## RESEARCH ARTICLE



# The contribution of road-based citizen science to the conservation of pond-breeding amphibians

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Handling Editor: Yolanda Wiersma

[Correction Note: The authors note an error in the version of the abstract originally published. A repetition of 'metamorphs' has been removed from the third paragraph of the abstract].

#### **Abstract**

- 1. Roadside amphibian citizen science (CS) programmes bring together volunteers focused on collecting scientific data while working to mitigate population declines by reducing road mortality of pond-breeding amphibians. Despite the international popularity of these movement-based, roadside conservation efforts (i.e. "big nights," "bucket brigades" and "toad patrols"), direct benefits to conservation have rarely been quantified or evaluated.
- 2. As a case study, we used a population simulation approach to evaluate how volunteer intensity, frequency and distribution influence three conservation outcomes (minimum population size, population growth rate and years to extinction) of the spotted salamander (Ambystoma maculatum), often a focal pond-breeding amphibian of CS and conservation programmes in the United States.
- 3. Sensitivity analysis supported the expectation that spotted salamander populations were primarily recruitment-driven. Thus, conservation outcomes were highest when volunteers focused on metamorph outmigration as opposed to adult in-migration—contrary to the typical timing of such volunteer events.
- 4. Almost every volunteer strategy resulted in increased conservation outcomes compared to a no-volunteer strategy. Specifically, volunteer frequency during metamorph migration increased outcomes more than the same increases in volunteer effort during adult migration. Small population sizes resulted in a negligible effect of volunteer intensity. Volunteers during the first adult in-migration had a relatively small effect compared to most other strategies.
- 5. Synthesis and applications. Although citizen science (CS)-focused conservation actions could directly benefit declining populations, additional conservation measures are needed to halt or reverse local amphibian declines. This study demonstrates a need to evaluate the effectiveness of focusing CS mitigation efforts on the metamorph stage, as opposed to the adult stage. This may be challenging, compared to other management actions such as road-crossing infrastructure. Current amphibian CS programmes will be challenged to balance implementing evidence-based conservation measures on the most limiting life stage, while retaining social and community benefits for volunteers.

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#### **KEYWORDS**

amphibians, citizen science, conservation, metamorph stage, migration, optimal resource allocation, population simulation model, spotted salamander

### 1 | INTRODUCTION

Citizen science (CS) programmes have been increasing in number and volunteer effort over the last two decades (Bonney et al., 2009; Dickinson & Bonney, 2012; O'Donnell & Durso, 2014). Successful programmes engage volunteers by offering opportunities to contribute to scientific understanding (Bonney et al., 2009; Cosentino et al., 2014), provide opportunity for personal growth and community enrichment (Asah & Blahna, 2012; Brossard, Lewenstein, & Bonney, 2005; Shirk et al., 2012) and influence conservation outcomes by affecting individual behaviour and socioecological systems (i.e. local conservation policy and decision-making; Lawson, Petrovan, & Cunningham, 2015; Shirk et al., 2012). Although most programmes focus on data collection, some also aim to directly improve conservation including protecting sharks (Hussey, Stroh, Klaus, & Chekchak, 2013), sea turtle nests (Cornwell & Campbell, 2012) and amphibians (Lustrat, 2005; Mechura, Gémesi, Szövényi, & Puky, 2012; Petrovan & Schmidt, 2016). An important factor driving volunteer engagement includes the perception that data collected or actions taken in CS efforts improve conservation planning and outcomes (Bonney et al., 2009; Shirk et al., 2012). To our knowledge, few CS programmes quantify the influence of volunteers on longterm conservation outcomes, which could help improve CS designs and long-term engagement.

