

Estimating survival of a streamside salamander: importance of temporary emigration, capture response, and location

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Abstract Estimating survival for highly secretive aquatic animals, such as stream salamanders, presents numerous challenges. Salamanders often spend a considerable time in refugia where they are difficult to capture. Few studies have calculated vital rates for stream salamanders, yet the need is substantial as they are threatened by a wide range of land-use stressors, especially urban development. In this study, we used 34 months of continuous field samples collected at an urban and undisturbed stream and robust design mark-recapture analysis to evaluate the importance of temporary emigration, capture response, and location on survival estimates of the salamander *Desmognathus fuscus*. We constructed a set of candidate models incorporating combinations of time- and location-varying capture and recapture probabilities, capture responses, temporary emigration, and survival

estimates and ranked models using Akaike's Information Criterion. We found strong support for month-specific capture probabilities, recapture probabilities, temporary emigration and a negative behavioral response to capture in the majority of months. We found no support for variation in capture probabilities, recapture probabilities, and temporary emigration between locations. However, we found that location strongly influenced survival estimates. Specifically, survival estimates were significantly higher at the undisturbed site than at the urban site. Our results emphasize the importance of estimating capture probabilities, recapture probabilities, capture response, and temporary emigration when evaluating survival in highly secretive aquatic animals. Failure to account for these population parameters will likely yield biased estimates of survival in freshwater animal populations.

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Introduction

Survival is a critical demographic metric in both basic and applied ecological research (Lebreton et al., 1992; O'Donnell et al., 2010; Smith et al., 2010). Estimating survival, however, presents numerous challenges, especially for secretive or cryptic semi-aquatic animals. Relying simply on the proportion of marked

animals released on one occasion and recaptured on the next occasion to estimate survival results in a biased estimate because the probability of effective capture is <1.0 (Lebreton et al., 1992; Williams et al., 2002). Effective capture probability is the product of two parameters: (1) conditional capture probability, which is the probability that an animal is captured given availability to be captured; and (2) temporary emigration probability, which is the probability that an animal is alive but not available for capture (Bailey et al., 2004a). Failure to disentangle conditional capture and temporary emigration probabilities can lead to low effective capture probability estimates and often results in survival estimates with large confidence intervals (Kendall et al., 1997). In addition, survival estimates may be biased if animals exhibit behavioral responses to initial capture, i.e., individuals become trap-happy or trap-shy after capture (Willson et al., 2011).

Relatively few studies have estimated survival of secretive, semi-aquatic animals while taking into account conditional capture probability, trap response, and temporary emigration (but see Church et al., 2007; Olivier et al., 2010). A mark-recapture analytical technique known as the robust design (Pollock, 1982; Kendall et al., 1997) combines both open- and closed-population models to provide unbiased estimates of survival, capture probability, trap response, and temporary emigration. The robust design consists of widely spaced primary sampling periods (e.g., years), across which survivorship is estimated using an open model approach. Each primary period consists of secondary samples (e.g., days), which are assumed to be demographically closed, across which population size, conditional capture probabilities, and trap response can be estimated. In addition, robust design models allow for estimates of temporary emigration.

Streamside salamanders are extremely cryptic, inhabiting underground refugia or other inaccessible habitats with surface activity often limited to particular seasons and/or climate conditions (Petranka, 1998; Hyde & Simons, 2001). At any given time the majority of individuals may be undetectable to survey efforts, thus estimating survival is particularly difficult. The importance of estimating survival for stream salamanders is underscored by several studies that highlight the negative effects of urbanization on salamander populations (Orser & Shure, 1972; Willson & Dorcas, 2003; Miller et al., 2007; Barrett

et al., 2010; Price et al., 2011). Although both adults and larval salamanders appear to be affected by urban development, the negative effects may differ between life-stage. For example, Price et al. (2011) found that urbanization resulted in reduction of occupancy of larval northern dusky salamanders (*Desmognathus fuscus* (Green)) (Plethodontidae) by 43%, yet adult occupancy remained near 100% 4 years post-urbanization of stream catchments. Furthermore, Barrett et al. (2010) indicates that survivorship appears to be low in larval southern two-lined salamanders (*Eurycea cirrigera* (Green)) (Plethodontidae) inhabiting urban streams, whereas adults persisted in urban catchments and have high reproductive output. High adult survivorship may be one factor that allows for persistence of salamander populations in urbanized streams, however, survival estimates of stream-dwelling Plethodontid salamanders are lacking. Thus, accurately estimating survival of adult salamanders is especially relevant from a conservation perspective.

