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Modeling the effects of life-history traits on estimation of population parameters for a cryptic stream species

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Abstract. Estimating demographic values and rates for populations of cryptic stream species frequently is difficult because of prohibitively low capture probabilities. When assessing cryptic populations, researchers often are forced to make simplifying assumptions that could alter their conclusions about a population. We constructed models based on different assumptions about cohort structure, behavioral responses to capture, temporary emigration, and survival in a cryptic, larval population of red salamanders (*Pseudotriton ruber*) and fitted models to capture-mark-recapture data. Overall, models based on 2 cohorts were favored over models based on 1 cohort. Models based on assumptions of constant survival, behavioral responses to capture, and random temporary emigration were ranked higher than models lacking these assumptions. Consistent behavioral responses to capture demonstrated that using uncorrected counts to assess trends for this, and perhaps other larval amphibian populations, yields misleading results. Counts that are not corrected for trap-shy behavior may inherently show negative temporal trends. Temporary emigration was a critical assumption when describing larval salamander demography because only 27% of the larvae were active on the surface (the rest were in substratum habitats). Our study demonstrates the importance of making appropriate assumptions about demographic parameters and shows how population models can quantify aspects of the natural history of cryptic species.

Key words: larvae, *Pseudotriton ruber*, salamander, survival, temporary emigration.

Cryptic animals pose problems for researchers attempting to estimate the status of populations. They often use habitats that are difficult to sample (e.g., underground areas) and, thus, can have prohibitively low capture probabilities. Many cryptic animals use multiple habitats or undertake extensive migrations (Kendall and Bjorkland 2001, Fujiwara and Caswell 2002, Trenham and Shaffer 2005), which can reduce capture probability in specific habitats or during certain times of year. Researchers often know little about the natural history of such animals, and they may be forced to use limited information, casual observations, or borrowed data from closely related species or populations when attempting to assess the status of populations of cryptic animals (MacKenzie et al. 2005, Conn et al. 2006, Mazerolle et al. 2007, Litt and Steidl 2010). Thus, low capture probability and lack of natural-history information may lead to imprecise inferences about the status of these populations.

Model development is often a critical component of estimating population parameters. Typically, only a subset of the population can be captured feasibly, so researchers use models to approximate demographic values and rates (Kendall et al. 1997, Bailey et al. 2004b). Models used to approximate demographic rates become less reliable when little is known about the natural history of animals. For example, conclusions about population status may be consistently negatively biased or show unexplained fluctuations through time when species have life-history traits, such as female parental care or ontogenetic shifts in habitat use, that are unknown to the researcher. Errors also can occur if researchers attempt to simplify models by removing information from the model that they hypothesize does not influence model fit to their data. For example, if researchers can survey only breeding habitats effectively, they may assume that the breeding site is closed to emigration and immigration during the breeding season. However, temporary emigration might need to be included in a model if animals move into other locations where

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they may experience different environmental pressures that could alter their vital rates (Pollock 1982).

Technological advances and computer software (e.g., program MARK; White and Burnham 1999) have improved the ability of researchers to estimate demographic parameters, and demographic values and rates, such as population size and survivorship, which are becoming widely used metrics of interest for biologists. Our objective was to test the sensitivity of parameter estimation to assumptions made by researchers about the natural histories and behaviors of cryptic animals. We fit capture-mark-recapture data for larval red salamanders (*Pseudotriton ruber*, Latreille 1801), an extremely secretive, stream-dwelling plethodontid salamander, to models based on different assumptions about cohort structure, behavioral responses to capture, and temporary emigration rates, and we evaluated model fit using an information-theoretic approach (Burnham and Anderson 2002). We show how different models can provide feedback useful for understanding aspects of the natural history of these salamanders and other cryptic species.

We developed 4 hypotheses to demonstrate the sensitivity of parameter estimation to assumptions about natural-history characteristics and behavior. First, we hypothesized that, like a wide variety of other organisms, larval *P. ruber* would show behavioral responses to capture (behavioral hypothesis; Bailey et al. 2004b, Kendall and Nichols 1995, Price et al. 2012). Second, we predicted that temporary emigration would have to be included to obtain accurate estimates of demographic parameters (temporary emigration hypothesis). We defined temporary emigration (γ) as the probability that an individual would leave the stream surface between sampling occasions (Bailey et al. 2004b). We evaluated these 2 hypotheses in 2 ways. First, we examined the influence of behavioral response to capture and temporary emigration on the fit of each model. Second, we evaluated how capture response and temporary emigration influenced estimates of demographic parameters. Third, because *P. ruber* has a multiyear larval period, we hypothesized that survivorship (φ) and capture probability would differ among cohorts with the 1^{st}-y cohort experiencing lower survival than the 2^{nd}-y cohort (survival hypothesis). Price et al. (2011) highlighted the need to identify threats to both larval and adult life stages, but different cohorts of species with multiyear larval periods may have different demographic rates. If researchers can assume that cohorts within a life stage behave similarly, less data and effort may be necessary to develop well defined population models (Biek et al. 2002), an important consideration when studying cryptic species for which data collection can be difficult. Our null hypothesis was that models assuming demographic variability between larval cohorts would receive greater support than models assuming similarity among all cohorts (cohort assumption).

