ABSTRACT

AMANDA PEROFSKY
Improving Population Size Estimation for Larval Stream Plethodontids
(Under the direction of John C. Maerz, PhD.)

Plethodontid salamanders are among the most abundant vertebrates of forested ecosystems in the eastern United States. Southern Appalachian streams are hotspots of diversity for semi-aquatic plethodontids. A single stream may include more than a dozen plethodontid species; however, estimates of their abundance are highly variable. Stream plethodontids are potentially important predators of first and second order streams and are likely to be important nutrient sinks. Measuring the importance of stream plethodontids requires accurate determination of their abundance. This research compares abundance estimation of four stream plethodontid species by mark-recapture across six streams at the Coweeta Hydrological Laboratory LTER site. The different categories of mark-recapture models include closed-population, open-population, and robust design models to demonstrate how different model assumptions can result in a wide range of population estimates. Our results indicate that the assumptions of the closed-population and open-population methods are violated by the occurrence of temporary emigration (i.e., the nonrandom movement of individuals into (or out of) the sampling area) and that only 5% of the total population is available for capture on the surface at a given time. We believe that Pollock's robust design model is the most appropriate population abundance estimator for stream plethodontids because of its capacity to incorporate variation in capture probabilities and to estimate temporary emigration probabilities. This study suggests that failure to consider temporary emigration can lead to significantly low-biased estimates of population size, which in turn diminishes the actual role of stream salamanders in ecosystem processes.

INDEX WORDS: capture-mark-recapture, plethodontid salamanders, abundance estimation, model selection, program MARK, robust design, temporary emigration, Coweeta Long Term Ecological Research (LTER)

IMPROVING POPULATION SIZE ESTIMATION FOR LARVAL STREAM

PLETHODONTIDS

by

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CHAPTER 1
INTRODUCTION

Understanding patterns of abundance is an integral component of the field of ecology. Accurately estimating abundance of wildlife is essential for the measurement of animal response to spatial and temporal environmental disturbances and for the assessment of their significance to community structure and ecosystem processes. As a consequence of escalating species extirpations, monitoring abundance has become a principal concern of conservation biology. In all circumstances, the quality of inference we derive from research is reliant upon the accuracy with which we can estimate this significant population parameter.

Approaches to the estimation of abundance have evolved from basic count statistics to more biologically realistic and practical methods. Relative abundance indices based on count data or return rates are the simplest approaches. These techniques assume a direct linear relationship between the index and population size and perfect or equal detection probabilities for individuals. The assumption of perfect or constant detection across space and time is unlikely to be met for many wildlife populations (Preston 1979, Nichols 1992, Pollock et al. 2002, Williams et al. 2002); hence, capture-mark-recapture (CMR) methods were developed to account for variation in detection probability.

The simplest CMR model, the closed-population model, assumes the population is closed to births, deaths, immigrants, and emigrants during the entire sampling period (the closure assumption), all animals are equally likely to be captured in each sample (equal capture probability), and no animal has probability of capture equal to zero, $p \neq 0$. The

equal capture probability assumption may be relaxed by allowing capture probabilities to vary as a result of time (t), behavioral (or trap) response (b), and heterogeneity between individuals (h). The assumption of closure is biologically unrealistic except for studies with very brief sampling periods and extremely large sampling areas. An alternative is the open-population model, which allows for population additions and losses. However, abundance is ephemeral (i.e., estimated separately for each sampling period) and cannot be calculated for the first or last sampling periods; in addition, mortality and emigration are confounded. In the case of the Cormack-Jolly-Seber (CJS) open-population model we used in this study, emigration is assumed to be permanent. This model does not account for the valid possibility that an animal can remain within the population yet temporarily emigrate to locations in which it cannot be detected.

Pollock's (1982) "robust design" model combines aspects of closed-population and open-population models by nesting secondary sampling periods that are temporally proximate (i.e., daily) within primary sampling periods divided by longer time intervals (Fig.1). The time between secondary sampling periods is brief enough to assume the population is closed (i.e., no births, deaths, immigration, or emigration). Births, deaths, immigration, and emigration can occur between primary periods. This sampling design allows the estimation of temporary emigration, the probability that an animal is alive but not available for capture during the sampling period. The incorporation of temporary emigration probability enables more accurate estimation of abundance by accounting for the possibility that a fraction of the total population cannot be sampled. This parameter may be particularly vital in determining population sizes and trends for 'secretive' animals

