Keeping salamanders off the streets: An assessment of one of the first amphibian road tunnels in the United States 30 years after installation

Brandon P. Hedrick[1,*], Abby Vander Linden[2], Edward Watt[3], Patrick M. O'Roark[3], Samantha A. Cordero[3], Christopher Sutherland[4]

[1]Department of Earth Sciences, University of Oxford, Oxford UK, [2]Graduate Group in Organismic and Evolutionary Biology, University of Massachusetts, Amherst MA USA, [3]Hitchcock Center for the Environment, Amherst, MA USA, [4]Department of Environmental Conservation, University of Massachusetts-Amherst, MA USA.

*Corresponding author. Email: bphedrick1@gmail.com, 07455 727337

ABSTRACT

Culverts are often installed under busy roads to help animals ranging from small frogs to bears safely cross roads that bisect their habitat. One of the first roadway culvert systems designed specifically for amphibian use in the United States was installed along Henry Street in Amherst, Massachusetts in 1987. The purpose of these under-roadway tunnels was to protect spotted salamanders (*Ambystoma maculatum*) during their annual migration from their hibernation area to their breeding pools, which are separated by a road. Anecdotal evidence from volunteers monitoring the site suggested that salamanders were no longer using the tunnels. To evaluate this concern, we conducted salamander counts to quantify the amount of tunnel use. In 2016, only 11% of the observed salamanders used the tunnels. Subsequently, we implemented two tunnel modifications in an effort to increase salamander tunnel usage above the baseline established in 2016. Unfortunately, neither retrofit was successful in increasing use. Previous studies have demonstrated that salamanders prefer minimum tunnel apertures of >0.4 meters, so it is likely that the 0.2 meter tunnel apertures used here are too small. This may create a differential in light and humidity between the environments inside and outside the tunnels that is recognized by the salamanders. While many studies have evaluated amphibian tunnel use in lab and field settings, ours is one of the first studies to have examined tunnel usage data long after initial tunnel installation. These long-term data are critical for evaluating what factors are necessary for maintaining tunnels over decade-long time scales.

KEY WORDS: Spotted salamanders, conservation, urban ecology, amphibian tunnels, *Ambystoma maculatum,* culverts

Roads and highways can cause substantial complications for wildlife, including habitat fragmentation, subdivision of once contiguous populations, and road mortality (Forman and Alexander 1998). Road mortality in particular is high for reptiles and amphibians, which move across roads slowly and often in large numbers (Gibbs and Shriver 2005, Holderegger and Di Giulio 2010). Previous studies have demonstrated that up to ten percent of amphibian populations can be lost annually to road mortality (Hels and Buchwald 2001) and, due to sex-bias in road crossing frequency, road mortality has the potential to alter sex ratios (Steen and Gibbs 2004, Steen et al. 2006). Given that an estimated one million vertebrates are killed on roads per day in the United States, a number that has increased due to human population growth and increased road density (Forman and Alexander 1998, Vos and Chardon 1998), finding approaches that facilitate safe road crossings for animals is an important challenge.

To attempt to reduce the effects of road mortality on indigenous fauna, the use of barrier fences and wildlife tunnels is becoming widespread, especially in Florida, Australia, and Europe (Forman and Alexander 1998, Taylor and Goldingay 2003, Dodd et al. 2004, Beebee 2013). The effectiveness of tunnels has been tested experimentally in closed conditions where workers have been able to vary tunnel parameters (Woltz et al. 2008) and in the field with wild populations (Jackson and Tyning 1989, Ashley and Robinson 1996, Hels and Buchwald 2001, Taylor and Goldingay 2003, Dodd et al. 2004, Aresco 2005, Gibbs and Shriver 2005, Yanes, et al. 2005, Patrick et al. 2010). These

studies have demonstrated that the combination of barrier fences and tunnels can drastically decrease the number of amphibian and reptile deaths resulting from road mortality. For example, Aresco (2005) recorded a decrease from 11.9 turtles killed/km/day to 0.09 turtles killed/km/day after drift fences funneling turtles to under-road tunnels were installed. Although these studies have helped clarify the issue of road mortality and the effectiveness of tunnels, there have been very few studies evaluating the continued success of older tunnel systems years after their installation.

One of the first amphibian tunnel systems in the United States was built in 1987 along Henry Street in Amherst, Massachusetts, to protect the spotted salamander (*Ambystoma maculatum*) during its annual migration (Jackson and Tyning 1989). This system has a set of two tunnels located 47 meters apart with associated barrier fences (Fig. 1). In this system, barrier fences are angled towards the tunnel mouth and are designed to 'funnel' salamanders into the tunnels. The eastern barrier fence is 128 meters long, while the western fence is 95 meters long (Fig. 1). Spotted salamanders hibernate on the eastern side of the road and then move to the breeding area on the western side of the road during rainy nights in early- to mid-March. Due to flooding issues, the eastern barrier fence is made of mesh so as to allow water to pass through. However, this makes the fences easily climbable, so the topmost five cm of the mesh fences have been curved over on the eastward-facing side to create an overhang that discourages climbing. Fence overhangs have been successful at keeping turtles from climbing fences in other drift fence systems (Aresco 2005). Since the early 1990s, volunteers have monitored this site during the spring migration and have carried salamanders that either climbed the drift fences or refused to use the tunnels across Henry Street safely.

Anecdotal evidence from these volunteers suggested that the tunnels have fallen into disrepair and no longer function as intended. Rather than use the tunnels, the suggestion is that salamanders balk at tunnel entrances and attempt to find other passageways across the street, often ending up on the road surface. To address these concerns as well as evaluate older tunnel systems more generally, we measured the effectiveness of the Henry Street tunnels in 2016, 2017, and 2018.

Retrofitting tunnels may be a cost-effective alternative to reinstalling tunnels, which often exceeds town conservation project budgets. In response to apparent decreased tunnel use in 2016 we tested two cost-efficient retrofits by experimentally manipulating one tunnel in subsequent years. In 2017, we investigated whether placing a light at the end of a tunnel would encourage use as suggested by Jackson (1996). In 2018, we constructed a platform leading down to the tunnel with a short drop-off just before the tunnel entrance to prevent salamanders from finding another passage across the street. Categorizing salamander count data into successful crosses, balks, and fence climbs, we estimated salamander mortality at this site and asked the following questions: (1) did more salamanders balk than use the tunnels?; (2) did either the light at the end of the tunnel or the tunnel platform increase tunnel usage? Further, we evaluated how current tunnel usage compares to usage just after tunnel installation in 1988 (Jackson and Tyning, 1989). In addition to improving the Henry Street wildlife tunnels, we sought to determine more generally if it is possible to retrofit older amphibian tunnel systems in a cost-effective manner if they fall into disrepair and are no longer used as intended.

