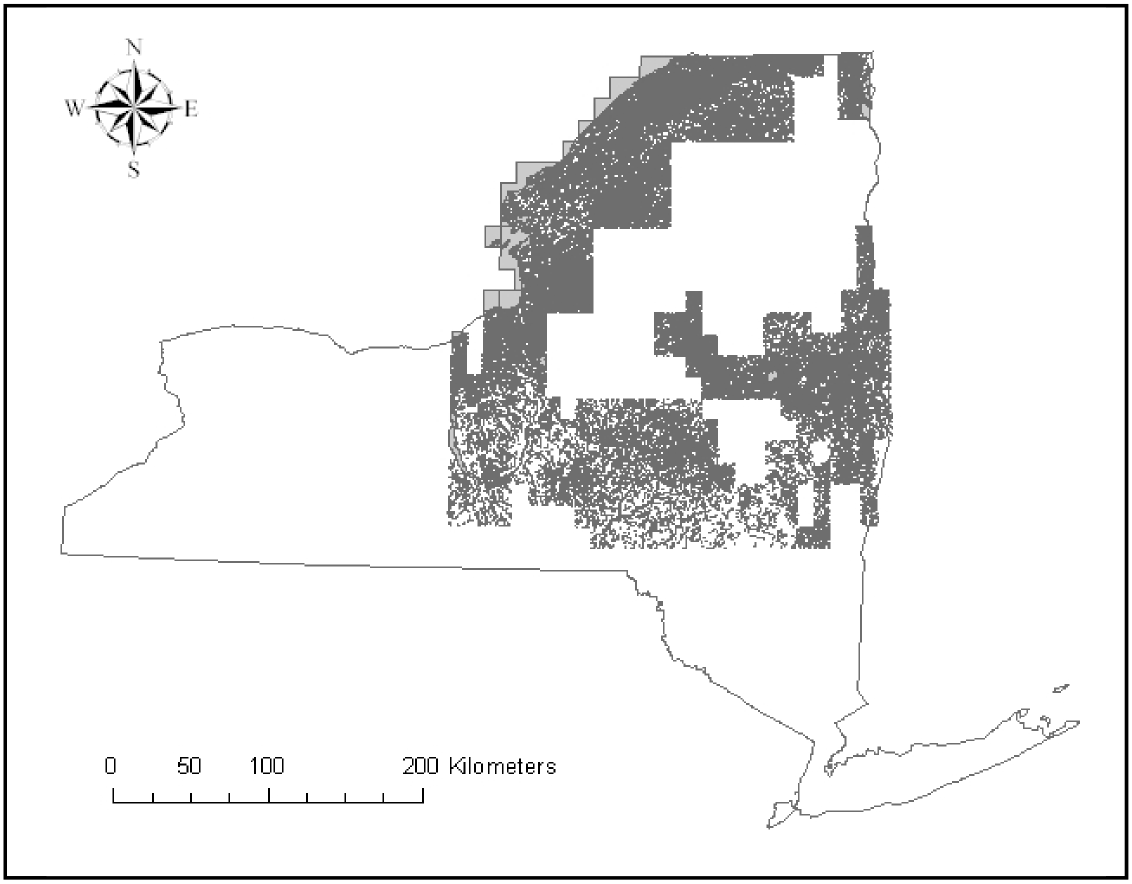
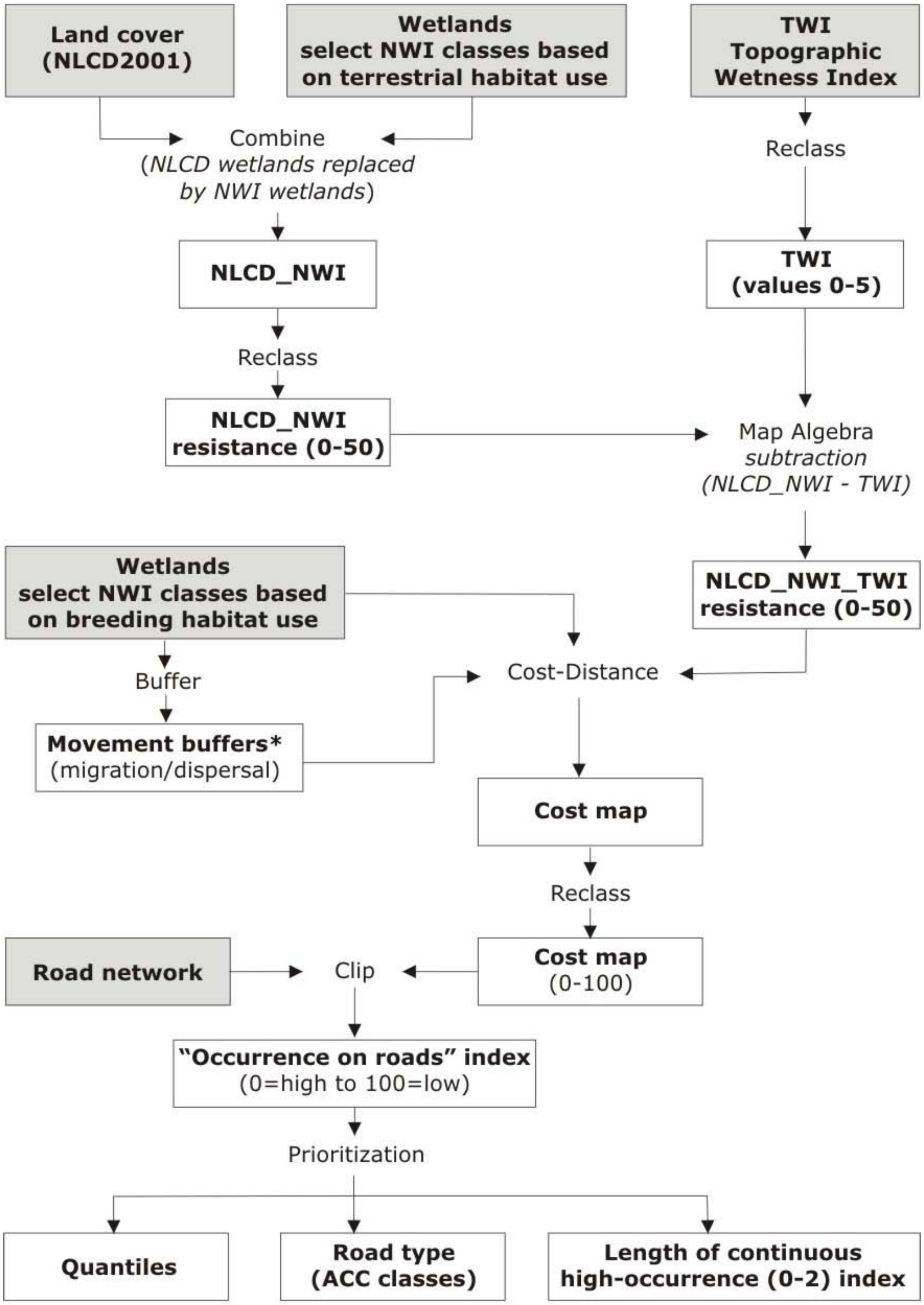


Figure 7.2. Stages in development of the road-hotspot models for 10 species of herpetofauna in New York State.



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

Figure 7.3. Example of the occurrence index output for all terrestrial habitat (rather than just roads), for (a) migrating spotted salamanders and (b) common snapping turtles with a darker color representing a higher probability of occurrence, aquatic habitat denoted by stippling (in this area aquatic habitat was suitable for both species) and roads indicated as dark lines.

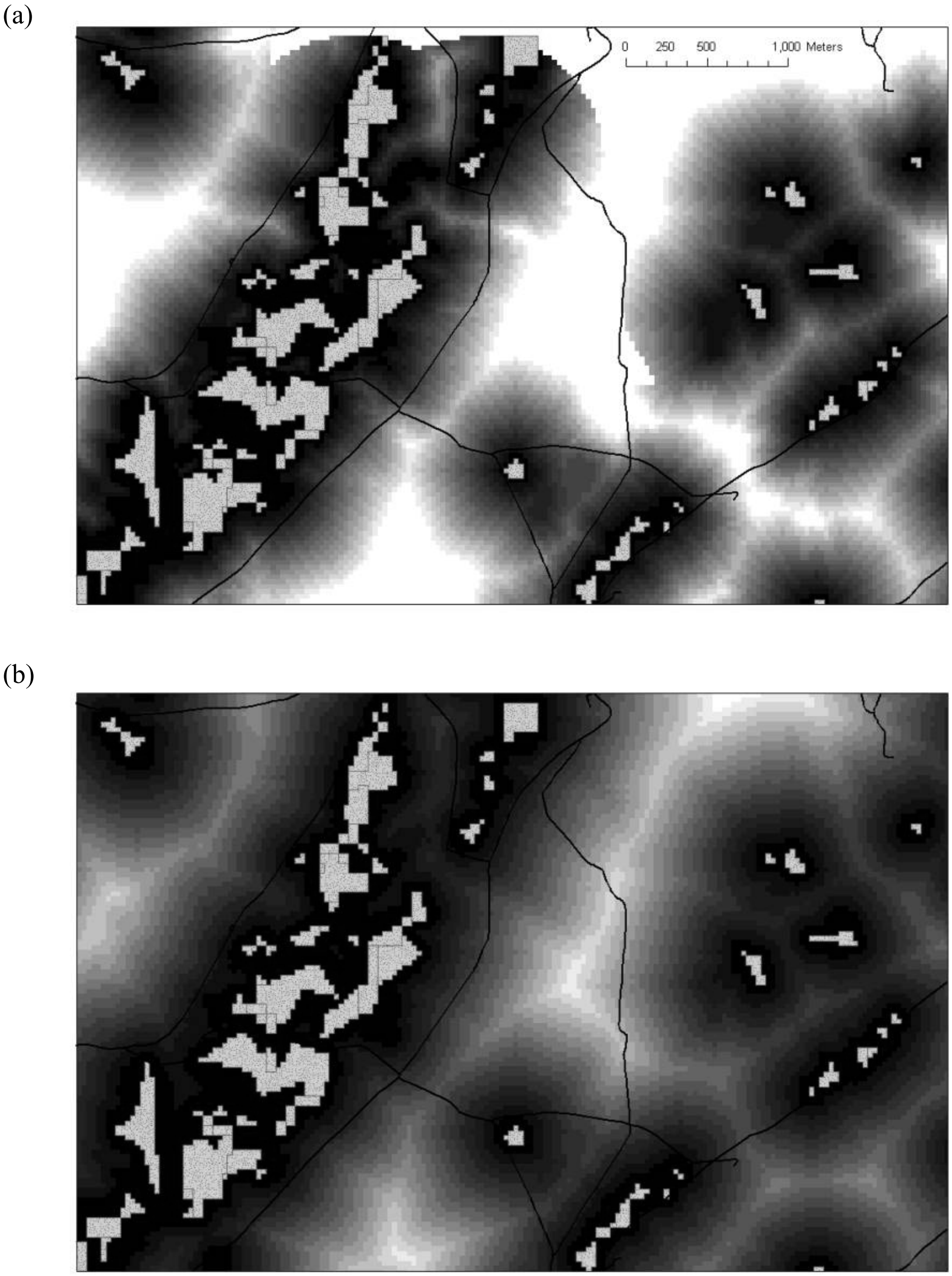


Figure 7.4. Example of the occurrence index output for all terrestrial habitat (rather than just roads), for (a) migrating adult wood frogs and (b) dispersing juvenile wood frogs with a darker color representing a higher probability of occurrence, aquatic habitat denoted by stippling and roads indicated as dark lines

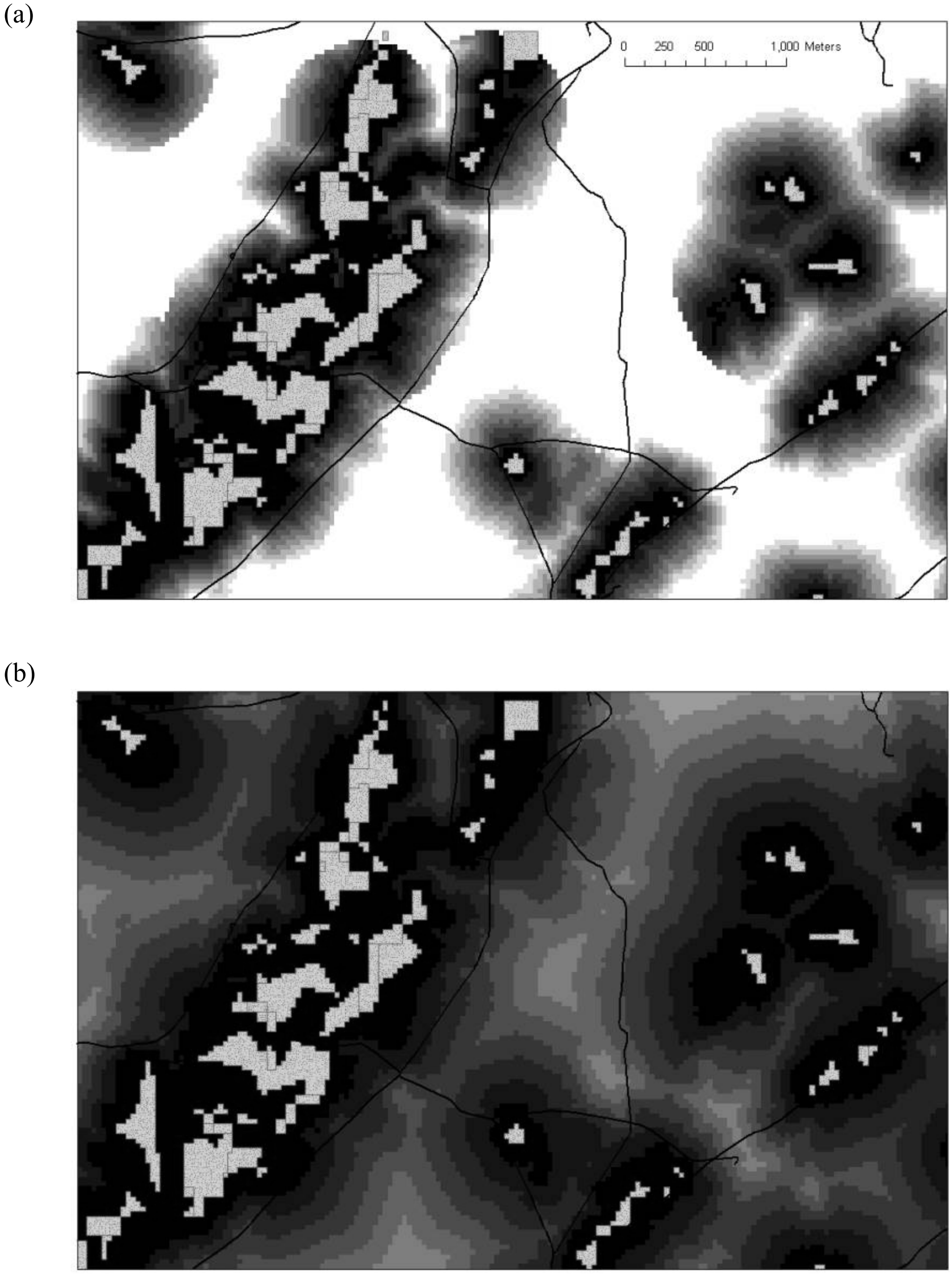
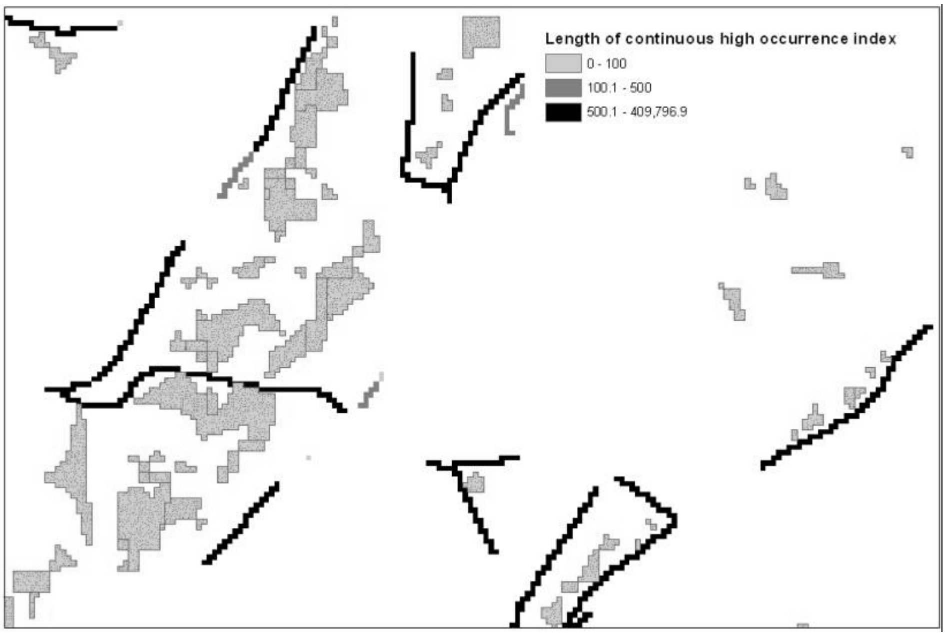