that are undetectable because they temporarily emigrate to locations that are inaccessible to researchers.
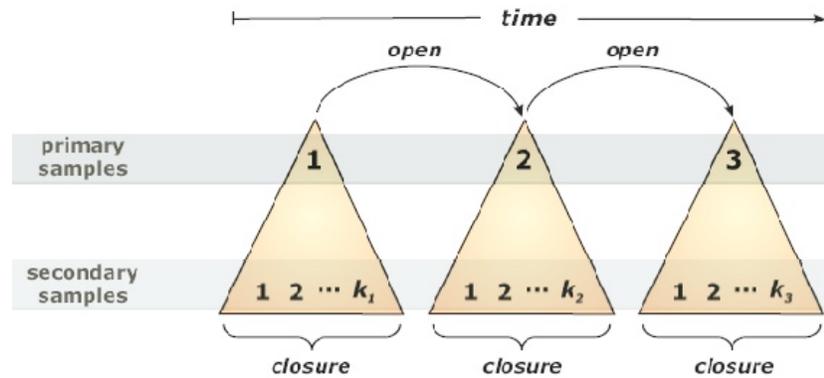
Figure 1. Pollock's (1982) robust design for a *k* period study. Our study contained four primary periods, each with 3 secondary samples (consecutive sampling days). Figure courtesy of 'Program MARK: A Gentle Introduction.'

Amphibians are an archetypal example of a group for which abundance estimation may significantly improve due to the application of robust design. Recent global-scale amphibian population declines and extinctions have necessitated the execution of more extensive and rigorous monitoring programs (Heyer 1994), which accordingly depend upon our ability to accurately measure their abundance (Blaustein et al. 1994, Wyman 1998, Pringle et al. 1999, Ranvestel et al. 2004, Johnson and Wallace 2005, Whiles et al. 2006). Most amphibian field surveys employ ad hoc methods, such as relative abundance indices based on count data or return rates, which assume equal or perfect capture probabilities for individuals. Amphibians, however, are classically difficult to detect in their natural environments. Many species are fossorial, have cryptic coloration, are nocturnal, or are active during only certain times of the year or under particular environmental conditions (Mazerolle 2006). Assuming equal capture probability and perfect detection is obviously not biologically realistic for these animals because there is high temporal

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variation in detection probability (Preston 1979, Nichols 1992, Pollock et al. 2002, Williams et al. 2002).

For instance, salamander populations are considered to be principally subterranean, with only a fraction of the total population near the surface and available for capture during a given sampling period (Taub 1961, Heatwole 1962, Hairston 1983, Petranka and Murray 2001). Additionally, site-specific habitat characteristics, climate, season, humidity, or seasonal behavioral patterns can affect the size of their surface populations (Bailey 2002). Historic research on terrestrial plethodontid salamanders suggested that 2% to 32% of individuals are active near the surface at a given time (Taub 1961), and recent work using Pollock's robust design (Bailey et al. 2004a) suggested 13% of individuals were available for capture at the surface during a given sampling period.

The headwater and first order streams in the Southern Appalachian Mountains of the southeastern United States are hotspots of diversity for semi-aquatic plethodontid salamanders, and a single stream may include more than a dozen plethodontid species. As abundant predators, it is presumed that the larvae of stream plethodontids may be important in stream processes, particularly in nutrient capture and retention; however, estimates of their abundance are highly variable and generally low (<1 larve/m^2 of stream; see review in Nowakowski and Maerz 2009). Most of these prior estimates used capture techniques with poor detection of individuals (e.g., visual searches) and did not incorporate CMR methods to account for imperfect detection probability.

A more recent study in the southeastern piedmont that incorporated CMR suggests that larval plethodontid abundance can exceed 10 individuals/m^2 and reported abundances as high as 150 larvae/m^2 (Nowakowski and Maerz 2009). However, this study calculated

closed-population estimates over a relatively broad time interval and did not account for temporary or permanent emigration; thus, its parameter estimates may be biased. No study has attempted to incorporate the robust design model to estimate abundance and to quantify temporary emigration for larval stream salamanders.

The objective of this study is to use Pollock's robust design to estimate larval stream salamander abundance and to contrast those results to estimates produced by simple count indices and closed-population estimates among six Appalachian headwater streams at the Coweeta Hydrological Laboratory Long Term Ecological Research (LTER) site in North Carolina. In particular, we focus on estimating temporary emigration and surface population and superpopulation sizes for *Desmognathus quadramaculatus*, a large and apparently abundant larval salamander presumed to be influential in stream processes and community dynamics within the headwater systems in the region.