The purpose of this study was to estimate survival in adult *D. fuscus* and determine the importance of temporary emigration, capture response, and location on the parameter estimate. Using robust design sampling, we monitored populations over 3 years in two first-order streams; one stream's catchment was urbanized just prior to the initiation of our study, and a second stream had an undisturbed catchment throughout the duration of our study. We hypothesized that inclusion of temporary emigration and capture response would be favored in model selection. In addition, we hypothesized that survival estimates would be lower in the recently urbanized location than in the undisturbed location.

Methods

Study sites and species

We conducted capture-mark-recapture (CMR) surveys at two first-order streams in the Piedmont physiographic province of North Carolina, USA. The Piedmont province is a rolling plateau geographically located between the Coastal Plain and Appalachian Highlands in eastern North America (Gade et al., 1986). The first stream, known hereafter as the undisturbed stream, was located on a nature preserve in northwestern Mecklenberg County and had a

catchment size of 35 ha, most of which was covered in forest (92% forested). Dominant tree species in the undisturbed catchment included *Fagus grandifolia* (Erhart), *Carpinus caroliniana* (Walter), *Quercus alba* (Linnaeus), and *Acer rubrum* (Linnaeus). The second stream, known hereafter as the urban stream, was located within a newly constructed neighborhood in Cabarrus County. The catchment of the urban stream was 42 ha and contained 41% forest cover; dominant tree species included *F. grandifolia*, *A. rubrum*, and *Liriodendron tulipifera* (Linnaeus). The remaining area (59%) of the urban catchment contained newly constructed homes, landscaped yards, and some (<5%) old field.

We focused our study on *Desmognathus fuscus*, a member of the family Plethodontidae, or lungless salamanders. This species is common in Piedmont streams, where densities can reach 1.42 metamorphosed individuals/m² (Spight, 1967). *Desmognathus fuscus* is highly aquatic and generally found under rocks, logs, and other debris along margins of low-order streams and seeps (Petranka, 1998). Reproduction is semi-aquatic; females lay eggs in protected microhabitats within or near water during mid- to late-summer (Juterbock, 1986). Hatchlings are often found in September and October and undergo metamorphosis during the following spring (i.e., May–June). Sexual maturity is reached at approximately 2 years of age (Danstedt, 1975), but life span in the wild is unknown. Adults occupy home ranges that vary, on average, from 1.4 to 48.4 m² (Barbour et al., 1969; Ashton, 1975).

Field methods

Starting in October 2005, we conducted salamander surveys for 34 consecutive months. Within this period, we used monthly samples as our primary samples, and our secondary samples consisted of 2 days within each month, separated by a maximum of 3 days during which we assumed population closure.

Within a 100 m section of each stream, salamanders were captured using a cover-controlled active search in which one person, moving upstream, turned rocks, logs, and other cover within the stream and within 0.5 m of the stream edge. Twenty coverboards (73 × 73 cm section of 11 mm plywood) were placed every 5 m along the 100 m section of stream to provide additional capture opportunities. Salamanders

were captured with a dip-net or by hand. After capture, all post-metamorphic salamanders were taken to the lab, anesthetized with 1 g of maximum strength Orajel[®] (Del Pharmaceuticals, Uniondale, NY; Cecala et al. (2007)) per 1 l of tap water, and individually marked by subcutaneous injection of visible implant elastomer (VIE; Northwest Marine Technologies, Shaw Island, WA). We restricted our analyses to salamanders >35 mm snout-to-vent length (SVL), which we considered adults (Orser & Shure, 1975; Jones, 1986). Because robust design studies require that all individuals be available for recapture within a secondary period, we always released salamanders 3 days prior to conducting our second day of secondary sampling. All surveys were conducted during daylight hours.