Figure 7.5. Illustration of three methods employed to prioritize hotspots of herpetofaunal occurrence on roads in New York State using migrating wood frogs as an example: (a) classifying occurrence index values based on 5 quantiles; (b) with the arterial classification code for roads overlaid (ACC); and (c) using the length of continuous high-occurrence rasters (divided into 3 categories based on length: short sections of road [length <100m]; (3) medium [length 100-500m]; and (4) long [length >500m]).

(c)



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APPENDIX

Effects of New York State Roadways on Amphibians and Reptiles: Background and Importance

David A. Patrick[1], James P. Gibbs[2] and Hara Woltz[3]

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Acknowledgments and Impetus

- NYSDOT grant #C-04-02:Development and placement of effective wildlife crossing structures for amphibians and reptiles across New York State transportation corridors. September 14th 2004
- Debra Nelson
- Gary Pratt
- Tim Baker
- Ilana Kanfer and the Onondaga County Planning Agency

Overview

1. Current state of knowledge regarding populations of herpetofauna (amphibians and reptiles)
2. Potential effects of roadways in New York State on these populations and the need to address these effects

Amphibians and reptiles in New York State

- 69 native species of amphibian and reptiles

missouristateyou.blogspot.com

savelakemartin.com

vernalpool.org

Many species of conservation concern

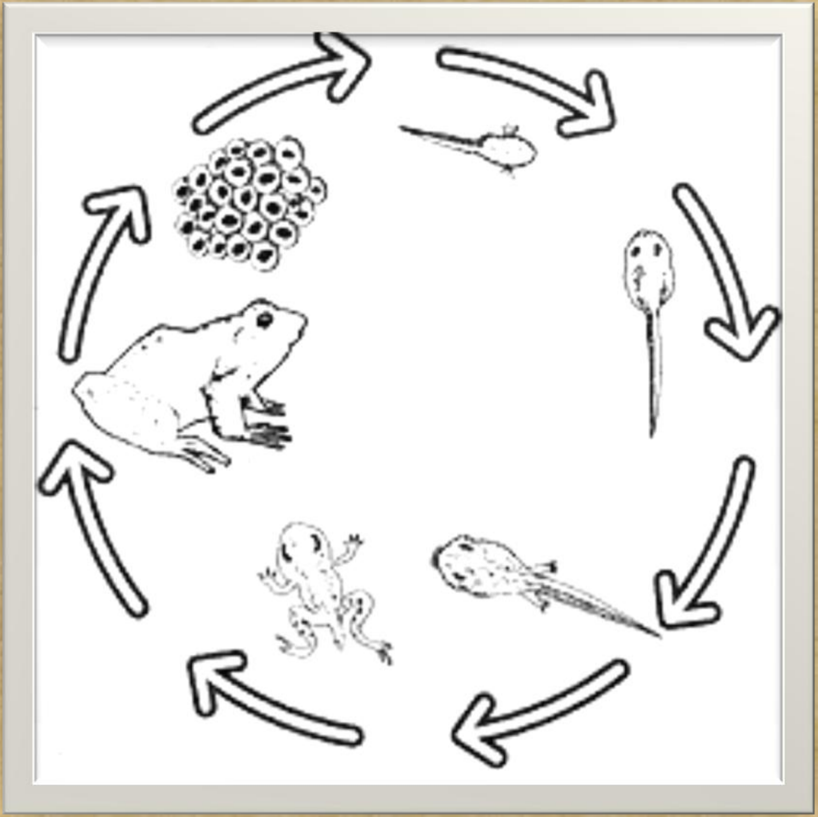
- Endangered = 9 species
- Threatened = 5 species
- Special concern = 13 species
- Total of 27 species, or 39% of species known from the state

commons.wikimedia.org

Biology of amphibians and reptiles

- Wide range of different “life-history strategies” comparing both among and within groups
- Many species rely on water for at least part of their life history cycle
- In New York State, all of the non-marine species are inactive during the winter

Life cycle of most frogs and salamanders



Exceptions to the rule

- Red-backed salamanders lay eggs under cover-objects on land where they hatch directly into miniature adults (no aquatic larval stage)

Explosive migration and breeding

- Adults of some species of amphibian emerge *en masse* in spring, and migrate into breeding pools within a few day
- This can result in thousands of animals on roads at once

Life cycle of turtles

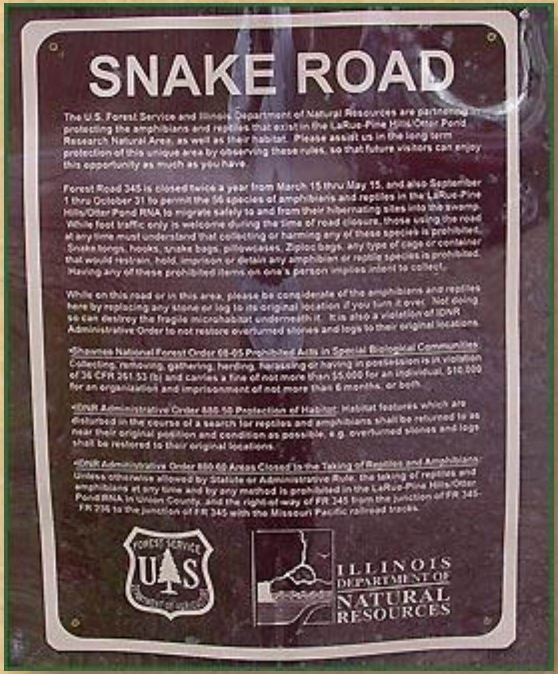
- Inland turtles in NY State fall along a gradient in terms of how “aquatic” they are
- All turtles come onto land to lay eggs (soft road margins are favored by some species)
- Some species of turtle roam widely to access food resources and suitable places for overwintering


junglewalk.com


bio.umass.edu

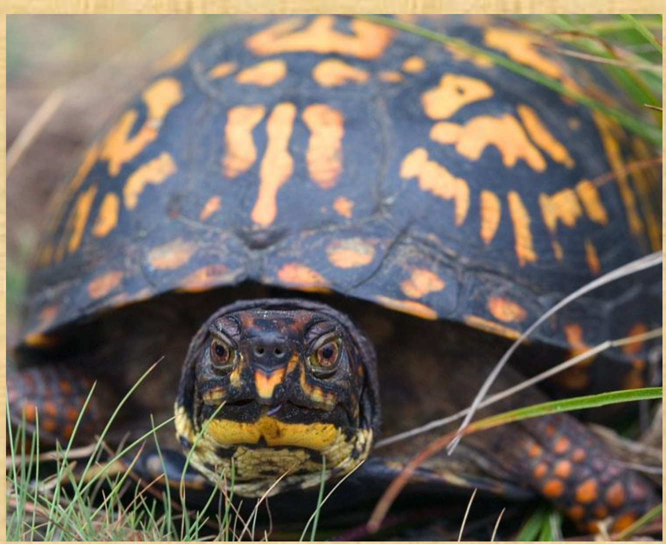
Life cycle of snakes

- Some snakes lay eggs, others give birth to live young
- Many species undergo annual migrations to and from “hibernacula”- suitable places for overwintering
- Some species of snake are closely associated with water (northern water snake and queen snake for example)
- Roads may be used by snakes as places to thermoregulate



How long do these organisms live for?

- In the case of a spring peeper (a small cryptic frog), not very long at all!
- In the case of some turtles, for many decades and possibly over a century



Longevity, fecundity, and population growth rates

- Long-lived species of amphibians and reptiles are characterized by high adult survival rates under natural conditions
- Long-lived species also tend to have low fecundity, with fewer eggs laid compared to shorter-lived species
- This means that populations of long-lived species cannot grow as fast as populations of short-lived species

- Individuals of long-lived species contribute fewer offspring on average per year
- Over the course of their life-time, however (assuming they experience their natural longevity), these few annual offspring add up
- If a turtle is killed as a young adult, however, all of those future offspring are lost

Patterns of habitat use

- Habitat specialists (e.g., forest dependent amphibians) compared with generalists
- Species may be generalists in some aspects of their life, but specialists in other aspects (e.g. nesting habitats)
- Many species have seasonal patterns of habitat use as previously mentioned

Movement distances

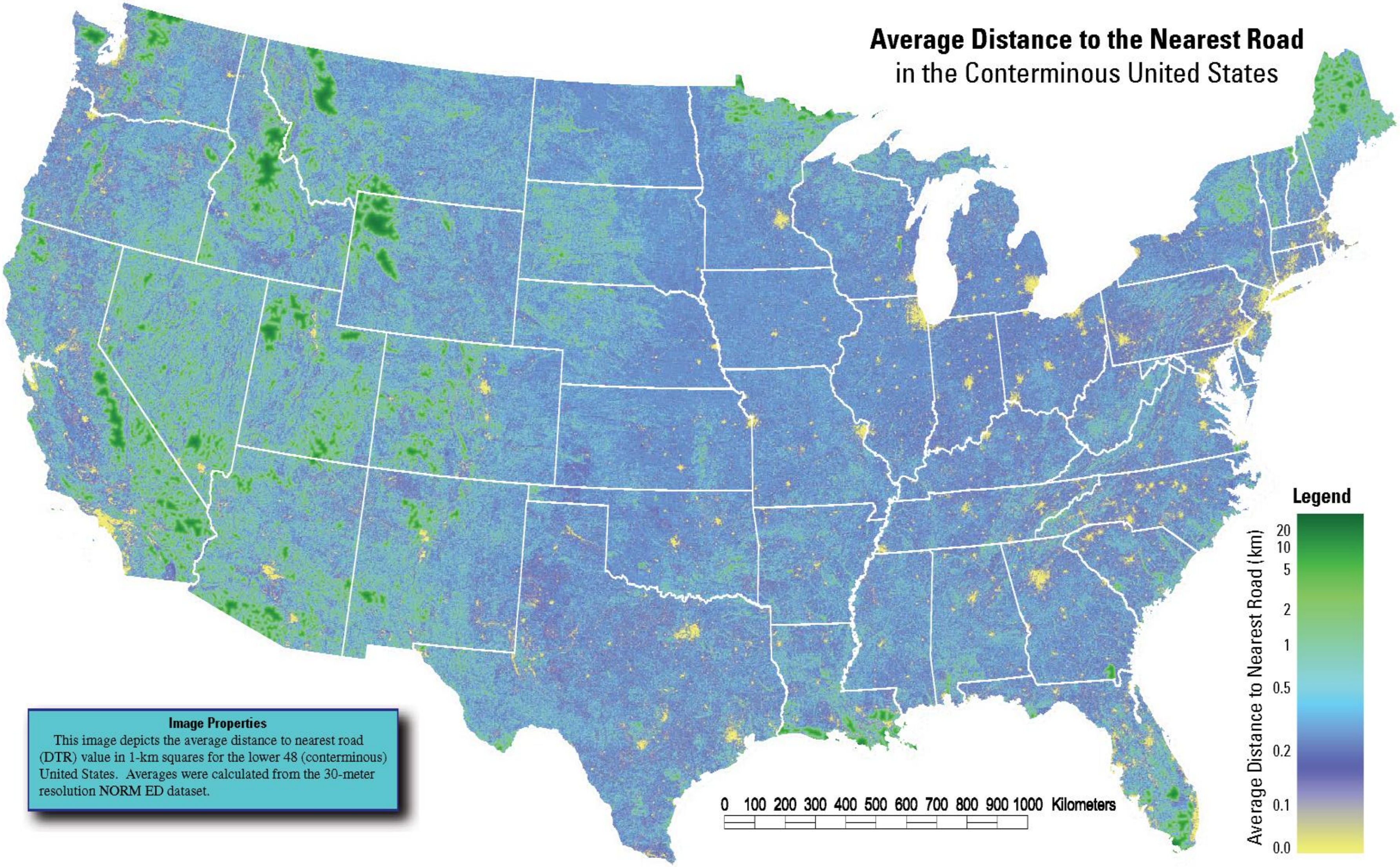
- Animals move for a variety of reasons including foraging, migration, and dispersal
- Some species are much more mobile than others
- Mobility can also vary depending on life-history stage: juveniles are often the dispersing life-history stage
- Movement can be constrained to particular habitats

Why the biology of species matters

- The life-history characteristics of species determine where and when they will be found on roads, how much of an effect the roads will have, and how effective mitigation is likely to be

An example

- Carr and Fahrig (2001) compared the effects of roads on two species of amphibians
- Northern leopard frogs are more vagile than green frogs
- An effect of road density was seen on leopard frogs, but not green frogs



Average Distance to the Nearest Road

in the Conterminous United States

Image Properties

This image depicts the average distance to nearest road (DTR) value in 1-km squares for the lower 48 (conterminous) United States. Averages were calculated from the 30-meter resolution NORM ED dataset.