CHAPTER 2
MATERIALS AND METHODS

Study Area

In the summer of 2008, we studied six Appalachian headwater streams at the
Coweeta Hydrological Laboratory LTER site near Franklin, North Carolina. Streams were
randomly selected from a group of streams with similar forest cover and stream discharge.
The Coweeta catchment is a 1624-ha drainage basin in the Blue Ridge physiographic
province of the southern Appalachian Mountains near the Georgia-North Carolina border.
The headwater streams drain forested catchments dominated by mixed hardwoods,
including oaks (*Quercus* spp.), hickories (*Carya* spp.), and yellow poplar (*Liriodendron
tulipifera*). A dense riparian understory of rhododendron (*Rhododendron maximum*)
shades the streams.

Field Methods

In May 2008, we initiated a three-month mark-recapture study of plethodontid
salamander larvae in the six Appalachian headwater streams. Streams were sampled with
six primary periods, each consisting of three consecutive sampling days (secondary
periods). Primary periods were separated by 12-14 days, and sampling was conducted from
10 May to 29 July.

For every stream, we designated ten-1m plots of in-stream habitat separated by
approximately 10m. Within each 1m transect, we placed a plastic litter trap. Leaf litter traps
were constructed with 1.75cm mesh netting with dimensions 56 X 23 X 6 cm, and packed

with deciduous leaf litter from the stream-bank. Each leaf-litter trap was secured by resting a rock on top of it. Daily sampling included checking leaf-litter traps and visual surveys of the plot. To remove salamanders from a leaf-litter trap, we lifted the leaf-litter trap from the water and immediately placed it within a plastic bin. We poured stream water over the trap and agitated the trap in the water to rinse the salamanders free from the leaf litter. Debris and salamanders were then poured into a dip net, and all salamanders were removed. This process was repeated twice to ensure that all salamanders were recovered. We then thoroughly surveyed the 1m transect of stream and checked under all refugia. Sweeps with a dip net were made parallel to the stream bank across the width of the stream, and the dip-net was checked for larvae after each sweep.

We identified individuals according to species and measured the mass and snout-vent length (SVL) to the nearest mm for each individual. All unmarked salamanders larger than 15mm (SVL) were individually marked using visual implant elastomer (VIE; Northwest Marine Technology, Shaw Island, Washington, USA; Bailey 2004). Individuals were marked uniquely by injecting a small amount of elastomer at up to 4 body locations (the base of each limb) using 4 elastomer colors (green, red, yellow, orange). Studies have shown that elastomer markings have long-term retention, minimal marking effects, and meet the assumptions of CMR studies (Davis and Ovaska 2001). Key assumptions of CMR include tag visibility to observers, tag retention throughout the study period, and negligible tag effects on life history behavior (Otis et al. 1978). VIE markings enabled us to identify individual salamanders on all future capture occasions. After marking, the salamanders were released into the leaf-litter trap.

Individual marks allowed us to compile a capture history for all salamanders (>15mm SVL), incorporating 18 sampling occasions (six primary periods X three secondary samples). Because spatial and temporal patterns of distribution and abundance are species-specific (Hyde and Simons 2001, Bailey et al. 2004b), we organized capture histories by species and estimated species-specific population parameters. We used program **MARK** to perform model selection under closed-population models, open-population models, and robust-design models. We evaluated models using Aikake's Information Criterion corrected for small sample size and overdispersion (QAIC$_c$; Akaike et al. 1973). All models with QAIC$_c$ < 2.0 were considered appropriate for a given dataset.

Closed Population Model

We used closed-population models to evaluate demographic parameters for *D. quadramaculatus, D. ocoee, D. monticola,* and *G. porphyriticus.* Estimates were obtained by pooling captures for all secondary periods within each primary period. For this model, we assumed the population was closed throughout the sampling period and that abundance was constant among primary periods. Schnabel's Method (Schnabel 1938) was used to calculate abundance for *D. ocoee,* because QAIC$_c$ > 2.0 when we attempted to perform model selection in program **MARK**. Closed-population model fit was evaluated using the median ĉ (χ^2/df) method. If the global model had evidence of fit (QAIC$_c$ < 2.0), the ĉ was adjusted, and we proceeded with model selection. To account for evidence of fit for multiple models, we obtained parameter estimates by using model-averaging tools available in program **MARK**. We considered six closed-population models (Table 1).

TABLE 1. Six models used in closed-population analysis of four species of larval plethodontids at the Coweeta Hydrological Laboratory LTER site in 2008. Symbols: N=abundance; p=capture probability; c=recapture probability.