STUDY AREA

The Henry Street spotted salamander site contains two wildlife tunnels, the 'north tunnel' and the 'south tunnel', installed 47 meters apart. The south tunnel was randomly chosen as the control and experimental modifications in 2017 and 2018 were made to the north tunnel. Tunnel entrances are constructed of concrete wingwalls with a sloped asphalt floor (Fig. 2A). The concrete tunnel roofs have repeated perforations along their length, which allows some outside light and moisture through (see Jackson and Tyning 1989 for a complete description).

METHODS

Spotted salamanders move in a mass migration from their hibernation areas to breeding pools once annually. Spotted salamander counts were conducted only during the migration from the hibernation area to the breeding area, not as they returned to their hibernation areas from the breeding pools. While the majority of a population migrates in a single night, often called the 'big night,' there are a small number of individuals that migrate either before or after the main migration event. Our analyses and assessments are based solely on 'big night' data collected on the 10th of March (2016), the 28th of March (2017), and the 29th of March (2018). Methods were carried out under IACUC 2016-0016.

Initial Assessment of Tunnel Functionality in 2016

Each year the tunnels were prepared for the migration in the same way several weeks prior to the anticipated migration event to ensure consistency. Tunnels were cleared of obstructions, areas near the tunnels were raked, and trash was collected in the

vicinity of the tunnels. Additionally, fences were checked for gaps and were repaired as necessary.

During each migration event, volunteer citizen scientists were given an orientation to the tunnels and the experiments run each year and then were asked to walk along the road to find salamanders. They were given 'write-in-the-rain' notepads to tally the number of salamanders that they found along the road. Upon finding a salamander, volunteers were asked to carry the salamander to the west side of the road where the salamanders breed to ensure that the salamanders were not crushed by cars. We note that road counts are conservative estimates because some salamanders were found dead on the road and other salamanders may have successfully crossed the road without being found. However, given the large volunteer force ($n > 20$), small patrol area, and small number of fatalities, we consider the estimate to be representative of the larger pattern of road crossing efforts. Fatalities were not considered because amphibian roadkill is notoriously difficult to identify to any taxonomic level and some of the roadkill was made up of wood frogs. BPH, AVL, PMO, and SAC took turns monitoring tunnel entrances for salamanders and tallying the numbers that balked or crossed through the tunnels. A salamander was considered a "balk" if it either crossed in front of the tunnel entrance rather than approached the tunnel, or if it entered the tunnel but subsequently turned around, exited the tunnel, and walked at least 50 cm away from the tunnel entrance. Upon balking, the salamander was carried safely across the street so that it would not be double-counted. The 2016 data served as a 'baseline' measure of the effectiveness of the tunnels prior to modifications in 2017 and 2018.

153 **A Light at the End of the Tunnel in 2017**

154 Anecdotal evidence from prior years suggested that adding a light to the far end of
155 the salamander tunnels increased tunnel usage (Jackson 1996). To test that hypothesis, we
156 placed a bright white-light LED lantern (Black Diamond Apollo Lantern, 200 lumens) in
157 a transparent, watertight plastic bag at the western end of the experimental (north) tunnel
158 in 2017. No light was placed at the south tunnel (control). The salamander crossing is a
159 popular tourist attraction in Amherst, MA and a large number of volunteers and
160 onlookers visit the tunnels to see salamanders. However, we strictly kept the southern
161 tunnel dark and only used flashlights with dim red lights to patrol the road for
162 salamanders that successfully crossed the fences and to monitor the tunnel cross and balk
163 events. Observation and tallying methods followed those of 2016.

164

165 **Salamander Platform in 2018**

166 We constructed a platform to place in front of the north tunnel entrance such that
167 salamanders that approached the tunnel would drop into a shallow pit with an 18 cm tall
168 ledge just in front of the tunnel (Fig. 2). Climbing out of the pit was made to be difficult,
169 such that climbing out was presumed to be more energetically costly than using the
170 tunnel. The goal was to use the platform to discourage balking and encourage tunnel use.
171 The platform was constructed of pine struts overlaid by a plastic mesh, which was
172 covered with soil to mimic natural ground cover (Fig. 2). As in 2017, the south tunnel
173 served as the control and was not modified. Observation and tallying methods followed
174 those of previous years.

175

176 **Statistics**

177 To analyze all of these data together and estimate the probability of tunnel
178 crossing versus balking (question 1), we used a binomial general linear model (GLM)
179 with individual responses as the binary variable (1 = crossed, 0 = balked). Using a series
180 of competing models (hypotheses), we examined whether the probability of tunnel use
181 varied. These models include:

182 1) *No covariates*: the null model assuming all year-tunnel combinations have the
183 same probability of tunnel-crossing success.
184 2) *Year*: a model testing for variation in crossing success by year assuming crossing
185 probabilities were the same in the north and south tunnels.
186 3) *Tunnel*: a model testing for variation in crossing success between the north and
187 south tunnels, assuming crossing probabilities were the same in both years.
188 4) *Year* + *Tunnel*: a model testing for the additive effect of both year and tunnel on
189 crossing success (i.e., year effect is the same for both tunnels and the tunnel effect
190 is the same for all years)
191 5) *Year* * *Tunnel*: a model testing for the interactive effect of both year and tunnel on
192 crossing success (i.e., crossing probabilities are estimated for all year-tunnel
193 combinations)

194 Models 1 through 4 assume that the light and platform 'treatments' have no effect on
195 crossing probability, whereas model 5, the model that allows for full variation among
196 year-tunnel combinations, tests whether the treatments have an effect on crossing
197 probability (question 2). We compared our 5 candidate models using Akaike
198 Information Criteria (AICc–Burnham and Anderson 2002) corrected for small sample

size, where the lowest AICc score represents the hypothesis best supported by the data. All analyses were carried out in the base stats package in R (R Core Development Team 2017).