Fact Sheet 2005-3011
January 2005

How can roads affect populations of amphibians and reptiles?

- Direct mortality reducing the number of individuals in a population
- Animals choosing not to cross a road or being killed while trying, resulting in “fragmentation” of populations
- Degradation (reduction in the quality) of remaining habitat

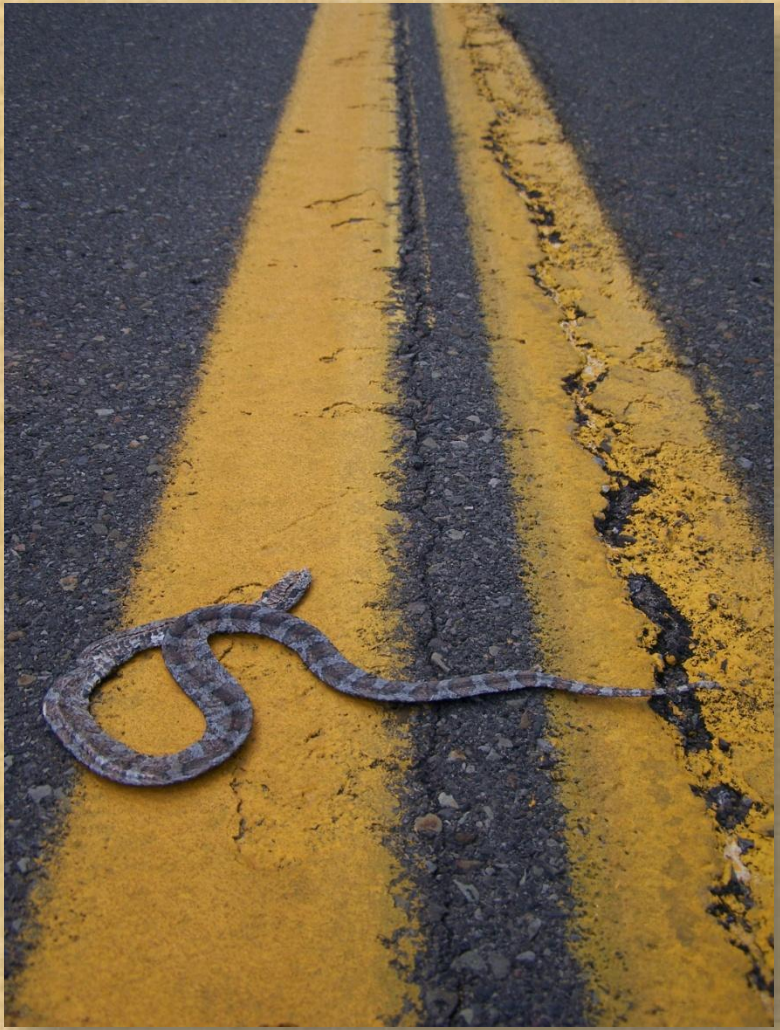
What these effects lead to

1. Reduction in the viability of “local” populations (the chance that they will persist into the future)
2. Reduction in the viability of “regional” populations
3. Reduction in the abundance of animals in a population (the population may still persist, but dramatically reduced in size)

Why would a reduction in abundance matter (beyond increasing the risk of extinction)?

- Amphibians in particular are extremely efficient in converting energy into body mass
- Adults carry energy and nutrients into wetlands at the start of breeding, depositing this material into the aquatic food-chain
- Emerging juvenile amphibians play the opposite role
- Reducing the number of individuals may therefore play a role in nutrient and energy dynamics across ecosystems

Road Effects Studies



1. Roads and reptiles
- Effects of roads on snake populations
- Effects of roads on turtle populations

2. Roads and amphibians
- Effects of roads on frog and salamander populations


Photo by James H. Harding

Snakes and roads: Cicero swamp

- Does proximity to roads influence abundance and distribution of snakes?

Patrick and Gibbs. 2009. Journal of Herpetology.

Methods

- Three old fields
- Road on one end (left of image)
- Metal road signs as cover-boards
- Observations made of snakes under boards

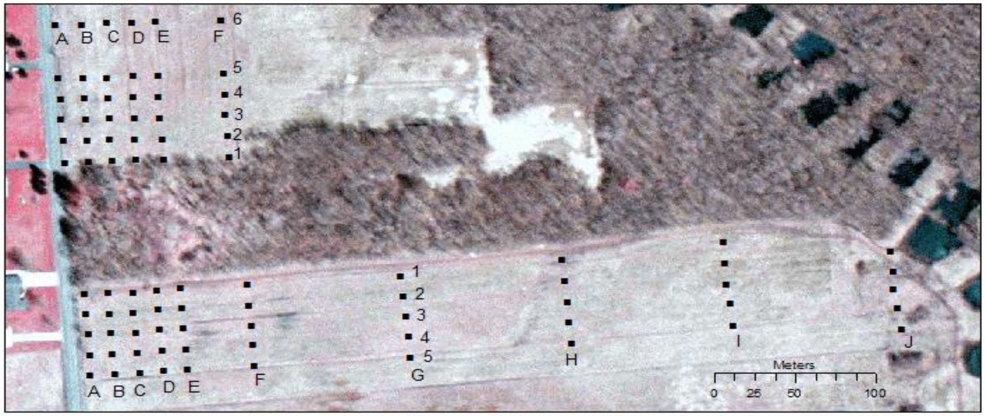


Figure 1: Cover sheet arrays in Short Grid field (top) and Ponds Grid field (Bottom).

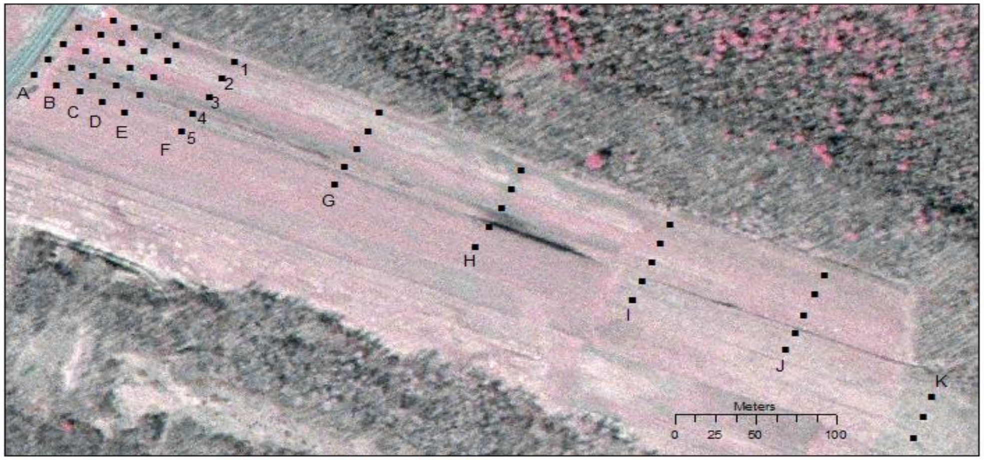


Figure 2: Coversheet array in Long Island field.

Results

- 1400 observations of 4 species of snake (garter, brown, northern water, and milk snake)
- Most captures of garter snakes (n = 1132) and brown snakes (n = 246)


© John White

- The distribution of snakes was not influenced by proximity to road
- For both brown snakes and garter snakes, significantly more snakes were found further from the forest edge (*P* <0.001)

Effects of roads on turtle populations

- How does road proximity affect turtle population structure and movement

Patrick and Gibbs. 2010. Landscape Ecology.

Research questions

Local Populations: How does urbanization, including roads, influence the sex-ratio and size/age of turtles?

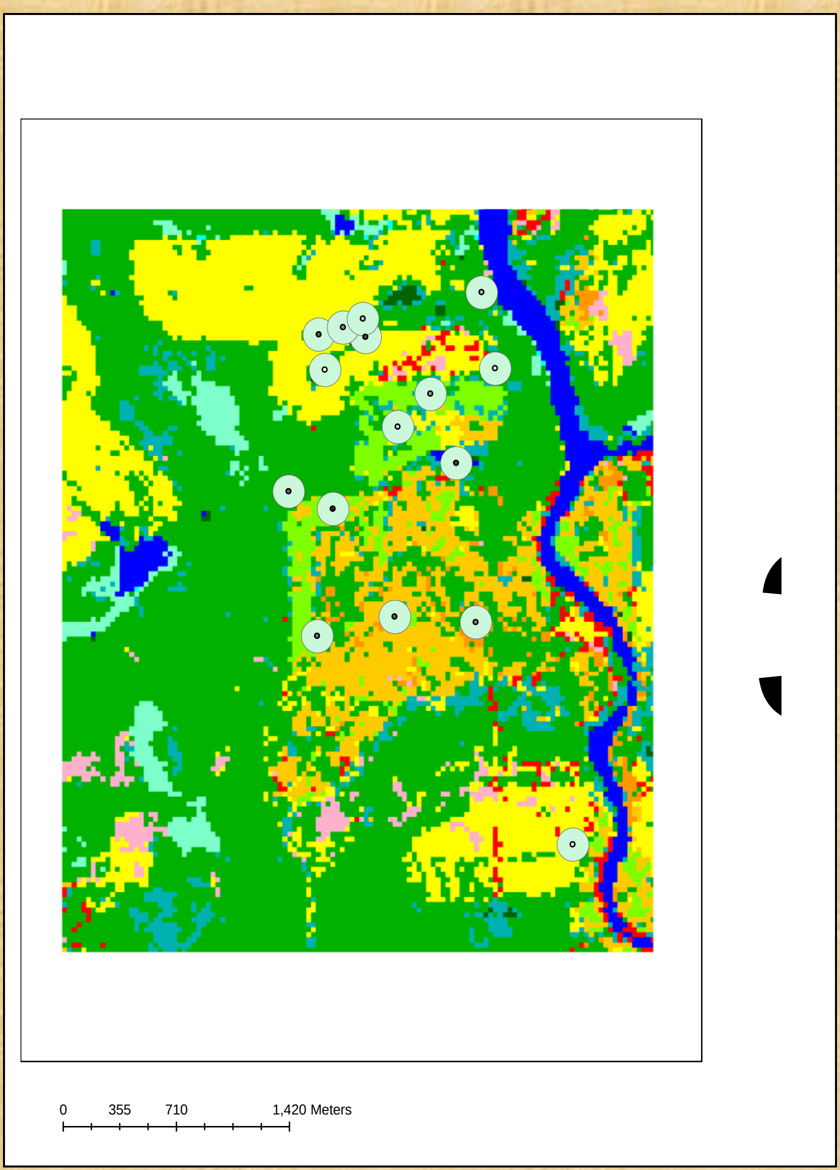
Regional populations: How does urbanization influence movement of turtles between ponds?

Methods

- 16 ponds surveyed in the Baldwinsville area of central New York
- Ponds chosen across a range of levels of disturbance of natural habitat

- Turtles captured using hoop nets baited with sardines
- Measured and individually marked by filing the shell

- Landscape including land cover type, canopy cover, and road cover around each pond calculated