Synchronous spring migratory breeding events for some species of amphibians present an annual opportunity for citizen scientists to contribute directly to local and regional conservation (Beebee, 2013; Petrovan & Schmidt, 2016). In the north-eastern United States, nocturnal breeding migrations of amphibians (i.e. spotted salamanders and wood frogs) in the spring are highly predictable and related to weather. Mass mortality of amphibian is typical when these migration events traverse roads in (e.g. 40%-100% of salamanders crossing; Ashley & Robinson, 1996; Gibbs & Shriver, 2005; Mazerolle, 2004; Wyman, 1990). These mass mortalities have spurred the development of grassroots CS programmes to quantify and reduce mortality by safely moving amphibians across roads on migration nights (variously termed "big night," "bucket brigades" or "toad patrols"; hereafter termed roadside efforts or programmes; Calhoun & Reilly, 2008; Petrovan & Schmidt, 2016). These roadside efforts are common in the north-eastern United States; for example, there are 71 active locations in south-western New Hampshire and southeastern Vermont across the last 11 years (2005-2016; Harris Center for Conservation Education; B.A. Thelen, pers. comm.). Despite the popularity of these programmes focusing on the first migration event  $% \left( 1\right) =\left( 1\right) \left( 1\right$ when adults migrate into ponds for breeding, the effectiveness of such efforts, and the optimal number of nights and volunteers for maximizing conservation outcomes remains largely unknown.

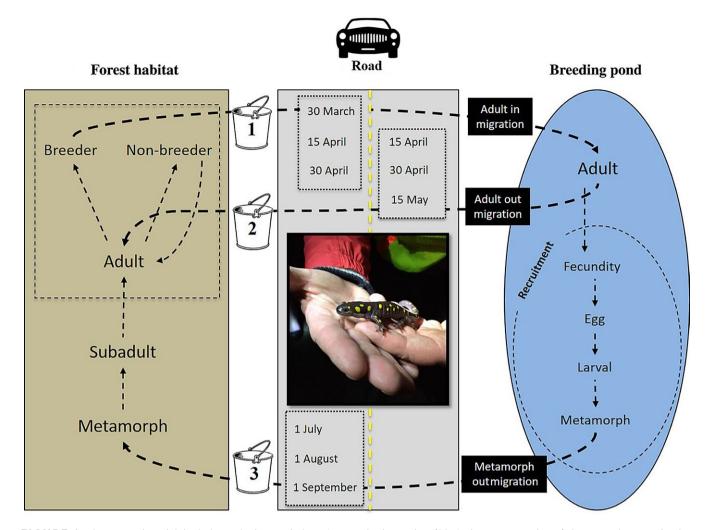
Although more than 30 peer-reviewed publications have estimated road mortality rates for amphibians across five continents, there remains considerable uncertainty in relative importance of reducing this source of mortality on long-term population outcomes (Beebee, 2013; Smith, Meredith, & Sutherland, 2015; but see Petrovan & Schmidt, 2016). Our objective was to assess the potential benefits of roadside efforts to local salamander populations by comparing the performance of a suite of diverse volunteer strategies in achieving conservation outcomes. Specifically, we evaluated impacts on three metrics representing fine to coarse scale long-term conservation outcomes: minimum adult population size (N at t = 50 years), population growth rate ( $\lambda$ ) and time to extinction (years). Minimum population size is more sensitive metric of the propensity for population decline when the risk of absolute extinction is small (McCarthy & Thompson, 2001).

Since many pond-breeding amphibian populations appear to be recruitment-driven (Green, 2003) and most roadside efforts focus on reducing adult mortality prior to breeding (Petrovan & Schmidt, 2016), we expected that volunteer effort focused on metamorph migration would have larger influence on population outcomes than adult-focused efforts. We evaluated alternative strategies that varied in intensity (number of volunteers per night), frequency (number of nights) and distribution of volunteers across three migration events when salamanders are vulnerable to road mortality (Figure 1): adult immigration into breeding ponds, adult migration out of breeding ponds and metamorph emigration out of ponds into forested habitats (Gibbs & Shriver, 2005; Timm, McGarigal, & Compton, 2007; Timm, McGarigal, & Gamble, 2007). By focusing on the spotted salamander (Ambystoma maculatum), a widely distributed habitat-specialist species frequently captured by volunteers across the north-eastern United States (Calhoun & Reilly, 2008; B.A. Thelen, pers. comm.) as a case study, we offer insights into the potential value of similar citizen scientist efforts (Petrovan & Schmidt, 2016) to benefit conservation of pond-breeding amphibian species.