In addition to conducting CMR on *D. fuscus*, we collected data on the environmental and habitat conditions of the two streams. Dissolved oxygen (% saturation), conductivity (μS), and water temperature (°C) were measured with a hand-held YSI 85 meter (YSI, Inc., Yellow Springs, OH) on five occasions during both March and April in 2005 and again in spring of 2008. Finally, we visually estimated the proportion of each transect covered with silt. We defined silt as any fine sediment accumulated in the stream bed. Environmental and habitat data collected in the spring of 2005 reflects pre-urbanization stream conditions, as our urban stream's catchment was not developed until fall of 2005. Data collected in 2008 are stream conditions after the urbanization process.

Mark-recapture modeling

We used Program MARK (v. 6.0; White & Burnham 1999) to construct models and evaluate the effects capture probability (p), recapture probability (c), and temporary emigration (γ) on survival (S) estimates. Population parameters were estimated using Huggins closed captures form of the robust design model (Huggins, 1989, 1991). Huggins robust design models derive population estimates separate from the model likelihood which, through reduction of parameters, tend to perform better with sparse data than traditional closed captures robust design models (Huggins, 1989, 1991). We assumed p and c within primary periods to be constant.

We first constructed 24 candidate models (Table 1) that varied in p , c , and γ , and we evaluated all possible

Table 1 Parameter variations in 24 competing models used to evaluate temporary emigration (γ), conditional capture probability (p), and capture response (c) in the salamander *D. fuscus*

Model	Parameters		Capture probability												
	Temporary emigration			Capture probability									Capture probability		
	None	Constant	Monthly	Time	Constant time, no capture response $p(\cdot) = c(\cdot)$	Time-dependent, no capture response $p(\text{time}) = c(\text{time})$	Month-specific, no capture response $p(\text{month}) = c(\text{month})$	Constant time, capture response $p(\cdot), c(\cdot)$	Time-dependent, capture response $p(\text{time}), c(\text{time})$	Month-specific, capture response $p(\text{month}), c(\text{month})$	Month-specific, capture response $p(\text{month}), c(\text{month})$	Month-specific, capture response $p(\text{month}), c(\text{month})$	Month-specific, capture response $p(\text{month}), c(\text{month})$		
$\gamma(\cdot) = 0$	$\gamma(\cdot)$	$\gamma(\text{month})$	$\gamma(\text{time})$	$\gamma(\cdot) = c(\cdot)$	$p(\text{time}) = c(\text{time})$	$p(\text{month}) = c(\text{month})$	$p(\cdot), c(\cdot)$	$p(\text{time}), c(\text{time})$	$p(\text{month}), c(\text{month})$	$p(\text{month}), c(\text{month})$	$p(\text{month}), c(\text{month})$	$p(\text{month}), c(\text{month})$	$p(\text{month}), c(\text{month})$		
1	X				X										
2	X					X									
3	X						X								
4	X							X							
5	X								X						
6	X									X					
7		X											X		
8		X				X									
9		X					X								
10		X						X							
11		X							X						
12		X								X					
13			X										X		
14			X					X							
15			X						X						
16			X							X					
17			X								X				
18			X									X			
19				X						X					
20				X							X				
21				X								X			
22				X									X		
23				X									X		
24				X									X		