Methods

Study organism

Plethodontid salamanders are extremely cryptic and make extensive use of substratum habitats (Taub 1961, Petranka 1998, Bailey et al. 2004b, Price et al. 2012). *Pseudotriton ruber* is a large-bodied plethodontid salamander that breeds in low-order streams and is found throughout the eastern US (Petranka 1998). Adult *P. ruber* breed in early autumn (Bruce 1978). Females deposit eggs in late autumn and early winter in cryptic locations in streams, seeps, and stream banks (Bruce 1978, Petranka 1998). The aquatic larval period of *P. ruber* can range from 2 to 3 y (Bruce 1974, Semlitsch 1983). Larvae prefer microhabitats with detrital stream substrate in areas of slow-moving water (Petranka 1998). No previous studies have documented population parameters for this species, and estimates of larval plethodontid survival are rare (Bruce 2008).

Field methods

We studied larval *P. ruber* in a 150-m 1^{st}-order stream in the Piedmont region of North Carolina, USA (Mecklenburg County). The stream was characterized primarily by glide-and-pool habitat with little change in elevation. The main substrate was detritus on a sandy base, but downstream (lower 20 m) and upstream (upper 15–30 m) reaches were characterized by deep mud (see Cecala et al. 2009 for more information on study site).

We sampled salamanders twice per month in June and July 2006 and once per month in May 2006 and August 2006 to April 2007 for a total of 14 primary periods. Sampling events consisted of 4 consecutive trapping days in May to July 2006 and 3 consecutive trapping days in August 2006 to April 2007 (see Cecala et al. 2009 for more sampling details). Logistic restraints prevented continued bimonthly sampling, but we accounted for differences in time among primary periods and within secondary periods in our modeling procedure (see *Model building* below). We sampled by placing 2 inverted bottle traps (Willson and Dorcas 2003) of 2 different sizes (2-L and ½-L bottles) in opposite directions within each meter of stream length (300 traps total). We checked traps daily. When a salamander was captured, we recorded the longitudinal position of the salamander in the stream and measured the salamander's snout–vent length (SVL) and total length (TL). We anesthetized individuals using a 1.0 g/L solution of Orajel® (Church and Dwight Co., Inc., Princeton, New Jersey; Cecala et al. 2007) and marked all animals individually with visual implant elastomer (Northwest Marine Technology, Shaw Island, Washington; Bailey 2004). We returned animals to their point of capture within the stream after processing and recovery from anesthesia.

Data analysis

We implemented a Pollock robust study design to model our data (Pollock 1982). Few individuals were captured from November to March ($n = 176$ captures in 5 mo), so we estimated demographic parameters for this population from May to October when *P. ruber* larvae were most active in the stream. The time between primary capture periods and within secondary capture periods varied, so we adjusted the intervals among secondary periods and the length of secondary periods to develop monthly estimates of demographic parameters conditional upon the sampling intervals. We assumed that any movement of larvae into or out of our study area could be attributed to temporary emigration to peripheral or subsurface areas of the study stream because it was isolated from other lotic water bodies by $\geq$300 m.

Pollock's robust design assumes that populations are closed during secondary sampling periods (Pollock 1982). We used the program CAPTURE (White et al. 1978) to test closure assumptions, to assess whether capture probabilities changed in response to time or previous capture, and to test for excessive differences among individuals with respect to capture probabilities (individual heterogeneity; Otis et al. 1978). We included temporal or behavioral responses or individual heterogeneity in our candidate model set (see *Model building* below) if these factors were deemed important via the CAPTURE analysis.