# 1.1 | Natural history

The spotted salamander (*A. maculatum*) is a vernal pool obligate species, with a broad distribution across the north-eastern United States. Adults become sexually mature at 3–7 years (depending on location) and may not breed each year (Savage & Zamudio, 2005). Migration occurs during warm and rainy nights in the spring when adults migrate to pools to deposit eggs. The species prefers vernal pools for breeding in addition to requiring surrounding upland woodlands for survival, and as such, populations are vulnerable to changes in the landscape and in biotic and abiotic parameters of the pool itself (Gibbs, 1998a, 1998b). Juveniles are especially susceptible to forest

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**FIGURE 1** Conceptual model depicting a single population of spotted salamanders (SS; Ambystoma maculatum) that occupies an upland forest habitat and migrates to a pond for breeding during three events (1 = adult in-migration, 2 = adult outmigration and 3 = metamorph outmigration. During each migration event, individuals have the potential to be picked up and saved from road mortality given the intensity (number) and distribution (migration event) of volunteers. At an annual time step, individual SS occur in one of three states (adult breeder, adult non-breeder or subadult) with migration and recruitment occurring between years. CS volunteer intensity (0, 2, 10 and 50 volunteers per night), frequency (1–4 nights during each migration event) and distribution (adult-focused or metamorph-focused) are evaluated in simulation strategies. Photograph credit: Sarah Wilson

condition (Rothermel & Semlitsch, 2006), with habitat loss increasing local extinction probability (Harper, Rittenhouse, & Semlitsch, 2008). Road mortality can be high with hypothesized impacts to at the population level (Gibbs & Shriver, 2005). Declines in occupancy have been observed within federally protected areas over the last decade (Miller & Grant, 2015).

## 2 | MATERIALS AND METHODS

# 2.1 | Population model

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We used a stochastic population simulation modelling approach to evaluate the cumulative, long-term conservation outcomes (minimum adult population size, population growth and time to extinction) of alternative volunteer strategies over 50 years for a single north-eastern United States spotted salamander population (Figure 1). Based on observed large migration events (i.e. >10% of the annual total number of individuals) in the north-eastern United States (Paton & Crouch, 2002; Timm et al., 2007a), we included four adult migration nights in the spring 14 days apart (30 March, 15 April, 30 April, 15 May) and three metamorph migration nights in the fall 30 days apart (1 July, 31 July, 30 August; Figure 1). However, we acknowledge that individuals may migrate in smaller numbers across more nights (i.e. six nights for adults and eight nights for metamorphs; Paton & Crouch, 2002). Adult abundance was censused each year for females prior to the onset of breeding, and we assumed equal sex ratio. Abundance was a function of initial adult and subadult population size ( $N_{t=1}^{A}$  and  $N_{t=1}^{S}$ , respectively), with each female having a probability of becoming a breeding individual (B) during any given time step (1 year). Each breeding female migrated from the forest into the pond by crossing a road and was subject to mortality from vehicle collision (probability of road mortality; MA1)

or being rescued by a volunteer, if available during the migration event. All females surviving the migration event were available to reproduce and females continued to survive in the pond for at least 14 days with a daily pond-specific survival rate ( $S^{APond}$ ). Surviving females were then available to move back across the road (surviving road mortality with a rate =  $1 - M^{A2}$ ) and survived in the forest for the remainder of the year (daily survival rate =  $S^{AForest}$ ), contributing to the adult population size in the next year ( $N^{A}_{t=2}$ ). Metamorphs randomly migrated out of the pond within 90–270 days after adults had entered the pond to initiate breeding and were subject to road morality ( $M^{M3}$ ) and survived in the forest as subadults (with daily rate =  $S^{SForest}$ ) until they became reproductively mature after 1 year and joined the adult population (Semlitsch & Anderson, 2016).