Model	Assumptions
1. {N, p(t), c(t)}	Time-specific capture and recapture probabilities
2. {N, p(t), c(.)}	Time-specific capture probability and constant recapture probability
3. {N, p(.), c(t)}	Constant capture probability and time-specific recapture probability
4. {N, p(t)=c(t)}	Equal and time-specific capture and recapture probabilities
5. {N, p(.), c(.)}	Constant capture and recapture probabilities
6. {N, p(.)=c(.)}	Constant and equal capture and recapture probabilities

Open Population Model

The open-population estimates were obtained by pooling all captures for each secondary period within each primary period similar to our closed-population models. Although these modeling techniques allow us to relax the closure assumption, all movement under these models is assumed to be permanent. Cormack-Jolly-Seber (CJS) open-population model fit was evaluated using 1,000 bootstraps. If the global model had evidence of fit, the $\hat{c}$ was adjusted, and we continued with model selection. We considered four CJS open-population models (Table 2).

TABLE 2. Four Cormack-Jolly-Seber (CJS) models used in open-population analysis of *D. quadramaculatus* at the Coweeta Hydrological Laboratory LTER site in 2008. Symbols: φ=survival probability; p=capture probability.

Model	Assumptions
1. {φ(.), p(.)}	Constant survival and capture probabilities
2. {φ(.), p(t)}	Constant survival probability and time-specific capture probability
3. {φ(t), p(.)}	Time-specific survival probability and constant capture probability
4. {φ(t), p(t)}	Time-specific survival and capture probabilities

Pollock's Robust Design

Pollock's (1982) robust design incorporates both closed-population and open-population models in one analysis. Primary sampling periods, *i*, contain *l* secondary sampling periods that are divided by a time interval short enough to assume the population is closed (i.e., no births, deaths, immigration, or emigration; Fig. 1). Primary periods are

divided by longer time periods during which population additions (immigration and births) and losses (deaths and emigration) can occur (Fig. 1). Data from secondary samples can be analyzed using closed-population models that allow for unequal capture probability (Otis et al. 1978). Closed-population models estimate conditional capture probabilities, recapture probabilities, and surface population size for each primary period. Information from both primary and secondary periods is used to estimate temporary emigration probabilities (Fig. 1; Nichols and Kendall 1995, Kendall et al. 1997, Kendall 1999).

Robust design models allow researchers to incorporate temporary emigration into population models and to distinguish between surface population size and superpopulation size. The surface population is defined as the population of salamanders near the surface and available for capture during a given sampling period. The superpopulation is both the population of salamanders near the surface (available for capture) and subterranean individuals (unavailable for capture) within a given sampling period. Temporary emigration probability (γ^*_i) is the probability that an animal is alive but not available for capture during a given sampling period. Random emigration implies that salamanders move into and out of the sampling area at random such that at any given time the surface population (N_i, i.e. the number of animals available for capture in the study area) is a random sample of a superpopulation (N°) of salamanders associated with that sample area.

$$E\ [N_i/N^\circ]=(1-\gamma^*_i)\ N^\circ$$

We assumed that temporary emigration refers to a salamander's vertical movement into the soil, onto the nearby stream bank, or wedging between rocks or into crevices in the streambed. Temporary emigrants cannot be detected by our surface sampling techniques. For completely random temporary emigration, the probability that a salamander is near the

surface at time i does not depend on its location at time $i - 1$. If random temporary emigration takes place during the sampling period, then population estimates from open- or closed-population models (Otis et al. 1978) are unbiased but are applicable to the superpopulation and not the surface population (Nichols and Kendall 1995, Kendall et al. 1997, Kendall 1999). Random temporary emigration causes effective capture probability to be lower and a reduction in precision for all other parameter estimates.

Markovian temporary emigration occurs when the probability that an animal is in the sampling area (i.e., available for capture) during primary period i depends on whether the animal was in (or out of) the sampling area at sampling occasion $i - 1$. Two probabilities must be considered:

(1) γ'_i = probability that an animal stays away from the study area in i, given that it was a temporary emigrant in $i - 1$; and

