

## Can road mortality limit populations of pool-breeding amphibians?

James P. Gibbs<sup>1,\*</sup> and W. Gregory Shriver<sup>2</sup>

<sup>1</sup>College of Environmental Science and Forestry, State University of New York, 350 Illick Hall, 1 Forestry Drive, Syracuse, New York 13210, USA; <sup>2</sup>U.S. National Park Service, Marsh-Billings-Rockefeller National Historic Park 54 Elm Street, Woodstock, VT 05091, USA; \*Author for correspondence (e-mail: jpgibbs@syr.edu; phone: +1-315-470-6764; fax: +1-315-470-6934)

Received 9 September 2003; accepted in revised form 9 July 2004

**Key words:** *Ambystoma maculatum*, Conservation, Demography, Pool-breeding amphibian, Road mortality, Spotted salamander

### Abstract

We integrated road maps, traffic volume data, and pool locations in a modeling study to estimate the potential effects of road mortality on populations of pool-breeding spotted salamanders (*Ambystoma maculatum* Shaw). Population projections based on spotted salamander life tables imply that an annual risk of road mortality for adults of > 10% can lead to local population extirpation; mitigation efforts (tunnels, road closures, and other measures) should seek to reduce road mortality rates to below this threshold. For central and western Massachusetts, we estimated that salamanders would be exposed to at least this threshold level of risk at 22–73% of populations (assuming a 100 vs. 500 m migration distance, respectively). We conclude that road mortality can be a significant source of additive mortality for individual spotted salamanders in many parts of the species' range. Efforts to prevent such mortality by transportation planners are likely warranted strictly on a biological basis in areas with road densities > 2.5 km per km<sup>2</sup> of landscape and traffic volumes > 250 vehicles/lane/day within the migration range of a breeding population of spotted salamanders.

### Introduction

Road mortality of amphibians is a worldwide conservation concern (e.g., Wyman 1991; Ashley and Robinson 1996; Hels and Buchwald 2001), and the United States is no exception. About one-fifth of the land area of the conterminous United States experiences some ecological effect of roads and traffic (Forman 2000), an effect that is increasing in concert with the expansion of the road network and increase in traffic volumes (National Research Council 1997).

Amphibians are one taxonomic group likely sensitive to this expansion because they frequently

are killed on roads, particularly during the highly synchronized overland migrations many pool-breeding species undertake annually (Wyman 1991). Mortality of dispersing juveniles, as well as adults, during the post-breeding period also occurs and could be significant, but is less well recognized, in large part because the phenomenon is more diffuse in time and space and therefore more difficult to study.

Amphibian migration is primarily nocturnal, when traffic volumes are highly reduced relative to their daytime rates (about 80% of traffic volume occurs during the day; Festin 1996). Moreover, amphibian demography, particularly that of anurans

(frogs and toads), is characterized by extraordinary potential for population increase (e.g., Ber-ven 1990). Thus, it is possible that amphibian road mortality is an unfortunate yet demographically insignificant phenomenon. The sparse research conducted on the topic to date, however, suggests otherwise.

Most research on the effects of road mortality on amphibians has entailed simple tallies of numbers of individuals killed at particular road crossing sites, in some cases yielding surprisingly large counts. For example, road-kill counts along a 3.6 km section of a two-lane paved causeway in Ontario, Canada over two seasons yielded > 32,000 individual amphibians (Ashley and Robinson 1996). Wyman (1991) reported average mortality rates of 50.3 to 100% for hundreds of salamanders attempting to cross a paved rural road in New York State, USA.

Attempts to translate such counts of road-killed animals into population-level assessments of the consequences of road mortality are few. Hels and Buchwald (2001) estimated that 10% of amphibian populations near roads were killed on roads annually at their study area in Denmark. Carr and Fahrig (2001) concluded that road mortality exerts more negative effects on populations of vagile species of frogs than on sedentary (largely aquatic) species in Ontario, Canada. In the same region, Fahrig et al. (1995) demonstrated that local frog populations decreased with increasing traffic volume. Only Gittins (1983), studying common toads (*Bufo bufo*) in Great Britain, concluded that road mortality had a minimal effect on populations.