Model building

We used the results from the CAPTURE analysis and our assumptions about the capture-mark-recapture data to develop 24 models to evaluate our 4 hypotheses. We compared parameter estimates among models based on different natural-history and behavioral assumptions about the larval salamander population. Population size (N) was assumed to be temporally stable because no mortality or hatching events that would drastically affect the superpopulation size were evident from May to October 2006. This stability assumption also simplified our comparisons of N among models. We also examined survivorship (φ) to assess whether it varied temporally between our 1- or 2-cohort (1G, 2G, respectively) models or between younger and older cohorts in the 2G models (survivorship hypothesis; Table 1).

To evaluate our cohort delineation hypothesis, we compared models assuming a single larval cohort (1G) with models accounting for their multiyear larval period. Bruce (1972) reported that *P. ruber* had a 3-y larval period in the mountains of North Carolina, but we found that this population had, in general, a 2-y larval period as seen in a Coastal Plain population (Semlitsch 1983, KKC, unpublished data). We based the 2-y cohort delineation (2G) on calculated growth rates from our mark-recapture data and formed 2 cohorts. Small, 1$^{\text{st}}$-y larvae were <37 mm SVL, whereas large, 2$^{\text{nd}}$-y larvae were $\geq$37 mm SVL (KKC, unpublished data). We used the cohort model that best reflected the larval period of this population (see below) to assess the effects of cohort (1$^{\text{st}}$- or 2$^{\text{nd}}$-y), behavioral response to capture, and temporary emigration on estimates of demographic rates and abundance (see below).

We evaluated behavioral response to capture in terms of likelihood of recapture. After initial capture (capture probability $= p$), an individual may become easier to capture (trap-happy), harder to capture (trap-shy), or show no response (recapture probability $= c$). We compared models with ($p \neq c$) and without ($p = c$) a behavioral response to capture (behavioral hypothesis; Table 1; Otis et al. 1978).

We explored the existence and type of temporary emigration in this population. If temporary emigration exists ($\gamma \neq 0$), it can be random (probability of emigrating from the sampling area [γ'] equals the probability of immigrating to the sampling area [γ'']; $\gamma' = \gamma''$) or Markovian (probability of emigrating differs from probability of immigrating; $\gamma' \neq \gamma''$; Table 1; Kendall et al. 1997).

Model evaluation

We evaluated model fit with the program RDSURVIV (Hines 1996), which uses a cell-pooling algorithm to assess model fit for robust design models. First, we evaluated fit of the most general model (Model 5: 2G, constant survival [S(.)], no behavioral response to capture [$p = c$], random temporary emigration [$\gamma' = \gamma''$]). If the results indicated lack of fit caused by overdispersion, we adjusted the variance inflation factor ($\hat{c}$) and proceeded with model testing.

TABLE 1. Models used to evaluate the effects of assumptions about cohort structure (1 cohort [1G] vs 2 cohorts [2G]), behavioral responses to capture (probability of capture [*p*] vs probability of recapture [*c*]), probability of temporary emigration (γ; random emigration [γ'] vs Markovian emigration [γ'']), and temporal variation in survival (S; no variation [.] vs variation [t]) on estimates of population size, survivorship, and temporary emigration parameters. See text for details.

Model number	Cohort structure		Survival		Behavioral response		Temporary emigration		
	2G	1G	.	t	$p \neq c$	$p = c$	$\gamma = 0$	$\gamma' = \gamma''$	$\gamma' \neq \gamma''$
Model 1	X		X		X		X		
Model 2	X		X		X			X	
Model 3	X		X		X				X
Model 4	X		X			X	X		
Model 5	X		X			X		X	
Model 6	X		X			X			X
Model 7	X			X	X		X		
Model 8	X			X	X			X	
Model 9	X			X	X				X
Model 10	X			X		X	X		
Model 11	X			X		X		X	
Model 12	X			X		X			X
Model 13		X	X		X		X		
Model 14		X	X		X			X	
Model 15		X	X		X				X
Model 16		X	X			X	X		
Model 17		X	X			X		X	
Model 18		X	X			X			X
Model 19		X		X	X		X		
Model 20		X		X	X			X	
Model 21		X		X	X				X
Model 22		X		X		X	X		
Model 23		X		X		X		X	
Model 24		X		X		X			X

We used an information-theoretic approach to assess the relative support for each of our hypotheses given the data. We used Akaike's Information Criteria (AIC; Akaike 1973) to evaluate the relative plausibility of each model, and we adjusted this value for small sample sizes ($\mathrm{AIC_c}$; Hurvich and Tsai 1989) in program MARK (White and Burnham 1999) with the number of marked individuals as our sample size. The most probable models were those with $\mathrm{AIC_c} < 2$ (Burnham and Anderson 2002). We calculated $\mathrm{AIC_c}$ weight (*w*) for each candidate model and assessed the fit of each model to the data by ranking models from highest to lowest *w* (Burnham and Anderson 2002).