$\gamma(\cdot) = 0$ indicates no temporary emigration, $\gamma(\cdot)$ indicates random, temporary emigration, $\gamma(\text{month})$ indicates monthly variation in temporary emigration and $\gamma(\text{time})$ indicates time-varying temporary emigration. No behavioral response to capture is indicated by $p = c$, whereas behavioral responses to capture are characterized by lack of equal sign between p and c

parameter combinations. We fixed γ to zero in models 1–6, indicating no temporary emigration, and modeled p and c as (1) constant capture probability with no capture response (i.e., $p(\cdot) = c(\cdot)$), (2) month-specific capture probability with no capture response (i.e., $p(\text{month}) = c(\text{month})$), (3) time-specific capture probability with no capture response (i.e., $p(\text{time}) = c(\text{time})$), (4) constant capture probability with constant capture response (i.e., $p(\cdot), c(\cdot)$), (5) month-specific capture probability with month-specific capture response (i.e., $p(\text{month}), c(\text{month})$), and (6) time-specific capture probability with time-specific capture response (i.e., $p(\text{time}), c(\text{time})$). Models 7–12 contained the same parameterization for p and c as models 1–6 but included constant γ (i.e., random, temporary emigration) rather than no temporary emigration. Models 13–18 contained the same parameterization for p and c as previous models but included month-specific γ . Finally, models 19–24 contained the identical parameterizations for p and c but included time-specific γ . Survival (S) was always modeled as constant but was allowed to vary between the undisturbed stream and urban stream during the evaluation of these 24 models.

We evaluated location-specific effects for the second stage in our model development. Including location-specific effects in our 24 candidate model set would have greatly increased the number of alternative models required to test all possible parameterizations. Thus, we evaluated the location-specific effects on p , c , and γ by modifying the most parameterized model (sensu Willson et al., 2011; Model 23; see Table 1). Our permutations of Model 24 included (1a) no location effect, (2a) location differences in γ , (3a) location differences in p and c , and (4a) location differences in all three parameters. If there was support for differences due to location in any of the three parameters, we allowed the affected parameter to vary between locations when testing the 24 candidate models to evaluate S . We compared the fit of the candidate models using Akaike's Information Criterion (AIC; Akaike, 1973) adjusted for small sample sizes (AIC_c; Burnham and Anderson, 2002).

After identifying our most parsimonious model for p , c , and γ , we evaluated various parameterizations of S . Our permutations of S included (1b) constant ($S(\cdot)$), (2b) location effect ($S(\text{location})$), (3b) month effect ($S(\text{month})$), (4b) time effect ($S(\text{time})$), (5b) month \times location effect ($S(\text{month} \times \text{location})$), and

(6b) time \times location effect ($S(\text{time} \times \text{location})$). Thus, the model with the most parameters possible in our model set included S that varied over time and between locations, p and c probabilities that varied over time and between locations and allowed for behavioral response to being captured (i.e., $p \neq c$), and constant random γ that varied over time and between locations. Again, we used AIC_c to select our best model(s) and used Akaike weights (w) to indicate the probability that the model is the best among the whole set of candidate models (Burnham & Anderson, 2002).

Results

The environmental conditions and habitat attributes of the two streams were similar prior to urbanization (i.e., 2005), with the exception of average percent of stream bed covered in silt, which was greater in the undisturbed stream (Table 2). Three years post-urbanization, we found that the urban stream values for minimum dissolved oxygen (% saturation), maximum conductivity (μS), April high water temperature ($^{\circ}\text{C}$), and average percent of stream bed covered in silt were greater than the undisturbed stream (Table 2). Furthermore, the conditions at the urban stream were dramatically different than those conditions collected prior to urbanization (Table 2).

We recorded 1,154 captures of 814 individuals at the undisturbed stream and 215 captures of 174 individuals at the urban stream from October 2005 through August 2008. Our analysis of p , c , and γ indicated that our most supported model (Model 18) contained month-specific γ , and month-specific p and c ($w = 0.99$; Table 3). Month-specific values of p ranged from 0.009 (1 SE = 0.004; 95% CI 0.004, 0.022) in July to 0.591 (1 SE = 0.10; 95% CI 0.383, 0.771) in September (Fig. 1). Our top model also indicated *D. fuscus* responded negatively to capture with c less than p in all months except June, July, and August (Fig. 1). In addition, our most parsimonious model indicated strong support for monthly γ with estimates ranging from $\gamma = 0.175$ (1 SE = 0.180; 95% CI 0.018, 0.715) in June to $\gamma = 0.943$ (1 SE = 0.017; 95% CI 0.898, 0.968) in September (Fig. 2).

