

ESTIMATING DETECTION PROBABILITY PARAMETERS FOR PLETHODON SALAMANDERS USING THE ROBUST CAPTURE–RECAPTURE DESIGN

LARISSA L. BAILEY,^{1,2} Cooperative Fish and Wildlife Research Unit, Department of Zoology, North Carolina State University, Campus Box 7617, Raleigh, NC 27695-7617, USA

THEODORE R. SIMONS, Cooperative Fish and Wildlife Research Unit, Department of Zoology, North Carolina State University, Campus Box 7617, Raleigh, NC 27695-7617, USA

KENNETH H. POLLOCK, Department of Statistics, Biomathematics, and Zoology, North Carolina State University, Campus Box 7617, Raleigh, NC 27695-7617, USA

Abstract: Recent concern over global amphibian population declines has highlighted a need for more extensive, rigorous monitoring programs. Two sources of variation, spatial variation and variation in detection probability, make the design and implementation of effective monitoring programs difficult. We used Pollock's robust design in a 3-year capture–recapture study to estimate detection probability and temporary emigration for *Plethodon* salamanders in Great Smoky Mountains National Park (Tennessee/North Carolina), USA. We used 12 competing models to determine the importance of temporary emigration, and we explored temporal and behavioral effects on conditional capture probabilities. The top 4 models all included random temporary emigration, and Akaike model weights indicated that this parameter was the most important. Models that contained behavioral effects in capture probabilities were selected more often than models with equal capture probabilities for marked and previously unmarked individuals. The "best" model contained random emigration and behavioral effects and was selected 4 times as often as any other model. When we included Markovian emigration, the probability of emigrating from the surface usually was less than the probability of remaining an emigrant (73% of site-years). Markovian emigration estimates often were similar and always had overlapping confidence intervals, thus the Markovian model rarely was chosen over the random emigration models (only 9.6% of site-years). Our study is the first to formally estimate temporary emigration in terrestrial salamander populations, and our results verify that significant proportions of terrestrial salamander populations are subterranean. We determined that the probability of capturing salamanders on the surface may also vary temporally within a sampling season. Therefore, we caution against using unadjusted count indices to compare salamander populations over time or space unless detection probabilities are estimated. Temporary emigration models will improve abundance estimates when a large proportion of the population is unavailable for capture during a given sampling period.

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Concern over amphibian populations has increased steadily in recent years with evidence of global-scale declines (Houlahan et al. 2000, Alford et al. 2001) and the unexplained disappearances of entire groups of species (Wake 1991, Blaustein et al. 1994). These declines have highlighted a need for more extensive and rigorous monitoring programs to detect and determine the causes of population declines (Heyer et al. 1994). Numerous organizations are attempting to document, measure, and monitor amphibian populations, especially those populations believed to be in decline (e.g., Amphibian Research and Monitoring Initiative, North American Amphibian

Monitoring Program, Partners in Amphibian and Reptile Conservation, Declining Amphibian Populations Task Force, and U.S. state and federal agencies). Amphibians can be categorized into 2 broad classes: aquatic (both pond breeding and streamside) or terrestrial (those with direct larval development or those that breed in small terrestrial water sources such as bromeliads). We described methods for estimating detection probability for terrestrial amphibians, specifically *Plethodon* salamanders. However, the methods could be applied to many aquatic amphibians or other species in which the population available to sampling is a subset of the total population inhabiting a given area.

Plethodon salamanders recently have been promoted as excellent indicators of biodiversity and forest ecosystem integrity (Welsh and Droege 2001). They are relatively long-lived, slow to mature, and

¹ Present address: Patuxent Wildlife Research Center, 11510 American Holly Drive, Laurel, MD 20708, USA.

² E-mail: lbailey@usgs.gov

have lower fecundity than most anurans (Petranka 1998). Plethodon salamanders are susceptible to a variety of natural and anthropogenic perturbations (see Welsh and Droege 2001 for a review) in part due to their permeable skin that is used for both respiration and osmoregulation.

The lack of long-term population studies and a generally poor understanding of the precision and accuracy of salamander sampling methods have hindered efforts to establish effective, large-scale monitoring programs (Hyde and Simons 2001, Pollock et al. 2002). Two sources of variation must be incorporated into a good monitoring design: spatial variation and detectability (Yoccoz et al. 2001, Pollock et al. 2002). A good spatial sampling design involves selecting sample units in a manner that permits inference about the entire area of interest (e.g., stratified random sample). Additionally, because not all animals are detected in a sampled area, monitoring programs must incorporate methods for estimating or removing effects of variations in detection probabilities (Pollock et al. 2002).

While some salamander studies incorporate a spatial design (e.g., Hyde and Simons 2001), few estimate detection probabilities (but see Tilley 1980, Jung et al. 2000, Smith and Petranka 2000, Salvadio 2001). Instead, most studies use a variety of sampling methods that produce relative abundance indices (usually count data) to estimate and compare population trends over time or space. Using count statistics as indices of abundance generally is unwarranted (Nichols and Conroy 1996, Yoccoz et al. 2001, Pollock et al. 2002). Two critical assumptions must be met for comparisons of indices to be valid. (1) A direct linear relationship must exist between the index and population size (i.e., the expected value of the count is directly proportional to population size):

$$E[C] = \beta \leftrightarrow N \text{ or } \hat{N} = \frac{C}{\beta}$$

for a known area, where C = number of individuals counted or caught, β = probability of detection, and N = population size. (2) The probability of detection must be constant over time and space:

$$E[C_1/C_2] = \beta_1 \leftrightarrow N_1/\beta_2 \leftrightarrow N_2 \approx N_1/N_2$$

if and only if $\beta_1 = \beta_2$ (Lancia et al. 1994).