We evaluated our model results by comparing parameter estimates from each model to parameter estimates from the best-fitting model to examine how different assumptions (i.e., temporal variability of survival, cohort structure, behavioral response to capture, and existence and type of temporary emigration) influenced estimates of the demographic parameters survivorship (φ), effective capture probability (p^*, see below), temporary emigration (γ), and size of the surface population (*N*). We obtained estimates of demographic parameters from linear models describing our various hypotheses that we implemented in program MARK (White and Burnham 1999, Williams et al. 2001). Our data indicated that this population had a 2-y larval period, so we used models based on cohort structure to compare demographic rates. We developed importance weights for each parameter by calculating the sum of the $\mathrm{AIC_c}$ *w*s for all models with the same cohort structure (1G or 2G) that included the parameter. We used importance weights to evaluate the hypothesis associated with each parameter (Burnham and Anderson 2002).

We used parameter estimates obtained from the best-fitting model to compute the abundance of salamanders per 10-m reach to identify stream areas of high potential biological importance. The surface population (*N*) included all individuals available for capture on the surface or in our traps, whereas the superpopulation (N_{super}) included the surface population *and* all individuals in substratum habitats (the stream substratum or regions of vertical or horizontal hyporheic flow) where they were unlikely to be encountered. We calculated the effective capture probability (p^*) as our estimated capture probability (*c*) corrected for temporary emigration (γ) and used p^*

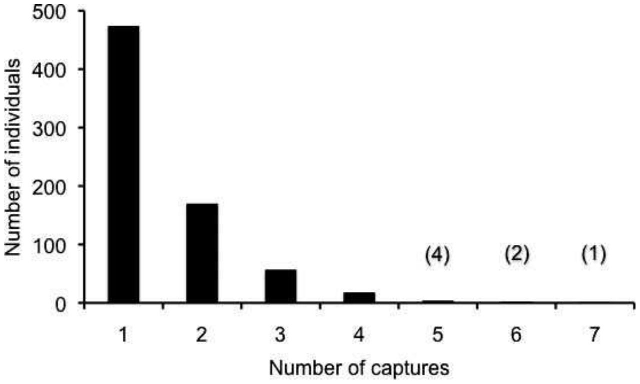

FIG. 1. Frequency distribution of captures of larval red salamanders.

to estimate N_{super} from capture counts in each primary period. We compared N with N_{super} to determine if including temporary emigration (γ) improved model fit.

Results

We captured 474 *P. ruber* individuals (726 total captures) during the 7-mo sampling period. Most (74%) animals were never recaptured, 18% were recaptured once, and 8% were recaptured more than twice (Fig. 1). All secondary periods were closed, and behavior was the only factor influencing capture probabilities (p) during secondary periods. Individual heterogeneity and behavioral responses to capture did not appear to influence p in 7 of 8 secondary periods.

Goodness-of-fit results varied. The more conservative G-test indicated fit ($G_{\text{df}=361} = 319.6$, $p = 0.94$), but the Pearson χ^2 test indicated some lack of fit ($\chi^2_{\text{df}=94} = 116.8$, $p = 0.056$). When we visually examined a plot of the residuals, we concluded that the evidence of lack of fit from the Pearson χ^2 test probably was caused by summing many low probabilities for rare events. The Pearson χ^2 test indicated overdispersion ($\hat{c} = 1.23$), whereas the G-test indicated underdispersion ($\hat{c} = 0.86$). Because of our concerns about the accuracy of the Pearson χ^2 test and to prevent underestimating the error of our estimates, we kept $\hat{c} = 1$ and evaluated the relative support of our models.

Overall, models assuming S(.) were better supported than models assuming that S varied temporally (S[t]) (Tables 2, 3). We concluded that monthly S was relatively constant in this population (Table 2), and used models assuming S(.) for further comparisons. Models assuming a behavioral response to capture ($p \neq c$) and random temporary emigration ($\gamma' = \gamma''$) were 2.7× more likely than the next best-fitting model assuming behavioral response but Markovian temporary emigration for 2 groups. All other models had little support as demonstrated by $\Delta\text{AIC}_c > 2$ (Table 2). Model *ws* also indicated that behavioral responses to capture were 1851× more likely than no behavioral response to capture confirming our behavioral hypothesis (Table 3). Summed AIC$_c$ *ws* for 2G models indicated that random temporary emigration was 2.6× more likely than Markovian temporary emigration. Models containing either of the temporary emigration assumptions had higher importance weights than models assuming no temporary emigration, a result supporting our hypothesis that temporary emigration is important when modeling cryptic populations (Table 3). These model rankings were consistent for all 1G and 2G models, but 2G models were more likely than 1G models (Tables 2, 3), a result supporting our cohort hypothesis.