## 2.2 | Parameters

We synthesized published literature on A. maculatum and closely related species to develop demographic and road mortality parameter values (Table 1 and Appendix S1) for use in our population model (Figure 1). We combined demographic rates across studies, sites and years to generate median expected values for recruitment parameters (fecundity = number of eggs per clutch multiplied by the number of clutches per female = 169 and survivorship of egg to larvae to metamorph = 0.0450), survival of metamorph and subadults in the upland forest (0.9986), time to maturity of subadults (1 year), daily survival of adults in upland forest during non-breeding periods (0.9992), and daily survival within the pond during breeding (0.9994), adult breeding probabilities (0.4230; i.e. adults may not breed every year; Savage & Zamudio, 2005). We also summarized movement rates, which included the timing of migration events for in- and outmigrating adults and out-migrating metamorphs, and road mortality. Uncertainty was included by drawing a new number of breeders, surviving adults and individuals subject to road mortality at each time step using a Bernoulli distribution. During each in-migration and outmigration event, we assumed individual A. maculatum were subject to vehicle mortality following Gibbs and Shriver (2005).

## 2.3 | Volunteer strategies

We created 360 volunteer strategies to evaluate the influence of volunteer intensity (number of volunteers per night; 0, 2, 10 or 50), frequency (number of nights; 1–4 for adult migration, 1–3 for metamorph migration) and distribution (in- versus outmigration for adults and outmigration for metamorphs) on population outcomes (see Appendix S2). We assumed that volunteers covered the entire migration route (i.e. a 100–150 m road transect) and spent several hours (i.e. up to four) to detect all migrating salamanders. We assumed that all migrating individuals were equally available for capture that each volunteer carried one bucket and could capture up to 20 individuals during a single migration event, and volunteers had perfect knowledge of the direction of travel of individual animals during synchronous adult in- and outmigration Strategies represented the range of effort reported across roadside volunteer events

Parameter values used in the population model and vital rate sensitivity analysis (lower 80% and upper 80% of median parameter value) with the resulting range in each population outcome (minimum population size, population growth rate and years to extinction)

	Parameter value	e		Minimum	Minimum population size (N)	ize (N)	Populatio	Population growth rate $(\lambda)$	א)	Years to e	Years to extinction	
Parameter	Median	Lower 80%	Upper 80%	Change	Lower 80% Upper 80%	Upper 80%	Change	Lower 80% Upper 80%	Upper 80%	Change	Lower 80% Upper 80%	Upper 80%
Larval mortality (egg to metamorph)	0.0450	0.0000	0.0810	27.87	28.63	0.76	0.4014	0.9905	0.5890	41.93	50.00	8.07
Fecundity (female eggs/female)	169	34	303	27.85	0.81	28.66	0.3871	0.6033	0.9905	41.83	8.18	50.00
Daily subadult survival in forest	0.9986	0.1997	1.00	16.45	4.05	20.50	0.0116	9026:0	0.9823	27.25	22.75	50.00
Breeding probability	0.4230	0.0846	0.7614	10.52	21.12	10.59	0.0227	0.9813	1.0040	0.002	50.00	49.99
Daily adult survival in forest	0.9992	0.1998	1.000	9.34	8.86	18.20	0.0353	1.0191	0.9838	0.70	49.30	50.00
Daily adult survival in pond	0.9994	0.1999	1.000	1.21	12.30	13.51	0.0045	0.9957	0.9912	0.00	50.00	50.00
Initial subadult population size	150	30	270	0.19	13.59	13.77	0.0138	0.9998	0.9860	0.04	49.96	50.00
Initial adult population size	150	30	270	0.08	13.72	13.64	0.0108	0.9977	0.9869	0	50.00	50.00

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in the north-eastern United States; however, most efforts mobilize only a few volunteers during the first adult in-migration event, with occasional large CS events with over 50 volunteers at a single site (B.A. Thelen and T. Watt, pers. comm.). Specifically, we compared outcomes from adult-only-focused strategies to metamorph-focused scenarios to evaluate the relative impact of volunteer effort focused on different life stages (Figure 1).

