

SPATIAL AND TEMPORAL VARIATION IN DETECTION PROBABILITY OF PLETHODON SALAMANDERS USING THE ROBUST CAPTURE–RECAPTURE DESIGN

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Abstract: Recent worldwide amphibian declines have highlighted a need for long-term, large-scale monitoring programs. Scientific or management objectives, appropriate spatial sampling, and detectability all must be considered when designing monitoring programs (Yoccoz et al. 2001). The ability to establish meaningful monitoring programs currently is compromised by a lack of information about amphibian detection probabilities. We used Pollock's robust design and capture–recapture models that included temporary emigration to test a priori hypotheses about spatial and temporal variation in salamander detection probability parameters for populations found in Great Smoky Mountains National Park (Tennessee/North Carolina), USA. We explored the effects of 3 large-scale habitat characteristics (disturbance history, elevation, vegetation type) and found that vegetation type and elevation were correlated with detection probabilities. Vegetation type was an important covariant in estimates of temporary emigration, conditional capture probability, and surface population size. Contrasts that isolated elevation effects were significant for all detection probability parameters except recapture probability, despite our small elevational range (330 m). When detection probability parameters have the potential to vary over time and space, investigators should develop monitoring designs that permit the estimation of detection probabilities.

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Recent worldwide amphibian declines have highlighted a need for long-term, large-scale monitoring studies to establish quantitative baseline data and document species range and status. Monitoring programs should have clear objectives (e.g., periodic assessment of population status), and the monitoring design should incorporate 2 important sources of variation: spatial variation and detectability (Yoccoz et al. 2001, Pollock et al. 2002). Although some recent amphibian studies have attempted to estimate spatial variability (e.g., Hyde and Simons 2001), most lack necessary geographic and temporal scale to reliably detect spatial and temporal patterns in abundance estimates. Although amphibian monitoring initiatives are widespread (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) most current moni-

toring programs are compromised because detection probabilities are not estimated. Surface counts are believed to comprise a small and variable proportion of the total populations, and the extent to which counts correlate to the total population may be poor (Smith and Petranka 2000). To our knowledge, no previous study has rigorously explored variation in salamander detection probabilities over time or space.

Previous studies have highlighted several ways that detection probability might vary. The size of the surface population may be influenced by large-scale habitat characteristics such as vegetation type, elevation or previous disturbance history (Petranka et al. 1993, DeMaynadier and Hunter 1998, Harpole and Haas 1999, Hyde and Simons 2001), or small-scale habitat characteristics such as the type and number of cover objects (Petranka et al. 1994, Grover 1998). Surface population size at a given site is expected to change temporally due to environmental conditions (Hairston 1987, Grover 1998, Petranka and Murray 2001) or seasonal behavioral patterns (DeMaynadier and Hunter 1998, Petranka 1998). Additionally, the capture probability for salamanders near the surface (conditional capture prob-

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ability) may vary spatially with habitat characteristics such as the amount of natural cover (Grover 1998) or temporally as a result of changing moisture conditions (Heatwole 1962, Jaeger 1980). Furthermore, salamander capture probabilities likely vary among species, possibly producing heterogeneity among individual capture probabilities (Grover 2000, Petranka and Murray 2001). Therefore, the salamander community composition may influence the overall salamander detection probability at a given location.

In Bailey et al. (2004), we demonstrated the usefulness of Pollock's robust design to separate and estimate population parameters important for salamander detection. Here we used estimates from capture–recapture models in a design-based framework to test a priori hypotheses about spatial and temporal differences in temporary emigration (the probability of being temporarily unavailable for capture; i.e., below the surface), conditional capture probabilities (the probability an animal is captured given it is available), and available (or surface) population sizes. We anticipated that these 3 parameters would differ: (1) spatially with large-scale habitat characteristics (disturbance history, vegetation type, elevation); (2) temporally among years; and (3) among species groups. We expected estimates of all 3 parameters to be highest on high-elevation, undisturbed, deciduous sites. Finally, we expected temporary emigration and conditional capture probability estimates to be higher for larger salamander species.

METHODS

Study Area and Field Methods

We conducted our study in Great Smoky Mountains National Park (GSMNP), USA, located along the Tennessee–North Carolina border. Containing the largest contiguous forest (205,665 ha) in the eastern United States, GSMNP is recognized for its rich temperate ecosystem and high salamander diversity (Petranka 1998).