Transportation policy makers are becoming increasingly aware of the issue of wildlife mortality and predisposed to addressing it (Forman et al. 2002). Unfortunately, we do not yet know whether road mortality is sufficient to pose a significant risk to the viability of local or perhaps even regional amphibian populations. Moreover, the few, site-specific studies of amphibian road mortality conducted to date have not provided the type of information needed to advance planning efforts. Particularly useful would be studies that identify threshold combinations of road density and traffic volume that lead to unacceptably high levels of road mortality in amphibian populations.

We implemented a modeling approach first described by Gibbs and Shriver (2002) to examine the magnitude of road mortality on pool-breeding amphibians. The modeling approach integrates

maps of actual road networks, data on traffic volumes, and simulated animal movements to estimate the effects of road density and traffic volume on animal demography. We used spotted salamanders (*Ambystoma maculatum* Shaw) as a model organism because (1) they are widespread in the eastern United States, (2) they are frequently a target of efforts to mitigate amphibian road mortality, and (3) their demography, characterized by extended generations times, and slow locomotion suggest that they would be among the amphibians most sensitive to additive sources of adult mortality, such as that generated by roads (Wyman 1991; Petranka 1998).

## Methods

### *Estimating mortality in relation to traffic volume*

The probability that a salamander would be killed as it attempted to cross a road,  $p_{\text{killed}}$ , was estimated based on an equation adapted from Hels and Buchwald (2001):

$$p_{\text{killed}} = 1 - e^{-Na/v}$$

where  $N$  = traffic volume in vehicles/min,  $a$  = width of the kill-zone on a road (m), and  $v$  = velocity (m/min) of the salamander moving through the kill-zone. The kill-zone was estimated as two times tire width (0.5 m total) per lane plus two times total salamander body length (snout-to-tail tip, see Hels and Buchwald 2001; data on mean adult length obtained from Petranka 1998). A conservative value was used for  $v$ , salamander velocity, that is, 1 m/min, based on our estimates of 12 adult *A. maculatum* crossing a road (see next paragraph); these animals averaged 1.3 m/min ( $\pm 0.63$  SD).

### *Assessing the validity of mortality estimates*

We assessed the validity of our mortality estimates in relation to traffic volume by measuring actual salamander mortality caused by fatal encounters with vehicles on roads between March 15 and May 1 in 2003. We conducted surveys on New York State Route 91 at Labrador Hollow (UTM 18 414312E, 4737775N [NAD27]) in Apulia, New York. At this site, salamanders descend from the forested slopes of Morgan Hill State Forest and

migrate across the highway en route to breeding pools in the Labrador Hollow Unique Area. We constructed 21, 3-m-long drift fences, spaced approximately 47 m apart, on the breeding-pool side of a 1 km length of highway (Figure 1). Drift fences were located 1 m from the road and angled  $10^\circ$  toward the road. Each drift fence was outfitted with one pitfall trap located in the center of the drift fence. Pitfall traps were metal cans 0.5 m deep and 7.5 cm in circumference. On six nights with sufficient precipitation to facilitate salamander movement, we monitored salamander crossings and vehicle passage. Observers repeatedly walked along the highway from fence 1 to 21 (a 'survey' of ca. 30 min) and counted and removed live and dead (or injured and presumably dying) animals. Live and dead salamanders were tallied (1) along segments of the highway between fences, and (2) from the segments of the highway facing drift fences where live animals captured in the drift fence pitfalls were included in the count. This sampling design provided two road crossing mortality estimates for salamanders (calculated as dead animals captured/total animals captured). We estimated 'true' mortality using salamanders captured on each survey in segments of the road facing drift fences and in drift fence pitfalls only

('true' because all salamanders would either be killed on the highway or captured in drift fences). We also estimated an 'inflated' mortality using road captures only ('inflated' mortality because all animals killed were counted, but some live animals escaped unnoticed between passes). Vehicle passage during surveys was recorded to the nearest second to later estimate traffic volume during a given survey period.

#### *Estimating mortality in relation to road density*

Annual road-associated mortality ( $d_{\text{road}}$ ) in spotted salamanders was estimated as

$$d_{\text{road}} = 1 - (1 - p_{\text{killed}})^{n_{\text{crossings}}}$$

where  $p_{\text{killed}}$  is the probability a salamander is struck by a vehicle on any given road crossing (see above) and  $n_{\text{crossings}}$  is the number of road crossings an individual salamander undertakes annually. The equation is derived from binomial probabilities (Zar 1984: 370–375) and estimates the likelihood that a salamander is struck (and presumably killed) during its cumulative road crossings each year.