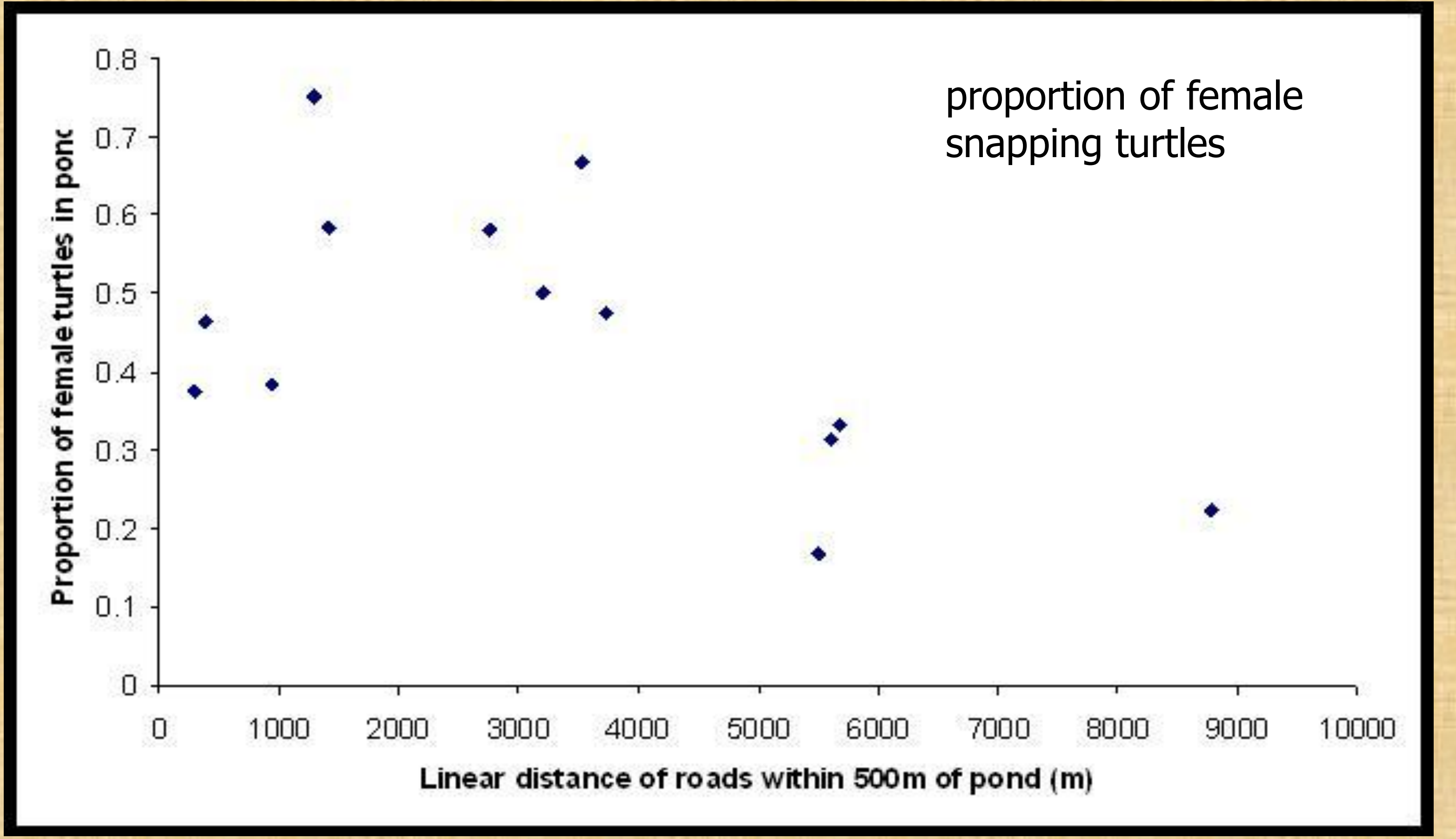


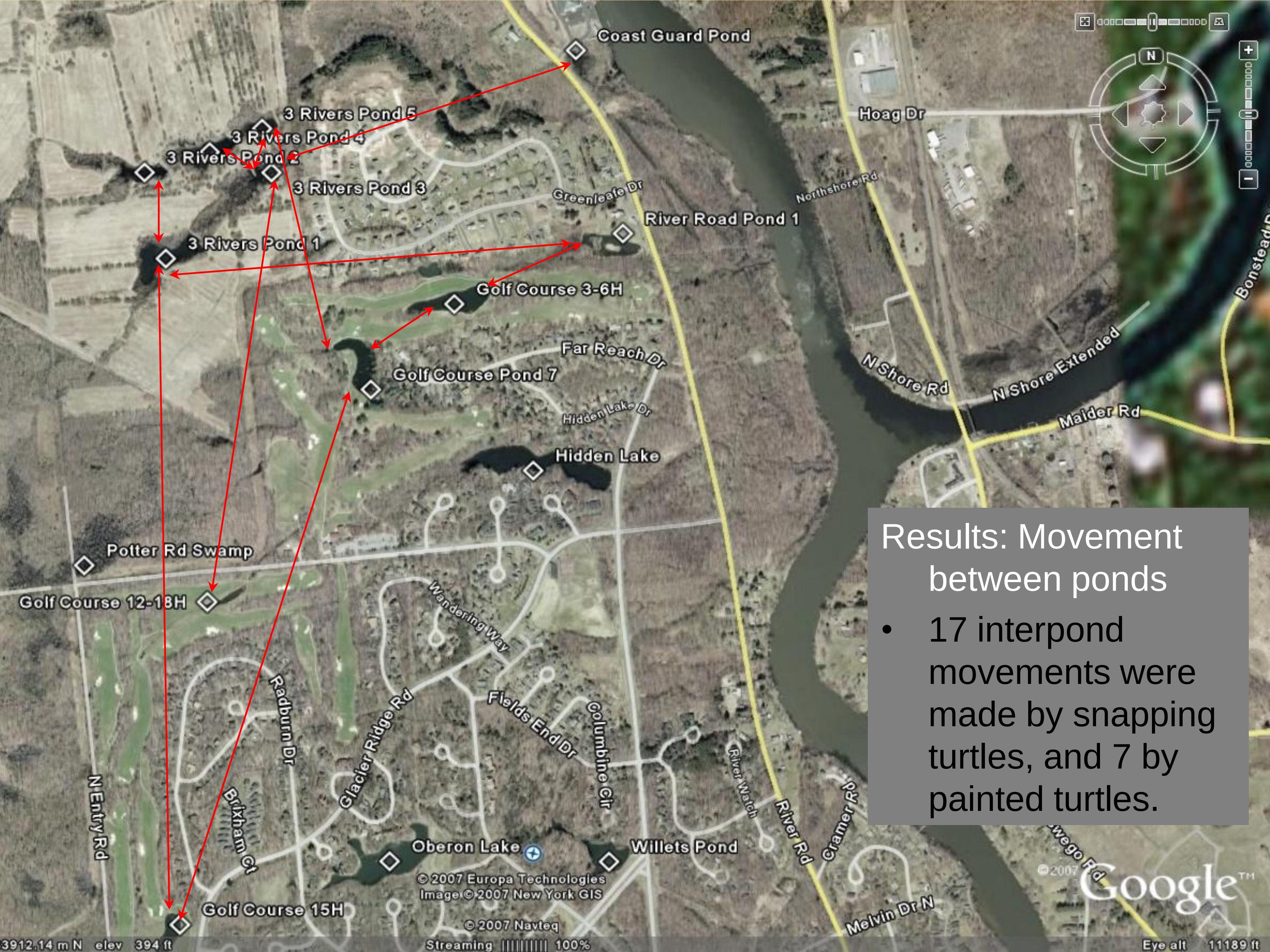
Results: Local population

- Three species of turtle captured (122 painted, 253 snapping, and 12 common musk turtle)

© Steve Barten

- The proportion of female snapping and painted turtles was best explained by the density of roads within 500m of the ponds





Results: Movement between ponds

- 17 interpond movements were made by snapping turtles, and 7 by painted turtles.

Can road mortality limit populations of pond-breeding amphibians?

- Estimated probability of a spotted salamander crossing a road being killed based on traffic volume
- Estimated the average number of times a salamander would cross a road for 500 breeding pools with different road densities
- Road density and traffic volume were then used to calculate predicted mortality for these 500 pools

Gibbs and Shriver 2005. Wetland Ecology and Management

- Population models were used to look at the demographic significance of increased mortality due to roads
- Found that >10% annual adult road mortality can lead to extirpation of local populations
- Depending on how far salamanders move on average, 22-73% of sampled populations were above this threshold

Does an increase in traffic intensity lead to declines in amphibian populations?

- Fahrig et al., (1995) compared amphibian densities using call surveys across a gradient of traffic intensity
- They also looked at road mortalities
- Road mortality increased with traffic intensity
- Frog and toad density as measured by calling decreased with traffic intensity
- They concluded that roads have the potential to reduce amphibian population viability

Summary points

- Roads clearly have the potential to affect populations of herpetofauna
- The susceptibility of species to road-effects will vary depending on life-history characteristics
- Life-history characteristics will also influence the efficacy of different approaches to mitigation

Some issues that remain unclear

- The combined effects of different stressors associated with roads (e.g., direct mortality and salt pollution)
- How adaptable populations are to road-effects, and what factors confer adaptability

Herpetofaunal crossing structure location and design

David A. Patrick, James P. Gibbs, and Hara Woltz

Overview

1. Introduction to the use of crossing structures
2. Life-history characteristics and the efficacy of crossing structures
3. Where to locate crossing structures
4. Considerations in crossing structure design

Using crossing structures

- Much of the road research involving herpetofauna has focused on crossing structures
- Crossing structures are extremely expensive and vary in efficacy, however
- Proactive road location and design can reduce the need to establish crossing structures and should be seen as a favorable option

Crossing structures can work

- Lake Jackson, Florida
- Incredible mortality of herpetofauna
- Implementation of crossing structure and barrier fence reduced this mortality dramatically

How life-history characteristics relate to crossing structure use

- For crossing structures to be effective animals have to use them
- This only works for animals that are concentrated in a predictable place
- Animals will be concentrated in space where there is limited suitable habitat

1. This might be on roads adjacent to discrete wetlands
2. Or where a limited area of suitable habitat crosses a road

When is a crossing structure unlikely to work?

- For habitat generalists
- ……especially if these generalists range widely
- Where there is a lot of suitable habitat
- As an example, researchers working in Maine with Blanding's turtle found it was not possible to identify specific locations where Blanding's and spotted turtles would cross (Beaudry et al., 2008. Biological Conservation)

© Zig Leszczynski

Where to locate crossing structures

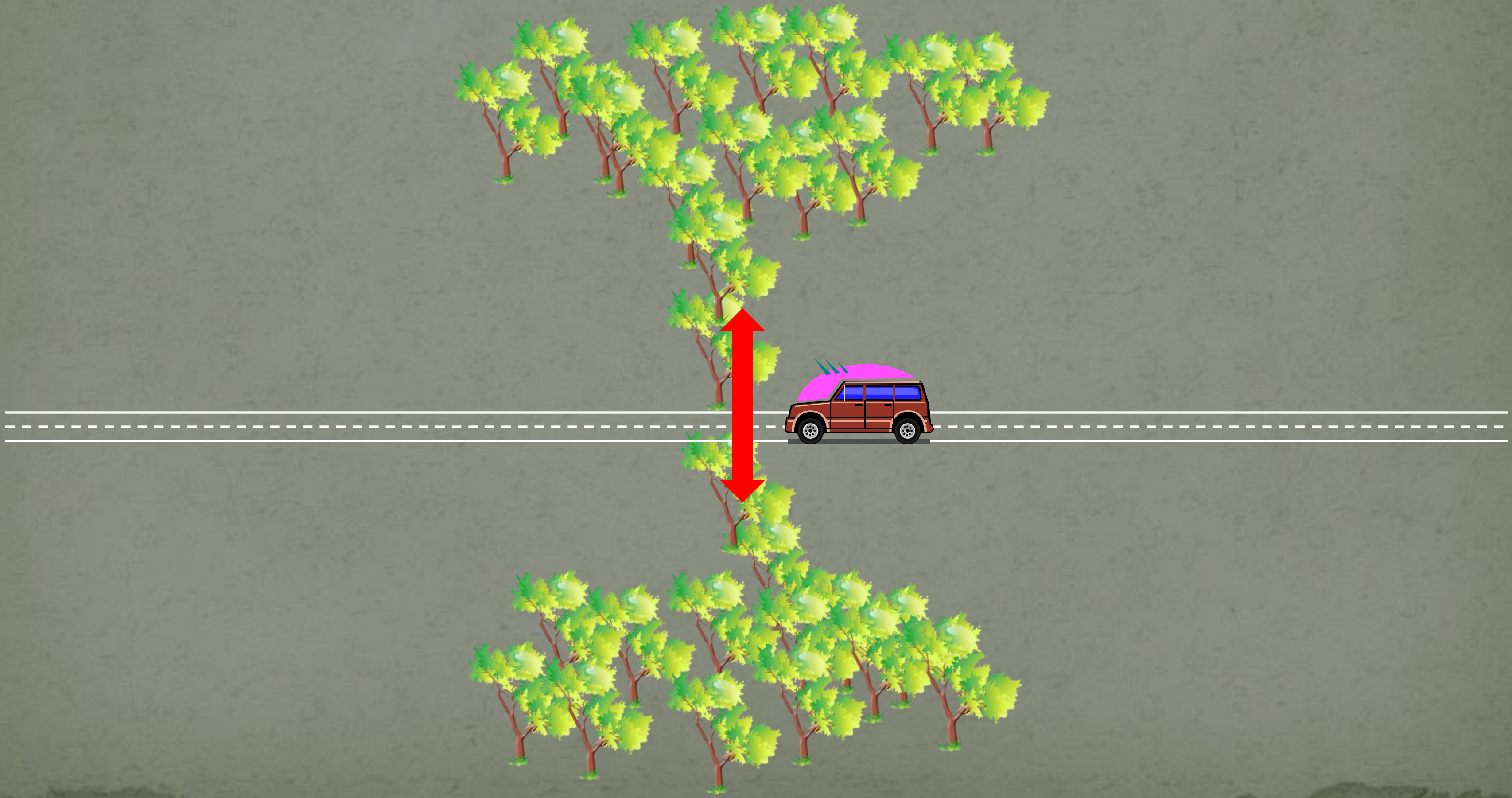
- Questions regarding where to place crossing structures relate to two scales

1. The first scale is establishing where concentrations of animals are found in general (i.e., the location of hotspots).
2. The second scale relates to within hotspots: where would crossing structures best be placed to facilitate their efficacy?

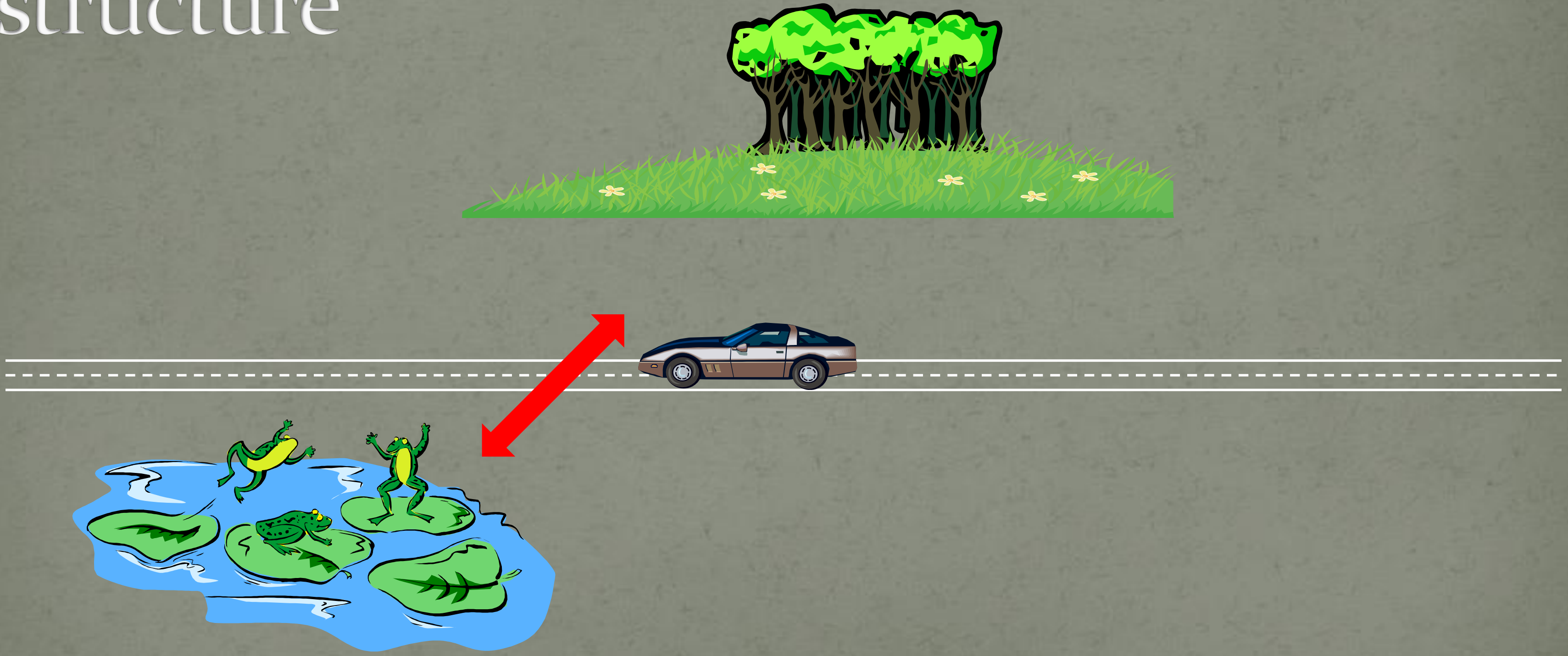
Patterns of habitat use and crossing structure placement

- Once we have identified the hotspot within which we want to place crossing structures, the next question is where exactly it should be placed
- To help us in making these decisions, we can consider the biology of the species or taxa we are focusing on and the makeup of the landscape