(2) γ''_i = probability that an animal in the study area in period $i - 1$ moves out of the study area for period i (Kendall et al. 1997; Fig. 2).
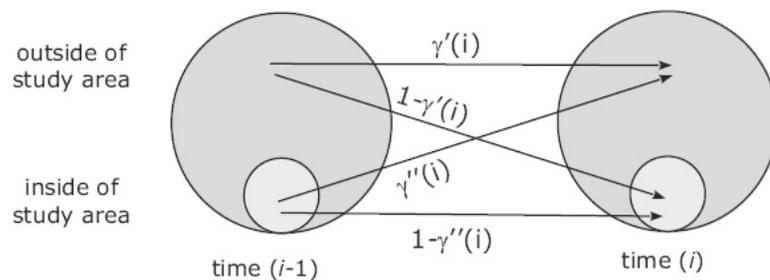
Figure 2. Relationships between γ' and γ''. The large circle represents the range of the superpopulation. The small circle (light grey) represents the fraction of the population available for capture (i.e., in the study area), whereas the darker part of the larger circle represents individuals unavailable for capture. Figure courtesy of 'Program MARK: A Gentle Introduction.'

The effect of Markovian temporary emigration on closed- and open-population estimates depends on the relationship between γ'_i and γ''_i, the change in this relationship over time,

and the size of the surface population prior to the initiating sampling (Kendall et al. 1997, Kendall 1999).

Pollock's robust design model estimates for *D. quadramaculatus* were obtained by using all 18 sampling occasions. All models assumed fixed apparent survival probability over primary periods using the survival probability value obtained from the best-fit CJS open-population model ($\varphi(.)=0.93$). Although published annual survival rates for salamander species are sparse, existing estimates suggest that annual survival rates are above 45% (Organ 1961, Tilley 1980, Hairston 1983). This translates to $\varphi(.)\approx0.93$ between our primary periods, assuming that survival is constant within a year. Goodness-of-fit models are not currently possible for robust design in program MARK. We used program MARK to fit 12 robust design models to the capture histories of *D. quadramaculatus* individuals. The three general categories of models were differentiated according to type of temporary emigration (i.e., no temporary emigration, random temporary emigration, and Markovian temporary emigration), and varied according to constant or time-specific capture and recapture probabilities. A quick reference for the 12 robust design models is provided in Table 3.

Model selection and parameterization can play vital roles in determining the demographic parameters of target populations. We compared parameter estimates obtained from closed-population models, open-population models, and robust design models to ascertain the most appropriate model for estimating demographic parameters of larval salamander populations. Lastly, we used Pollock's robust design model to evaluate the importance and type of temporary emigration in a 'secretive' salamander group and to distinguish the difference between the surface population size and superpopulation size.

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TABLE 3. A reference chart and model selection results for parameter variations of 6 competing closed-population models, 4 competing open-population models, and 12 competing robust design models. Closed-population analysis was applied to populations of *D. quadramaculatus*, *D. monticola*, and *G. porphyriticus* at Coweeta Hydrologic Laboratory LTER site in 2008; only the results for *D. quadramaculatus* are shown (closed-population analysis results for *D. monticola* and *G. porphryticus* are provided in Table 4 and Table 5). Open-population and robust design model selection results are shown for *D. quadramaculatus*. Closed-populations and open-population models were evaluated using Akaike's Information Criteria corrected for small sample size and overdispersion (QAIC$_c$). Robust design models were evaluated using Akaike's Information Criteria (AIC$_c$). Symbols: M=Markovian; R=random; (.)=constant; (t)=time-specific.

Model	# of parameters (K)	Temporary Emigration		Capture prob. (p)		Recapture prob. (c)			Survival prob. (φ)		Abundance (N)	Akaike weight (*w$_i$*)
		M	R	(.)	(t)	(.)	(t)	Equal to p	(.)	(t)	(.)	
Closed Population												
1	3			X		X					X	0.45723
2	7				X	X					X	0.36723
3	7				X		X	X			X	0.09156
4	7			X			X				X	0.04040
5	11				X		X				X	0.03180
6	2			X		X		X			X	0.01178
Open Population												
1	2			X					X			0.85052
2	6				X				X			0.09188
3	6			X						X		0.05266
4	9				X					X		0.00494
Robust Design												
1	6	X		X		X					X	0.43769
2	8		X	X		X					X	0.34928
3	11	X		X			X				X	0.06862
4	11	X			X	X					X	0.05332
5	13		X	X			X				X	0.05105
6	13		X		X	X					X	0.02946
7	16	X			X		X				X	0.007
8	18		X		X		X				X	0.00359
9	8				X	X					X	0.0
10	13				X		X				X	0.0
11	3			X		X					X	0.0
12	8			X			X				X	0.0

CHAPTER 3
RESULTS

A total of 1298 salamanders of five species were captured and marked during our three-month study. The five salamander species captured were *D. quadramaculatus* (N=326), *D. ocoee* (N=150), *D. monticola* (N=69), *G. porphyriticus* (N=51), and *E. wilderae* (N=702). Individual encounter histories could not be compiled for *E. wilderae* because most captured animals were too small to mark (<15 mm SVL). Of the total individuals captured, 62% of *D. monticola,* 38% of *D. ocoee*, 78% of *G. porphyriticus*, and 83% of *D. quadramaculatus* were sufficient in size to mark.