The assumption of constant detection probability is unlikely to be met for many terrestrial salamanders because detection probability is thought to vary for several reasons. First, the cap-

ture probability for salamanders near the surface may vary spatially due to habitat characteristics or temporally with changing environmental conditions. Furthermore, terrestrial salamander populations are believed to be largely subterranean, with only a few individuals near the surface and available for capture on a given sampling occasion (Taub 1961, Heatwole 1962, Petranka and Murray 2001). Site-specific habitat characteristics, environmental conditions, or seasonal behavioral patterns may influence the size of the available surface population.

Estimation of salamander detection probability has several key elements. First, a distinction is made between the "surface population" and the "superpopulation" of salamanders associated with a sampled area. We define surface population as the population of salamanders near the surface and available for capture during a given sampling period. Superpopulation refers to the population of salamanders both near the surface (available for capture) and subterranean individuals (unavailable for capture) within the sampled area.

Two parameters influence salamander detection probability:

(1) Conditional capture probability (p_i^*) is the probability that an animal is captured given that it is near the surface during sampling period i ($i = 1, 2, \dots, k$, where k = total number of sampling occasions).

(2) Temporary emigration probability (γ_i^*) is the probability that an animal is alive but not available for capture during sampling period i ($i = 1, 2, \dots, k$, where k = sampling occasions). In our study, we restricted horizontal emigration (see Methods) and assumed that temporary emigration involves salamanders moving temporarily below the surface.

Thus, the probability of detecting a given salamander in the superpopulation at a particular time is the product $(1 - \gamma_i^*) \leftrightarrow p_i^*$. This probability of detection, referred to as the effective capture probability (Kendall 1999), is the capture probability reported in most salamander capture-recapture studies (e.g., Jung et al. 2000). Not surprisingly, effective capture probability estimates usually are low (often < 0.10) and result in population estimates with large confidence intervals (e.g., Howard 1987).

The occurrence of temporary emigration often violates key assumptions for both open- and closed-population capture-recapture models.

Closed-population models assume that neither emigration nor immigration occurs within the sampling area during the study. Open-population models, such as the Jolly-Seber (JS) model (see Seber 1982), assume that all emigration from the sampling area is permanent (see Pollock et al. 1990). Violations of these assumptions result in biased estimates of population parameters. The presence, severity, and direction of the bias depend on the proportion of emigrants and whether the emigration is completely random or Markovian (Kendall and Nichols 1995, Kendall et al. 1997, Kendall 1999, Potak-Zehfuss et al. 1999).

Our objectives were to use a robust capture–recapture design to estimate temporary emigration, conditional capture probability, recapture probability, effective capture probability, and surface population size for terrestrial salamander populations. We fit 3 years of capture–recapture data from plots in Great Smoky Mountain National Park (GSMNP) to 12 competing models using program MARK (White and Burnham 1999) to test a series of a priori hypotheses about salamander population parameters. We predicted a high prevalence of temporary emigration at all sites and explored whether temporary emigration was random or Markovian. Additionally, we explored whether conditional capture probabilities showed any time or behavioral effects (trap-shy or trap-happy response). Finally, we tested whether surface population size estimates varied across primary sampling periods.

STUDY AREA

Great Smoky Mountains National Park, USA, is at the forefront of efforts to develop long-term natural resource inventory and monitoring on National Park Service lands. Located along the Tennessee–North Carolina border, GSMNP is internationally recognized for its rich temperate forest biodiversity. Geography and geology, along with steep, complex topography, create temperature and moisture gradients across the GSMNP's 205,665 ha of contiguous forest. These gradients produce high levels of temperate species diversity in many taxa, including salamanders. Approximately 10% of the world's salamander species are found in the southern Appalachian region (Petranka 1998). These salamanders are a high priority taxon for GSMNP's inventory and monitoring program due to the high diversity, large number of endemic species, and the limited amount of data on the distribution, abundance, and natural history of most species.

METHODS

Types of Temporary Emigration

Completely Random Emigration.—Completely random temporary emigration implies that animals move into and out of the study 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 animals associated with the sampled area:

$$E[N_i / N^*] = (1 - \gamma_i^*) N^*.$$

In our study, individuals could move in and out of the study area vertically, but their horizontal movement was restricted. Temporary emigration thus refers to an individual's movement down into the soil, where temporary emigrants were unavailable to surface sampling techniques. The probability that a salamander is near the surface at time i does not depend on its location at time $i - 1$. If temporary emigration exists within the study period, but is completely random, then population estimates from open- (JS) or closed-population models (Otis et al. 1978) are unbiased, but apply to the superpopulation not the surface population (Kendall and Nichols 1995, Kendall et al. 1997, Kendall 1999). In the presence of random temporary emigration, effective capture probability is lower and precision on all other parameter estimates is reduced.

Markovian Emigration.—Markovian emigration represents a situation where the probability that an animal is in the study area (i.e., available for capture) during primary period i depends on whether the animal was in (or out of) the study area at sampling occasion $i - 1$. In the case of Markovian emigration, 2 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).

Forming generalizations about the effect of Markovian temporary emigration (within a specified study period) is difficult using either open- or closed-population estimates because the potential bias strongly depends on the relationship between γ_i' and γ_i'' , the change in this relationship over time, and the available proportion of the super-

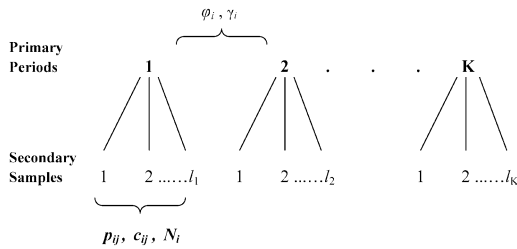


Fig. 1. Pollock's (1982) robust design for a k -period study. Each primary period i contains l_i closely-spaced secondary samples. Conditional capture probability (p_{ij}), recapture probability (c_{ij}), and surface population size (N_i) are estimated over secondary samples using closed-population models. Survival (ϕ_i) and temporary emigration rates (γ_i) are estimated between primary periods using open-population models (e.g., Jolly-Seber). Our salamander study contained capture–recapture data from 14 sites in 1999 and 19 sites in 2000 and 2001 (52 site-years). All site-years contained 4 primary periods each with 3–4 secondary samples (consecutive sampling days).

population in the study area prior to the start of sampling (Kendall et al. 1997, Kendall 1999).