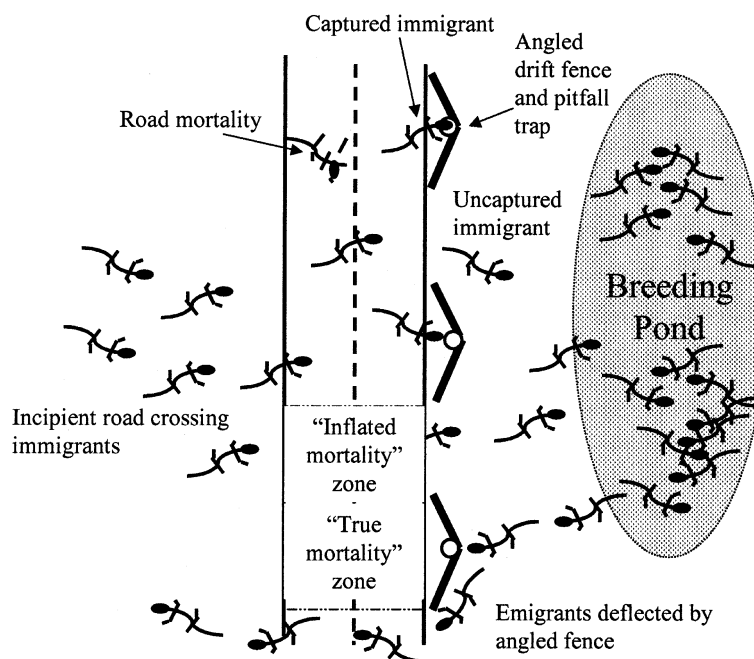


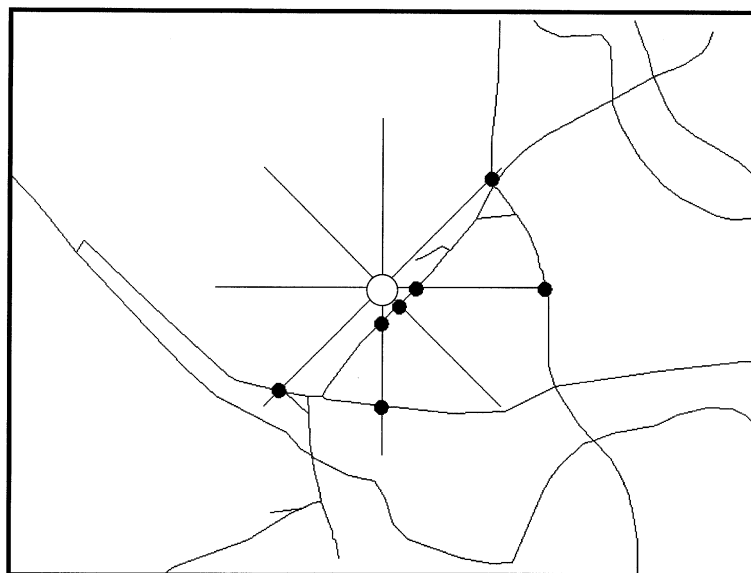
Figure 1. Sampling design used to estimate rates of road mortality of adult spotted salamanders in relation to traffic volume at Labrador Hollow, Apulia, New York, March–May 2003.

We used spatially explicit simulations of movements of individual salamanders on round-trip movements between upland territories and breeding pool areas to estimate the relationship between  $n_{\text{crossings}}$  and road density based on actual road networks (Figure 2). Salamander movements were simulated in landscapes within a 7224 km<sup>2</sup> region of central and western Massachusetts (Figure 3), which encompassed the Connecticut River Valley as well as portions of the Berkshire Mountains. All geographic data were obtained from MassGIS (<http://www.state.ma.us/mgis/massgis.htm>) and analyzed with ArcView 3.2 software and associated extensions. We randomly chose 500 breeding pools within this area (from the data layer created based on the survey conducted by Burne [2001]), and counted the average number of times a single salamander would have to cross a road on eight, roundtrip, linear movements (to the N, NE, E, SE, S, SW, W and NW) oriented upon the breeding pool (Figure 2). Two dispersal distances were evaluated – 100 and 500 m away from the pool – to bracket the low and high estimates of average adult salamander movement distances (125 m) reported by Semlitsch (1998). Road density in a

corresponding circle of radius 100 or 500 m of each breeding pool was also calculated by dividing the total length of roads present by the area of the circle (as km roads/km<sup>2</sup> of landscape). From these data ( $n = 500$  pairs of road density vs. salamander road crossing frequency for each dispersal distance) the relationship between road density and average  $n_{\text{crossings}}$  was estimated via least-squares linear regression analysis (with intercepts forced through zero).