## 2.4 | Simulations and sensitivity analysis

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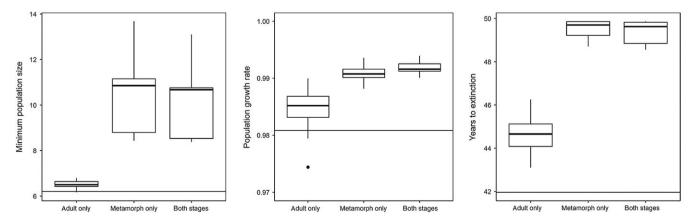
We excluded road mortality and volunteer efforts to ensure that our simulated population represented a closed population that occurs within the north-eastern United States in terms of number of adults and eggs observed in field studies. This first represents an isolated population, for example, within a forest fragment, and second allows us to evaluate the effect of mitigation of road mortality independent of any rescue by adjacent populations. Given the simulated population behaved reasonably similar to wild populations, we ran 500 simulations with a low adult road mortality rate (0.2) and elevated adult road mortality rate (0.4; Gibbs & Shriver, 2005; Shoop, 1974) using a modified popsim function in R (version 3.3.2). We assumed similar mortality rates for adult in-migration and outmigration. We conducted a vital rate sensitivity analysis to identify which rates have the greatest influence on population growth, time to extinction and minimum population size. We varied each of the 8 parameters by ±80% while holding the others constant at their median value to capture uncertainty in reported empirical rates (Table 1). The average minimum population size, population growth rate and years to extinction across simulations for each volunteer strategy were retained for comparison.

## 3 | RESULTS

Population simulations of the baseline strategy (i.e. no volunteers on any migration night) without road mortality resulted in an average  $\lambda$  of 0.9808, 41.96 years to extinction, and a minimum population size

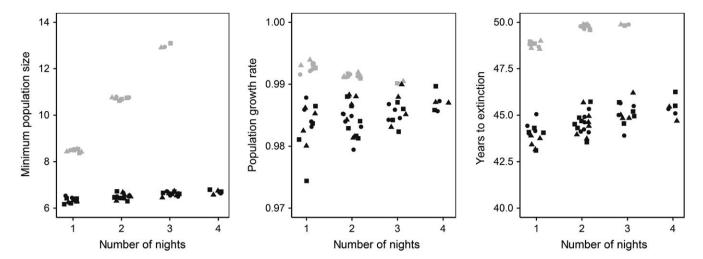
of 6.20 females. The average total population size ranged from 20 to 40 females (median = 30) was similar to empirical observations from ponds across the north-eastern United States (E. Grant, unpublished data). All population outcomes were most sensitive to increases in larval mortality, with a substantial reduction in minimum population (28.6–0.76), population growth rate (0.9905–0.5890) and years to extinction (50–8.07 years) when larval mortality was ±80% of the median value (Table 1). Fecundity had a similarly large influence on all population outcomes compared to larval mortality (Table 1). Subadult survival had a moderate influence on minimum population size and years to extinction, with breeding adult survival in the forest as the next most influential parameter for population growth rate (Table 1). Initial population size and survival of adults in the pond were the least influential demographic rates.

Almost all volunteer strategies increased minimum population size, population growth rate and years to extinction compared to having no volunteer conservation effort (Figure 2). All population outcomes were, on average, greater for strategies with low road mortality compared to high mortality (see Appendix S2); thus, we report results from high road mortality only to explore potential maximum benefits of volunteer efforts on Ambystoma spp. populations. Minimum population size was most sensitive to changes in volunteer intensity, frequency and distribution while population growth rate was least sensitive (many strategies performed similarly well; see Appendix S2). In terms of minimum population size, the optimal strategy consisted of 10 volunteers per night for all seven nights (i.e. for all adult and metamorph migration events), resulting in a minimum population size of 13.68. However, 38 other strategies also maintained qualitatively similar minimum population size. The least effort to achieve at least 13 individuals consisted of two volunteers during three metamorph outmigration events and one adult in-migration night. The optimal strategy to obtain the maximal population growth rate ( $\lambda$  = 0.9939) over 50 years included 10 volunteers during one metamorph migration night, but 231 other strategies also resulting in  $\lambda > 0.990$ . The least effort to obtain  $\lambda$  > 0.990 included two volunteers on one adult migration and one