Pollock's Robust Design

Recent advances in capture–recapture theory have resulted in models that incorporate and estimate both types of temporary emigration (Kendall et al. 1997, Kendall 1999). Data collected using Pollock's (1982) robust design are most appropriate for these models. Under the robust design, primary sampling periods, i , contain l_i secondary sampling periods that are separated by a time interval short enough to assume the population is effectively closed (i.e., no births, deaths, immigration, or emigration; Fig. 1). Primary periods are separated by longer time intervals during which population additions (immigration and births) and deletions (emigration and deaths) are likely to occur (Fig. 1). Data from secondary samples within each primary period can be analyzed using closed-population models that allow for unequal capture probability (Otis et al. 1978, White et al. 1982). The closed-population models estimate conditional capture probabilities, recapture probabilities, and surface population size for each primary period. Data within each primary period are pooled to estimate survival rates and both primary and secondary period information is used to estimate temporary emigration rates (Fig. 1; Kendall and Nichols 1995, Kendall et al. 1997, Kendall 1999).

Field Methods

We designed our field methods to test the efficacy of several common salamander abundance

indices and estimate different components of salamander detection probability. Individual capture histories for all salamanders at each site were used to estimate population parameters from capture–recapture models. We then compared population size estimates derived from these models to relative abundance indices from paired, independent sites to determine whether a constant, linear relationship existed for any of the indices. In this paper, we present only the robust capture–recapture results. The efficacy of relative abundance indices and a comparison among different capture–recapture models is the subject of companion papers (Bailey 2002, Bailey et al. unpublished data).

From 1999 to 2001, we sampled salamanders from 15 \leftrightarrow 15-m plots within the Roaring Fork Watershed (Mt. LeConte U.S. Geological Survey Quadrangle). We sampled 15 plots in 1999 and 20 plots in 2000 and 2001. Plots were located off-trail, but near permanent Global Positioning System-referenced census points where both large and fine-scale vegetation and soil information had been collected prior to our study. Each plot was enclosed with a silt fence to inhibit horizontal salamander movement to or from the plot. We raked the perimeter of each plot and buried the bottom edge of the silt fence 10–15 cm into the soil around the perimeter of each plot. The remainder of the fence was raised and stapled to 60 cm tall wooden stakes. We draped the top 15 cm of the fence toward the inside of the plot, creating a lip to make it difficult for salamanders to crawl over the fence and escape. We established 3 parallel transects, following the method of Hyde and Simons (2001), to estimate relative abundances. Within each plot, we established a natural-cover transect (15-m long \leftrightarrow 3-m wide), 5 coverboard arrays (placed 3 m apart along a 15-m transect), and 5 leaf-litter search locations (1 \leftrightarrow 1 m; placed 3 m apart along a 15-m transect).

We collected capture–recapture data from each plot during 4 primary sampling periods between early April and mid-June. Each plot was sampled for 3–4 consecutive days (secondary periods) within each primary period (Fig. 1). Primary periods were separated by 6–10 days. The sampling order of the plots was rotated so that plots were not searched at the same time each sampling day. Plots were not searched when it was raining.

During each sampling occasion, we sampled the 3 transects first, turned the remaining natural cover next, and searched the inside edge of the fence last. This procedure ensured that every

salamander on the surface had a probability of being captured. We marked the location of individual salamanders as they were caught and recorded the following information for each individual: species, presence of previous marks, snout-vent length (SVL), substrate under which the individual was caught, and age and sex (if possible). All unmarked salamanders over 18 mm SVL were individually marked using fluorescent elastomer (Northwest Marine Technology, Inc., Shaw Island, Washington, USA). Individuals were marked uniquely by injecting a small amount of elastomer at up to 4 body locations (base of each limb) using 3 elastomer colors (yellow, red, orange; Jung et al. 1997, Hyde 2000). Recent studies show that elastomer markings have good long-term retention, minimal marking effects, and meet the assumptions required in capture-recapture studies (Davis and Ovaska 2001, Bailey in press). Permutations of colors and position allowed the salamanders to be uniquely identified on all future capture occasions. We sterilized injection syringes with alcohol between each marked salamander. After marking, the animals were released at the marked plot locations where they were caught.

Demographic Closure and Heterogeneity

A variety of models can be fit to data collected using Pollock's robust design. Those that include temporary emigration parameters are detailed in Kendall and Nichols (1995) and Kendall et al. (1997). Most temporary emigration models assume demographic closure over secondary samples, and no heterogeneity in capture probabilities. We used program CAPTURE (Otis et al. 1978, Rexstad and Burnham 1991) to fit our 1999 data to a series of closed-population models to explore for the presence of heterogeneity and violations of the closure assumption over secondary sampling periods. Program CAPTURE selects a "best" model from a set of 8 closed-population models in which capture probability may vary due to time (t), heterogeneity (h), and trap response (b) in all possible combinations (M_o , M_b , M_h , M_t , M_{bh} , M_{bt} , M_{th} , M_{tbh} ; Otis et al. 1978). In addition, program CAPTURE performs a test for demographic closure using M_h as the null hypothesis (Otis et al. 1978). Other closure tests are available (Stanley and Burnham 1999), but these tests use model M_t as the null model in the absence of behavioral effects. We found this model extremely unlikely given our data.