#### *Demographic significance of road mortality*

We estimated mortality for each of the 500 breeding pools assessed in Massachusetts, using the observed road density surrounding each site as well as a statewide, night-adjusted traffic volume estimate. This value was estimated to be 160 vehicles/lane/day, based on the number of all motor vehicles registered in Massachusetts multiplied by the annual miles traveled by an average vehicle in the United States in 1998 divided by the lane ‘mileage’ in the state (FHA 1999). Traffic volumes were reduce by 80% to conform to the



*Figure 2.* Example of simulated patterns of movement by an individual adult spotted salamander moving on 8 round-trips (straight lines) from a breeding pool (open dot) and crossing (filled dots) roads (solid lines). In this case the average frequency of road crossing was 1.75 (average of 0, 0, 0, 2, 2, 2, 2, 4 and 4). Road density was subsequently estimated within a circular area of radius = migration distance and centered upon the same pool. Simulated movements were subsequently replicated 500 times for two movement distances (100 and 500 m away from pools).

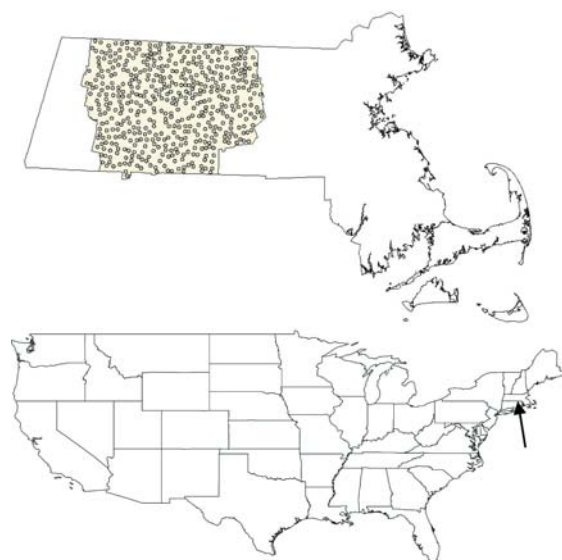


Figure 3. Area of central and western Massachusetts, USA, where salamander movements were simulated in relation to roads (upper). Circles represent the 500 randomly chosen breeding pools mapped by Burne (2001) used in the analysis. Arrow on map of the United States (lower) indicates location of Massachusetts.

proportion of overall traffic volume that occurs between 1800 and 0600 h (Festin 1996), the peak period of the salamanders' nocturnal movements (Petranka 1998).

We evaluated the potential significance of additive road mortality to spotted salamander population viability by integrating published estimates of vital rates into a population projection model that estimated the number of adults ( $N_{a,t}$ ) in a given year ( $t$ ) as:

$$N_{a,t+1} = N_{a,t} * \sigma_a + N_{e,t} * \sigma_m * (K_l - N_{e,t}) / K_l * \sigma_j$$

where ( $N_{e,t}$ ) is the number of eggs produced in a given year ( $t$ ):

$$N_{e,t+1} = N_{a,t} * \sigma_a \varphi \quad \text{and}$$

$\sigma_a$  = adult annual survival rate,  $\varphi_m$  = average eggs produced per individual,  $\sigma_m$  = survival rate from egg to metamorphosis,  $\sigma_j$  = survival rate of juveniles through their first winter,  $K_l$  = the carrying capacity of larval habitat.

The model reflects limitation of adult populations through density dependent process in the larval stage, typical of most pool-breeding amphibians (see Vonesh and de la Cruz 2002).