We assessed how different assumptions about temporary emigration and behavioral response to capture affected parameter estimates. Without inclusion of random or Markovian temporary emigration, we were unable to distinguish between N and N_{super} although total estimates were similar to those obtained from models including temporary emigration. In this population, N yielded mean density estimates of 1 salamander larva/m^2, but N_{super} yielded estimates indicating that true density might be as large as 8 larvae/m^2.

We compared parameter estimates of the best-fitting 2G model (Model 2, 2G, S[.], $p \neq c$, $\gamma' = \gamma''$) to that for the best-fitting 1-cohort model (Model 14; 1G, S[.], $p \neq c$, $\gamma' = \gamma''$) to test the effect of cohort structure on model performance. A single, constant estimate of S overestimated 2$^{\text{nd}}$-y φ but underestimated 1$^{\text{st}}$-y φ, and 2$^{\text{nd}}$-y γ'' and p were underestimated in Model 14. By assuming 1 cohort, we obtained a more precise but less accurate estimate of N_{super} (Table 3).

We compared parameter estimates between our best-fitting model (Model 2; 2G, S[.], $p \neq c$, $\gamma' = \gamma''$) and the model assuming random temporary emigration but no behavioral response to capture (Model 5; 2G, S[.], $p = c$, $\gamma' = \gamma''$). Estimates of φ appeared to remain constant, but estimates of γ'' and p decreased when we assumed no behavioral response to capture (Table 3).

Random temporary emigration appeared in the model with the most evidence of fit to this population (Model 2; 2G, S[.], $p \neq c$, $\gamma' = \gamma''$), so we compared other models to random temporary emigration models. Models assuming no temporary emigration (Model 1; 2G, S[.], $p \neq c$, $\gamma = 0$) significantly reduced p, but not c. Models assuming no γ overestimated N by 3× and underestimated φ for large larvae (Table 3). Models assuming Markovian temporary

TABLE 2. Results of model evaluation using Akaike's Information Criterion for small sample size (AIC_c) weights (w) to assess the relative fit of each model to capture-mark-recapture data for a population of larval *Pseudotriton ruber*. Larger values indicate higher levels of support for the model. See Table 1 and text for an explanation of notation. K = number of parameters, ΔAIC_c = difference between model AIC_c and AIC_c of the most general model (Model 5: 2G, S[.], $p = c$, $\gamma' = \gamma''$).

Model number	Model	K	AIC_c	ΔAIC_c	w
Model 2	2G, S(.), $p \neq c$, $\gamma' = \gamma''$	10	−349.73	0.00	0.725
Model 3	2G, S(.), $p \neq c$, $\gamma' \neq \gamma''$	12	−347.78	1.95	0.274
Model 5	2G, S(.), $p = c$, $\gamma' = \gamma''$	8	−333.87	15.86	<0.001
Model 6	2G, S(.), $p = c$, $\gamma' \neq \gamma''$	10	−333.18	16.56	<0.001
Model 8	2G, S(t), $p \neq c$, $\gamma' = \gamma''$	22	−333.14	16.59	<0.001
Model 9	2G, S(t), $p \neq c$, $\gamma' \neq \gamma''$	24	−330.91	18.82	<0.001
Model 1	2G, S(.), $p \neq c$, $\gamma = 0$	8	−322.89	26.84	<0.001
Model 11	2G, S(t), $p = c$, $\gamma' = \gamma''$	20	−317.40	32.33	<0.001
Model 12	2G, S(t), $p = c$, $\gamma' \neq \gamma''$	22	−315.79	33.94	<0.001
Model 4	2G, S(.), $p = c$, $\gamma = 0$	6	−314.45	35.28	<0.001
Model 7	2G, S(t), $p \neq c$, $\gamma = 0$	20	−307.13	42.60	<0.001
Model 10	2G, S(t), $p = c$, $\gamma = 0$	18	−299.14	50.59	<0.001
Model 11	1G, S(.), $p \neq c$, $\gamma' = \gamma''$	5	−280.80	68.93	<0.001
Model 15	1G, S(.), $p \neq c$, $\gamma' \neq \gamma''$	6	−279.26	70.47	<0.001
Model 20	1G, S(t), $p \neq c$, $\gamma' = \gamma''$	11	−274.05	75.68	<0.001
Model 21	1G, S(t), $p \neq c$, $\gamma' \neq \gamma''$	12	−272.08	77.65	<0.001
Model 17	1G, S(.), $p = c$, $\gamma' = \gamma''$	4	−228.78	120.95	<0.001
Model 18	1G, S(.), $p = c$, $\gamma' \neq \gamma''$	5	−227.47	122.26	<0.001
Model 23	1G, S(t), $p = c$, $\gamma' = \gamma''$	10	−222.14	127.60	<0.001
Model 24	1G, S(t), $p = c$, $\gamma' \neq \gamma''$	11	−220.21	129.53	<0.001
Model 13	1G, S(.), $p \neq c$, $\gamma = 0$	4	−195.74	153.99	<0.001
Model 16	1G, S(.), $p = c$, $\gamma = 0$	3	−191.28	158.45	<0.001
Model 19	1G, S(t), $p \neq c$, $\gamma = 0$	10	−189.93	159.80	<0.001
Model 22	1G, S(t), $p = c$, $\gamma = 0$	9	−186.05	163.68	<0.001