Kendall et al. (1997) derived an additional ad hoc estimator for random temporary emigration

when capture probabilities are heterogeneous. This method requires many recaptured individuals; thus, we used data from 1 of our best sites to calculate ad hoc temporary emigration estimates and compared them to temporary emigration estimates obtained from the method described below.

Model Description and Selection

We developed 12 models to test our a priori hypotheses about salamander population parameters. The models have variations of the following basic parameters:

N_i = available, surface population size during primary period i ($i = 1, 2, 3, 4$);

γ_i = probability of temporary emigration (probability of being absent from the study area) for primary period i ($i = 1, 2, 3, 4$);

p_{ij} = probability that a salamander is captured on secondary sampling occasion j of primary period i , given that the salamander is available for capture (conditional capture probability); and

c_{ij} = probability that a salamander is recaptured during secondary sampling occasion j in primary period i , given that the salamander was available for capture.

Conditional capture and recapture probabilities are assumed to be constant over secondary samples, but may vary among primary periods. More general models are theoretically possible (see Kendall et al. 1997), but the combination of small sample sizes and low detection probabilities often did not allow us to explore more complex models. All 12 models assumed that fixed apparent survival rate over primary periods is 1 (i.e., $\phi(\cdot) = 1$). Initially, we tried to estimate $\phi(\cdot)$ with a more general model, but $\phi(\cdot)$ estimates were often nonsensical and unstable. While published annual survival rates are lacking for most terrestrial salamander species, estimates that do exist suggest that annual survival rates are above 45% (Organ 1961, Tilley 1980, Hairston 1983). Primary periods in our study were separated by only 6–10 days, suggesting that survival rates should be near 1. Even a conservative annual survival estimate of 30% would translate to $\phi(\cdot) \approx 0.955$ between primary periods, assuming that survival was constant within a year. A more realistic value of 50% would translate to $\phi(\cdot) \approx 0.974$. We substituted an ultra-conservative survival rate between primary periods of $\phi(\cdot) = 0.95$ into our best model to verify that this level of survival rate reduction had negligible effects on detection probability estimates. We used program MARK

Table 1. Reference chart for parameter variations of 12 competing models.

Model	Parameters							
	Temporary emigration		Capture probabilities				Surface population size	
	None $\gamma(.) = 0$	Random $\gamma(.)$	Constant time No trap response $p(..) = c(..)$	Time- specific No trap response $p(i.) = c(i.)$	Constant time Trap response $p(..), c(..)$	Time- specific Trap response $p(i.), c(i.)$	Constant time $N(.)$	Time- specific $N(i)$
							$N(i)$	
1		X			X		X	
2	X				X		X	
3		X				X	X	
4		X				X		X
5	X					X	X	
6	X					X		X
7		X		X			X	
8		X		X				X
9	X			X			X	
10	X			X				X
11		X	X				X	
12	X		X				X	

(White and Burnham 1999) to fit the following 12 models to the capture histories for each site in each year. A quick reference for the 12 models is provided in Table 1.

Models 1 and 2.—Constant conditional capture probability ($p(..)$); constant recapture probability ($c(..)$); constant surface population ($N(.)$); and either constant random temporary emigration ($\gamma(.)$; Model 1), or no temporary emigration ($\gamma(.) = 0$; Model 2). These models are equivalent to the closed-population behavioral model M_b over secondary samples (Otis et al. 1978) and JS open-population Model D for primary periods (Pollock et al. 1990).

Models 3 and 4.—Conditional capture probabilities vary across primary periods ($p(i.)$); constant recapture probability; constant random temporary emigration; and either constant surface population ($N(.)$; Model 3), or time-specific surface population ($N(i)$; Model 4). These models are equivalent to closed-population behavioral model M_b and JS Model B but with random temporary emigration included.

Models 5 and 6.—Same as Models 3 and 4 but ignoring temporary emigration ($\gamma(.) = 0$).

Models 7 and 8.—Conditional capture and recapture probabilities equal and time specific ($p(i.) = c(i.)$); constant random temporary emigration; and either constant surface population (Model 7), or time-specific surface population (Model 8). These models are equivalent to closed-population null model M_o and JS Model B but with random temporary emigration included.

Models 9 and 10.—Same as Models 7 and 8 but ignoring temporary emigration ($\gamma(.) = 0$).

Models 11 and 12.—Constant and equal conditional capture and recapture probabilities ($p(..) = c(..)$); constant surface population; and either constant random temporary emigration (Model 11), or no temporary emigration (Model 12). These models are equivalent to closed-population null model M_o and JS Model D but with random temporary emigration included. Models 11 and 12 are the most restricted models possible, and although they are biologically unrealistic, they may serve as suitable null models for comparisons with more general models.

We based model selection on Akaike's Information Criterion corrected for overdispersion and small sample size (QAIC_c; Akaike 1973, Burnham and Anderson 2002). We assessed uncertainty about the best overall model across all combinations of sites and years (site-years) by tabulating the frequency that each model was selected best by QAIC_c methods. To provide further information regarding model selection uncertainty within site-years, we calculated mean Akaike weights for each model across all site-years. We assessed the relative importance of each parameter (e.g., temporary emigration) by summing mean Akaike weights across all models containing the given parameter.

Goodness-of-fit tests are not currently possible for the robust design in program MARK. We therefore fit our most general model (Model 4: $\gamma(.)$, $p(i.)$, $c(..)$, $N(i)$) to each of our datasets using program RDSURVIV (see Kendall et al.