Based on Petranka's (1998) synopsis of the scientific literature on spotted salamander biology, annual adult survival rate,  $\sigma_a$ , was estimated at 0.7, survival rate of egg to metamorphosis was estimated at 0.04, and  $\sigma_j$  = survival rate of juveniles through their first winter was estimated at 0.6. The clutch size parameter,  $\varphi$ , incorporates number of eggs per mass (ca.80), number of egg masses laid per female per year (ca.2), and annual breeding probability (ca.0.38), all halved to reflect contributions by both males and females. Last, starting populations were set at 10,000 eggs and 100 breeding adults (an approximately stable age distribution) and  $K_l$ , carrying capacity of the larval habitat, was set at 10,000. Under this scenario, a spotted salamander population was projected over 25 years under varying levels of adult survival ( $\sigma_a = 0.4, 0.5$  and  $0.6$ ), each reflecting varying levels of additive road mortality in relation to the scenario of no road mortality ( $\sigma_a = 0.7$ ).

## Results

### *Estimating mortality in relation to traffic volume*

Mortality estimates were highly and positively correlated with volume of traffic that passed during the same interval:  $p_{\text{killed}} = 1.537 * \text{vehicles/min} - 0.0048$ ,  $R^2 = 0.927$ , Figure 4).

### *Assessing the validity of mortality estimates*

We counted 330 live and dead spotted salamanders on road crossing surveys. Mortality rate at drift fences ('true' mortality rate) was estimated at 19% (16 dead/70 live) whereas mortality estimated from captures on the road between drift fences ('inflated' mortality rate) was 25% (61 dead/183 live). We used road mortality estimates from 5 surveys along the road during which we collected >10 animals between drift fences, reduced these estimates by 6% (the inflation factor between true and inflated estimates), and found that field estimates of mortality were nearly identical (Figure 4) to those predicted by the equation of Hels and Buchwald (2001).

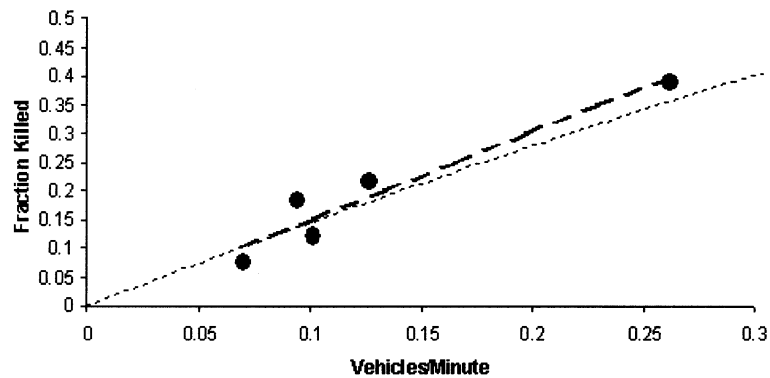


Figure 4. Relationship between road mortality predicted on the basis of traffic volume, salamander rate of locomotion, and salamander length (based on Hels and Buchwald 2001) vs. that estimated in the field during five surveys at Labrador Hollow, Apulia, New York, in 2003.

#### *Estimating crossing frequency in relation to road density*

The relationship between road density (RD) and expected road-crossing frequency ( $n_{\text{crossings}}$ ) (Figure 5) was linear and positive for two migration distances, with slope increasing but model fit declining as dispersal distance increased: 100 m,  $n_{\text{crossings}} = 0.0658 \cdot \text{RD}$  ( $R^2 = 0.81$ ) and 500 m,  $n_{\text{crossings}} = 0.356 \cdot \text{RD}$  ( $R^2 = 0.54$ ).

#### *Demographic significance of road mortality*

Based on our probability model that integrated traffic volume and road density, we estimated that

for the 500 breeding pools assessed in Massachusetts, the median road mortality rate was 17% annually for animals moving 100 m and 37% for animals moving 500 m. Population projections indicated that a spotted salamander population with a starting number of eggs = 10,000 (at a breeding pool's carrying capacity) and starting number of adults = 100 would (after achieving a stable age distribution) attain an equilibrium adult population size of about 200 after 20 years (Figure 6). Additive road-associated mortality of 10% would lead to a stable adult population, albeit at a lower equilibrium level, of about 80 individuals (Figure 6). Road mortality levels of 20 and 30% would lead to population extirpation (Figure 6) within 25 years. Thus, a threshold rate