For *D. quadramaculatus* and *G. porphyriticus*, closed-population models demonstrating the highest level of fit assumed constant capture and recapture probabilities (Model 1; QAIC$_c$ w_i=0.457 for *D. quadramaculatus*, Table 3; QAIC$_c$ w_i=0.58 for *G. porphyriticus*, Table 4). However, the model containing time-specific capture probability and constant recapture probability also had a high Aikake weight for both species (Model 2; QAIC$_c$ w_i=0.367 for *D. quadramaculatus*; QAIC$_c$ w_i=0.199 for *G. porphyriticus*). Therefore, model averaging of Models 1 and 2 was used to estimate abundance and capture and recapture probabilities. Model-averaged capture probabilities for *D. quadramaculatus* and *G. porphryiticus* are 0.53 ± 0.02 and 0.42 ± 0.06, respectively. Model-averaged recapture probabilities for *D. quadramaculatus* and *G. porphryiticus* are 0.026 ± 0.007 and 0.008 ± 0.009, respectively. Estimated densities are 5.97 *D. quadramaculatus* individuals/m^2 and 0.80 *G. porphyriticus* individuals/m^2. Model 2 containing time-specific capture probability and constant recapture probability fit the *D.*

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monticola population better than competing models (QAIC$_c$ w_i=0.34; Table 5). However, Model 1 (QAIC$_c$ w_i=0.275) containing constant capture and recapture probabilities and Model 6 (QAIC$_c$ w_i=0.248) containing equal and constant capture and recapture probabilities also had high Aikake weights. Model-averaged capture and recapture probabilities are 0.646 ± 0.038 and 0.068 ± 0.025, respectively. We obtained a density estimate of 0.816 *D. monticola* individuals/m^2. Because QAIC$_c$ > 2.0 for *D. ocoee* and thus did not demonstrate model fit, we used Schnabel's Method to calculate abundance for this species. Density estimates yielded approximately 3.78 individuals/m^2.

Because we captured few *D. ocoee, D. monticola,* and *G. porphyriticus,* we were unable to conduct open population analysis or Pollock's robust design for these species. The CJS open-population model containing constant survival and capture probabilities (Model 1; QAIC$_c$ w_i=0.851) fit the *D. quadramaculatus* data better than competing models (Table 3). Survival probability was very high as predicted (0.928 ± 0.168), and capture probability was very low (0.031 ± 0.015) compared to the estimate obtained from closed-population analysis.

Our robust design model analysis revealed strong evidence for temporary emigration. The model containing Markovian temporary emigration with constant capture and recapture probabilities (Model 1; QAIC$_c$ w_i=0.438; Table 3) was favored over any models containing random temporary emigration or no temporary emigration. However, the model containing random temporary emigration also had a very high Akaike weight (Model 2; QAIC$_c$ w_i=0.349) and produced almost identical parameter estimates. Thus, we used model averaging to produce estimates of surface population abundance and capture and recapture probabilities. The parameter estimates of temporary immigration and

emigration between primary periods were very high (γ'=0.955 ± 0.019; γ''=0.952 ± 0.020) and almost identical; thus, we were unable to distinguish between the two types of temporary emigration. Because the estimates of γ' and γ'' were similar with overlapping confidence intervals, the probability that an animal stays away from the study area in i, given that it was a temporary emigrant in i-1, is just as likely as the probability that an animal in the study area in i-1 moves out of the study area for period i. In other words, the probabilities were the same for a salamander to remain unavailable for capture than for a salamander to emigrate to a location inaccessible to sampling efforts. According to the model averaging of Models 1 and 2, the average surface population density is 1.30 individuals/m^2, which is less than the closed-population density estimate of 5.97 individuals/m^2. Capture probability is 0.432 ± 0.042, and recapture probability is 0.063 ± 0.012.