RESULTS

Salamander Tunnel Usage (2016–2018)

Comparing our five hypotheses, there was compelling support for the hypothesis that tunnel crossing success varied both by year and by tunnel (top three models in Table 1: $\Sigma_{1:3} = 0.81$). However, the model that allowed for variation by treatment effect (*Year * Tunnel*) was the lowest ranked model, receiving relative model support of just AICω = 0.05. This strongly suggests that there were negligible effects of both the installation of a light at the end of the tunnel and the addition of a platform. However, despite the large support for the year and tunnel effects, there was still no clear top model. To account for this model uncertainty and to produce estimates of crossing probabilities for each year-tunnel combination, we generated a model-averaged prediction for each year-tunnel combination (Table 2, Fig. 3).

While the marginal effects of tunnel and year were not significant, retaining the tunnel and year effects separately was supported using AIC model selection (Table 1), and suggested that between-tunnel differences were larger than that of between-year differences. For example, salamanders were, on average, less likely to cross Henry Street using the south tunnel than the north tunnel: the estimated regression coefficient from the tunnel effect model was $\beta_{south} = -0.55 \pm 0.33$ ($p=0.08$– Fig. 3). Relative to 2016, the year used as the reference level, the likelihood that salamanders would cross using tunnels was

222 higher in 2017 and lower in 2018: the coefficients from the year effect model
223 were $\beta_{2017} = 0.53 \pm 0.36$ ($p=0.13$) and $\beta_{2018} = -0.19 \pm 0.33$($p=0.055$) respectively (Fig.
224 3). Tunnel crossing probabilities ranged from a high of 0.19 ± 0.05 in the north tunnel in
225 2017 to a low of 0.10 ± 0.03 in the south tunnel in 2018 (Table 2).
226
227 **DISCUSSION**
228 When roads impinge upon amphibian habitats it is necessary to implement
229 conservation measures to ensure that slow-moving amphibians are not locally extirpated.
230 Amphibian tunnels or culverts in combination with drift fences have become a popular
231 and successful method for mitigating the risks roads pose to wildlife (Gibbs and Shriver
232 2005, Yanes et al. 2005, Woltz et al. 2008); however, future maintenance services are not
233 commonly included in tunnel installation packages. It is therefore important to regularly
234 return to old tunnel systems to ensure that they are functioning properly and determine
235 methods to improve their functionality if necessary. Older tunnels, such as those installed
236 at Henry Street in 1987 (which have not been monitored quantitatively since the time of
237 their installation) should be carefully monitored over long timescales. In 2016 we
238 discovered that at Henry Street only 11% of migrating salamanders were successfully
239 using the tunnels. In 2017 and 2018 we implemented and tested the efficacy of cost-
240 effective solutions to retrofit the tunnels, but unfortunately neither of the attempted
241 methods increased tunnel usage (Figs. 3, 4).
242 Prior to testing tunnel use by spotted salamanders, we first examined changes in
243 vehicular road use at Henry Street since the installation of the tunnels in 1987 and found
244 that there has been no significant change in traffic volume on Henry Street since

installation in spite of high variability ($p = 0.743$, $R^2 = 0.004$ – Fig. S1A). This is fortunate, because increased traffic volume increases road mortality. For example, from 1977 to 2001 the chance of turtles successfully crossing a highway in Florida decreased from 32% to 2% as a result of a 162% increase in traffic volume (Aresco 2005). To determine if there was a continued need for salamander tunnels at Henry Street, we used the road mortality model developed by Hels and Buchwald (2001) and modified by Gibbs and Shriver (2005). This equation has been shown to be very accurate for reptiles and amphibians (Hels and Buchwald 2001, Aresco 2005), including the spotted salamander (Gibbs and Shriver 2005). Our results demonstrated that in the absence of human intervention an average of 84% of the observed spotted salamanders would die as a result of road mortality annually with a standard deviation of $\pm$ 3.2% (Fig. S1B). Gibbs and Shriver (2005) show that adult mortality greater than 10% can lead to local extirpation and that between 22% and 73% of salamander populations in Western Massachusetts are above that threshold, demonstrating the importance of functional amphibian tunnels.

Jackson and Tyning (1989) quantified the fence and tunnel effectiveness for the Henry Street tunnel system one year after installation. They found that in 1988, a total of 68.4% of the total salamanders present crossed through the tunnels, with 75.9% of salamanders that reached the tunnel entrance crossing through the tunnels. Jackson and Tyning (1989) did note some tunnel balking and ascribed this as potentially being a result of temperature, humidity, illumination, and/or airflow differences between the interior and exterior of the tunnels, or human disturbance. These numbers suggest that a much higher proportion of salamanders used the tunnels successfully just after installation in comparison with 2016–2018 (Figs. 3, 4). It is possible that monitoring populations too

soon after wildlife tunnel construction may lead to inaccurate tunnel usage numbers and many authors call for long-term tunnel monitoring data (Glista et al. 2009, Beebee 2013).

Jackson (1996) suggested that a lack of light might lead to salamander hesitation and that the placement of a light at the far entrance of the salamander tunnels might increase use. However, their data were not conclusive. The idea of increased light affecting tunnel use has been debated based on laboratory-based experiments where light permeability was shown to not be a significant factor affecting frog or turtle tunnel usage (Woltz et al. 2008). Based on data from 2017, we showed that only 11 out of 44 salamanders used the lit tunnel (25%), whereas 9 out of 30 salamanders used the same tunnel the previous year in the absence of light (30%) (Fig. 4b Supplemental Table 2). This suggests that illumination does not have a substantial impact on salamander tunnel use.

In 2018, we placed a platform in front of the north tunnel entrance to trap salamanders directly in front of the tunnel entrance to encourage tunnel use and discourage balking (Fig. 2). However, of 113 salamanders that fell in the pit, only 20 crossed through the tunnel (17.6%) (Fig. 4c, Supplemental Table 2). Salamanders would enter the tunnel, travel less than half a meter into the tunnel, and then turn around. These salamanders then spent hours trying to climb out of the pit rather than use the tunnel that directed them toward their breeding area. We note that because we did not have replicates for either our light or ramp experiments given the presence of only two tunnels across two years, our statistical power for detecting small differences was limited. However, given the magnitude of our trends, it is unlikely that additional replicates would overturn our conclusions.