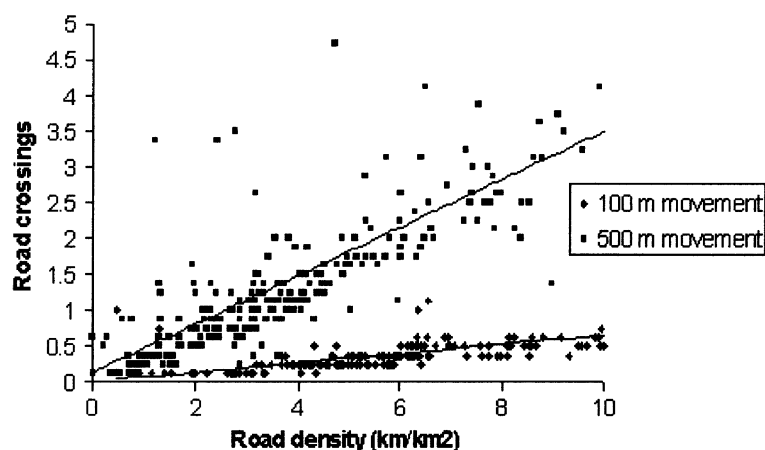


Figure 5. Relationship between road density and estimated road crossing frequency for spotted salamanders moving at two distances (100 and 500 m).

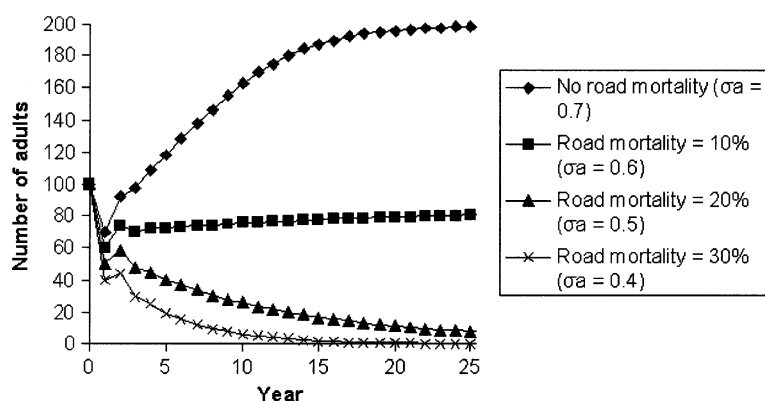


Figure 6. Projections of a single spotted salamander population over 25 years under scenarios of adult survival = 0.7 (typical estimate of adult survival in areas without heavy road mortality) vs. road-mortality reduced levels of adult survival = 0.6, 0.5 and 0.4. The model reflects limitation of adult populations through density dependent processes in the larval stage, that is 10,000 eggs, with starting population of 100 adults and 10,000 eggs, with the population achieving a stable age distribution between years 1 and 5.

of somewhere between 10 and 20% likely occurs above which population declines owing to road mortality would be expected to ensue.

### Discussion

Can road mortality limit populations of pool-breeding amphibians? These analyses imply that road mortality could be a significant source of additive mortality for spotted salamanders in central and western Massachusetts. Moreover, our population projections, which integrate these road mortality estimates with the demography of the spotted salamander, indicate that road mortality alone could lead to local population extirpation in many areas. Our estimates are somewhat conservative insofar as they consider only mortality during breeding migrations whereas some movements do occur outside the breeding season and may further expose adults and migrating juveniles to road mortality.

Notably, our population projections suggest that the 'dose-response' curves between sizes of salamander populations and levels of road mortality are not a simple linear relationship. Scenarios for patterns of local population decline with increasing exposure to road mortality are likely quite complex in amphibians and low levels of road mortality may have little effect on salamander populations. This is because many population processes in amphibians are the result of density-

dependent interactions in the larval stage (e.g., Berven 1990). Thus, initial road-caused declines in the adult population may be partially compensated for by increased juvenile recruitment, as reduced input of eggs results in less larval crowding, and hence higher rates of metamorphosis (e.g., Vonesh and de la Cruz 2002). Once egg input of adults drops below that needed for saturation of larval habitats, however, the number of metamorphs produced and the number of breeding adults will be linearly and positively related. Thus, we expect the relationship between the intensity of road mortality and populations of spotted salamanders is one in which salamander populations remain stable in the face of increasing road mortality and then go into rapid decline after a threshold has been crossed, a pattern largely borne out by the outputs of the population model (Figure 6). Further research is needed to understand these processes and estimate critical thresholds of road mortality on salamander population persistence.