We restricted our sites to the Roaring Fork Watershed (Mt. LeConte U.S. Geological Survey Quadrangle) in GSMNP. Our capture–recapture sites were located near a subset of count-index sites established by Hyde and Simons (2001). Their sites were located near trails, usually within 50 m, and spaced approximately 250 m apart, beginning at a random point at least 250 m from each trail head (Hyde and Simons 2001). We selected a subset of Hyde and Simons' (2001)

sites stratified according to previous land-use history, a factor we believed could have a strong effect on salamander population size and detection probability components. Land-use history was determined from maps (Pyle 1985) that described 5 disturbance history classes: undisturbed, settlement areas, and 3 types of logging (selective, light commercial, industrial cut). All sites currently are completely forested following the establishment of GSMNP in 1934. We combined disturbance history into 2 classes: undisturbed and disturbed (settlement and all logged classes). Forest-community classifications of 90-m Landsat imagery (MacKenzie 1993) were combined into 2 vegetation types: mixed deciduous (cove hardwood, mixed mesic, tulip poplar) and mixed pine (pine-oak and pine). We assigned sites to 1 of 3 120-m elevation classes beginning at 740 m.

We captured and marked salamanders from 15 plots (15 × 15 m) in 1999 and 20 plots in 2000 and 2001. For a detailed description of plot layout and sampling methods, see Bailey et al. (2004). Plots were sampled according to Pollock's robust design (Pollock 1982, Bailey et al. 2004). From 1 April to mid-June, we searched each plot during 4 primary periods each consisting of 3–4 consecutive sample days (secondary samples). Primary periods were separated by 6–10 days. Captured animals were inspected for marks, and unmarked animals were marked with colored elastomer (Northwest Marine Technology, Inc., Shaw Island, Washington, USA) at 4 body locations for individual identification (Bailey et al. 2004).

Model Description and Selection

Numerous capture–recapture studies have demonstrated the advantages of Pollock's robust design over standard open-population sampling (Nichols et al. 1984, 1998; Kendall et al. 1995, 1997; Schwarz and Stobo 1997). A variety of models can be fit to data collected in this manner, including models that estimate temporary emigration (Kendall and Nichols 1995, Kendall et al. 1997). In previous studies, we used model-based analysis to test a priori hypotheses about the nature and importance of different salamander detection probability parameters within our experimental units (site-years; referred to as Stage 1 in Bailey et al. 2004). The series of a priori models had definite—and differing—interpretations with regards to understanding relationships among population processes. Our data supported one model as convincingly best across site-years using 2 different model selection strate-

gies (Bailey et al. 2004). This best model contained seasonally invariant random temporary emigration ($\gamma(\cdot)$) and average surface population size ($N(\cdot)$) and included a trap-shy behavioral response with different conditional capture ($p(\cdot)$) and recapture ($c(\cdot)$) probabilities. We used this model to test for changes in salamander population parameters across time and space because: (1) the model was 4 times more likely than any other competing model, based on 2 different selection criteria; (2) parameter estimation under this model was possible for nearly all sites in all years; and (3) the model allowed us to test our a priori hypotheses on sites with both high and low temporary emigration rates.

Next, we used replication-based tests (Stage 2) with our model-based point estimates, to address our a priori research hypotheses about the effects of large-scale habitat characteristics and time. Our purpose was to focus on variation in parameter estimates over datasets in a planned, design-based approach. The 2-stage technique currently is favored by several authors (Coffman et al. 2001, Schwarz 2002, Williams et al. 2002:493) but is not without problems (see Link 1999). Incorporating "random effects" into capture-recapture models is an active field of research (Burnham and White 2002, Burnham and Anderson 2002, Schwarz 2002), and better approaches likely will be developed. However, given the current state of theoretical development, we feel that our 2-stage method is reasonable.

Summary of the Analysis

We used program MARK (White and Burnham 1999) to compute parameter estimates under our chosen model for each site in each year (site-year). We modeled parameter estimates as a function of large-scale habitat characteristics chosen (previous disturbance history, vegetation type, elevation class). These habitat characteristics often are confounded within GSMNP because disturbed sites usually are found at lower elevations. In addition, one of our disturbed, mixed-pine sites had insufficient numbers of salamanders for parameter estimation. We eliminated this site from the analysis, leaving few mixed-pine sites for vegetative comparisons. We therefore condensed the habitat characteristics into 5 different habitat treatments: disturbed/deciduous/low-elevation, disturbed/pine/low-elevation, disturbed/deciduous/mid-elevation, undisturbed/deciduous/mid-elevation, and undisturbed/deciduous/high-elevation.