291 Tunnel aperture is likely one of the most important variables in wildlife tunnel
292 construction (Mata et al. 2008, Woltz et al. 2008). The Henry Street tunnel entrances are
293 0.2 meters wide and 0.25 meters tall. Woltz et al. (2008) found that two species of frogs
294 and turtles preferred tunnel apertures between 0.5–0.6 meters in diameter over both
295 smaller and larger tunnels. Beebee (2013) further found that the optimal tunnel design
296 had apertures greater than 0.4 meters. In contrast, Patrick et al. (2010) found that spotted
297 salamanders did not choose tunnels on the basis of entrance aperture. However, the
298 smallest aperture that they tested had a diameter of 0.3 meters, 50% wider than the Henry
299 Street tunnels. It is possible that tunnel aperture may have been a primary factor leading
300 to tunnel disuse at Henry Street. As this was a field experiment, we were not able to vary
301 tunnel aperture and thus were not able to assess with certainty that this was the cause of
302 balking among salamanders at Henry Street.
303 Since amphibians require moisture to survive, Woltz et al. (2008) argued that the
304 substrate of the tunnels needed to be wet to reduce desiccation risk, which could be
305 accomplished by having a grated roof along the tunnels (Beebee 2013). However, Patrick
306 et al. (2010) found that species did not consider desiccation risk in crossing location
307 choice. At Henry Street, there are small slots in the top of the tunnels that run the length
308 of the tunnels measuring 1.5 cm in width and 6.5 cm in length, spaced 2.5 cm apart
309 parallel to the road and 4 cm apart perpendicular to the road (Fig. S2). Although these
310 slots allow enough moisture into the tunnels to ensure the substrate is wet, it is possible
311 that the small size of these slots is affecting the relative humidity inside the tunnels. We
312 speculate that it is these two combined factors (tunnel aperture and tunnel roof
313 construction) that are most likely contributing to the salamanders' aversion to using the

tunnels due to a change in moisture levels within the tunnels relative to outside the tunnels (Jackson 1996). Future experimental studies should seek to confirm this outside of a field setting to determine an acceptable moisture range and tunnel opening design for amphibians.

Fences play a critical role in wildlife tunnel systems (Cunnington et al. 2014). Aresco (2005) found 100% mortality in turtles at wildlife tunnels without fences. While Dodd et al. (2004) showed that after tunnel installation road kill counts dropped dramatically, animals such as tree frogs that were able to climb barrier fences were unaffected by the presence of the wildlife tunnels. In 1988, of 95 salamanders marked at Henry Street, 87 reached the tunnels. This suggests that only 8.4% climbed the fences that year (Jackson and Tyning 1989). In contrast, the percentage of observed salamanders climbing the fences was 45% in 2016, 34% in 2017, and 37% in 2018. Fences can quickly fall into disrepair and must be maintained (Baxter-Gilbert et al. 2013). It was evident that the Henry Street fences needed annual maintenance, with new holes and broken fence components found prior to the salamander migration every year. Even with this annual maintenance, each year from 2016–2018 a substantial number of salamanders climbed the drift fences and made it onto the road without reaching the tunnels. Although the plastic mesh fencing was put in place to allow water to pass through the fences and reduce erosion (Jackson and Tyning 1988), the salamanders can easily climb the mesh using the perforations as toeholds. Additionally, the height of the fences (<20 cm tall in many sections) makes them relatively easy for the salamanders to climb. Fences taller than 0.6 meters (Beebee 2013) with a substantial overhang (Aresco 2005) would discourage climbing and improve the system.

While temporary road closures have the potential to greatly lessen the effect of road mortality on migrating amphibians (Forman and Alexander 1998), the fact that spotted salamanders only migrate during rainfall, which is unpredictable, makes scheduling road closures sometimes untenable and thus tunnels are likely the most effective way to combat road mortality. Although road signs indicating crossing events have been shown to likely be ineffective (Coulson 1982, Jochimsen et al. 2004, Glista et al. 2009), leaving signs up year-round may cause drivers to take detours to avoid the impinging road(s) during migration events (Griffin 2015). Adding year-round signs referencing the migration event at Henry Street would potentially cut down on traffic on migration nights in a cost-effective manner, which would be safer for both salamanders and volunteers.

CONCLUSIONS

Based on these data, we conclude that the Henry Street salamander tunnels are being used by a small percentage of observed salamanders. Mitigation attempts to improve the tunnel in a cost-effect manner such as lighting the tunnels and building structures to discourage balking proved ineffective. Although this was not tested as part of our experiment, we hypothesize that the aperture of the Henry Street tunnel entrances is too small to encourage salamander use. The small size of the tunnel apertures and the lack of adequately large perforations along the tunnel roofs may be creating a differential in moisture and light between the tunnels and the outside environment (Jackson, 1996). It is likely the large citizen science force that has been mobilized through the Hitchcock

Center for the Environment, rather than the presence of the wildlife tunnels, has kept these salamanders from being locally extirpated (Sterrett et al., 2019).

Citizen science played a crucial role in this project due to the large number of salamander monitors necessary to ensure accurate data collection (Sterrett et al., 2019). However, while volunteers can help salamanders cross streets, they only help in one direction because salamanders do not move en masse from their breeding area back to their hibernation area. Consequently, volunteers alone cannot prevent decline (Beebee 2013).

It is unknown if other older wildlife tunnel systems have similar issues to the Henry Street tunnels. We echo many workers who lament the lack of long-term data on amphibian tunnel use and call for more studies examining the effectiveness of wildlife tunnels after initial installation (Glista et al. 2009, Beebee 2013). Preferences in tunnel design appear to differ between taxa and there is no unique solution to tunnel design that will work for all species (Lesbarrères et al., 2004). Additional studies will help to elucidate species-specific patterns so tunnel systems may be optimized for the specific taxon that they are meant to aid.

ACKNOWLEDGMENTS

We thank the many Hitchcock Center for the Environment volunteers who made this project possible, as well as assistance from the University of Massachusetts Wildlife Club and Shotokan Karate Club. We also thank David Munteanu (Clemson University), Zena Casteel (Cornell University), Kallin Lang, and Patricia Brennan (Mount Holyoke College) for help with fieldwork. We would like to especially thank David Dunn for

construction of the salamander platform. Finally, we thank Michael Forstner (Texas State University), Scott Jackson (UMass–Amherst), Jacob Kubel (Mass Wildlife), Arianne Messerman (University of Missouri), Reed Noss (Florida Institute for Conservation Science), Molly Grace (University of Central Florida), Rhett Rautsaw (Clemson University), and the Town of Amherst Conservation Commission for discussions regarding experimental set-up.

Funding

This research was partially supported by the National Science Foundation (Grant #: 1612211 awarded to BPH) and the Town of Amherst.