Although we have validated a critical component of the model, that is, road mortality in relation to traffic volume (Figure 4), substantial uncertainties remain with the relationship between road crossing frequency and road density. In particular, our analysis assumed that salamanders traverse the landscape in a linear fashion and cross any road encountered. That salamanders navigate completely independently of roads, however, is naive. In fact, roadbeds and ditches may physically

prevent road crossings and the salamanders themselves may avoid crossing roads. Some salamanders may remain on road surfaces for extended periods, either arrested physiologically by debilitating compounds associated with salts used to de-ice road surfaces or to linger upon the warmer surfaces for purposes of thermoregulation. Detailed behavioral studies of movements of individual salamanders in relation to roads would greatly clarify these issues and suggest ways to model them more accurately. We expect, for example, that high levels of road mortality such as those estimated do indeed occur where salamanders must cross roads to reach vital habitats (e.g., isolated breeding ponds that limit population recruitment in an area such as our study site in Labrador Hollow) that are separated by roads from adult habitat on uplands (e.g., Wyman 1991). However, aversions to road crossing, coupled with options for habitat choices, would deflate our mortality estimates to an unknown degree.

It must be emphasized that this study was performed at a regional spatial scale to examine the question of whether road mortality could lead to the extirpation of regional *A. maculatum* populations. Mortality at any particular site could be dramatically greater or less than what we estimate depending on local road densities and traffic volumes. For example, daily traffic volumes on 'main roads' and other arteries in this part of the United States can be on the range of 1000–10,000 vehicles per day. Some restricted access highways carry 10,000–100,000 vehicles/day (FHA 1999). Roads with such traffic volumes are wholly lethal to any migrating salamander.

The applicability of our findings to other amphibians and regions is unclear. Frogs and toads move more quickly across roads and are less vulnerable to road mortality (Wyman 1991). Frogs may be more mobile, however, particularly during the post-breeding period (e.g., Carr and Fahrig 2001) and hence may undertake road crossings at greater frequency over an entire season. Frogs are also more active diurnally, when traffic volumes are dramatically higher (Festini 1996). Even for other salamanders, variation in life history may make application of these results tenuous. For example, the red-spotted newt (*Notophthalmus viridescens*) wanders for years prior to sexual maturation during which time it is likely highly vulnerable to road mor-

tality. Notably this species is among the most sensitive to habitat fragmentation (Gibbs 1998) and chronic road mortality may contribute to this sensitivity. Conversely, plethodontid salamanders may be more limited in their movements than *Ambystoma* and hence less vulnerable. From a geographical perspective, these results are likely applicable to other regions that are urbanized to a similar degree as the region studied in central Massachusetts (for example, much of the northeastern United States excluding northern New England and Northern New York).

To convert our analyses into policy relevant information, we identified the combinations of traffic volume and road density that produce a predicted level of 25% or more additive mortality associated with roads (Figure 7). Based on this analysis, we estimated that combinations road densities  $>2.5$  km per km<sup>2</sup> of landscape and traffic volumes  $>250$  vehicles/lane/day within the dispersal and migration range of a particular breeding population of spotted salamanders could generate demographically significant mortality levels (Figure 6). Although interactions among salamander movement, road mortality, and population persistence remain unclear, it is apparent that conservation planning should accommodate local movements and breeding migrations of salamanders if local and perhaps even regional populations are to remain secure. Moreover, if efforts are successful in limiting rates of traffic-caused mortality to  $<10\%$  (See Figure 6) of all individuals attempting to cross

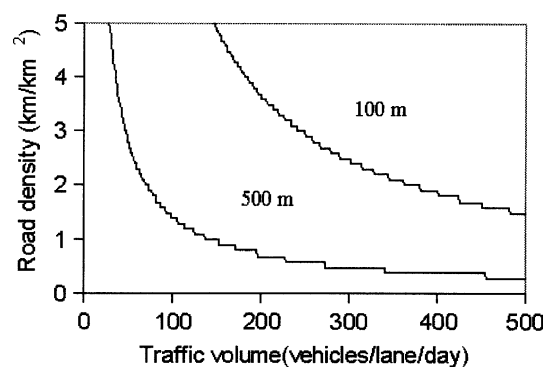


Figure 7. Combinations of road density and daily traffic volume that produce an estimated level of annual road-associated mortality of 25% in adult spotted salamanders migrating to two different distances (100 and 500 m).

roads during migration circuit to a particular pond, e.g., by tunnel construction, road closure, or physically transporting individuals, then those efforts are likely warranted to stave off local population extirpation.