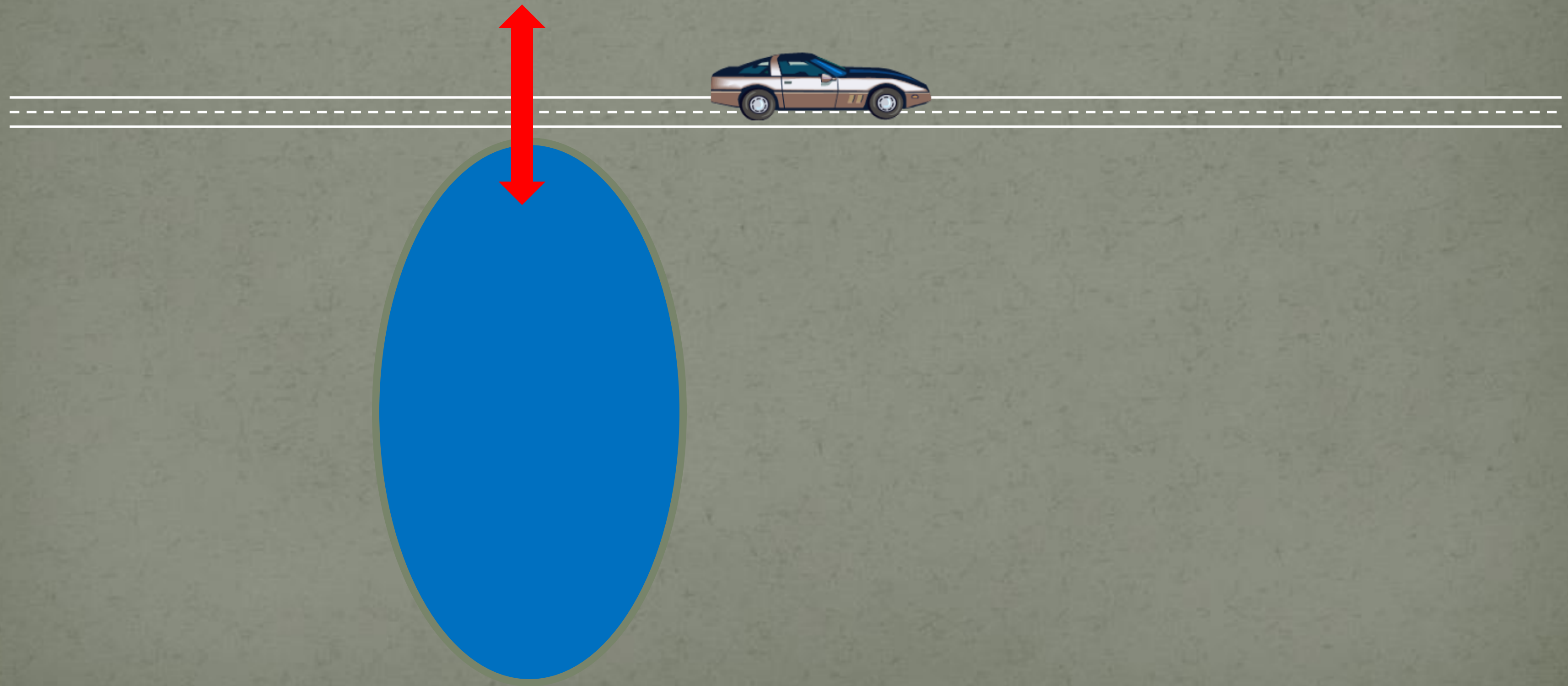
If we have an obvious corridor of suitable habitat bisected by the road, we can place the crossing structure at this point



If we know that an organism is crossing between two patches of habitat, we can use this information to place the crossing structure



Because animals tend to be concentrated closer to a wetland edge, we can also use proximity to locate crossing structures (everything else being equal)



But what if we have a large hotspot without much variation in habitat?

- A good example of this scenario is Labrador Hollow, near Apulia, NY
- Amphibians cross along a 1-km long stretch of road
- Establishing barrier fences and underpasses along this entire length would be extremely costly
- We conducted research to see if we could predict where spotted salamander and American toad would cross within this area based on more subtle variation in habitat

Patrick, Schalk, Gibbs, and Woltz. 2010. Journal of Herpetology

Methods

- Study site description
- Transect establishment- 10-m long sections
- Habitat sampling:

1. Distance to nearest culvert
2. Distance to nearest wetland
3. Presence of seeps

Results

- 551 spotted salamanders and 92 American toad were recorded in a 4-night period during peak migration
- We did not find compelling patterns of habitat specific movement linked to the biology of the two focal species
- In a nutshell, we cannot use fine-scale variation within the habitat to place culverts in a hotspot where the habitat is all fairly suitable

What attributes of crossing structures make them palatable to herpetofauna?

- Once we have decided where to locate crossing structures, we need to make sure animals will choose to use them
- A number of studies have been conducted assessing what makes a crossing structure work

Culverts for drainage and herpetofaunal passage

- An important question is whether we can use existing drainage culverts for herpetofaunal passage
- Some species of amphibian move in early spring during rain events
- This period of time coincides with very high rates of run-off from melting snow
- Animals will not enter fast-flowing water gushing through culverts

Study 1)Road crossing structures for amphibians and reptiles: Informing design through behavioral analysis

- Behavioral choice arrays were used to assess response of frogs (green frog and northern leopard frog) and turtles (common snapping and eastern painted turtles)

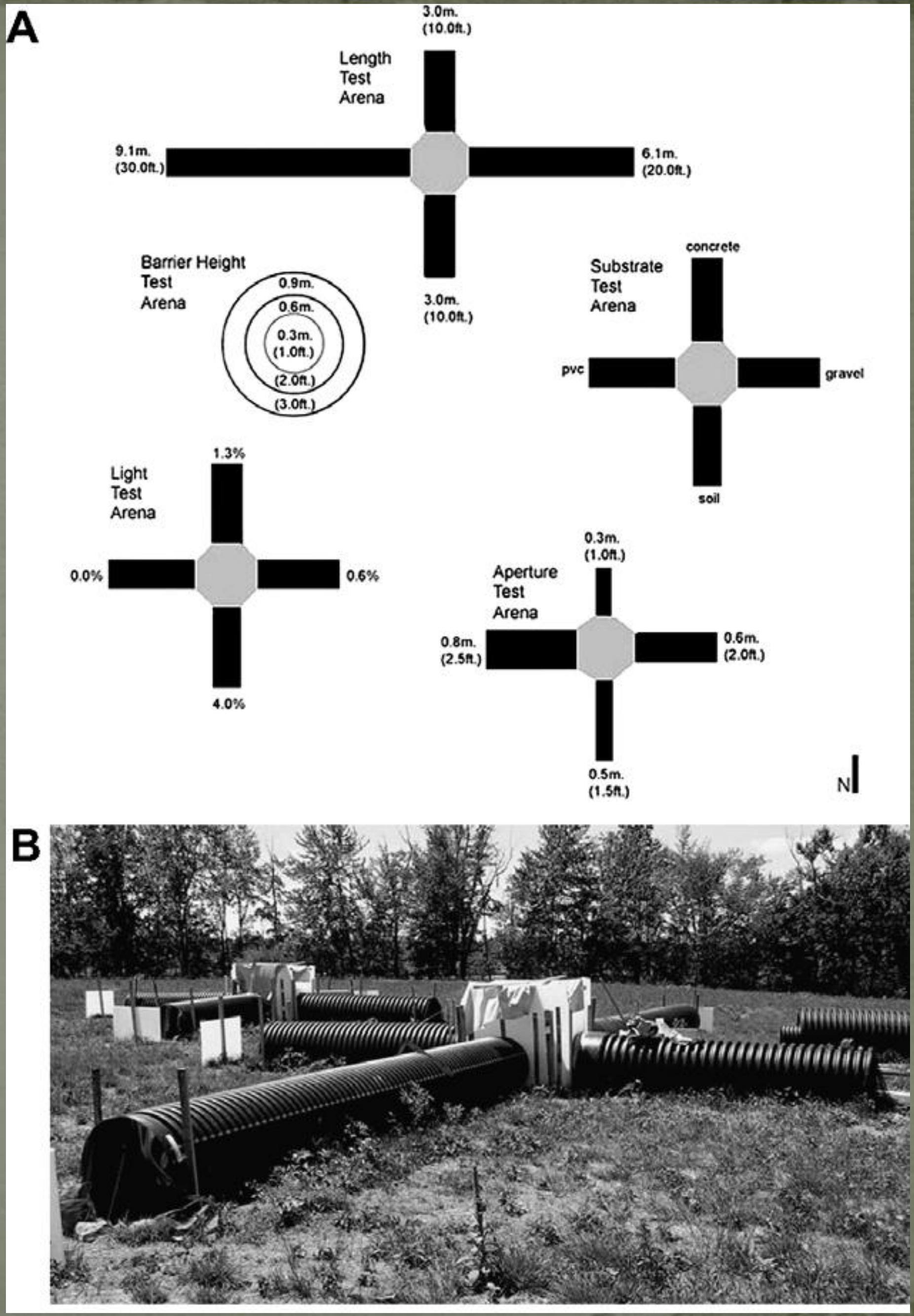
Woltz, Gibbs, and Ducey 2008. Biological Conservation

Methods: treatments

- Focused on attributes of corrugated plastic culverts including:
- Aperture diameter (0.3, 0.5, 0.6, and 0.8 m)
- Substrate type (concrete, soil, gravel, or bare PVC)
- Length (3, 6.1, and 9.1 m)
- Light permeability (0%, 0.65%, 1.3%, or 4.0% of the pipe’s surface area, rendered by drilling 0.5 cm holes in the upper surface of pipes)

Methods: experimental arrays

- Animals were placed in center of enclosure and provided with choice



Results

Aperture diameter:

- Turtles were more discerning than frogs, significantly preferring the mid-sized aperture

Substrate type:

- Only green frogs showed any significant preference, choosing culverts with soil and gravel over bare pipes and concrete

Pipe length:

- Strong signals were not seen, although leopard frogs and painted turtles appeared to avoid the longest pipes

Light permeability:

- Again, preference was not strong, but both frog species favored the culvert with the most light

Conclusions

- tunnels > 0.5m in diameter lined with soil or gravel would best facilitate road crossing for these and likely other frog and turtle species

Study 2) Effective culvert design to facilitate passage of amphibians across roads

- This second study built upon the results of Woltz et al., by examining the response of amphibians undergoing their natural migration to attributes of culverts
- Migration is when we expect the majority of culvert use to occur for this taxa

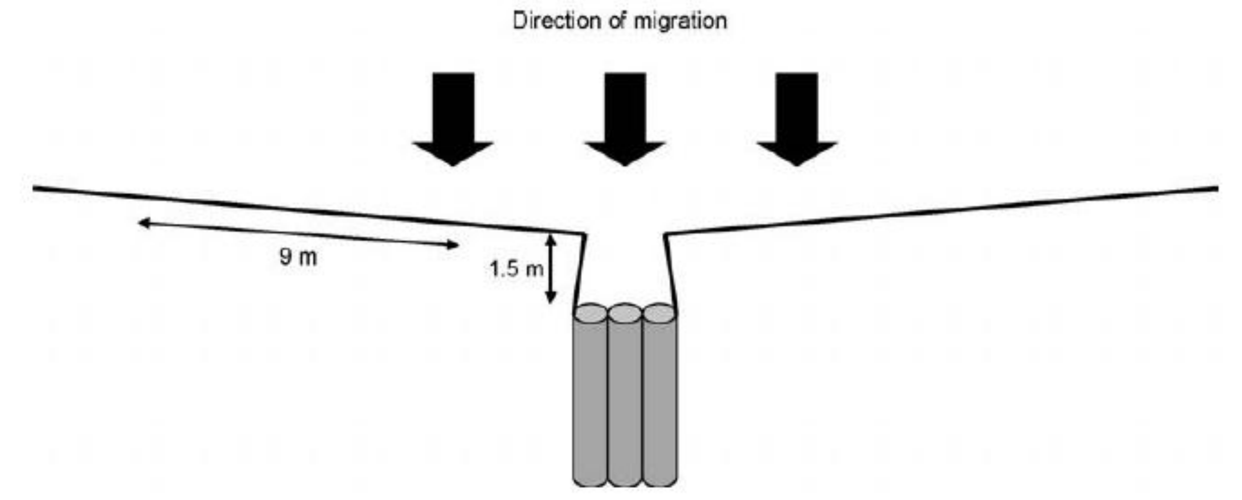
Patrick and Gibbs. 2010. Journal of Herpetology

Methods: treatments

- Study conducted at Labrador Hollow with spotted salamander
- Again focused on attributes of corrugated plastic culverts including:
- Aperture diameter (0.3, 0.6, and 0.8 m)
- Substrate type (concrete, river gravel, or bare PVC)
- Length (3, 6.1, and 9.1 m)

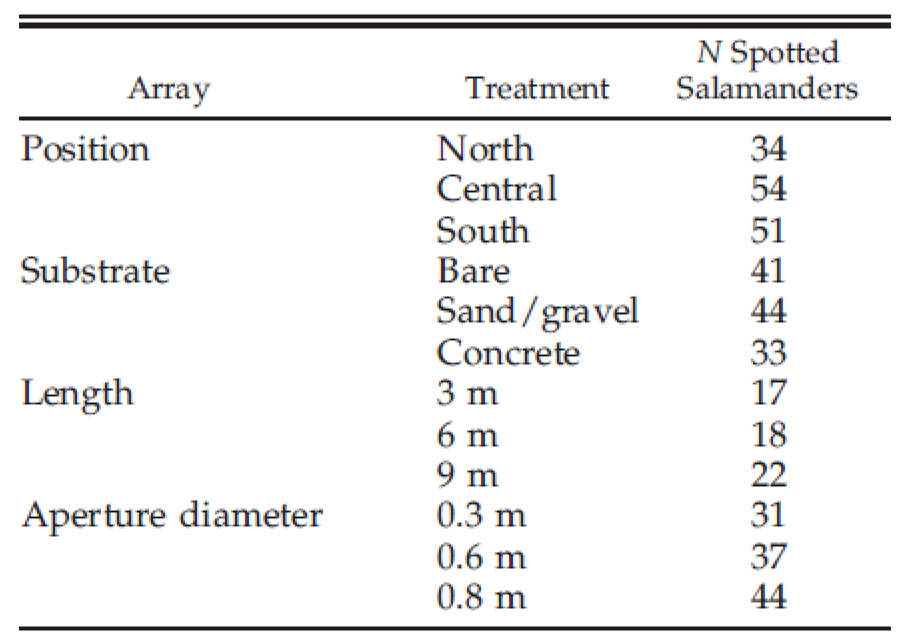
Methods: experimental arrays

- Migrating salamanders were funneled into arrays where they chose between three culverts with different attributes
- To account for possible choice based on the position of the culvert within the array, pipes were switched after each session



Results

- 446 spotted salamanders captured in 5 nights
- Salamanders did not show strong preference for attributes of culverts, moving through all treatments



Array	Treatment	*N* Spotted Salamanders
Position	North	34
	Central	54
	South	51
Substrate	Bare	41
	Sand/gravel	44
	Concrete	33
Length	3 m	17
	6 m	18
	9 m	22
Aperture diameter	0.3 m	31
	0.6 m	37
	0.8 m	44