1997 for details). Program RDSURVIV uses a cell-pooling algorithm to compute Pearson's χ^2 test statistic, and we calculated the variance inflation factor (\hat{c}) by hand for each data set (Kendall et al. 1997, Burnham and Anderson 2002).

Our a priori models have definite, and differing, interpretations with regard to understanding relationships among population processes. Thus, our purpose in using AIC methods was to select 1 model from a range of alternatives that most adequately described the data with as few parameters as possible (Burnham and Anderson 2002). We stress that these models are only an approximation of reality, chosen a priori to compare several hypotheses concerning salamander population parameters. The model selected as best does not necessarily represent all of the biological processes that influenced our salamander populations.

We used a 2-stage technique to address a priori hypotheses about variations in salamander detection probability parameters across time and space (Bailey et al. 2004, this issue). Stage 1 (described in this paper) was a model-based analysis that explored sources of variation in parameter values within our experimental units (site-years). In Stage 2, we used resulting point estimates in replication-based tests to address our a priori research hypothesis concerning variations across times and space (see Bailey et al. 2004). Using parameter estimates from different models may introduce unknown biases in these comparative tests, as mentioned by Boulinier et al. (1998); thus we fit the single best model to all site-years to obtain estimates of random temporary emigration, conditional capture probability, and average surface population size. We reported the means of these estimates here, but refer readers to Bailey et al. (2004) for more detailed, replication-based analysis. Because most capture-recapture studies of terrestrial salamanders report the effective capture probability, we used our estimates to estimate effective capture probability as $\hat{p}^o(.) = (1 - \hat{\gamma}(..))\hat{p}(..)$ for each site-year. On rare occasions, program MARK was unable to fit parameters reliably, so we only included parameter estimates when the estimate was less than the standard error of the estimate, corrected for overdispersal (Burnham and Anderson 2002).

Finally, we modified the most commonly selected model to include first-order Markovian emigration. A salamander's presence on the surface is believed to be influenced by seasonal behavioral patterns and environmental factors such as surface moisture and temperature. These influ-

ences could result in either random or Markovian temporary emigration; thus we explored the possibility of either type of temporary emigration. Due to data limitations, we assumed Markovian emigration was constant across primary periods.

RESULTS

We analyzed 14 sites in 1999 and 19 sites in 2000 and 2001 for a total sample of 52 site-years. The number of captures varied widely among site-years from 19 to 428. Mean number of marked individuals was 102.58 per site-year (SE = 11.62, $n = 52$ site-years) and 29.30 per primary period (SE = 2.06, $n = 208$ primary periods). Mean recapture rates were 18.71% (SE = 0.93%, $n = 52$) within the sampling season and 9.04% (SE = 0.54%, $n = 208$) within primary periods.

Demographic Closure and Heterogeneity

Using our 1999 data and program CAPTURE, we checked for demographic closure and the presence of heterogeneity over secondary samples. Twenty of 56 possible closed populations (14 sites each with 4 primary periods) contained at least 2 recaptures within secondary samples and could thus be used to test for closure and heterogeneity. The closure test was rejected on only 1 of 20 eligible populations. In addition, all but 2 of the 20 closed populations selected either the null model (M_0 ; chosen best 13 of 20 times) or a model with time or behavioral effects. Therefore, subsequent evaluations of robust design models assumed no heterogeneity and demographic closure over secondary samples. In addition, we suspected behavioral (trap-shy) effects to be present in conditional capture probabilities. We recognize that the tests to detect heterogeneity have low power for our field sample sizes, but homogeneous models (i.e., models without heterogeneity) allow for maximum likelihood estimation and are available in program MARK. These considerations contributed to our decision to not use models containing heterogeneous capture probabilities.

Model Selection and Parameter Estimation

Goodness-of-fit analysis using program RDSURVIV indicated that the most general model fit the data adequately for 32 of the 52 site-years (i.e., P values > 0.05), and estimates of variance inflation factors were relatively low (mean $\hat{c} = 1.86$, median $\hat{c} = 1.56$). Only 4 of the 52 site-years had \hat{c} estimates > 2.3. These results suggest that the model structure was adequate and that model parameter estimates should be unbiased; however, we

Table 2. Frequency and number of site-years ($n = 52$ total site-years) that models were selected, based on Akaike's Information Criteria adjusted for sample size and overdispersion (QAIC_c), for 12 different models explaining salamander population parameters in Great Smoky Mountain National Park, USA, 1999–2001. Mean Akaike weights across all site-years are also given for each model. The relative importance of a given parameter is found by summing mean Akaike weights for all models containing the parameter. All models assume apparent survival rate is fixed at $\phi(\cdot) = 1$. By all standards, Model 1 was selected 4 times more often than any other competing model.

	Models											
	$p(\cdot), c(\cdot)$		$p(i), c(\cdot)$				$p(i) = c(i)$				$p(\cdot) = c(\cdot)$	
	1	2	3	4	5	6	7	8	9	10	11	12
Frequency model was chosen best (total number of site-years)	0.54 (28)	0.0 (0)	0.06 (3)	0.02 (1)	0.02 (1)	0.0 (0)	0.08 (4)	0.0 (0)	0.08 (4)	0.02 (1)	0.12 (6)	0.08 (4)
Mean (SE) Akaike weight	0.41 (0.05)	0.05 (0.01)	0.11 (0.03)	0.04 (0.02)	0.04 (0.01)	0.02 (0.01)	0.09 (0.02)	0.02 (0.01)	0.05 (0.01)	0.02 (0.01)	0.11 (0.02)	0.06 (0.01)

acknowledge that slight overdispersion existed, probability due to mild heterogeneity, possibly caused by factors such as size, age, species, or sex. Thus, we reported adjusted standard errors for parameter estimates using variance inflation factors estimated for each site-year (i.e., $\sqrt{\hat{c}} \leftrightarrow \text{SE}(\hat{\theta})$).