### Acknowledgments

We are grateful to R. Brooks and P. Paton for inviting us to the Vernal Pools Symposium at The Wildlife Society Conference in Burlington, Vermont, in 2003, thereby motivating us to undertake this analysis. We also thank them for insightful comments and helpful editing, which was similarly provided by two anonymous reviewers. Many undergraduate and graduate students at SUNY-ESF kindly assisted with road surveys at Labrador Hollow, particularly Joel Strong, Debra Endriss, Nancy Karraker, Sara Ashkannejhad, Stephanie Smith, and Matthew Young. Mary Clements of the New York State Department of Transportation arranged permission and material support for us to conduct the road surveys, for which we are grateful.

### References

- Ashley E.P. and Robinson J.T. 1996. Road mortality of amphibians, reptiles and other wildlife on the Long Point Causeway, Lake Erie, Ontario. *Can. Field-Nat.* 110: 403–412.
- Berven K.A. 1990. Factors affecting population fluctuations in larval and adult stages of the wood frog (*Rana sylvatica*). *Ecology* 71: 1599–1608.
- Burne M.R. 2001. Massachusetts Aerial Photo Survey of Potential Vernal Pools. Natural Heritage and Endangered Species Program, Westborough, MA, USA.
- Carr L.W. and Fahrig L. 2001. Impact of road traffic on two amphibian species of differing vagility. *Conserv. Biol.* 15: 1071–1078.
- Fahrig L., Pedlar J.H., Pope S.E., Taylor P.D. and Wagner J.F. 1995. Effect of road traffic on amphibian density. *Biol. Conserv.* 73: 177–182.
- FHA (Federal Highway Administration). 1999. Highway Statistics – 1998. Office of Highway Policy Information, FHA, Washington, DC, Available from <http://www.fhwa.dot.gov/ohim/hs98/hs98page.htm>.
- Festini S.M. 1996. Summary of National and Regional Travel Trends: 1970–1995. Office of Highway Information Management, Federal Highway Administration, Washington, DC, Available from: <http://www.fhwa.dot.gov/ohim/bluebook.pdf>.
- Forman R.T.T. 2000. Estimate of the area affected ecologically by the road system in the United States. *Conserv. Biol.* 14: 31–35.
- Forman R.T.T., Sperling D. and Swanson F.J. 2002. Road Ecology: Science and Solutions. Island Press, Covelo, California, USA.
- Hels T. and Buchwald E. 2001. The effect of road kills on amphibian populations. *Biol. Conserv.* 99: 331–340.
- Gibbs J.P. 1998. Distribution of woodland amphibians along a forest fragmentation gradient. *Landscape Ecol.* 13: 263–268.
- Gibbs J.P. and Shriver W.G. 2002. Estimating the effects of road mortality on turtle populations. *Conserv. Biol.* 16: 1647–1652.
- Gittins S.P. 1983. Population dynamics of the common toad (*Bufo bufo*) at a lake in mid-Wales. *J. Anim. Ecol.* 52: 981–988.
- National Research Council. 1997. Towards a Sustainable Future: Addressing the Long-term Effects of Motor Vehicle Transportation on Climate and Ecology. National Academy Press, Washington, DC, USA.
- Petranka J.W. 1998. Salamanders of the United States and Canada. Smithsonian Institution Press, Washington, DC, USA.
- Semlitsch R.D. 1998. Biological delineation of terrestrial buffer zones for pond-breeding salamanders. *Conserv. Biol.* 12: 1113–1119.
- Vonesh J. and de la Cruz O. 2002. Complex life cycles and density dependence: assessing the contribution of egg mortality to amphibian declines. *Oecologia* 133: 325–333.
- Wyman R.L. (ed.) 1991. Global Climate Change and Life on Earth. Routledge, Chapman and Hall, New York, NY, USA.
- Zar J.H. 1984. Biostatistical Analysis. 2nd edn. Prentice Hall, NJ, USA.