**FIGURE 2** Average minimum population size (N), population growth rate (lambda) and years to extinction (n = 500 simulations) across volunteer strategies focused on adult-only migration, metamorph-only migration and both stages of migration when road mortality is high (0.4) and across the frequency (# nights) and intensity of volunteers (2–50). Expected values for scenarios with no volunteers are indicated by the line

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**FIGURE 3** Average minimum population size (*N*), population growth rate (lambda) and years to extinction (*n* = 500 simulations) for volunteer strategies focused on the adult stage (black) or metamorph stage (grey). Scenarios ranged from 1 to 4 nights for adult-focused strategies and 1–3 nights for metamorph-focused strategies and varied in the level of volunteer intensity (2 = circle, 10 = triangle and 50 = square)

metamorph migration night. Years to extinction ranged from 41.96 to 49.88 years, with 72 strategies resulting in the longest time to extinction (49.88). The least effort to obtain >49 years to extinction (which occurred in 276 strategies) included two volunteers assisting salamander on either two metamorph nights or on one metamorph and one adult night (see Appendix S2).

Generally, a volunteer effort that included metamorph migration nights increased all measures of population outcomes more than efforts focused only on adult migration nights (Figure 2). There was a marginal increase in population outcomes for adding more than one night to either adult or metamorph migration events (Figure 3). For example, minimum population size on average increased by two individuals with every additional night during metamorph migration period. In contrast, increasing effort during the adult migration showed negligible improvements (<0.1 increase in minimum population size, <0.002 increase in lambda, <1.2 years to extinction; Figure 3). Volunteer intensity (0, 2, 10 or 50 persons per night) had the least influence on all population outcomes because two volunteers could capture most individuals migrating on any given night (i.e. 20 individuals per person per night) and the number of A. maculatum migrating was always less than 40.

# 4 | DISCUSSION

Our simulated amphibian pond-breeding population indicated that long-term conservation outcomes (minimum population size, population growth and years to extinction) are largely driven by recruitment into the adult population. Therefore, we were not surprised that focusing on metamorph migration events had greater positive effects on conservation outcomes compared to efforts focused on traditional adult migration-focused events, which only had marginal positive influence. We consistently found that the distribution of volunteers was more important than volunteer intensity and frequency, with two volunteers on a single metamorph migration night having larger benefits than many volunteers (>2 during all four adult

migration events [in- and outmigration]). If volunteer CS conservation efforts want to maximize population outcomes, our results suggest volunteers engaged in roadside conservation events should shift focus to reducing road mortality during metamorph migration, as many amphibian populations are recruitment-driven (Green, 2003; Scheele et al., 2015) To maximize range-wide population gains, large community volunteer events (i.e. >10 volunteers) may benefit most by dispersing volunteers into smaller groups to assist more populations—opposite the current paradigm.

Despite our results being robust to uncertainty (best performing strategy was not influenced by variation in demographic rates), our simulation likely overestimated the potential realized benefits of volunteer effort on amphibian conservation for several reasons. First, we assumed that a given scenario would occur every year for 50 years and that demographic rates were constant over time. Second, the entire effective area of migration was assumed to be surveyed by volunteers and had a constant maximum effect on saving migrating salamanders from road mortality (20 per volunteer). However, the effective area of migration may be larger (i.e. 150-300 m; Wells, 2008) and result in reduced detection of migrating salamanders, resulting in higher mortality. Citizen scientist roadside conservation efforts in the north-eastern United States have reported a single volunteer capturing from 0 to 100 salamanders per night, with 1-20 dead salamanders (B.A. Thelen, pers. comm.). Third, we assumed a mortality rate based on estimates from males and females (Gibbs & Shriver, 2005), but mortality could be higher for females because of lower movement speeds across roads (Finkler, Sugalski, & Claussen, 2003). Lastly, we did not include metapopulation dynamics in our evaluation of the volunteer effort, even though adult dispersal among ponds could be a critical source of recovery and ultimately sustain populations with low abundances from local extinction (Heard et al., 2015), though ponds subject to road mortality may function as demographic sinks.