The addition of location to our most parameterized model of p , c , and γ revealed no unequivocal support

Table 2 Environmental variables and habitat conditions collected at an urban and undisturbed stream in the North Carolina Piedmont, USA

Environmental conditions	Pre-urbanization (2005)		Post-urbanization (2008)	
	Urban	Undisturbed	Urban	Undisturbed
Max. conductivity (μS)	116.1	128.9	178.2	137.8
Min. DO_2 (% saturation)	55.2	65.5	40.8	22.2
Max. water temp. ($^{\circ}\text{C}$)—March	15.3	16.5	13	13.4
Min. water temp. ($^{\circ}\text{C}$)—March	11.6	11.1	7.8	7.2
Max. water temp. ($^{\circ}\text{C}$)—April	15.4	16.1	22.4	16.3
Min. water temp. ($^{\circ}\text{C}$)—April	10	12.4	11.8	11.5
Avg. % silt (± 1 SE)	25 (± 7.36)	47.5 (± 4.789)	95 (± 2.887)	46.25 (± 3.75)

Maximum conductivity (μS), minimum dissolved oxygen (% saturation), and maximum and minimum water temperature ($^{\circ}\text{C}$) were measured on five occasions during both March and April prior to urbanization and again in spring of 2008, after the urban stream's catchment became developed. The average percent of silt was measured visually, and reflects the average percent of silt within four, 10 m sample transects located within each study stream

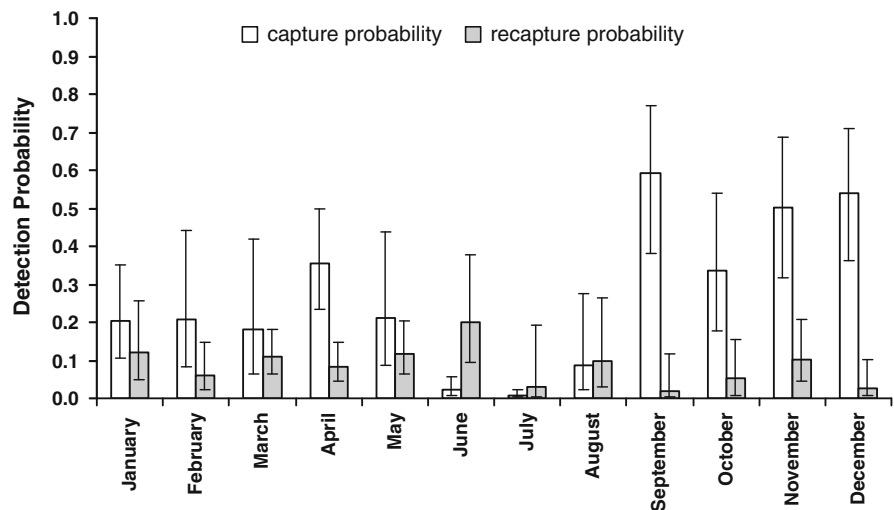
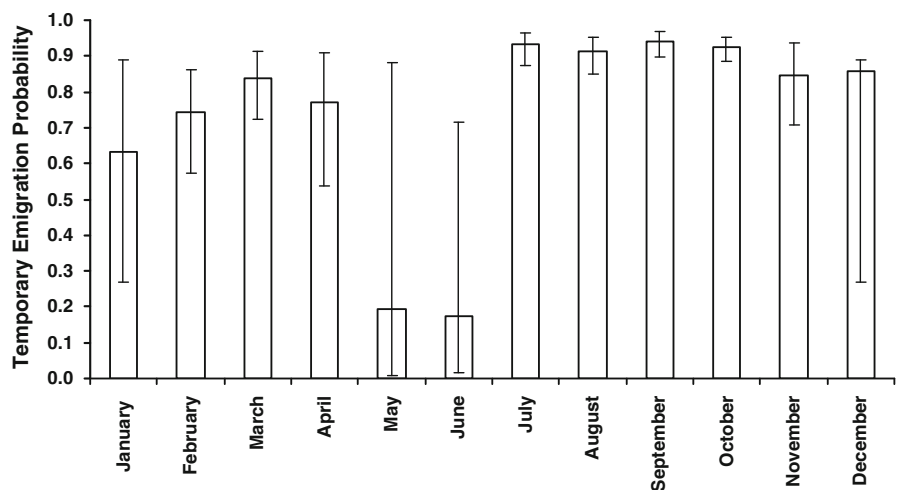
Fig. 1 Monthly variation in conditional capture probability (p) and recapture probability (c) of the salamander *Desmognathus fuscus* captured at two, first-order streams in the Piedmont of North Carolina, USA. Bars represent 95% CI**Fig. 2** Monthly variation in probability of temporary emigration (γ) of the salamander *Desmognathus fuscus* captured at two, first-order streams in the Piedmont of North Carolina, USA. Bars represent 95% CI