emigration (Model 3; 2G, S[.], $p \neq c$, $\gamma' \neq \gamma''$) overestimated φ of large larvae (Table 3).

Our models indicate that small larvae make up most of the individuals on the surface and in the super population (Table 3). Estimates of φ, γ, p, and c were relatively stable for 1G and 2G models. After accounting for different larval cohorts in this population, φ appeared to be higher for small than for large larvae, a result contrary to our hypothesis that large larvae would experience higher φ (Table 3). Moreover, p and c appeared to be higher for large than for small larvae (Table 3). When we corrected our data for different assumptions, we discovered high density in upstream reaches (Fig. 2).

Discussion

Our results demonstrate the importance of accounting for variation in natural history and behavior when estimating demographic parameters of cryptic, stream-dwelling animal populations. In particular, behavior of animals after capture and the capacity for temporary emigration are critical components of an accurate description of population parameters for larval stream plethodontids. Failure to evaluate these 2 assumptions could lead researchers to very different conclusions about population trajectory or the importance of these traits in the natural history of this organism.

Assumptions regarding behavioral responses to capture strongly influenced the model fit for this population. Larval salamanders appeared to be trap-shy following capture, so little support exists for the use of indices or estimators that assume $p = c$. Count indices and models like the Lincoln–Peterson estimator frequently are used for rapid assessments of populations because they require little effort to complete (Schnabel 1938, Mazerolle et al. 2007, Nowakowski and Maerz 2009). These methods are based on the assumption that observed counts are directly and consistently proportional to the true population abundance of an area. For the larval salamanders we studied, these assumptions were violated as a result of the differences between p and c (Pollock et al. 2002). In this instance, count estimates would inherently indicate negative temporal trends because previously captured animals would be recaptured with a lower probability (trap-shy). Counts should not be used to

TABLE 3. Parameter estimates for 2 cohorts of larval salamanders obtained from linear models implemented in the program MARK (White and Burnham 1999). Models were selected to compare effects on demographic parameters of assumptions about cohort structure (Model 2: 2 cohorts [2G] vs Model 14: 1 cohort [1G]), probability of temporary emigration (γ; Model 1: no temporary emigration vs Model 2: probability of random emigration [γ'] vs Model 3: probability of Markovian emigration [γ'']), behavioral response to capture (Model 2: probability of capture [p] $\neq$ probability of recapture [c] vs Model 5: no behavioral response to capture [$p = c$]). w = Akaike Information Criterion for small samples weight, φ = population survivorship, N = estimated surface population size, p^* = effective capture probability or the probability that an individual on the surface will be captured, N_{super} = superpopulation abundance or estimated abundance of all individuals in the study stream.

