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SHORT RESEARCH NOTE

# Contrasting road effect signals in reproduction of long- versus short-lived amphibians

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**Abstract** Despite an increasing understanding of the effects of roadways on amphibian populations, no studies have examined road effects on demographic traits other than survival. We predicted that road mortality could exert a disproportionate effect on fecundity in long-lived species due to shifts in population age structures to younger individuals of smaller size that produce commensurately smaller egg masses. To test this hypothesis, we assessed egg mass sizes of a long-lived amphibian (spotted salamander, *Ambystoma maculatum*) and short-lived one (wood frog, *Rana sylvatica*) in wetlands near and far from highways. Egg mass sizes of *A. maculatum* were smaller in wetlands near highways. In contrast, those of *R. sylvatica* were similar among wetlands regardless of the distance from highways. We conclude that paved highways with moderate traffic volume may be having important effects on populations of long-lived amphibians through mortality-mediated depression of reproduction.

**Keywords** Road effect · Road mortality · Egg mass size · *Ambystoma maculatum* · *Rana sylvatica* · Reproduction · Amphibian

Roads have been estimated to influence as much as 20% of the land area in the United States (Forman, 2000) and negatively affect a wide range of species via direct mortality, barriers to movement, and behavior alteration (Trombulak & Frissell, 2000). In the case of amphibians, abundances and species richness are lower in habitats near roads due to road mortality (e.g., Carr & Fahrig, 2001; Eigenbrod et al., 2008). Road mortality for amphibians migrating to breeding sites, reported at levels ranging from 19% (Gibbs & Shriver, 2005) to as high as 98% (Hels & Buchwald, 2001), rapidly increases with slight changes in traffic intensity (Mazerolle, 2004). Moreover, roads can pose significant barriers to movements of some amphibians. In the U.S., movements in three families of salamanders (deMaynadier & Hunter, 2000) were inhibited by wide, heavily used logging roads, thereby potentially restricting gene flow (Marsh et al., 2008).

Much of the previous research of the effects of roads on amphibian demography has focused on road-related mortality. Yet amphibian demography is a combined function of migration, reproduction, and survival, and human-caused disturbances affecting any of these vital parameters can constrain populations and limit long-term viability. We were interested in determining

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if roads reduce the fecundity of long-lived amphibians and chose to compare a long-lived salamander and a short-lived frog, both of which migrate to breeding ponds on an annual basis. *Rana sylvatica* females first breed at 2 years (Berven, 1990; Berven, 2009) and they live 2–4 years (Sagor et al., 1998); thus most individuals breed once or twice in their lifetimes. *Rana sylatica* are explosive breeders and females lay a single mass of tightly clustered eggs each year. Body size and egg mass size are positively related in this species (Berven, 1988). In contrast, *A. maculatum* females generally breed for the first time at age 2, live up to 32 years (Flageole & Leclair, 1992), and although probably not reproducing every year (Husting, 1965), they may breed many times in their lives. Females deposit two to four egg masses during each brief breeding season (Petranka, 1998) with the entire complement constituting a clutch. *Ambystoma maculatum* continue to grow throughout their lifetimes (Blackwell et al., 2003), and there is a well-documented relationship between egg mass size and body size (Wilbur, 1977; Kaplan & Salthe, 1979). If life expectancy within the population of a long-lived animal, such as *A. maculatum*, was reduced due to road mortality, we would expect to see smaller average egg mass sizes. We would not see such an effect for *R. sylvatica* which has a short lifespan, breeding only once or twice. Thus, our objectives were to (1) compare egg mass sizes for *A. maculatum* and *R. sylvatica* in wetlands near to and far from roads, (2) compare egg mass sizes for *A. maculatum* in a large wetland with a high-traffic road on one side and a low-traffic road on the other side; and (3) determine whether characteristics of breeding sites were related to any differences in observed egg mass sizes.

Spotted salamanders and wood frogs have been the focus of several road-related studies (deMaynadier & Hunter, 2000; Mazerolle, 2004; Gibbs & Shriver, 2005) and serve as good model organisms for studying the effects of roads on amphibians. Both species are abundant where suitable habitats exist and they have broad distributions across North America (Martof, 1970; Petranka, 1998). Adults of both species are considered strongly philopatric to breeding sites (Husting, 1965; Berven & Grudzien, 1990; Vasconcelos & Calhoun, 2004) and occupy forested, terrestrial habitats between breeding periods. *Rana sylvatica* move up to 340 m (Baldwin et al., 2006; Rittenhouse & Semlitsch, 2007), and *A. maculatum* can range up to 210 m from ponds following the breeding season (Kleeberger & Werner, 1983; Madison, 1997).