Table 3 Model rankings for estimating capture (p), recapture (c), and temporary emigration (γ) in the salamander *Desmognathus fuscus* sampled at two, first-order streams in the Piedmont of North Carolina, USA from October 2005 to August 2008

Model	Parameters			No. parameters	AIC _c	Δ AIC _c	AIC _c wt
	γ	p	c				
18	(month)	(month)	(month)	38	4987.770	0.000	0.998
24	(time)	(month)	(month)	59	4999.783	12.013	0.002
12	(.)	(month)	(month)	27	5010.949	23.179	0.000
17	(month)	(time)	(time)	82	5016.494	28.725	0.000
14	(month)	(time)	$p = c$	48	5030.005	42.235	0.000
15	(month)	(month)	$p = c$	26	5030.461	42.691	0.000
11	(.)	(time)	(time)	71	5034.050	46.281	0.000
16	(month)	(.)	(.)	16	5035.964	48.194	0.000
6	0	(month)	(month)	26	5036.612	48.842	0.000
8	(.)	(time)	$p = c$	37	5037.233	49.464	0.000
13	(month)	(.)	$p = c$	15	5037.336	49.566	0.000
9	(.)	(month)	$p = c$	15	5038.030	50.260	0.000
19	(time)	(.)	$p = c$	36	5040.337	52.567	0.000
23	(time)	(time)	(time)	102	5040.427	52.658	0.000
22	(time)	(.)	(.)	37	5041.757	53.988	0.000
21	(time)	(month)	$p = c$	47	5051.769	63.999	0.000
20	(time)	(time)	$p = c$	69	5054.022	66.252	0.000
5	0	(time)	(time)	70	5060.522	72.753	0.000
2	0	(time)	$p = c$	36	5065.072	77.302	0.000
3	0	(month)	$p = c$	14	5068.130	80.361	0.000
10	(.)	(.)	(.)	5	5085.653	97.883	0.000
7	(.)	(.)	$p = c$	4	5107.573	119.804	0.000
4	0	(.)	(.)	4	5119.252	131.482	0.000
1	0	(.)	$p = c$	3	5153.604	165.835	0.000

Survivorship (S) in all models was constant but allowed to differ between locations

for location-specific effects. The AIC_c w of our top model (i.e., $\gamma(\text{time}) p(\text{time}) c(\text{time})$) in the location model set was 0.999, thus we did not allow these parameters to vary between the locations in our model. Various parameterizations of S revealed strong support for location-specific survival (Table 4; $w = 1.000$). Survival estimates were 0.88 (1 SE = 0.009; 95% CI 0.861, 0.898) at the undisturbed stream and 0.758 (1 SE = 0.030; 95% CI 0.694, 0.813) at the urban stream.

Discussion

Estimating demographic parameters for cryptic, semi-aquatic species such as stream salamanders can be particularly difficult. In this study, we found clear

evidence that conditional capture probability, recapture probability, and temporary emigration varied from month to month and models containing both a capture response and temporary emigration were favored in model selection, suggesting the importance of these parameters in estimating survival of *D. fuscus*. Furthermore, we found evidence that survival was constant among primary periods but differed between the urban and undisturbed stream.