		Model 2	Model 3	Model 1	Model 5	Model 14
Parameter	Cohort	2G, $p \neq c$, $\gamma' = \gamma''$	2G, $p \neq c$, $\gamma' \neq \gamma''$	2G, $p \neq c$, $\gamma = 0$	2G, $p = c$, $\gamma' = \gamma''$	1G, $p \neq c$, $\gamma' = \gamma''$
w		0.725	0.274	<0.001	<0.001	<0.001
φ	1st-y	0.874 ± 0.044	0.866 ± 0.058	0.868 ± 0.044	0.877 ± 0.044	0.800 ± 0.036
φ	2nd-y	0.609 ± 0.066	0.733 ± 0.142	0.507 ± 0.058	0.614 ± 0.067	
γ''	1st-y	0.726 ± 0.080	0.729 ± 0.081	0	0.567 ± 0.089	0.818 ± 0.27
γ''	2nd-y	0.726 ± 0.080	0.737 ± 0.071	0	0.519 ± 0.137	
γ'	1st-y	–	0.708 ± 0.122	–	–	–
γ'	2nd-y	–	0.893 ± 0.088	–	–	
p	1st-y	0.123 ± 0.037	0.123 ± 0.037	0.031 ± 0.005	0.072 ± 0.010	0.264 ± 0.023
p	2nd-y	0.296 ± 0.042	0.293 ± 0.042	0.110 ± 0.028	0.131 ± 0.021	
c	1st-y	0.069 ± 0.010	0.069 ± 0.010	0.069 ± 0.010	–	0.076 ± 0.009
c	2nd-y	0.094 ± 0.018	0.094 ± 0.018	0.094 ± 0.018	–	
N	1st-y	152 ± 37	153 ± 37	517 ± 87	238 ± 31	79 ± 4
N	2nd-y	44 ± 3	44 ± 3	73 ± 14	66 ± 8	
p^*	1st-y	0.034	0.033	0.031	0.031	0.048
p^*	2nd-y	0.081	0.077	0.110	0.063	
N_{super}	1st-y	556 ± 277	562 ± 280	517 ± 172	550 ± 141	433 ± 35
N_{super}	2nd-y	159 ± 19	166 ± 20	73 ± 28	136 ± 34	

infer patterns or trends in and among populations of stream-dwelling salamanders without a rigorous test of the behavioral hypothesis. Furthermore, models assuming no behavioral response to capture can inflate estimates of N because of large reductions in estimates of effective capture probabilities ($[1 - \gamma]p$), but the severity of this problem may vary depending on the relative difference between p and γ (Kendall et al. 1997, Kendall 1999, Bailey et al. 2004b).

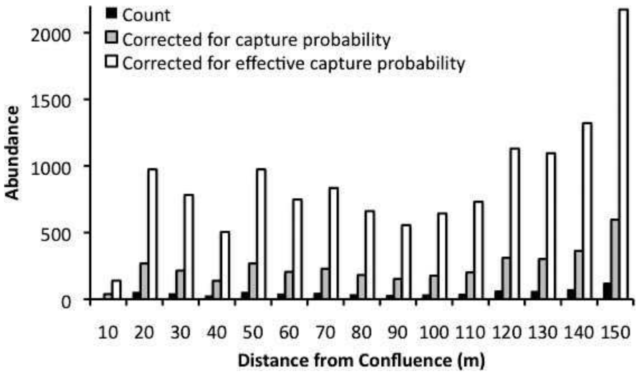

FIG. 2. Raw counts of individual captures, number of individuals estimated based on capture probability, and number of individuals estimated based on capture probability corrected for temporary emigration (effective capture probability). Estimates were obtained from Model 2 with 2 cohorts based on larval size (Table 1, see text for details).

Temporary emigration is common for many animals, including terrestrial and marine mammals, birds, and fish, but many investigators have studied these populations when they are breeding in defined areas (e.g., grey seals [*Halichoerus grypus*], Schwarz and Stobo 1997; Hawksbill sea turtles [*Eretmochelys imbricate*], Kendall and Bjorkland 2001). Few investigators have studied animals, such as small terrestrial mammals, marine mammals, salamanders, fish, and benthic invertebrates, that use vertical movement strategies (but see Kendall et al. 1997, Fujiwara and Caswell 2002, Bailey et al. 2004b). Kendall et al. (1997) showed that temporary emigration occurred during cool months of torpor in meadow voles and was a relevant demonstration of how demographic models may inform researchers about the natural history of cryptic animals. Bailey et al. (2004c) showed that cryptic terrestrial salamanders requiring high humidity for terrestrial activity had higher temporary emigration rates in drier, disturbed forests. Our study further shows that conclusions drawn without consideration of temporary emigration may be misleading (see Bailey et al. 2004b).