LITERATURE CITED

Aresco, M. J. 2005. Mitigation measures to reduce highway mortality of turtles and other herpetofauna at a north Florida lake. Journal of Wildlife Management 69:549–560.

Ashley, E.P. and J. T. Robinson. 1996. Road mortality of amphibians, reptiles and other wildlife on the Long Point Causeway, Lake Erie, Ontario. Canadian Field-Naturalist 110:403–412.

Baxter-Gilbert. J., D. Lesbarrères, and J. D. Litzgus. 2013. On the Road Again: Measuring the Effectiveness of Mitigation Structures for Reducing Reptile Road Mortality and Maintaining Population Connectivity. Proceedings of the 2013 International Conference on Ecology and Transportation :1–19.

Beebee, T. J. C. 2013. Effects of Road Mortality and Mitigation Measures on Amphibian Populations. Conservation Biology 27:657–668.

Burnham, K., and D. Anderson. 2002. Model selection and multimodal inference. Springer, New York.

Coulson, G. M. 1982. Road-kills of macropods on a section of highway in Central Victoria. Australian Wildlife Research 9:21–26.

Cunnington, G. M., E. Garrah, E. Eberhardt, and L. Fahrig. 2014. Culverts alone do not reduce road mortality in anurans. Ecoscience 21:69–78.

Dodd, C. K. J., W. J. Barichivich, and L. L. Smith. 2004. Effectiveness of a barrier wall and culverts in reducing wildlife mortality on a heavily traveled highway in Florida. Biological Conservation 118:619–631.

Forman, R. T. T. and L. E. Alexander. 1998. Roads and their major ecological effects. Annual Review of Ecology and Systematics 29:207–231.

Gibbs, J. P. and W. G. Shriver 2005. Can road mortality limit populations of pool-breeding amphibians? Wetlands Ecology and Management 13:281–289.

Glista, D. J., T. L. DeVault, J. A. DeWoody 2009. A review of mitigation measures for reducing wildlife mortality on roadways. Landscape and Urban Planning 91:1–7.

Griffin, C. 2015. Effects of road-induced habitat fragmentation on reptile and amphibian species at risk in North America: impacts and mitigation efforts. University of Ottawa. 1–55.

Hels, T. and E. Buchwald. 2001. The effect of road kills on amphibian populations. Biological Conservation 99:331–340.

Holderegger, R., and M. Di Giulio. 2010. The genetic effects of roads: A review of empirical evidence Author links open overlay panel. Basic and Applied Ecology 11:522–531.

Jackson, S. D. 1996. Underpass systems for amphibians. Pp. 240–244 *in* G. L. Evink, P. Garrent, D. Zeigler and J. Berry, eds. Trends in Addressing Transportation Related Wildlife Mortality, proceedings of the transportation related wildlife mortality seminar. State of Florida Department of Transportation, Tallahassee, FL.

Jackson, S. D., and T. F. Tyning 1989. Effectiveness of drift fences and tunnels for moving spotted salamanders *Ambystoma maculatum* under roads. Pp. 93–99 *in* T. E. S. Langton, ed. Amphibians and Roads: Proceedings of the toad tunnel conference. ACO Polymer Products, Shefford, England.

Jochimsen, D. M., C. R. Peterson, K. M. Andrews, J. W. Gibbons, and E. Drawer. 2004. A literature review of the effects of roads on amphibians and reptiles and the measures used to minimize those effects. Idaho Fish and Game Department, USDA Forest Service.

Lesbarrères, D., T. Lodé, and J. Merilä. 2004. What type of amphibian tunnel could reduce road kills? Oryx 38:220–223.

Mata, C., I. Hervás, J. Herranz, F. Suárez, and J. E. Malo. 2008. Are motorway wildlife passages worth building? Vertebrate use of road-crossing structures on a Spanish motorway. Journal of Environmental Management 88:407–415.

Patrick, D. A., C. M. Schalk, J. P. Gibbs, and H. W. Woltz. 2010. Effective Culvert Placement and Design to Facilitate Passage of Amphibians across Roads. Journal of Herpetology 44:618–626.

Petranka, J. W. 1998. Salamanders of the United States and Canada. Smithsonian Institution Press, Washington, DC, USA.

R Core Development Team. 2017. language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Steen, D. A. and J. P. Gibbs. 2004. Effects of Roads on the Structure of Freshwater Turtle Populations. Conservation Biology 18:1143–1148.

Steen, D. A., M. J. Aresco, S. G. Beilke, B. W. Compton, E. P. Condon, C. K. J. Dodd, H. Forrester, J. W. Gibbons, J. L. Greene, G. Johnson, T. A. Langen, M. J. Oldham, D. N. Oxier, R. A. Saumure, F. W. Schueler, J. M. Sleeman, L. L. Smith, J. K. Tucker, and J. P. Gibbs. 2006. Relative vulnerability of female turtles to road mortality. Animal Conservation 9:269–273.

Sterrett, S. C., R. A. Katz, W. R. Fields, and E. H. C. Grant. 2018. The contribution of road-based citizen science to the conservation of pond-breeding amphibians. Journal of Applied Ecology:1–8.

Taylor, B. D. and R. L. Goldingjay. 2003. Cutting the carnage: wildlife usage of road culverts in north-eastern New South Wales. Wildlife Research 30:529–537.

Vos, C. C. and J. P. Chardon. 2002. Effects of habitat fragmentation and road density on the distribution pattern of the moor frog *Rana arvalis*. Journal of Applied Ecology 35:44–56.

Woltz, H. W., J. P., Gibbs, P. K. Ducey. 2008. Road crossing structures for amphibians and reptiles: Informing design through behavioral analysis. Biological Conservation 141:2745–2750.

Yanes, M., J. M. Velasco, F. and Suárez. 1995. Permeability of roads and railways to vertebrates: the importance of culverts. Biological Conservation 71:217–222.

Tables

Table 1. AIC-ranked model table including all models, the number of parameters included in each model (K), the AIC*c* score (the *c* denotes that the correction for small samples was used), the differences between each model and the most supported model (ΔAIC*c*), the AIC model weight which represents the relative support for each model (AICω), and finally, the cumulative model weights ($\Sigma_{1:j}$).