Our estimates of conditional capture probability were similar to estimates provided in other investigations of salamander populations. Bailey et al. (2004a) found that conditional capture probabilities for several Plethodontid salamander species ranged between 0.20 (SE = 0.04) and 0.35 (SE = 0.03). Bailey et al. (2004a) suggested that differences in conditional capture probability depended on species groups,

Table 4 Model rankings for estimating survival (S) in the salamander *Desmognathus fuscus* sampled at two, first-order streams in the Piedmont of North Carolina, USA from October 2005 to August 2008

Model	S	No. parameters	AIC _c	Δ AIC _c	AIC _c wt
2b	(location)	38	4987.770	0.000	1.000
1b	(.)	37	5009.755	21.986	0.000
5b	(month \times location)	60	5010.014	22.244	0.000
3b	(month)	48	5017.023	29.253	0.000
4b	(time)	69	5048.686	60.916	0.000
6b	(time \times location)	102	5075.055	87.285	0.000

Note that all models contained month-specific values for temporary emigration, conditional capture probability, and recapture probability

behaviors, and temporal factors such as environmental changes. In our study, temporal (i.e., monthly) variation in capture probability was highly supported. We found *D. fuscus* was least detectable during summer months (i.e., June, July, and August) and most detectable during spring and fall months. Temporal differences in conditional capture probability have long been considered typical of stream salamander populations as surface activity is often seasonal and/or dependent on environmental conditions (Barbour et al., 1969; Ashton, 1975; Orser & Shure, 1975; Connette et al., 2011); however, our study is the first to quantify these temporal differences. The low conditional capture probabilities during June, July, and August may be the result of several factors including low levels of surface activity because of low water levels during summer months (e.g., Keen, 1984) or the relative inactivity of females during this time period due to oviposition and nest attendance (Organ, 1961; Danstedt, 1975; Juterbock, 1986). Failure to account for the monthly variation in conditional capture probabilities we observed would have resulted in reduced precision of our survival estimates.

Behavioral responses to capture (i.e., difference in capture probability between unmarked and previously marked individuals) have been documented in a wide variety of animals (Nichols et al., 1984), but rarely documented for amphibians. We detected a negative behavioral response to capture, as recapture probabilities were less than initial capture probabilities in 9 of the 12 months. Bailey et al. (2004a) also detected a negative capture response in terrestrial, Plethodon salamanders. The negative capture response we observed may be due to a variety of factors, however, Nichols et al. (1984) notes that negative capture

responses may be a result of handling techniques that stress the animal. Several aspects of our study may have resulted in stressed salamanders, including capturing by hand or by net, anesthetizing prior to injection with VIE, injecting with VIE, or microclimate degradation under coverboards, rocks and/or logs that were previously overturned. The techniques we employed to capture and mark salamanders are widely used in amphibian population studies (e.g., Bailey et al., 2004a; Rothermel & Semlitsch, 2006; Cecala et al., 2009; Grant et al., 2010). If CMR techniques result in a negative capture response, the failure to account for negative trap response in such studies will result in considerable bias in vital rate parameter estimates (Nichols et al., 1984; Pollock et al., 1990).

The importance of estimating probability of temporary emigration has been demonstrated in a variety of animals, especially species that breed in defined areas [i.e., sea turtles (Kendall & Bjorkland, 2001); pond-breeding amphibians (Bailey et al., 2004b; Muths et al., 2006; Kinkead & Otis, 2007); marine mammals (Schwarz & Stobo, 1997)] and those that utilize subterranean refugia [i.e., voles (Kendall et al., 1997)]. Our results, as well as those by other researchers (i.e., Bailey et al., 2004a; Kinkead & Otis, 2007), collectively support the notion that Plethodontid salamander populations exhibit significant levels of temporary emigration. Previous studies of terrestrial Plethodontid salamanders have documented high rates of temporary emigration, with an average of 87% of individuals being unavailable for capture during each primary period (Bailey et al., 2004a). Our study documented that temporary emigration also occurs at particularly high rates (i.e., $\gamma > 0.900$ in some months) in stream-inhabiting Plethodontid salamanders.