Conclusions

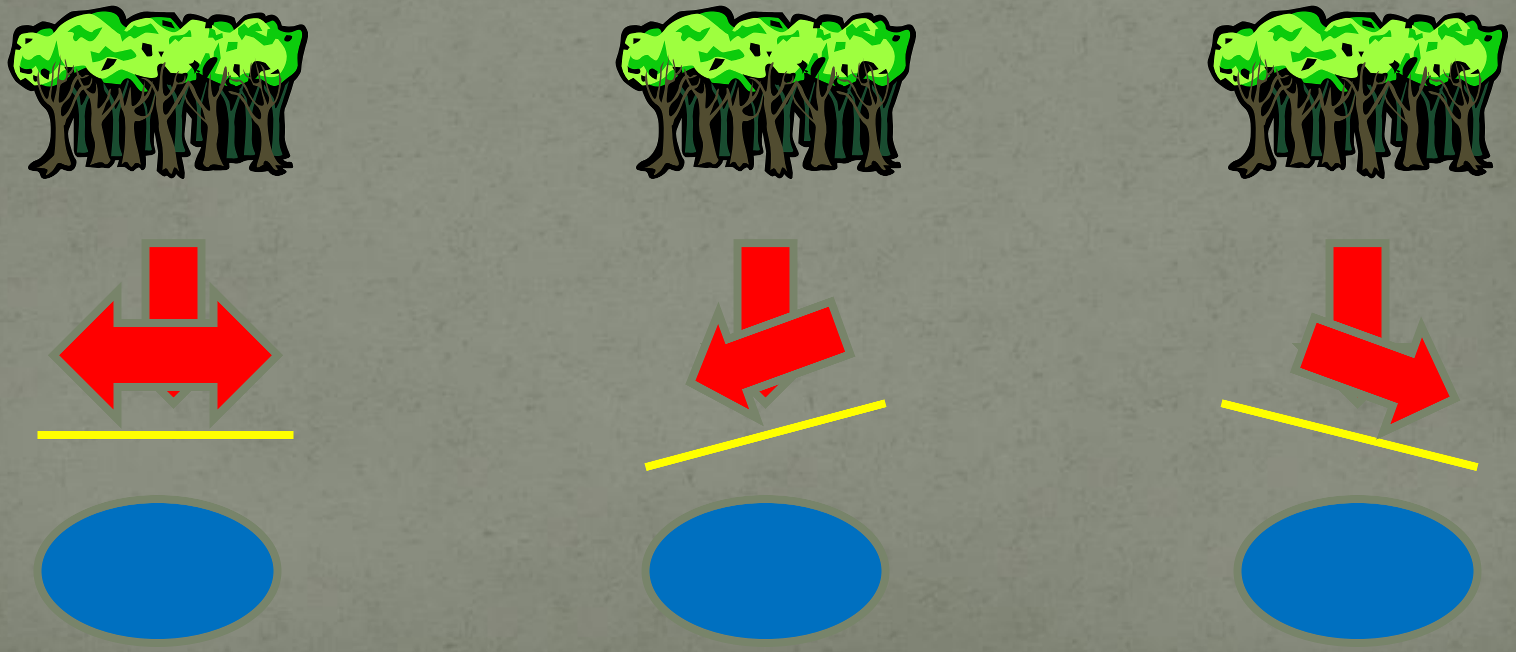
- Spotted salamanders during active migration appear to be relatively tolerant of variation in the attributes of culverts within the range of treatments tested

Barrier fences

- Barrier fences are incredibly important
- Studies have shown that if animals are forced to walk too far along a fence they may not reach a culvert
- Woltz et al. (2008) found that fences 0.6-m high stopped frogs and turtles
- Animals tend to follow the direction of the fence that best approximates the direction they would like to take to reach their destination:

Barrier fence and direction of movement (based on observation)

- Understanding the direction animals are likely to be moving is likely to be important when constructing an effective barrier fence (animals migrate both ways!)



Conclusions

- Crossing structures are only likely to work for certain species
- Barrier fences should be arranged in relation to the direction of movement
- Animals may be relatively tolerant of variation in culverts if they are using them during active migration
- In general, culvert should be as short as possible and not narrow
- Natural substrates are likely to work better than artificial
- Culverts cannot receive high rates of water flow during times of use by animals

Further discussion/research

- Weighing up when to install crossing structures and when to allow animals to cross the road can be challenging
- We still don’t know how adaptable local populations can be to the presence of a road: If animals have an option, do they avoid moving in direction of the roadway?
- More research into how to best design barrier fences to funnel animals in the right direction is needed

Multi-scale habitat-resistance models for predicting road mortality hotspots for reptiles and amphibians

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Overview

1. How can we predict where animals will be found on roads?
2. Hotspot models
3. Validation data
4. Conclusions derived from models
5. Strengths of this approach
6. Limitations
7. Next steps

How can we tell where animals will be found on roads?

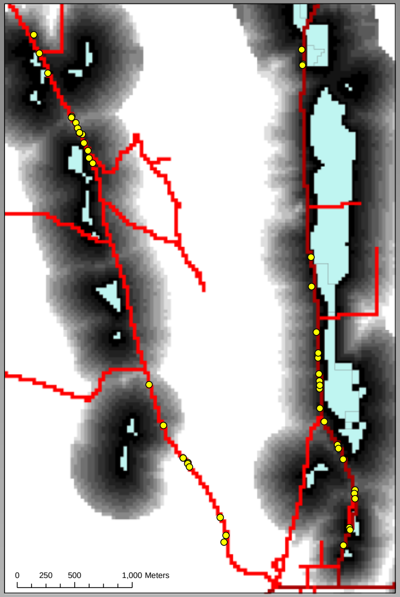
1. Direct observation
2. Models based on existing road occurrences
3. Models based on knowledge of the life-history characteristics of organisms

Models using existing road occurrences

- Data gathered via roadside surveys
- Remote sensing used to assess surrounding habitat characteristics
- Statistical models used to identify habitat characteristics best explaining occurence
- These habitat associations can be used to predict where other hotspots may be found
- For example, Langen et al., (2008) found that most mortalities of herpetofauna in St Lawrence County occurred on causeways between wetlands

Models using knowledge of life-history characteristics

- First step in models is gathering information about life-history of species
- This information is used to predict where individuals will be distributed across the landscape based on factors such as distance from breeding sites and how suitable intervening habitat is
- We can then overlay a road network to estimate where animals are likely to be found



Comparison of modeling approaches

Existing road occurrence

- Locally accurate
- May not be accurate at larger scales as environment or species characteristics can vary
- Road surveys not suitable for rare species
- Cannot use approach if roads have yet to be built

Life-history characteristics

- Unlikely to capture local variability in life history characteristics
- Regionally applicable
- Life-history data may not be available for all focal species

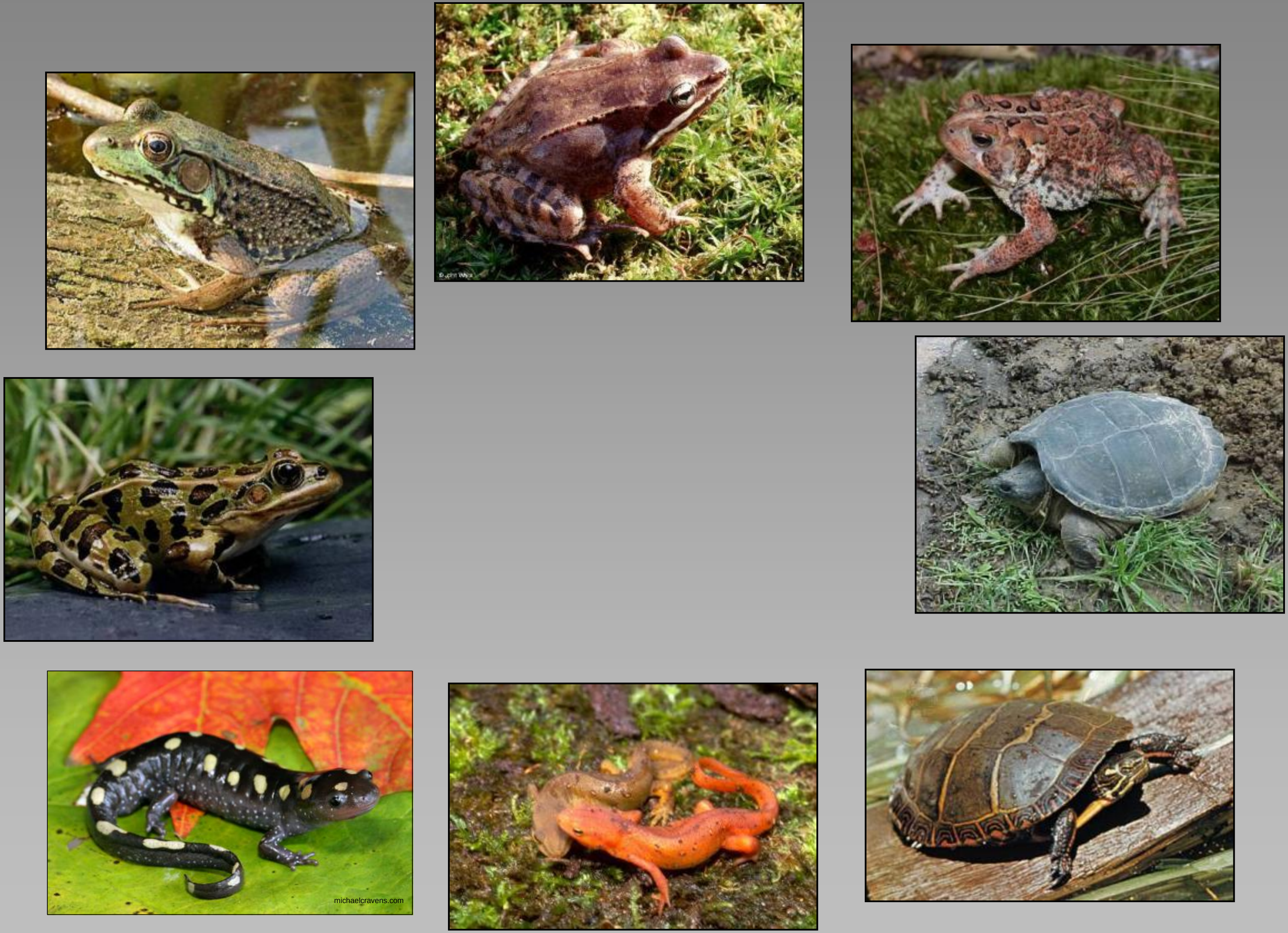
Hotspot models

- ❑ Based on goal of developing models for region-wide application we chose to use fundamental organism-habitat relationships as basis for models

Goals and objectives of hotspot models

- ☐ To develop spatial models predicting where herpetofauna are likely to be concentrated on roads in New York State
- ☐ Models should be species/life-history specific
- ☐ Models should provide sufficient data to guide mitigation efforts by the Department of Transportation

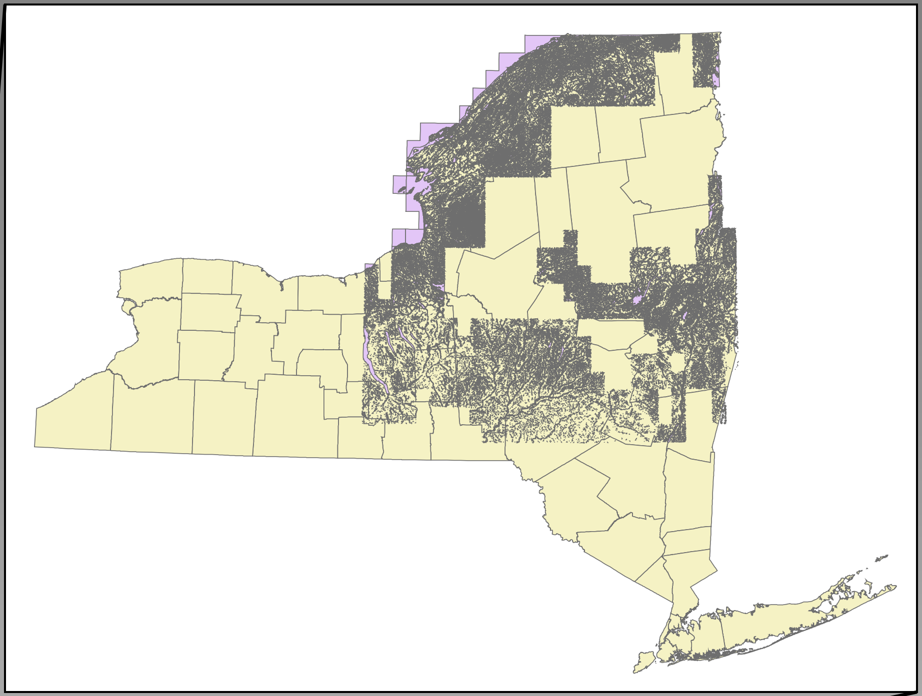
Methods: Study species

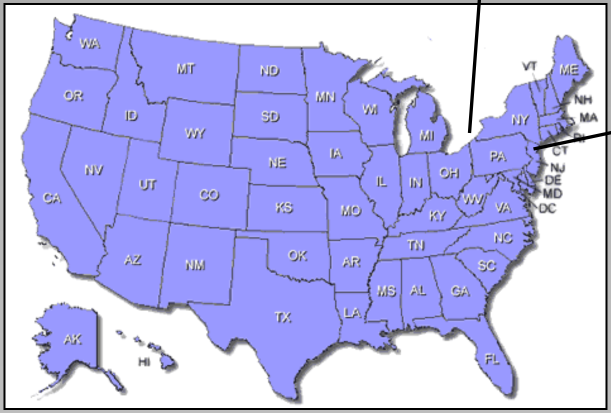


Juveniles and adult amphibians

- Juveniles and adult amphibians were modeled separately for wood frogs, spotted salamanders, and American toads
- Juveniles are the dispersing life history stage, therefore move farther
- Juveniles are also more sensitive to habitat change