Roadside CS, conservation-based programmes are increasing in popularity across the north-eastern United States. Amphibian species such as A. maculatum, Ambystoma jeffersonianum and Lithobates

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sylvaticus are listed as species of greatest conservation concern in many U.S. states (2015 State Wildlife Action Plans; U.S. Fish and Wildlife Service) and are often the primary targets of such roadside volunteer efforts. Our population simulation can easily be applied to larger salamander populations by increasing initial population sizes and increasing volunteer intensity levels and to other species which could be targeted by roadside CS efforts for amphibians with biphasic life histories (i.e. A. jeffersonianum, L. sylvaticus, Bufo bufo and Rana temporaria). We acknowledge that the spotted salamander is well studied; thus, rates were relatively easy to synthesize from the literature. However, the parameters can be replaced with other species' rates (even if poorly known) and the model can be used to evaluate the sensitivity of the decision (how many nights and which nights) to assist in roadside migration efforts and over what combination of vital rates a given strategy would be successful; these rates can be considered in the light of what is known about a species' ecology to determine whether a strategy would improve persistence. If the decision varies depending on what rates are used, CS coordinators can determine where more research is needed-that is, to improve the precision of estimates for which the decision is sensitive. Roadside CS programmes are poised to utilize such an approach, as data collection activities can be altered over time to reduce critical uncertainties influencing volunteer conservation strategies (i.e. adaptive management; Lyons, Runge, Laskowski, & Kendall, 2008).

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To maximize conservation benefits of volunteer conservation events for pond-breeding amphibians, programmes may need to change the emphasis from coordinated adult translocations to "on call" juvenile rescue. Although both adult and metamorph migrations are triggered by large rainfall events, adult movement is also triggered by change in temperature, whereas abiotic weather-related drivers of metamorph migration are less likely (Paton & Crouch, 2002; Timm, McGarigal, & Compton, 2007). This lack of cues for mobilizing volunteer effort to assist metamorph migration across roads represents a severe logistical challenge. Additionally, amphibian road-crossings have become well-established community events with coordinators investing resources to mobilize networks of volunteers during the onset of spring. Many CS programmes, including roadside conservation efforts, provide additional, diverse, social benefits (i.e. raising local awareness, community engagement and education; Tulloch, Possingham, Joseph, Szabo, & Martin, 2013), which may in fact prevent volunteers from shifting to the more optimal, metamorph-focused strategy (Asah & Blahna, 2012). Globally, volunteer conservation programmes may be challenged to find strategies that balance focusing actions on the most limiting life stage while providing social benefits. If conservation outcomes are highly valued in CS programmes, then either incentives may be needed to ensure long-term engagement or other strategies to increase participant satisfaction will need to be considered. Many roadside programmes may already implement actions that may be more effective at reducing metamorph mortality, such as installing road-crossing infrastructure including fences, tunnels and/or bridges (Kyek, Kaufmann, & Lindner, 2017; Rytwinski et al., 2015;

Schmidt & Zumbach, 2008). However, the effectiveness of these alternatives remains largely unknown and should be evaluated before reducing volunteer roadside efforts at specific sites.

#### **ACKNOWLEDGEMENTS**

We thank Brett Amy Thelen and the Harris Center for Conservation Education for access to CS data in New Hampshire and Ted Watt for discussion related to Henry Street amphibian tunnels in Amherst, MA. This is contribution #679 of the Amphibian Research and Monitoring Initiative (ARMI) of the US Geological Survey. Any use of trade, firm or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

#### **AUTHORS' CONTRIBUTIONS**

S.C.S. and E.H.C.G. conceived the ideas and designed methodology; S.C.S. and R.A.K. collected population parameters from literature; R.A.K. and W.R.F. built the model and analysed the data; S.C.S., R.A.K. and E.H.C.G. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

#### **DATA ACCESSIBILITY**

Data available via the Dryad Digital Repository https://doi.org/10.5061/dryad.v67003c (Sterrett, Katz, Fields, & Grant, 2018).

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#### SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

How to cite this article: Sterrett SC, Katz RA, Fields WR, Campbell Grant EH. The contribution of road-based citizen science to the conservation of pond-breeding amphibians. *J Appl Ecol.* 2019;56:988–995. https://doi.org/10.1111/1365-2664.13330