Hypothesis	K	AIC*c*	ΔAIC*c*	AICω	$\Sigma_{1:j}$
Year + Tunnel	4	366.9	0.00	0.34	0.34
Tunnel	2	367.4	0.50	0.26	0.60
Year	3	367.8	0.96	0.21	0.81
Null	1	368.6	1.71	0.14	0.95
*Year * Tunnel*	6	370.8	3.96	0.05	1.00

Table 2. Model averaged predictions of the probability that a salamander uses a tunnel to cross the road.

Year	Tunnel	Probability	SE
2016	North	0.148	0.031
2017	North	0.190	0.050
2018	North	0.133	0.028
2016	South	0.110	0.033
2017	South	0.142	0.052
2018	South	0.097	0.031

Figures:

Figure 1. Site map of the spotted salamander road-crossing site. Henry Street bisects the salamander hibernation area and breeding area. The tunnels are marked in orange and the fences are marked in blue. The red lines show the full extent of the salamander crossing, although the vast majority of salamanders cross within the range of the fences.

Figure 2. (**a**) Northern tunnel eastern entrance. (**b**) Salamander ramp with drop-off installed in front of northern tunnel entrance. (**c**) Salamander ramp covered with soil as was in place during the migration event in 2018. Scale = 0.5 meters.

Figure 3. Model averaged predictions of the probabilities of tunnel crosses for each tunnel for each year. The north tunnel had a higher probability of crossing each year, but this was not significantly impacted by tunnel retrofits in years 2017 and 2018.

Figure 4. Salamander crossing data (2016–2018) showing the proportion of salamanders that crossed the fences prior to reaching the tunnels (red), salamanders that balked at the tunnel entrance (yellow), and salamanders that successfully used the tunnels (green). The northern and southern tunnel data are presented separately to show how well each tunnel performed (right). (**a**) 2016 data (control year). (**b**) 2017 data comparing the northern tunnel (lit tunnel) and the southern tunnel (unlit tunnel). (**c**) 2018 data comparing the tunnel with the salamander ramp and the control tunnel. For 2018, salamanders that fell into the pit following the ramp and climbed out are shown in blue while salamanders that did not reach the pit are in yellow.

510

511 **Supplementary data**

512 Supplementary Text:

513 Annual average daily traffic volume data since 1987 were collected from the
514 Massachusetts Department of Transportation (MassDOT) (https://www.mass.gov/traffic-
515 volume-and-classification). We then compared our field data to the road mortality model
516 [Equation 1] developed by Hels and Buchwald (2001) and adapted by Gibbs and Shriver
517 (2005) to estimate how road use changes at Henry Street since the tunnels were installed
518 may have affected spotted salamander mortality.

519 [1] $p_{killed} = 1 - e^{-Na/v}$

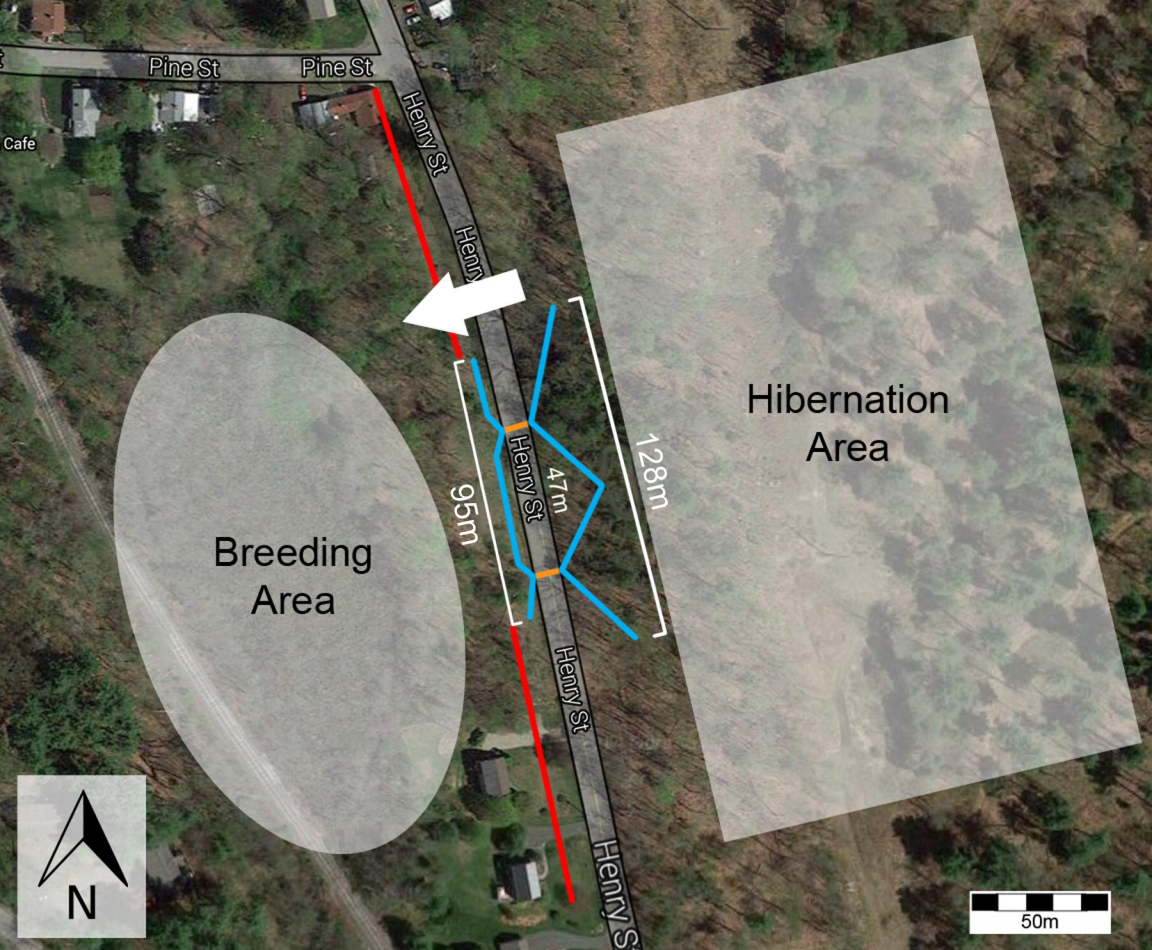
520 In this model, p_{killed} is the probability of an animal being killed from a single road
521 crossing, N is 80% of the traffic volume in number of vehicles per minute, a is the width
522 of the kill-zone on the road (2 times the average tire width times the number of lanes plus
523 two times the average snout-vent salamander length (m)), and v is the average velocity of
524 the animal (m/min). Most amphibians move at night, so time of day is correlated with
525 amphibian deaths (Ashley and Robinson 1996). This leads workers using the Hels and
526 Buchwald (2001) equation to decrease traffic volume by 20% from the annual average
527 daily traffic volume to compensate for reduced traffic volumes during the evening and
528 night (Aresco 2005, Gibbs and Shriver 2005). For our analysis, width of the kill zone (a)
529 was set to 1.22 meters, assuming an average 215 mm wide tire and an average spotted
530 salamander length of 180 mm (Petranka 1998, Gibbs and Shriver 2005). Salamander
531 velocity was set to 1m/min based on velocities measured by Gibbs and Shriver (2005) for
532 *Ambystoma maculatum*.