Our study was conducted in the Huntington Wildlife Forest and adjacent Finch-Pryun forestlands in the central Adirondack Mountains (hereafter Adirondack study area; 43°58′11.35″N; 74°13′14.70″W) of northern New York and at Labrador Hollow State Wildlife Preserve in central New York (hereafter Labrador Hollow study area; 42°47′26.79″N; 76°03′05.90″W). The Adirondack study area contains protected forestland and commercial timberland which is bisected by a two-lane state highway with traffic volume averaging 1,231 vehicles per day (New York State Department of Transportation, http://www.dot.state.ny.us/tech_serv/high/tvwebpag.html, accessed online June 2005). Labrador Hollow is a protected area consisting of a 50-ha wetland situated in a narrow valley. The wetland is bordered on the east by a paved county highway and on the west by an unpaved road that serves a single house and a small picnic area. Traffic volume on the paved county highway averages 2,062 vehicles per day (New York State Department of Transportation, 2005) and on the unpaved road averages approximately 15 vehicles per day (N. Karraker, personal observation). Traffic volume remains moderate on the paved county highway after dark, when amphibians migrate, but nearly ceases on the unpaved road.

In April 2005, we determined egg mass sizes of *A. maculatum* in Adirondack vernal pools and at the Labrador Hollow wetland, and of *R. sylvatica* in Adirondack vernal pools in April 2006. In the Adirondacks, we randomly selected 15 of 23 pools located farther than 500 m from the highway (hereafter forest pools) and included all 15 vernal pools located within 200 m of the highway (hereafter roadside pools), which contained egg masses in previous years (Karraker et al., 2008). At Labrador Hollow, we collected egg masses along the western edge of the wetland adjacent to the paved road and along the eastern edge adjacent to the unpaved road. We used a systematic protocol for sampling egg masses in wetlands in order to avoid unintentionally "selecting" particular egg masses and biasing our sample. To do this, in vernal pools, we collected and determined egg mass sizes for all present in smaller pools or for larger pools by starting at one end and collecting all egg masses, while walking in a clockwise direction for a portion of the pool. In the large wetland, we collected all *A. maculatum* egg masses encountered while walking in a northerly direction for approximately 100 m along the edges of each side of the wetland. We were unable to collect data on *R. sylvatica* egg masses in the large wetland at Labrador Hollow. We estimated egg mass sizes for both species using an ovagram, a device which presses egg masses between gridded, transparent plastic sheets enabling precise estimates of egg mass size (Karraker, 2007).

We used a tape measure to determine distance from the road of vernal pools within 200 m of the highway (hereafter, roadside pools) at the Adirondack study area. For pools located farther than 500 m from the highway (hereafter, forest pools), we determined distance from the road using a geographic information system. We also measured maximum pool depth, and pool perimeter, and canopy closure above each pool with a convex spherical densiometer. In the large wetland at Labrador Hollow, we measured water depth and canopy closure at five equidistant locations within the areas searched for egg masses on each side of the wetland.

In the Adirondacks, egg mass sizes of *A. maculatum* from forest pools were 30% larger ($t = 3.45$, $P = 0.002$, df $= 29$) than those from roadside pools (Table 1; Fig. 1). *Ambystoma maculatum* egg mass sizes increased with increasing distance from the road ($R^2 = 0.46$, $P < 0.0001$) and with decreasing percent canopy closure ($R^2 = 0.22$, $P = 0.008$). There was no relationship between egg mass size and pool maximum depth ($R^2 = 0.09$, $P = 0.12$) or pool perimeter ($R^2 = 0.02$, $P = 0.50$). Egg mass sizes of *R. sylvatica* from roadside and forest pools in the Adirondacks did not differ ($t = 0.08$, $P = 0.93$, df $= 16$; Fig. 1). At the Labrador Hollow wetland, *A. maculatum* egg masses on the low-traffic side of the wetland were more than 50% larger ($t = 4.96$, $P < 0.001$, df $= 71$) than those on the high-traffic side (Table 1). Canopy closure averaged 30% higher ($t = 4.21$, $P < 0.01$, df $= 9$) on the low-traffic side, but water depth was not different ($t = 0.21$, $P = 0.83$, df $= 9$) between the two sides of the wetland.