The model containing no temporary emigration produced a smaller capture probability (0.011 ± 0.002), an identical recapture probability (0.063 ± 0.012), and a significantly larger surface density estimate (24.6 individuals/m^2). Table 6 illustrates the variation among estimates of abundance, density, capture probability, and recapture probability obtained for *D. quadramaculatus* from different types of models (closed-population, open-population, robust design). Robust design models that included temporary emigration yielded the lowest population estimates. We feel these models estimated the population of salamanders near the surface and available for capture at a given sampling occasion (i.e., surface population). Closed-population models and robust design models that did not incorporate temporary emigration yielded higher estimates. We believe the robust design model without temporary emigration estimated the

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superpopulation size. Using the robust design, the temporary emigration probability, γ"=0.952 ± 0.020, was incorporated to estimate the superpopulation density of *D. quadramaculatus* individuals as 27.1 individuals/m^2, which resembled the estimate from robust design without temporary emigration.

TABLE 4. Model selection results from analysis of mark-recapture closed-population of *Gyrinophilus porphyriticus* at the Coweeta Hydrological Laboratory LTER site in 2008.

Model	Number of parameters (K)	Akaike weight (w_i)
{N, p(.), c(.)}	3	0.58009
{N, p(t), c(.)}	7	0.19919
{N, p(.)=c(.)}	2	0.12905
{N, p(.), c(t)}	7	0.04006
{N, p(t)=c(t)}	7	0.03972
{N, p(t), c(t)}	11	0.01188

TABLE 5. Model selection results from analysis of mark-recapture closed-population of *Desmognathus monticola* at the Coweeta Hydrological Laboratory LTER site in 2008.

Model	Number of parameters (K)	Akaike weight (w_i)
{N, p(t), c(.)}	7	0.34027
{N, p(.), c(.)}	3	0.27544
{N, p(.)=c(.)}	2	0.2479
{N, p(t)=c(t)}	7	0.11412
{N, p(t), c(t)}	11	0.01155
{N, p(.), c(t)}	7	0.01071

TABLE 6. Population parameter estimate comparisons between closed-population, open-population, and robust design models for *D. quadramaculatus* at the Coweeta Hydrological Laboratory LTER site in 2008. Note: 'γ' refers to temporary emigration.

Model	Parameters			
	Capture probability (p)	Recapture probability (c)	Abundance across 6 streams (N)	Density (individuals/m²)
Closed population	0.53 ± 0.02	0.026 ± 0.007	358.04 ± 39.67	5.97
Open Population	0.03 ± 0.015			
Robust Design (including γ)	0.43 ± 0.04	0.063 ± 0.012	78.04 ± 3.23	1.3
Robust Design (no γ)	0.011 ± 0.002	0.063 ± 0.012	1475.74 ± 326.27	24.6

CHATPER 4
DISCUSSION

Estimation of abundance is an essential component of ecological studies and wildlife monitoring and management programs. There are numerous estimation methods available for wildlife, and the accuracy of a method depends upon its underlying assumptions and how these assumptions relate to the ecology of the species of interest. Population size estimates derived from count data and mark-recapture methods varied significantly for a population of larval stream salamanders found in the Appalachian headwater streams at the Coweeta Hydrological Laboratory site. An inspection of the assumptions of count-based indices and closed- and open-population mark-recapture models can explain why there is such variation in abundance estimates.

Abundance estimates based on count indices assume that there is a constant, linear relationship between the index and true population size and that detection probability is perfect (i.e., the probability of detecting an individual of a particular species is 1.0) and/or constant. For one of the most abundant larval plethodontid species in our sampling areas, *D. quadramaculatus*, our average density estimates from closed-population and robust design analyses (5.87 individuals/m^2 and 1.30 individuals/m^2, respectively) exceeded our average density estimate generated from counts (0.88 individuals/m^2) by factors of 8 and 1.5, respectively. This discrepancy is not attributable to greater capture rates because our densities based on count data are comparable to the results from previous studies (Burton and Likens 1975, Barr and Babbitt 2002a, Johnson and Wallace 2005). These

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comparisons are evidence that studies relying solely on count data tend to produce results that are significantly low-biased.