Bailey et al. (2004b) estimated that 13% of the adult population of salamanders was surface active. This estimate falls within the range of Taub's (1961) estimates of 3 to 32% for adult terrestrial plethodontids. We found that 27% of the larval plethodontid population was surface active. Our estimates may be higher than those previously reported because moisture limitations experienced by adult plethodontid salamanders are not present in an aquatic life stage (Feder 1983). Alternatively, if model assumptions of closure within secondary periods were violated in our study, the proportion of surface-active individuals would be overestimated. Models have been developed to relax this assumption, but they allow only 1 transition or require detection when individuals leave the sampling area, which were conditions that did not apply in our study system (Schwarz and Stobo 1997, Bailey et al. 2004a). The distribution of our recaptures also could have led to overestimation of *N*. Most individuals were never recaptured, so our model structures probably underestimated φ and γ. Furthermore, only 68% of our recaptures occurred among primary periods and were used to estimate γ. Thus, we hypothesize that γ probably was higher than estimated for these salamanders.

Larval salamanders are fully aquatic organisms and have gills that are absorbed during metamorphosis (Petranka 1998). In isolated streams without hydrologic connectivity to other low-order streams, these populations are closed to permanent larval emigration or immigration. However, we showed that extensive temporary larval emigration can occur into areas of the stream that cannot be sampled (e.g., for larval *P. ruber*, $\gamma = 0.73 \pm 0.08$ [SE] between primary periods). These areas can include subsurface areas of hyporheic exchange or lateral water movement (Poole et al. 2008). By correcting our data for parameters estimated from the population models, we were able to distinguish significantly higher densities of salamanders adjacent to the seep (10- to 20-m downstream of the surface seep) than count data indicated. These results were consistent with the hypothesis of extensive substratum habitat use and upstream-biased movement indicating that stream seeps may be important habitat refuges for larval salamanders where access to subsurface habitat was higher (Petranka 1998, Lowe 2003, Bailey et al. 2004b, Cecala et al. 2009). Confirmation of these hypotheses by considering population parameters illustrates how well informed population models for cryptic species may improve our understanding of their natural histories.

Contrary to our hypothesis, we discovered that small larvae had higher monthly S relative to large larvae, but our estimates of yearly φ are higher than other values published for larval stream salamanders (our study: 0.189, Bruce 2008: 0.074). Our estimates of S for large larvae could have been biased by our assumption that all movement was temporary. In summer when large larvae begin metamorphosis, terrestrial juveniles may emigrate permanently from the stream. The changes and stress associated with the process of metamorphosis also may reduce the likelihood of movement (decreased *p*). Our models will respond to the effect of these changes in parameters by yielding values indicative of a reduction in φ. Models based on the assumption that demographic parameters may vary among cohorts could provide important information about the size structure of this population.

Three potential explanations exist for the sharp decline in abundance of 2^{nd}-y larvae. First, our trapping methods may have been biased toward catching higher proportions of small larvae. We were unable to measure the true size-class ratio for our population, but previous research indicates that our methods are biased against capture of small individuals (Willson and Dorcas 2003). Second, S was constant from May to October, but overwintering individuals may experience much higher mortality. We found very little evidence for this hypothesis. Third, abiotic or biotic conditions in this stream could have been very different during the years before our study so that hatching success was low in the previous year or larvae hatched in the year before our study experienced much higher mortality than larvae hatched in the year of our study. Unfortunately, without previous information regarding annual φ or previous conditions, we cannot explain why this population was composed primarily of 1^{st}-y larvae despite high estimates of φ. Because of the differences between S of larval cohorts and little support for models assuming that 1^{st}- and 2^{nd}-y larvae behaved similarly, we caution researchers against assuming that all cohorts of a life stage have similar demographic rates.

Capture-mark-recapture studies can be time and labor intensive, but they provide critical information about the status and trajectories of cryptic populations that often use difficult-to-sample habitats. Before initiating capture-mark-recapture studies on cryptic species, researchers should decide whether behavioral traits, such as response to capture or use of difficult-to-sample regions, warrant inclusion in the demographic model. Our results indicate that temporary emigration may be an important process to quantify even in regions presumed to be closed to immigration and emigration. Researchers may be tempted to consider the population as a whole to reduce the effort necessary to estimate important parameters. However, information about individual cohorts may be critical in identifying threats to the future viability of these populations. Our models indicate that substratum densities of benthic stream vertebrates may be much higher than previously thought. In our study system, the density of salamanders active on the surface at any one time was only ~1 individual/m^2, whereas true densities were much higher (up to 8 individuals/m^2 in some areas). Knowledge of this difference between surface and total populations may be important. For example, *P. ruber* is the most abundant species of larval salamanders in the stream, but 4 other coexisting species in this stream contribute to the total salamander population size and surface density. Our results show that the models we used can provide insight into life-history traits of cryptic organisms by providing a more quantitative understanding of difficult-to-observe behaviors, such response to capture and temporary emigration.

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