Egg mass sizes of *A. maculatum* were larger in pools located farther than 500 m from a highway compared with those in pools located within 200 m of the highway in the Adirondacks, and egg mass size increased with distance from highway. At Labrador Hollow, egg mass sizes were larger on the side of the wetland bordered by the low-traffic volume, unpaved road than on the side of the wetland bordered by a paved highway with much higher traffic volume. We speculate that spatial variation in egg mass size is due

**Table 1** Egg mass sizes for *A. maculatum* and *R. sylvatica* at roadside and forest wetlands in New York

| Location wetland type | Mean (SD) | Range | Number of egg masses | Number of wetlands |
|---|---|---|---|---|
| Adirondacks | *A. maculatum* | | | |
| Roadside | 58.8 (12.8) | 8–148 | 137 | 15 |
| Forest | 77.0 (16.1) | 7–155 | 140 | 15 |
| Labrador Hollow | | | | |
| Roadside | 56.2 (34.1) | 10–123 | 30 | 1 |
| Forest | 107.1 (50.0) | 26–228 | 26 | 1 |
| Adirondacks | *R. sylvatica* | | | |
| Roadside | 693.9 (81.6) | 514–1012 | 36 | 8 |
| Forest | 689.8 (70.3) | 529–939 | 40 | 9 |

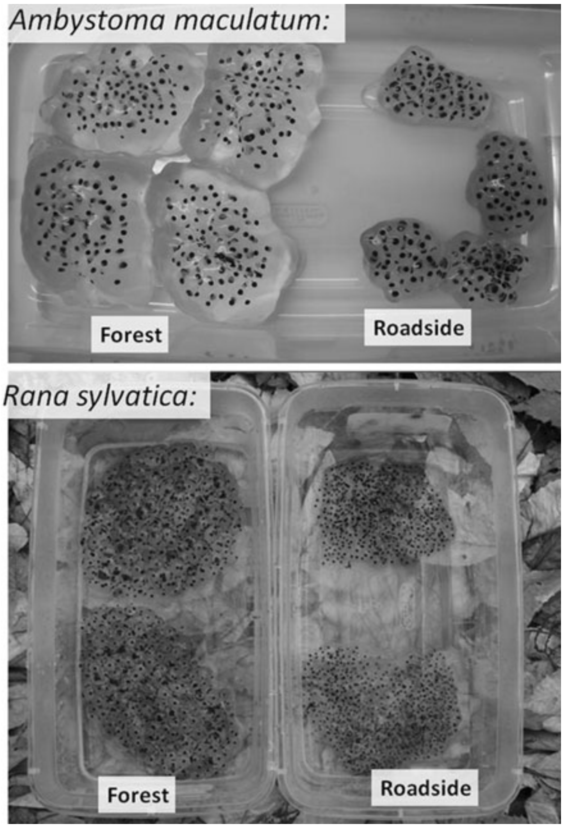

**Fig. 1** Photographs of representative egg masses of *A. maculatum* and *R. sylvatica* from forest and roadside pools in the Adirondack Mountain Region of New York

to differences in body sizes of females ovipositing in these wetlands and that these differences in body size are a function of road mortality. At the Adirondack site, the highway bisects forestland. *A. maculatum* are known to move up to about 200 m (Kleeberger & Werner, 1983; Madison, 1997) and *R. sylvatica* up to nearly 350 m (Baldwin et al., 2006; Rittenhouse & Semlitsch, 2007) from wetlands into adjacent forests after breeding. Thus, it is likely that some proportion of the animals breeding at a wetland near a road will have to cross the highway to breed each year. At Labrador Hollow, where both the high-traffic road and the low-traffic roads are immediately adjacent to the wetland and there is intact forest upslope of the roads on both sides of the wetland, nearly all *A. maculatum* will have to cross a road to breed each year. We do not have any data on road mortality of amphibians from the Adirondacks. We estimate that between 19 and 25% of *A. maculatum* (Gibbs & Shriver, 2005) and up to 30% of *R. sylvatica* (J.P. Gibbs, unpublished data) are killed by cars while crossing the high-traffic side of the wetland in Labrador Hollow. These estimates are for immigration and thus do not include additional mortality during emigration.