The inflated density estimate derived from the closed-population model (5.87 individuals/m^2) compared to that of robust design model (1.30 individuals/m^2) could be the result of the inherent assumptions of the closed-capture model. All closed-population models assume the population is closed over sampling occasions, with no mark loss or observer bias. Marking studies have shown that elastomer mark loss and misidentification are rare (Davis and Ovaska 2001, Bailey 2004); thus the assumptions regarding mark retention and identification were possibly met. Although survival probabilities are not well known for stream salamanders, several studies of terrestrial salamanders have suggested that annual survival rates are above 45% (Organ 1961, Tilley 1980, Hairston 1983). Therefore, the survival probability during our three-month sampling period should approach 1. Correspondingly, growth rates are sufficiently low (Petranka 1998) so that we would not expect a significant number of new recruits into the population (>15 mm SVL salamanders) during our study. Thus, the discrepancy between closed-population and robust design estimates could be the result of movement of salamander larvae violating the closure assumption. Over the course of our study we did not record movement between trap sections, which suggests that linear migration is limited. We believe the movement of larvae below the surface or onto the nearby stream bank or between rocks and crevices explains the potential lack of closure. Although the closed-population model (Model 1) exhibiting best fit for the *D. quadramaculatus* and *D. monticola* data contained constant capture probability, the model containing temporal variation in capture probability (Model 2) also had a high Aikake weight for both species. Model averaging indicated temporal

variation in capture probabilities. Thus, we believe that the equal capture probability assumption was most likely violated.

The most dramatic results were 1) temporary emigration probabilities between primary periods are very high (γ'=0.955 ± 0.019; γ"=0.952 ± 0.020); and, 2) the large discrepancy between surface population and superpopulation size for *D. quadramaculatus.* Temporary emigration violates the closure assumption, but if the temporary emigration is completely random, closed-population and open-population models should yield unbiased estimates of the superpopulation in a sampling area (Bailey et al. 2004a). The superpopulation density calculated using the robust design temporary emigration probability (27.1 individuals/m^2) was significantly greater than the density estimate obtained from closed-population analysis (5.87 individuals/m^2), which suggests that the closed-population estimates are potentially biased and that temporary emigration could be non-random (i.e., Markovian). The surface density obtained from the robust design model without temporary emigration (24.6 individuals/m^2) resembles the superpopulation density.

Because model selection could not discern between Models 1 and 2 (ΔQAIC$_c$ <2.0) and estimates of γ' and γ" were similar with overlapping confidence intervals, we were unable to distinguish between the two types of temporary emigration. In our study the robust design model containing Markovian temporary emigration with constant capture and recapture probabilities (Model 1) was slightly favored over a model containing random temporary emigration with constant capture and recapture probabilities (Model 2). All models that did not include temporary emigration had zero Akaike weight, which provides strong evidence for temporary emigration. Robust design superpopulation estimates for *D. quadramaculatus* exceeded surface population estimates by 18 orders of magnitude and

closed-population estimates by 5 orders of magnitude. These density estimates certainly suggest that salamander larvae densities are extremely high in southern Appalachian streams but that the majority of individuals are impossible to detect during a given sampling period.

Some studies have recognized temporary emigration (e.g. Jung et al. 2000, Smith and Petranka 2000, Hyde and Simons 2001, Petranka and Murray 2001), and Bailey et al. (2004) has estimated its magnitude for terrestrial salamanders. Taub (1961) conducted one of the few studies to directly address the phenomenon of temporary emigration. Through experimental field cages, she found that between 2% and 32% of the total population of salamanders in a given sampling area were on the surface and available for capture during a given sampling occasion. Similar to the results of Bailey et al. (2004b), which reported that 13% of terrestrial plethodontids are available for capture at the surface, our results suggest that on average 5% of larval stream salamanders are available for capture during a given sampling period. Although our study is consistent with temporary emigration as Markovian and not random, we acknowledge that the ability to distinguish between the two types is weak due to low numbers of recaptured individuals.

Conclusions

Our results have important implications for the monitoring of stream salamander populations in that they indicate a large fraction of stream salamander populations are unavailable for capture during a given sampling occasion. Plethodontid salamanders have numerous unique attributes that designate them as prospective indicators of biodiversity and ecosystem integrity, e.g. longevity, small territory size, site fidelity, sensitivity to natural

and anthropogenic disturbances, and tendency to occur in high densities (Welsh and Droege 2001). The failure to consider temporary emigration can lead to significantly low-biased estimates of population size, which in turn diminishes the importance of stream salamanders in ecosystem processes. In addition, our results suggest that capture probability is <1 for individual salamanders and can vary temporally due to seasonal behavioral patterns and changing environmental conditions; therefore, studies should not assume constant or perfect detection without first testing this assumption. This is consistent with the results of previous studies (Hyde and Simons 2001, Bailey et al. 2004b), which have also indicated that detection can vary through space and according to species and behavior. Mark-recapture estimation methods are costly and time-consuming compared to simple count indices, but our results emphasize the importance of incorporating variability in capture probability and temporary emigration rates instead of relying on unadjusted observed occupancy data.

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