Study area





- Focal area shown in shaded grey
- Limited to regions with wetland data

Framework of hotspot models

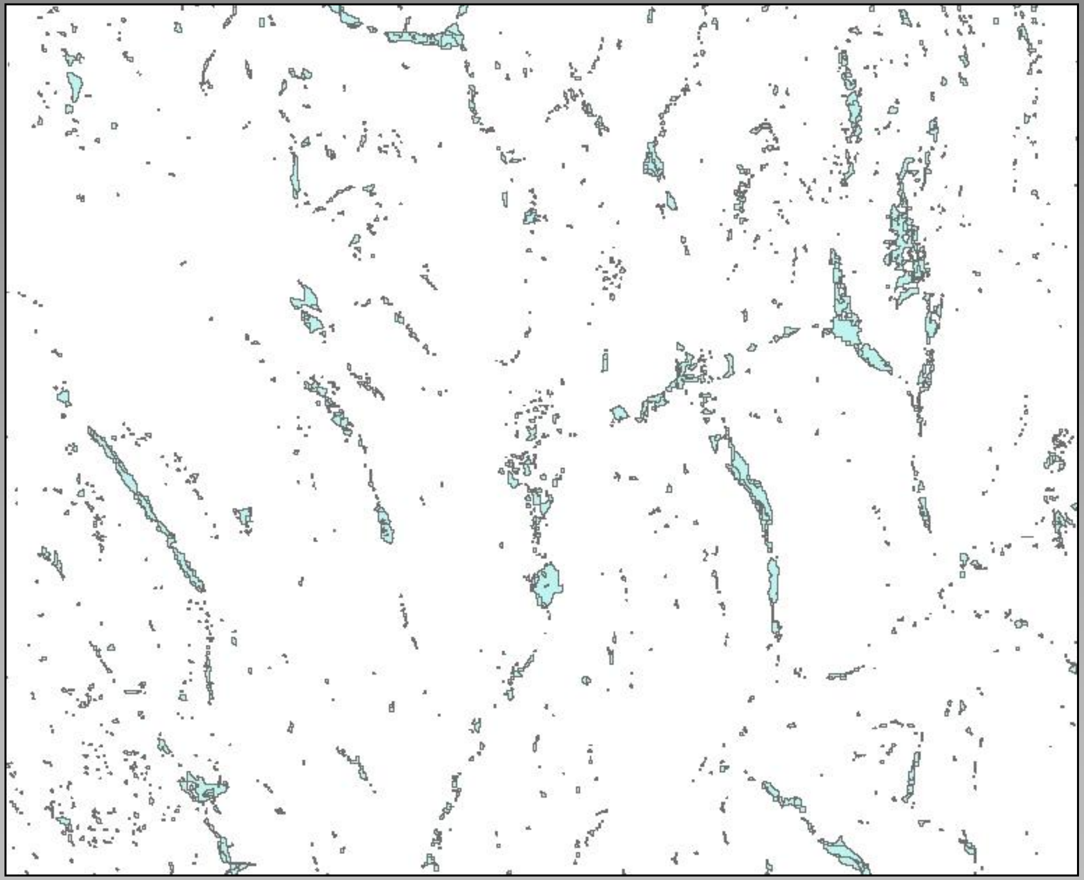
- Hotspot models based on habitat suitability for each species
- Literature data gathered on life-histories
- Suitable aquatic habitat selected for each species

Framework of hotspot models

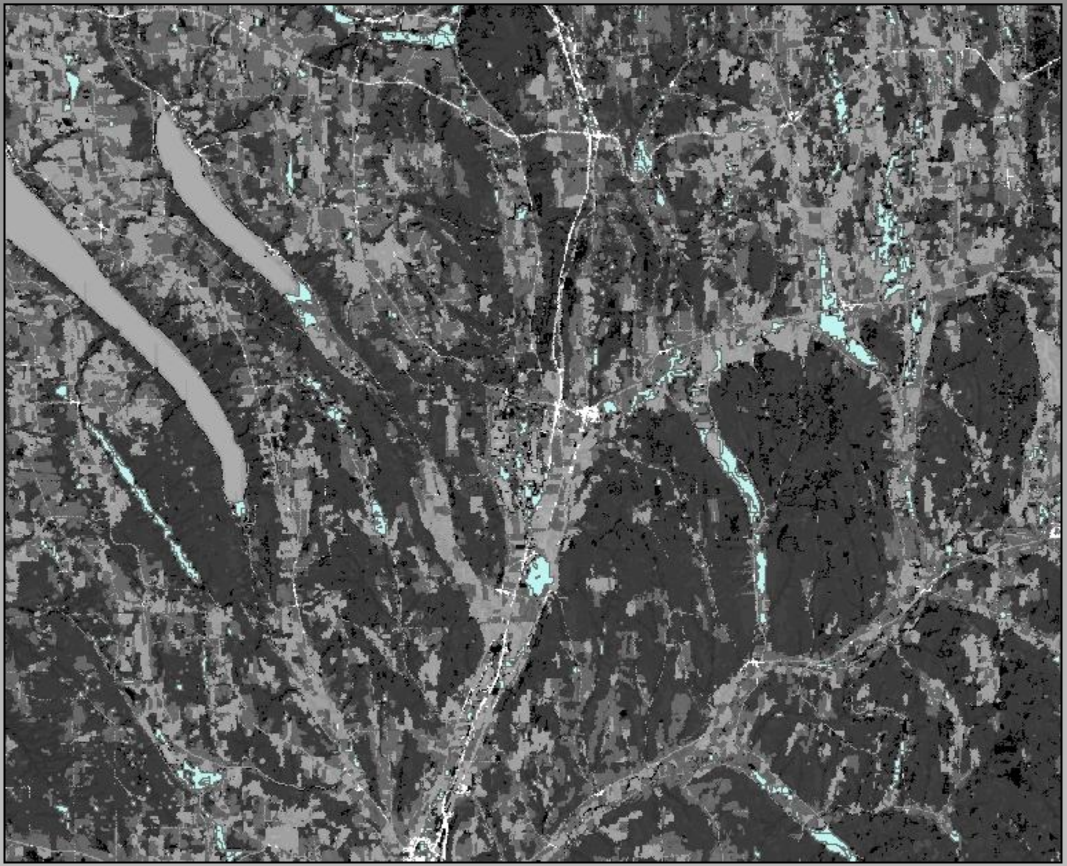
- For each species, terrestrial habitat assigned a “resistance” value
- This value represents the willingness of an animal to cross the habitat, the physiological cost and the increased risk of mortality
- Resistance value rescaled based on a Topographic Wetness Index (wet being favorable)

Results: Migrating spotted salamanders as an example

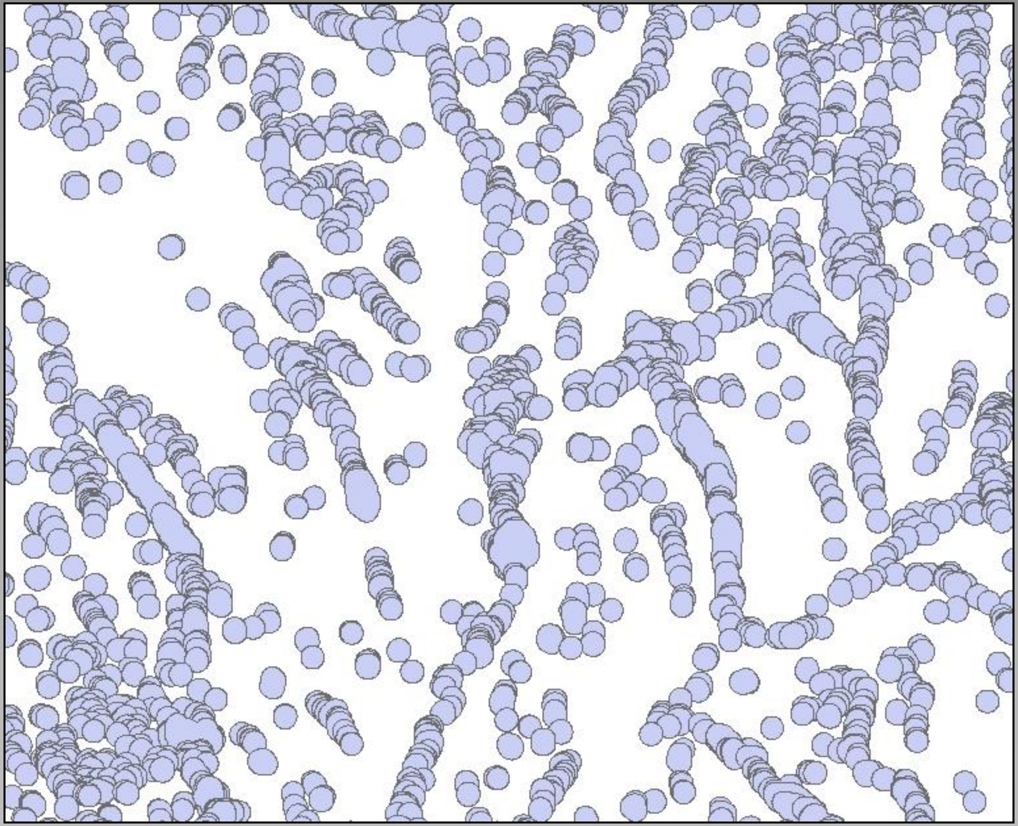
Suitable aquatic habitat selected (National Wetlands Inventory [NWI])



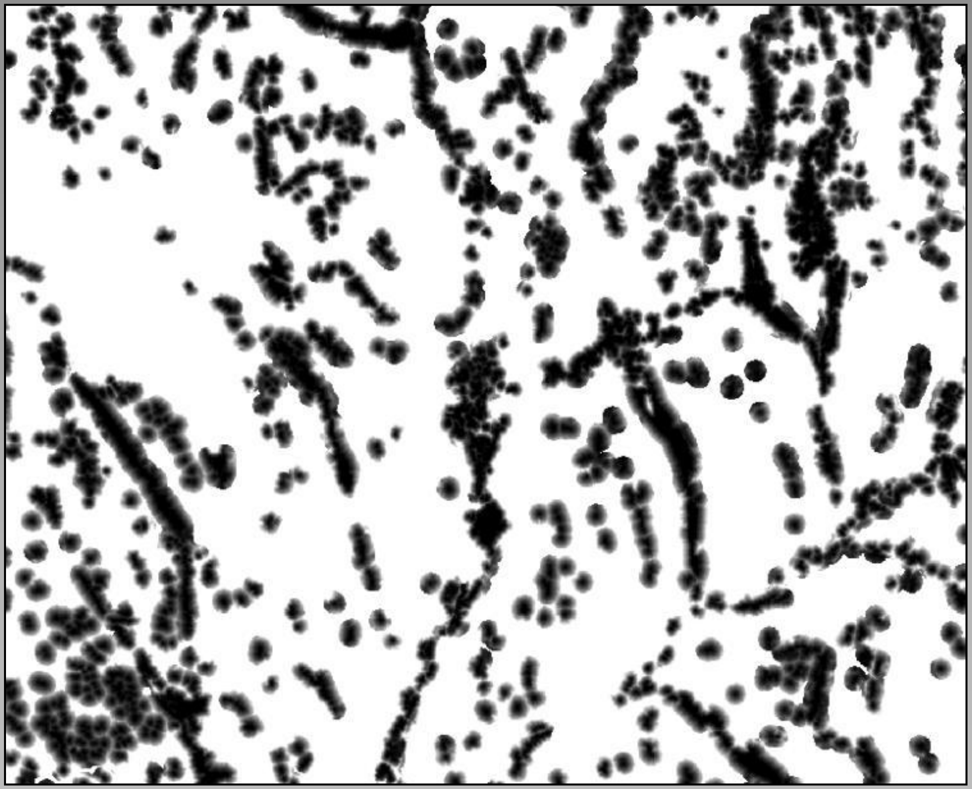
National Land Cover Data and NWI data combined and resistance values assigned. Values rescaled by topographic wetness index



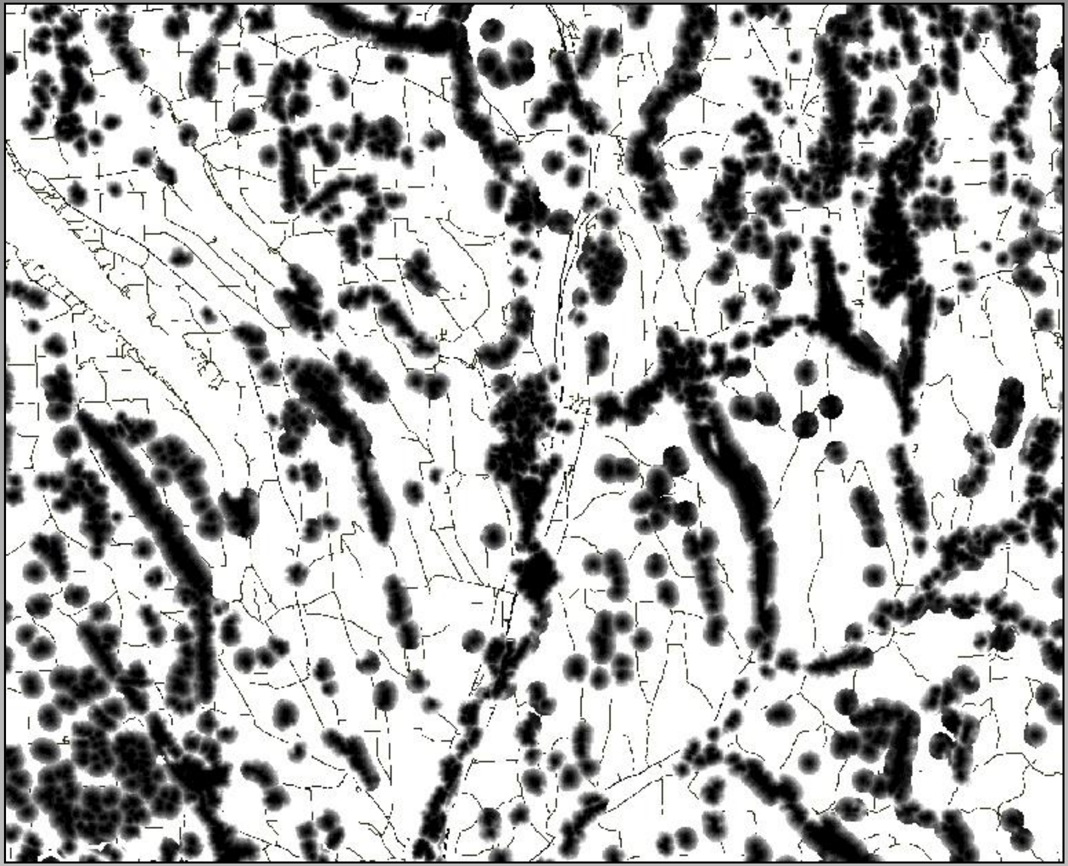
Movement buffer established around each wetland using maximum movement distance of species/life-history stage