Overall, Model 1 was selected best more often than any other competing model (Table 2). Referees expressed concern that a positive relationship may exist between the number of marked individuals (i.e., sample size) and the number of parameters in chosen models for each site-year. Burnham and Anderson (2002) found that if sample sizes increase substantially (e.g., an order of magnitude), more parameters can be reliably estimated. Sample sizes did vary considerably among site-years (range = 19–428); thus we explored the potential for an increasing, linear relationship between sample size and number of parameters in the selected model for each site-year. While we did observe a slight positive relationship, sample size accounted for little variation in the number of parameters in selected

models ($R^2 = 0.09$).

Our model-based analysis revealed strong evidence of temporary emigration and trap-shy response in capture probabilities and some evidence of temporal variation in conditional capture probabilities. Models that included a random temporary emigration parameter (Models 1, 3, 4, 7, 8, and 11) were chosen more often (80.7%) than models with no emigration terms (19.3%). Akaike weights suggest that the top 4 models all included random temporary emigration and the relative importance of this parameter was higher than any other parameter. None of the remaining models was consistently selected (<10% of site-years), nor did the remaining models have high mean Akaike weights (Table 2). Models incorporating behavioral or trap-shy effects (Models 1–6) were selected more often (63.5%) than those without behavioral effects (Models 7–12, 36.5%). The sum of mean Akaike weights for models containing behavioral effects (0.67) was nearly twice that of models without behavioral effects (0.35; Table 2). When behavioral effects were removed, estimates of condi-

Table 3. Time-specific estimates of conditional capture probability ($p(i)$), recapture probability ($c(i)$), and surface population size ($N(i)$) for salamanders on a study site in Great Smoky Mountain National Park, USA, 2000. One hundred and sixteen individuals were caught; 28 individuals were captured on >1 sampling occasion. (n = number of animals captured in each primary period). Model 4 contains time variation and behavioral (trap-shy) effects. Model 8 contains time variation but no behavioral effects. Estimates for period 1 were imprecise with high standard errors for Model 4. Standard error estimates are inflated by: $\sqrt{\hat{c}} \leftrightarrow \text{SE}(\hat{\theta})$; $\hat{c} = 1.14$. All models were evaluated using Akaike's Information Criteria adjusted for sample size and overdispersion (QAIC_c).

Primary period	n	Model 4: $\gamma(\cdot), p(i), c(\cdot), N(i)^a$						Model 8: $\gamma(\cdot), p(i) = c(i), N(i)^b$					
		$\hat{p}(i)$	$\text{SE}\hat{p}(i)$	$\hat{c}(\cdot)$	$\text{SE}\hat{c}(\cdot)$	$\hat{N}(i)$	$\text{SE}\hat{N}(i)$	$\hat{p}(i) = \hat{c}(\cdot)$	$\text{SE}\hat{p}(i) = \text{SE}\hat{c}(\cdot)$	$\hat{N}(i)$	$\text{SE}\hat{N}(i)$		
1	52	0.01	0.01	0.09	0.03	—	—	0.08	0.04	172.36	72.68		
2	34	0.58	0.13			36.14	3.53	0.18	0.07	73.77	25.23		
3	42	0.35	0.12			50.62	9.40	0.10	0.04	121.12	43.79		
4	13	0.04	0.03			96.38	81.61	0.02	0.02	161.45	75.37		

^a $\Delta\text{QAIC}_c = 0.0$; Akaike weight = 0.98.
^b $\Delta\text{QAIC}_c = 12.10$; Akaike weight = 0.00.

Table 4. Estimated rates of temporary emigration parameters ($\gamma'(\cdot)$ and $\gamma(\cdot)$) and recapture probability ($c(\cdot)$) for salamanders on 1 study site in Great Smoky Mountain National Park, USA, 2001. Fifty-seven individuals were caught; 13 individuals were captured on >1 sampling occasion. In Model 1 and Markovian, $p(\cdot)$ represents conditional capture probability; for Model 2, $p(\cdot)$ resembles an effective capture probability. In Model 1 and Markovian, $N(\cdot)$ is interpreted as surface population. Apparent survival rate is fixed at $\phi(\cdot) = 1$, and all parameters are constant across primary sampling periods. Standard error estimates are inflated by: $\sqrt{\hat{c}} \leftrightarrow SE(\hat{\theta})$; $\hat{c} = 1.66$. All models were evaluated using Akaike's Information Criteria adjusted for sample size and overdispersion (QAIC_c).

Parameter	Model 2: $\gamma(\cdot) = 0^a$		Model 1: $\gamma(\cdot)^b$		Markovian: $\gamma'(\cdot)^c$	
	Estimate	SE	Estimate	SE	Estimate	SE
$\gamma(\cdot)$			0.92	0.04	0.91	0.05
$\gamma'(\cdot)$					0.93	0.04
$p(\cdot)$	0.02	0.01	0.44	0.08	0.44	0.08
$c(\cdot)$	0.05	0.03	0.05	0.03	0.05	0.04
$N(\cdot)$	209.10	86.79	30.06	2.19	30.06	2.19

^a $\Delta QAIC_c = 17.32$.

^b $\Delta QAIC_c = 0.0$.

^c $\Delta QAIC_c = 2.20$.

tional capture probabilities declined and surface population estimates increased dramatically (Table 3). The second most likely model, judging from Akaike weights (Model 3), contained both time and behavioral effects and indicated that conditional capture probabilities may have varied among primary sampling periods.