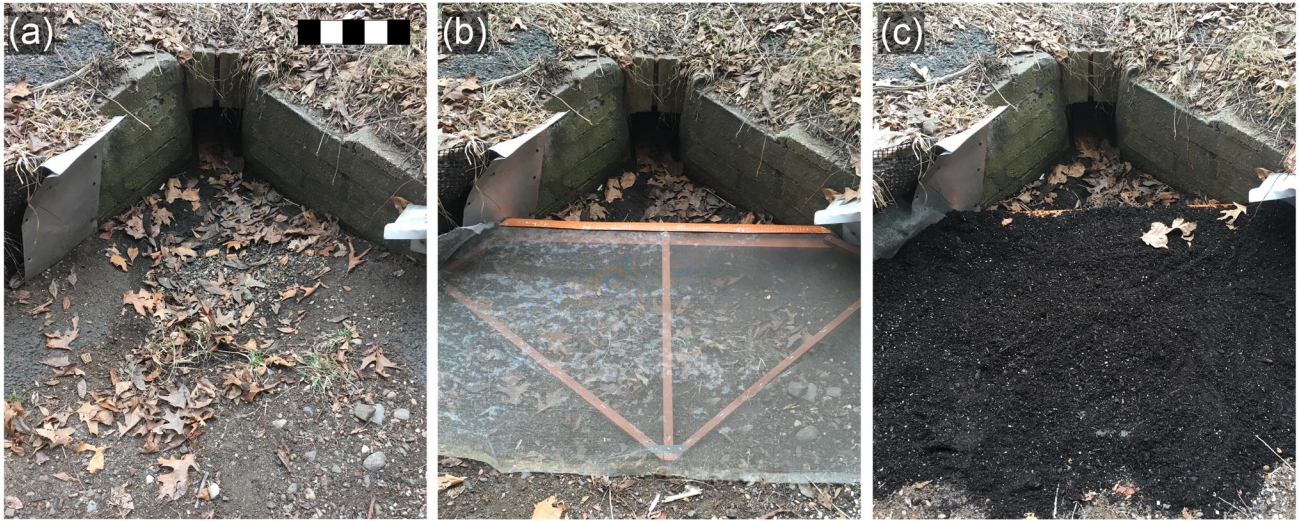
Supplemental Table 1: Road use data for Henry Street with annual average daily traffic volume per year. Data were collected by MassDOT (Massachusetts Department of Transportation; https://www.mass.gov/traffic-volume-counts).

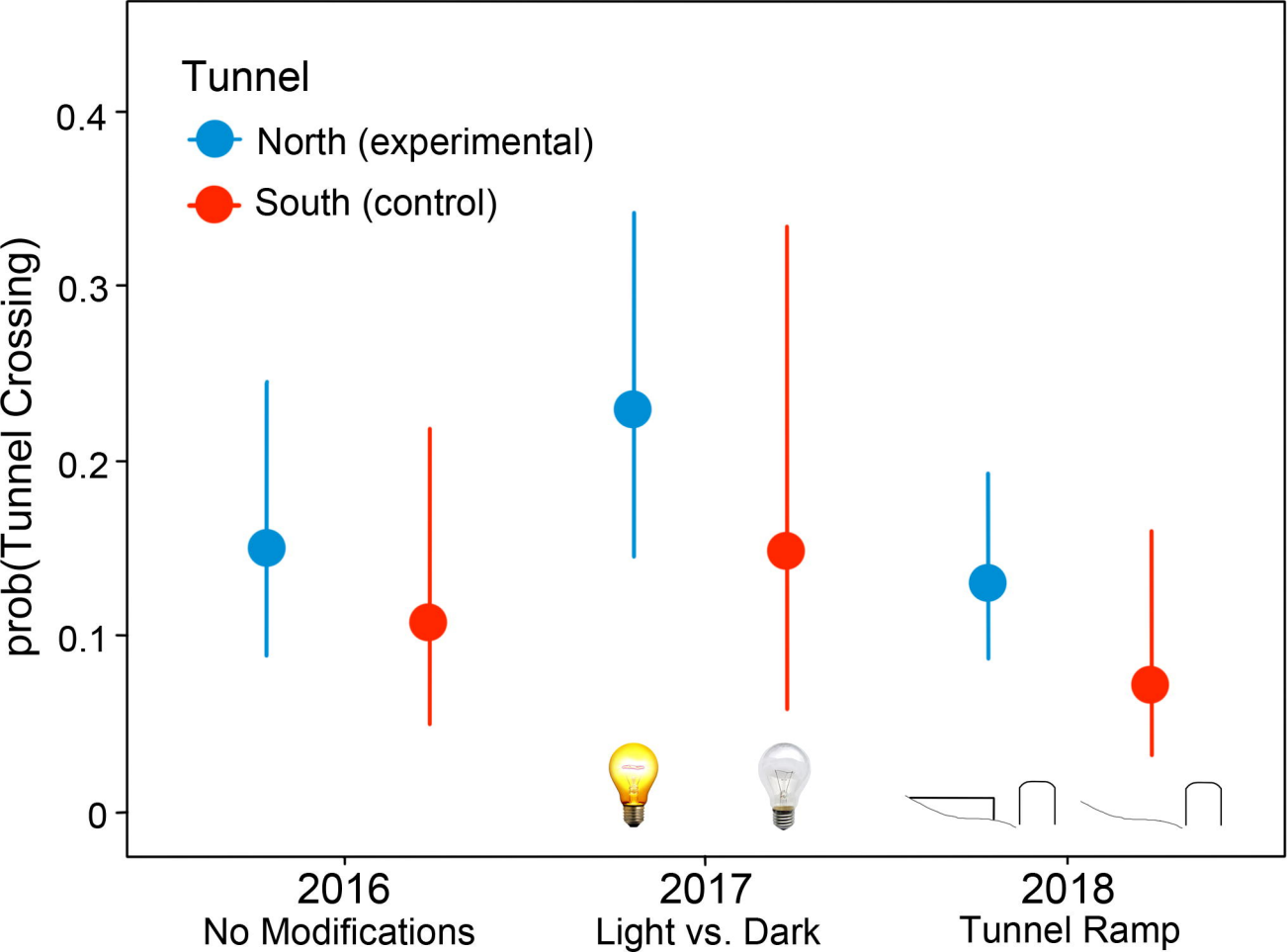
Supplemental Table 2: Salamander count data for migration nights with the greatest number of salamanders and additional smaller migration nights. Only the "big night" data were used in these analyses since additional nights lacked the volunteer numbers to collect accurate road monitoring data.