An alternative explanation for the phenomenon we observed may be that roadside pools in the Adirondacks or the high-traffic side of the wetland at Labrador Hollow had poorer habitat quality than forest pools or the low-traffic side of the wetland. While at the Adirondack site, one could argue that quality or quantity of food for *A. maculatum* may be lower closer to the road due to edge effects, the same could not be said for the Labrador Hollow site as there is mature, intact and seemingly similar forest on both sides of the large wetland. As further support, we expect that limitation of resources would have similarly affected *R. sylvatica* such that we would have observed smaller egg mass sizes where it breeds near high-traffic roads. Differences that potentially affect body condition of females, such as chemical contaminants being transported from roads into nearby breeding sites, could be responsible. Females in poorer body condition would reasonably have smaller egg mass sizes, as in these individuals there would be a proportionally greater allocation of resources to growth and maintenance than to reproduction. However, if this were the case, we should have seen a similar effect in *R. sylvatica*.

Another possible explanation for the patterns we observed is that female *A. maculatum* may have made the reproductive trade-off near roads of allocating more resources to individual ova, thereby increasing ova size and decreasing egg mass size. For *A. maculatum*, a strong relationship has not been documented between egg mass size and ova size, and among individuals there is high variation in both (Wilbur, 1977), so it is unlikely that a reallocation of resources from egg mass size to individual ova is responsible for our observations. In contrast, a strong positive relationship between egg mass size and body size has been demonstrated for both *A. maculatum* (Wilbur, 1977; Kaplan & Salthe, 1979) and *R. sylvatica* (Berven, 1982).

Alternatively, the differences we documented may be related to the sizes of egg masses deposited by *A. maculatum*. Selection favors female amphibians that mate with fitter males, and this is accomplished in species with internal fertilization, such as *A. maculatum*, by females choosing their mate and through cryptic choice such as sperm competition or selection (Halliday & Verrell, 1984). However, in habitats with dense breeding congresses or species with external fertilization, a female may not be able to choose her mate. Perhaps, female *A. maculatum* breeding in wetlands near high-traffic roads deposit smaller egg masses because most males attempting to breed in these habitats are of apparent low quality. Females may store sperm (Tennessen & Zamudio, 2003), and egg masses can be sired by up to eight males, thereby increasing the probability that some eggs will be fertilized by higher quality males (Myers & Zamudio, 2004). This explanation cannot be discounted and warrants further investigation.

We note that inferences from our results on the large wetland at Labrador Hollow are limited by a lack of replication, but differences in egg mass sizes near and far from the highway were substantial. Further investigations of this relationship with adequate replication would be valuable. Another limitation of our study is that we were unable to examine egg mass sizes for both species in the Adirondacks in the same year. Either species may exhibit inter-annual variation in egg mass size potentially confounding our results. However, even though inter-annual differences in climate or another factor might affect body condition, we think it is highly unlikely that there could be enough of a difference in body condition due to such factors in a single year as to render a significant difference in egg mass sizes of *R. sylvatica*, particularly since they lay an average of about 600 eggs per mass. For egg mass sizes to be statistically different, increased body size accrued over 1 year would have to be substantial. Given the extremely short growing season for *R. sylvatica* in the Adirondacks (approximately May–October) and the long, harsh winters, significant body size increases over 1 year are highly unlikely. Significant inter-annual differences in egg mass size due to body size/environmental factors would be more likely in species with smaller egg mass sizes, such as *A. maculatum*, and in more hospitable climates with longer growing seasons, such as at the southern edges of their ranges.

Finally, we do not know the degree to which egg mass sizes correlate with clutch sizes for *A. maculatum* in our study areas. This species lays two to four egg masses, comprising a clutch, in a short breeding season, but in the field it is impossible to determine which egg masses belong to a clutch unless oviposition of all masses in a clutch is directly observed or determined through genetic means. We hypothesize, however, that there must be a strong correlation and that our observations are not simply female *A. maculatum* near highways laying more egg masses of smaller size and females far from roads laying fewer egg masses of larger size. We urge further study into habitat disturbance and egg mass size/clutch size relationships.

Studies of the effects of roads on amphibians have focused heavily on road-associated mortality, and our study suggests that there may be other, less easily observed impacts of roads on populations. We urge other researchers to include studies of these effects in their efforts to understand how roads influence amphibian populations.

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