We explored the possibility of Markovian temporary emigration by modifying our best model (Model 1) to include constant Markovian emigration. We found this model was likely ($\Delta QAIC_c < 2.0$) for 17 of the 52 possible site-years and was chosen best for only 5 site-years (9.6%). We were unable to fit the model to data from 7 site-years, primarily because the $\gamma'(\cdot)$ parameter failed to converge. Parameter estimates of $\gamma'(\cdot)$ usually were greater than $\gamma''(\cdot)$ estimates (73% of site-years), indicating that emigrants at a given time period were more likely beneath the surface during the previous time period than on the surface. In other words, we found a higher probability for an individual to remain beneath the surface than for an individual on the surface to emigrate into the soil. However, estimates of $\gamma'(\cdot)$ and $\gamma''(\cdot)$ were usually similar and their confidence intervals always overlapped, thus the Markovian emigration model was rarely favored over random temporary emigration models.

Conditional capture probability estimates were severely reduced in models without temporary emigration (Table 4). Estimates of conditional capture probability and average surface population size showed no differences among models

with random and Markovian emigration because these parameters were fit with the closed-population models across secondary samples (Table 4).

The average estimate of random temporary emigration (using Model 1) across site-years was high (0.87 ± 0.01 [$\hat{\gamma}(\cdot) \pm SE(\hat{\gamma}(\cdot))$], $n = 50$ site-years). The average conditional capture probability estimate was 0.30 ± 0.01 ($\hat{p}(\cdot) \pm SE(\hat{p}(\cdot))$; $n = 48$ site-years). Combining these 2 estimates, $\hat{p}^o(\cdot) = (1 - \hat{\gamma}(\cdot))\hat{p}(\cdot)$, yielded an effective capture probability of 0.03 ± 0.002 ($\hat{p}^o(\cdot) \pm SE(\hat{p}^o(\cdot))$; $n = 48$ site-years). Changing survival rate to $\phi(\cdot) = 0.95$ in Model 1 reduced estimates of random temporary emigration by ≤ 0.03 , and other parameter estimates were unaffected. Temporary random emigration estimates using the ad hoc estimator of Kendall et al. (1997) were similar to estimates from Model 1 (Table 5), indicating that individual heterogeneity may not have biased results on our sites.

DISCUSSION

We used Pollock's robust design (Pollock 1982) to estimate and explore a priori hypotheses about temporary emigration, conditional capture probability, and surface population size for terrestrial salamanders. We found strong evidence for temporary emigration on all of our study sites. This phenomenon has been recognized previously (e.g., Smith and Petranksa 2000, Jung et al. 2000, Hyde and Simons 2001, Petranksa and Murray 2001), but its magnitude has not been estimated. Taub (1961) conducted 1 of the few studies to address this issue directly. Through experimental field cages, she found that between 2 and 32% of the total salamanders in a given sampling area were on the surface and available for capture during a single sampling occasion. Our results suggest that on average, 13% of our salamanders were

Table 5. Estimated rates of random temporary emigration ($\gamma(i)$) for salamanders on 1 study site in Great Smoky Mountain National Park, USA, 2001. Model 1 has been modified to include time-specific random temporary emigration and contains behavioral (trap-shy) effects in conditional capture probability. Ad hoc estimates were calculated using equations 11 and 12 in Kendall et al. (1997). Ad hoc estimates allow for either heterogeneous variation or both heterogeneous and behavioral variation in conditional capture probabilities. Apparent survival rate for all estimators is assumed to be 1.

Parameter	Model 1: $\gamma(i)$		Ad hoc: M_h		Ad hoc: M_{bh}	
	Estimate	SE	Estimate	SE	Estimate	SE
$\gamma(2)$	0.63	0.15	0.58	0.09	0.71	0.10
$\gamma(3)$	0.86	0.08	0.82	0.05	0.87	0.01

available for capture during a given sampling period. Furthermore, our study is consistent with temporary emigration as a random process, rather than Markovian. However, we acknowledge our ability to distinguish between the 2 types of temporary emigration is weak because of low numbers of recaptured animals and poor precision in both $\gamma'(\cdot)$ and $\gamma''(\cdot)$ estimates. However, the trend for $\gamma'(\cdot) \neq \gamma''(\cdot)$ is interesting and warrants further investigation of biological mechanisms that would produce such a trend.

Variations in conditional capture probability govern our ability to detect salamanders at a given location. Our findings suggest that conditional capture probabilities vary due to a strong trap-shy response and possibly temporal factors that may reflect changing environmental conditions (e.g., temperature and soil moisture) or seasonal behavioral patterns. Conditional capture probabilities also may reflect temporal variation in the size of the surface populations (i.e., conditional capture probability may be a function of surface population size, $p_{i,j} = f(N_i)$).

Evidence of behavioral effects on capture probabilities suggests that estimation methods assuming equal capture probabilities (e.g., Lincoln-Peterson, Schnabel, or Schumacher-Eschmeyer methods—see Pollock et al. 1990 for details) may not be appropriate for terrestrial salamanders. These methods are highly sensitive to unequal capture probability and applying them to species exhibiting a trap-shy behavioral response often leads to an overestimate of population size (Pollock et al. 1990). As an example, our Model 8, assumed equal capture and recapture probability and produced substantially higher surface population estimates and standard errors than models incorporating behavioral effects (Table 3). Models incorporating unequal capture probabilities for marked and previously unmarked individuals were selected for most site-years (approx 63%).