This study demonstrated that temporary emigration can vary temporally within a population. Variation in temporary emigration among months may be due to ecological and behavioral factors. It is well-known that many stream salamanders have low energetic requirements, allowing them to spend prolonged periods underground or under cover (Petranka, 1998), with activity limited to periods of ideal abiotic conditions (Barbour et al., 1969; Ashton, 1975; Orser & Shure, 1975; Connette et al., 2011). Low levels of temporary emigration during May and June suggest a higher degree of surface activity than during other months. Our temporary emigration estimates could have been inflated if individuals move outside the capture area or have home ranges that only partially overlap with the sampling area. Regardless of the source of temporary emigration, failure to account for temporary emigration reduces precision of vital rate estimates (Kendall et al., 1997; Bailey et al., 2004a).

We found strong evidence for location-specific survival. Salamanders had survival estimates among primary sampling periods of 0.88 (1 SE = 0.009; 95% CI 0.861, 0.898) at the undisturbed stream compared to survival estimates of 0.758 (1 SE = 0.030; 95% CI 0.694, 0.813) at the urban stream. If we extrapolate these estimates over 1 year (e.g., 0.88^{12}) these data equal annual survival estimates of 0.216 (95% CI 0.166, 0.275) at the undisturbed site and 0.036 (95% CI 0.012, 0.083) at the urban stream. Our survival estimates for the undisturbed stream are similar to estimates reported by Danstedt (1975) who estimated that survival ranged from 0.238 to 0.420 per year for males and from 0.268 to 0.426 for females. However, our survival estimates from the urban location are substantially lower than those reported by Danstedt (1975). Differences in survival estimates between our study and investigations by other researchers (Organ, 1961) support the suggestion by Danstedt (1975) that patterns of survival in *D. fuscus* vary among populations. Danstedt (1975) hypothesized that variation in survival may be due to competition among females for nest sites, especially when in the presence of other members of the genus *Desmognathus* (i.e., *D. monticola* (Dunn)) and/or predation pressures by other stream salamanders, such as the spring salamander (*Gyrinophilus porphyriticus* (Green)) and the red salamander (*Pseudotriton ruber* (Latreille)). Our data, however, do not support these hypotheses as *D. fuscus* was the only member of the genus *Desmognathus*

present in our study streams and *G. porphyriticus* and *P. ruber* were only detected in our undisturbed stream, which had a higher monthly survival estimate for *D. fuscus*.

Differences in adult survival between the locations may reflect differences in either permanent emigration or true survival, both of which could be linked to urban development. Although our findings provide limited inference due to the small number of sites sampled, our study does provide some additional insight on the effects of urbanization on stream salamanders. We found that the habitat conditions at the urban stream dramatically changed after the urbanization of the stream catchment. These changes in environmental conditions, including increased siltation, increased water temperature, and increased conductivity, are consistent with conditions that characterize urban streams (Paul & Meyer, 2001). Furthermore, these conditions have been correlated with low salamander abundances (Willson & Dorcas, 2003; Miller et al., 2007), which we noted in our urban stream only after urbanization of the stream catchment. In fact, prior to urbanization, we captured more adult *D. fuscus* ($n = 11$) at the urban stream than at the undisturbed stream ($n = 8$) (Price et al. unpub. data). Previous studies attributed low abundances to low values of larval survivorship (Barrett et al., 2010; Price et al., 2011). Our results suggest that adult survival may also be depressed in urban streams.

Monitoring vital rates, such as survivorship, of freshwater animals is becoming increasingly important in order to quantify anthropogenic impacts and evaluate the effectiveness of management and restoration on freshwater systems. This study suggests that in order to accurately estimate survival of secretive semi-aquatic animals, such as salamanders, evaluation of conditional capture probability, recapture probability, and temporary emigration is important. If temporary emigration, capture responses, and/or conditional capture probabilities are ignored, survivorship estimates will likely be biased and assessments of freshwater animal populations may be inaccurate.

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