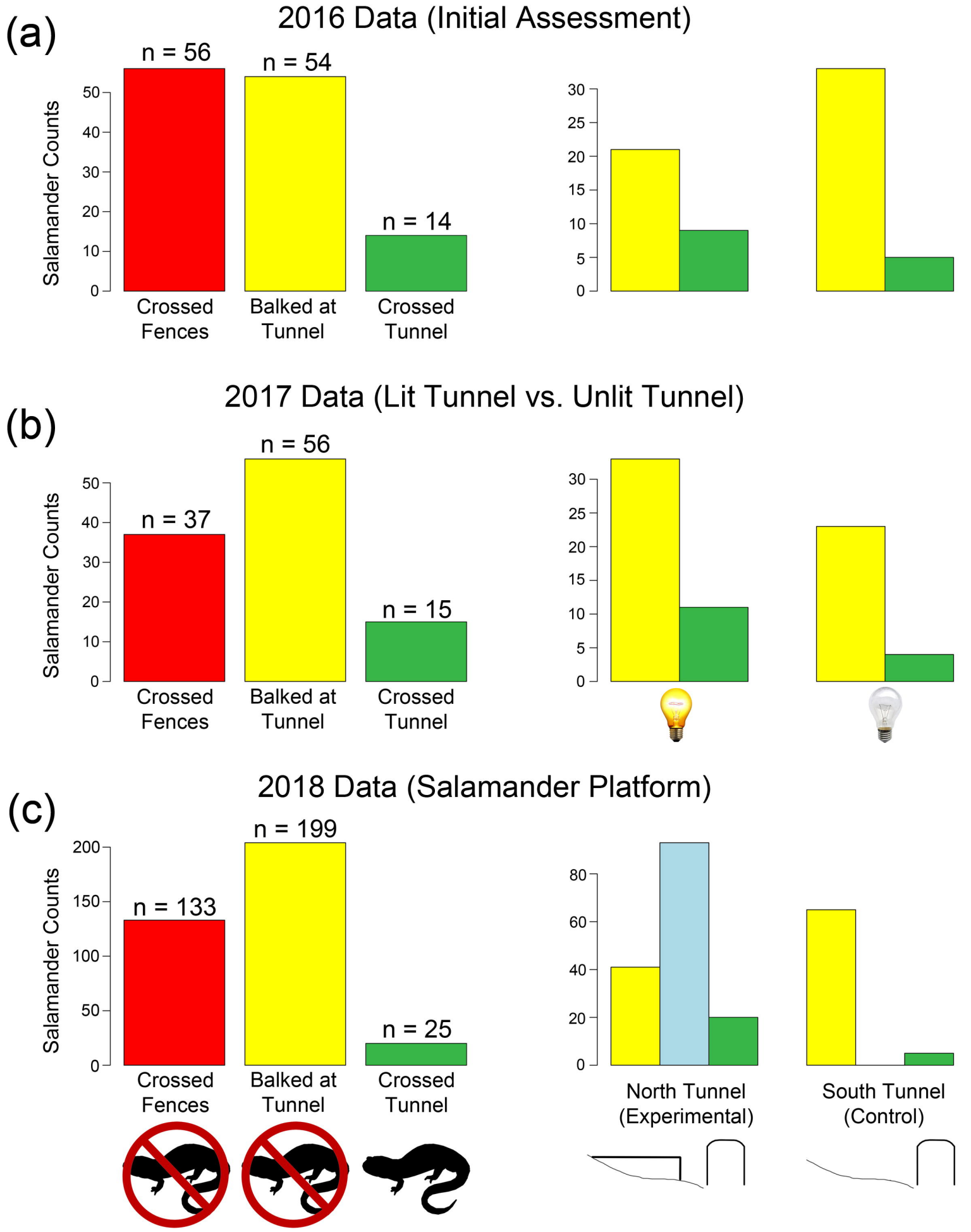
Supplemental Figure 1: (a) Annual average daily traffic volume on Henry Street from 1987 to 2015 showing no statistically significant increase in traffic volume over time. (b) Likelihood of salamander mortality while crossing Henry Street in the absence of tunnels over time based on models from Hels and Buchwald (2001). Upwards of 84% of salamanders would die annually from road mortality in the absence of human intervention.

Supplemental Figure 2: Tunnel roof along the road showing the spacing of slots.


Pine St
Pine St
Cafe
Henry St
Henry St
Henry St
Henry St
Henry St
Hibernation Area
Breeding Area
128m
95m
47m
N
50m


(a)
(b)
(c)


Tunnel
North (experimental)
South (control)
prob(Tunnel Crossing)
0.4
0.3
0.2
0.1
0
2016
No Modifications
2017
Light vs. Dark
2018
Tunnel Ramp


(a)
2016 Data (Initial Assessment)
n = 56
n = 54
n = 14
Salamander Counts
0
10
20
30
40
50
Crossed Fences
Balked at Tunnel
Crossed Tunnel
0
5
10
15
20
25
30
(b)
2017 Data (Lit Tunnel vs. Unlit Tunnel)
n = 37
n = 56
n = 15
Salamander Counts
0
10
20
30
40
50
Crossed Fences
Balked at Tunnel
Crossed Tunnel
0
5
10
15
20
25
30
(c)
2018 Data (Salamander Platform)
n = 133
n = 199
n = 25
Salamander Counts
0
50
100
150
200
Crossed Fences
Balked at Tunnel
Crossed Tunnel
0
20
40
60
80
North Tunnel (Experimental)
South Tunnel (Control)