Conditional capture probability and temporary emigration are confounded in estimates of effective capture probability reported in traditional capture-recapture models (Kendall et al. 1997, Kendall 1999). We used our temporary emigration and conditional capture probability estimates for each site-year to calculate effective capture probabilities that could be compared to other salamander studies. Our overall estimate (0.03 ± 0.002 ; $n = 48$ site-years) is within the range of similar studies on terrestrial salamanders (Jung et al. 2000, Smith and Petranksa 2000). Random temporary emigration will not bias estimates of effective cap-

ture probability, but it will reduce the precision of parameter estimates. Random temporary emigration also limits population estimates to the superpopulation only (Kendall 1999). This constraint is clearly illustrated by our results in Table 4 in which the population estimate under Model 2 (no temporary emigration) is 7 times the surface population estimate under identical models that contain temporary emigration terms. The precision of the Model 2 population estimate ($CV = 32.2$ [$CV = 1 \text{ SE/estimate} \leftrightarrow 100$]) is much less than that of the surface population estimates for the temporary emigration Model 1 ($CV = 3.7$). The benefits of incorporating temporary emigration into models include the ability to partition the different components of the effective capture probability, allowing more precise estimates of the surface population size.

Pollock's robust design and temporary emigration models have their own set of limiting assumptions. The models assume demographic closure and no heterogeneity in capture probabilities over secondary samples. These assumptions need to be tested before using temporary emigration models in program MARK. We tested both assumptions using the closed-population program CAPTURE. The closure test included in program CAPTURE allows heterogeneity in capture probabilities but is sensitive to the presence of time or behavioral variation (Otis et al. 1978). Other closure tests are available but assume time-specific variation in capture probabilities (Stanley and Burnham 1999). We found time variation to be the least likely of the possible capture probability effects (null, time, heterogeneity, behavior) from our analysis over secondary samples in 1999 (Bailey 2002); thus we chose to use the closure test in program CAPTURE. However, both types of closure tests are insensitive to temporary emigration when it occurs in the middle of the study, and both tests perform poorly when the number of captured animals is low (Stanley and Burnham 1999).

Heterogeneity of capture probabilities is expected in many wildlife populations due to factors such as age, sex, size, or social status (Pollock et al. 1990). Heterogeneity may be present in salamander capture probabilities due to variations among species (Petranksa and Murray 2001, Bailey et al. 2004) or age or size (Tilley 1980, Salvadio 2001) and could be the source of the slight lack-of-fit we observed in our goodness-of-fit tests. The model selection procedure in program CAPTURE yielded little evidence of heterogeneity

over secondary sampling periods. The null model (M_0) was chosen most often, but this may reflect low recapture rates and a lack of power to reject the null model. Thus, assumptions of demographic closure and no heterogeneity over secondary samples are supported for our data, but low recapture rates, typical of salamander capture–recapture studies (Jung et al. 2000, Smith and Petranksa 2000), make that support equivocal. We were able to investigate the potential impact of heterogeneous capture probabilities on 1 site-year using Kendall et al.'s (1997) ad hoc estimator. We found good consistency between the ad hoc and Model 1 temporary emigration estimates, indicating that individual heterogeneity may have a minor impact on temporary emigration estimates at our sites.

Our approach can be applied to a wide variety of organisms and environments. Kendall et al. (1997) explored situations in which terrestrial mammals might move out of a study area by temporarily migrating out of the trapping grid or retreating into burrows during a torpor state. Marine mammals may be visible only in certain locations and only when they are near the surface of the water (Marsh and Sinclair 1989, Fujiwara and Caswell 2002). Probably the most common use of temporary emigration models involves situations in which only breeding individuals are observable. Temporary emigration models have been applied to snow geese (*Anser caerulescens*; Kendall and Nichols 1995), grey seals (*Halichoerus grypus*; Schwarz and Stobo 1997), Hawksbill sea turtles (*Eretmochelys imbricate*; Kendall and Bjorkland 2001), and gulf sturgeon (*Acipenser oxyrinchus desotoi*; Potak-Zehfuss et al. 1999) in situations where the available population is composed of breeding individuals. We feel that these models have tremendous potential for pond breeding amphibians, in which breeding populations fluctuate widely with hydroperiod length (Pechmann et al. 1991, Semlitsch et al. 1996). In these situations, temporary emigration and available sample populations may vary over time, but size of the superpopulation could remain quite stable.

MANAGEMENT IMPLICATIONS

Long-term, large-scale amphibian monitoring studies currently are being planned by many organizations (e.g., Amphibian Research and Monitoring Initiative, North American Amphibian Monitoring Program, Partners in Amphibian and Reptile Conservation, and Declining Amphibian Populations Task Force). These pro-

grams likely will use relative abundance indices (count data) or capture–recapture methods to monitor population status. Detection probabilities are likely heterogeneous over time and space in these studies. Our results have 2 important management implications for programs whose objectives include monitoring salamander populations. First, our results indicate that large proportions of terrestrial salamander populations are subterranean and unavailable for capture during a given sampling occasion. Ignoring this temporary emigration will result in reduced estimates of effective capture probability and imprecise and possibly biased population estimates. The ability to estimate temporary emigration and surface populations allows us to examine how these parameters vary spatially and temporally (see Bailey et al. 2004). We believe that using unadjusted count indices to compare populations over time and space without estimating detection probability is unjustified. A second management implication of our results stems from our finding that the capture probability of individual salamanders varies due to behavioral (trap-shy) and time effects. Therefore, we caution against using capture–recapture methods that assume equal capture probability without first testing this assumption.

Admittedly, capture–recapture methods are costly compared to simple count indices. We therefore recommend a double-sampling design for large-scale studies (Pollock et al. 2002) when estimating detection probability at every sampling location is not feasible. Our suggested approach relies on a good sampling design to select a large number of sites in a variety of habitats and the use of count indices or "proportion of area" occupied as state variables (MacKenzie et al. 2002). The double-sampling design uses capture–recapture studies on a subset of reference sites to estimate detection probabilities and calibrate counts for the more extensive sampling effort. We believe that this approach may provide better monitoring data than programs based solely on count indices.

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