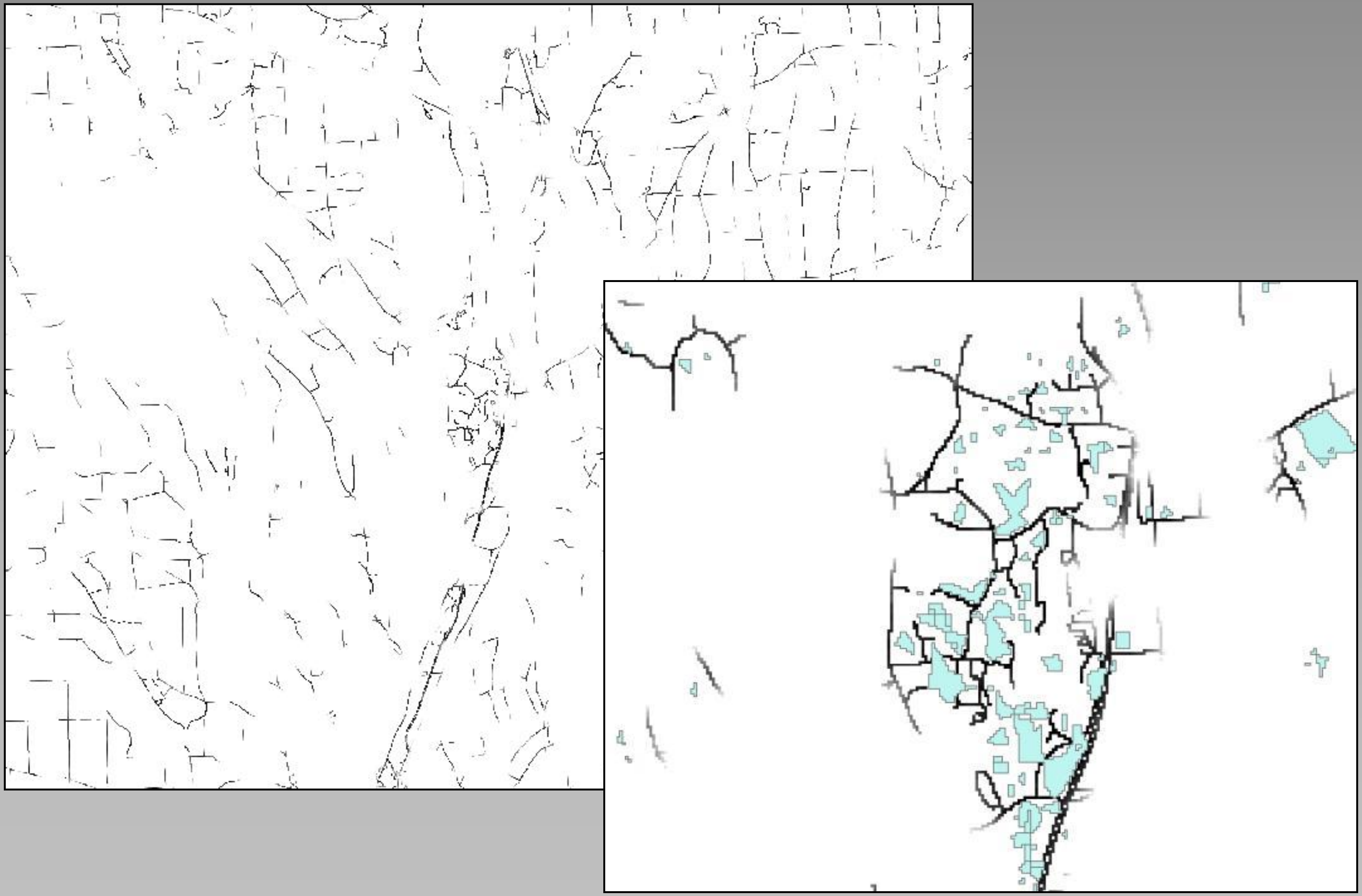
Resistance landscape clipped by buffers. Cumulative cost-distance calculated from aquatic nexus to edge of buffer. Rescaled from 0-100



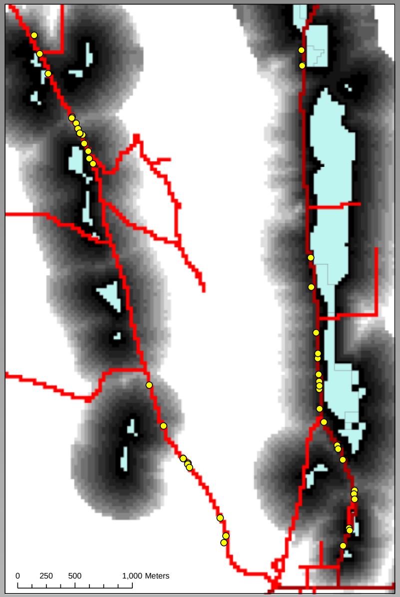
Road network overlaid on this ‘occurrence index’



Occurrence index clipped by road network to produce map of relative likelihood of a spotted salamander being present on the road



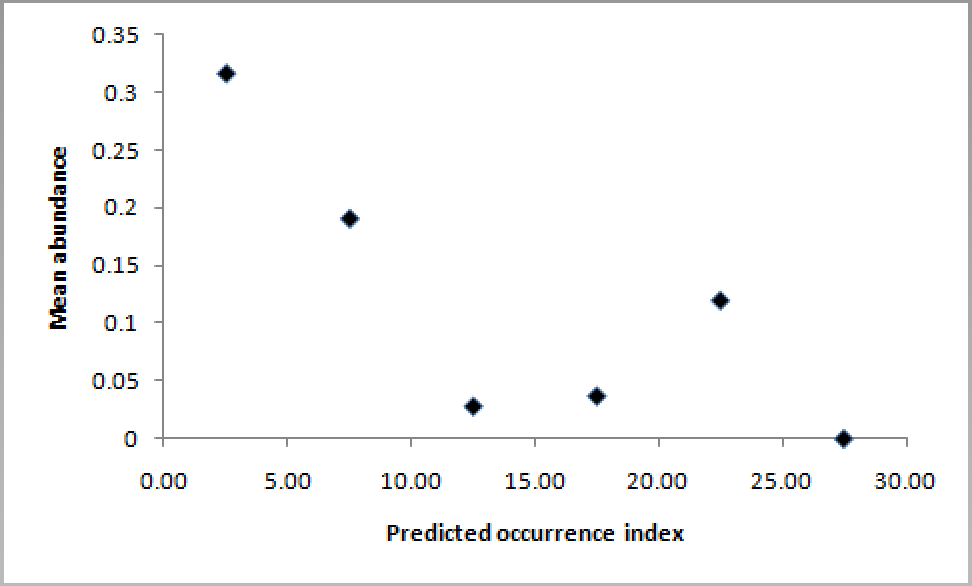
Validating models



Methods

- Models were validated using road surveys along two routes in central New York
- Roads were cruised either by car or by bicycle
- The observed occurrences of species were then compared to predicted occurrences from our models

- Total of 590 individuals of 8 species observed on the two loops
- Abundance of spotted salamanders, and occurrence of wood frogs and newts was significantly related to predicted occurrence indices
- Green frogs and toads were not well predicted by models



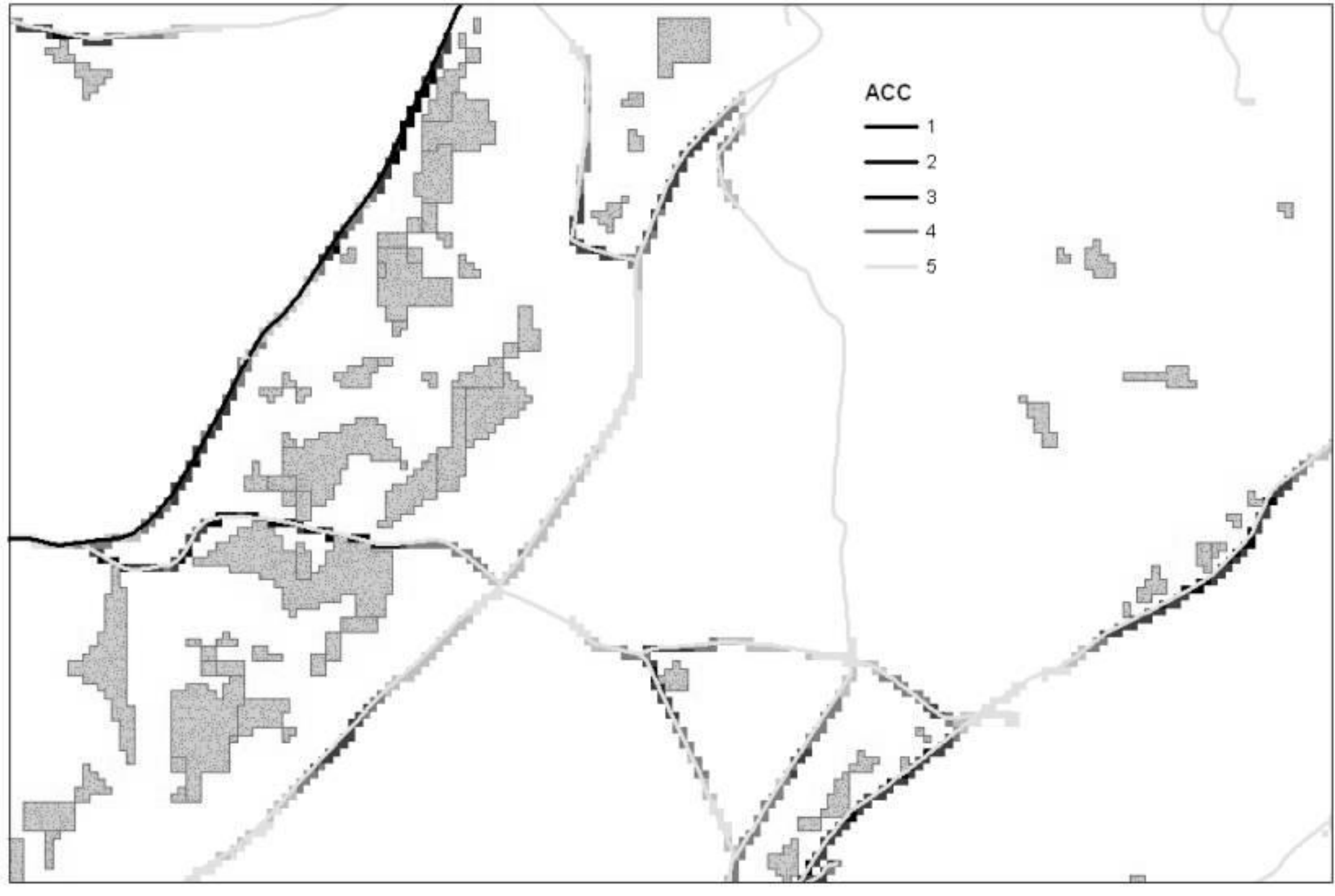
Spotted salamander predicted versus observed occurrence

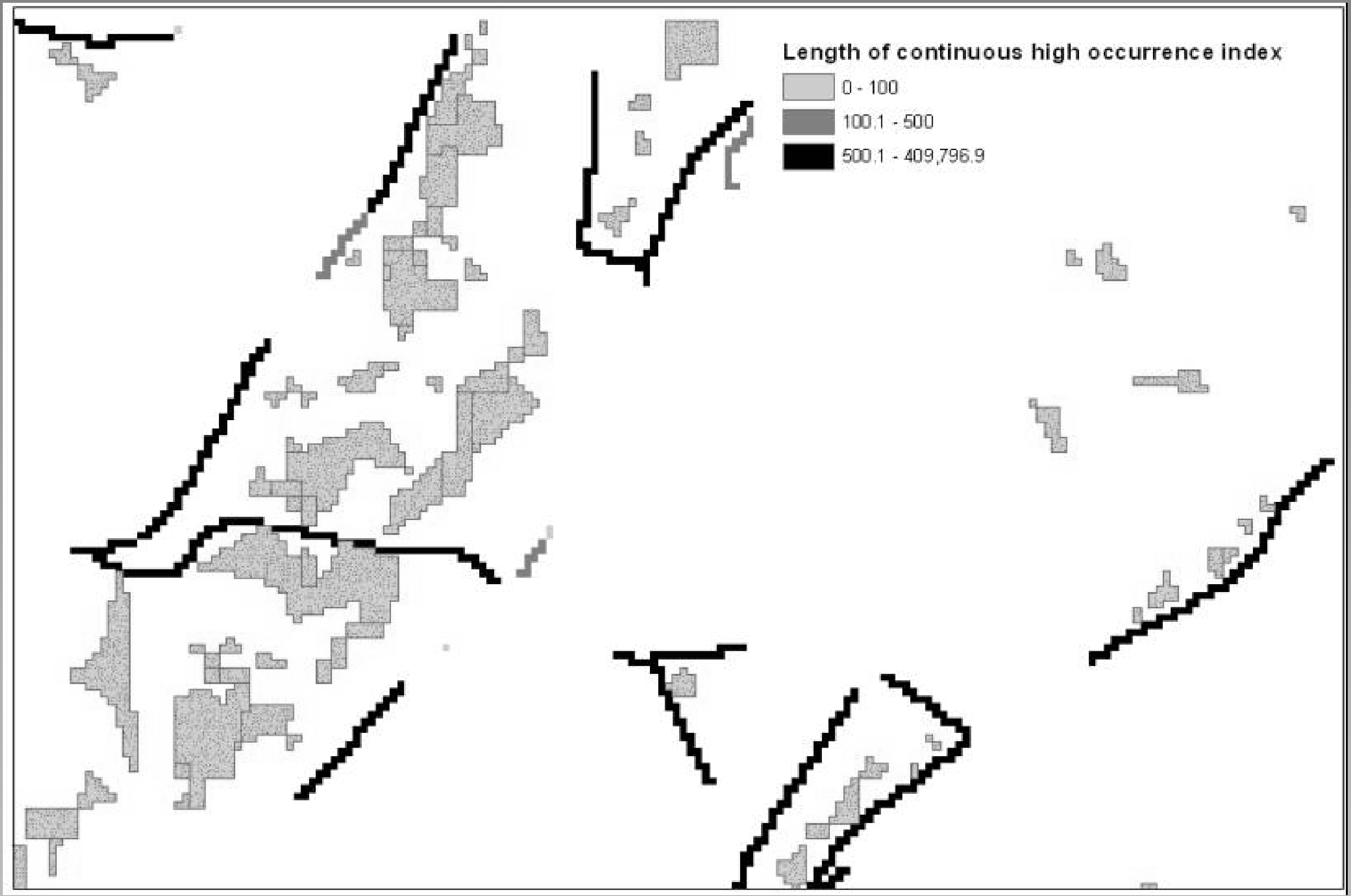
Prioritizing information: how to use models

- Models generate a large amount of information, including predicting occurrence of at least one species on most sections of road
- How do we prioritize this information?

- We developed two prioritization metrics:

1. Overlaying the arterial classification code (ACC) over our occurrence index to identify roads with high traffic volume and a high probability of occurrence
2. Using the length of continuous high-occurrence rasters to identify places where we expect to see large numbers of animals on roads


ACC
1
2
3
4
5


Length of continuous high occurrence index
0 - 100
100.1 - 500
500.1 - 409,796.9

- We can also choose focal species as indicators for the taxa in general
- For example wood frog occurrence is well-predicted by models and this species also provides a good indicator for where we might expect other forest dependent amphibians to occur

Conclusions drawn from models

- Herpetofauna are more likely to occur in close proximity to suitable aquatic habitat and in high-quality terrestrial habitat
- Roads running parallel and close to the edge of wetlands have highest probability of occurrence
- Differences in life-history have clear implications for patterns of occurrence on roads

Strengths of this approach

- Large-scale approach allowing predictions to be made across a wide spatial scale
- Based on readily available data, therefore transferable to different species and regions
- Allows predictions to be made where no roads currently exist

Limitations and caveats

- ☐ Spatial data limitations- for example smaller wetlands are often missed from available data layers and GIS data may be limited in extent
- ☐ Less accurate than occurrence-based models at a local scale
- ☐ Risk of compiling species attributes from across a range creating a combination of characteristics that does not exist anywhere (although validation data suggests not an issue)

Questions and feedback?