We used parameter point estimates as response variables and explored differences among 5 habitat treatments using a split-plot Analysis of Variance (ANOVA) to handle the repeated measurement of sites over years (PROC GLM; SAS Institute 1999). Average surface population size estimates were modeled as $\log(\hat{N})$. The models included habitat treatments as the whole plot factor, and year and habitat \times year as the repeated measurement factors. Site-years were considered random, not fixed, effects. We tested for a habitat treatment main effect and habitat treatment \times year interaction. We used contrast statements to test for (1) vegetation effect among disturbed, low-elevation sites; (2) elevation effect among disturbed, deciduous sites; (3) elevation effect among undisturbed, deciduous sites; (4) disturbance effects among deciduous, mid-elevation sites; and (5) low-elevation, disturbed sites versus high-elevation, undisturbed sites with deciduous vegetation type only. On rare occasions, program MARK yielded poor or nonsensical estimates for certain site-years, usually due to low numbers of recaptured animals. We eliminated parameter estimates in which the variance inflated standard error (estimate) was greater than the estimate. Thus, we included only those site-year estimates that we felt were reliable. For comparison, we also performed a weighted split-plot ANOVA where weights were $\frac{1}{(SE)^2}$.

Most capture-recapture salamander studies report an effective capture probability (Kendall 1999, Bailey et al. 2004). This probability is interpreted as the probability that an animal is captured given it is in the superpopulation, but not necessarily near the surface (Kendall 1999). Superpopulation refers to the population of salamanders both on and beneath the surface within a sampled area. We used our estimates of temporary emigration and conditional capture probability to estimate effective capture probability ($\hat{p}^o(\cdot) = (1 - \hat{\gamma}(\cdot))\hat{p}(\cdot)$) for each site-year. We ran the same split-plot, repeated measures ANOVA using this derived parameter to obtain estimates that could be compared to studies that do not estimate temporary emigration. In addition, we tested for spatial and temporal differences in effective capture probability.

We refer to 4 taxonomic and size groupings similar to those described by Smith and Petranka (2000). The large *Plethodon* group contains the *glutinosus* complex (including *P. glutinosus* and *P. oconluftee*), *P. jordani*, and hybrids. The small *Plethodon* group includes *P. cinereus* and *P. serratus*. The large *Desmognathus* group contains *D. imita-*

Table 1. Split-plot analysis of variance results testing the effects of 5 habitat treatments (combinations of disturbance history, vegetation type, and elevation) and site on the probability of temporary emigration (probability of being temporary absent from the study area) for salamanders in Great Smoky Mountains National Park. Temporary emigration estimates were obtained at each site-year using a model with seasonal invariant random temporary emigration, conditional capture probability, recapture probability, and average surface population size ($n = 50$ site-years). Type III sums of squares (SS) and tests of the effects of the pairwise interaction involving year also are reported.

Source	df	Type III SS	F	P
Habitat treatment	4	0.139	6.29	0.004
Site (Habitat treatment)	14	0.078	1.38	0.246
Year	2	0.028	3.53	0.048
Habitat treatment × Year	8	0.088	2.76	0.030
Error	21	0.063		

Contrasts	df	Contrast SS	F	P
Vegetation type within				
Disturbed/Low-elevation	1	0.059	10.71	0.006
Elevation level within				
Disturbed/Deciduous	1	0.005	0.85	0.372
Elevation level within				
Undisturbed/Deciduous	1	0.066	11.93	0.004
Disturbance type within				
Deciduous/Mid-elevation	1	<0.001	0.06	0.814
Low-elevation/Disturbed vs.				
High-elevation/Undisturbed				
– Deciduous only	1	0.054	9.78	0.007

tor, *D. ocoee*, and members of the *fuscus* complex (including *D. conanti*, *D. santeelah* and *D. fuscus fuscus*). The species *D. wrighti* was considered as its own group. Parameter estimation was not possible for each species group on all site-years. Each site-year had a unique composition of species; therefore, we used only species-specific parameter estimates from site-years in which the model yielded reliable values (i.e., SE (estimate) < estimate). We used split-plot, repeated-measures ANOVA, with species as the whole plot factor and year and species × year as the repeated measurements factors, to test for species and year differences in temporary emigration, conditional capture probability, and recapture probability estimates.

RESULTS

Weighted and unweighted split-plot analyses were similar, thus we only reported the unweighted results. In each case, parameter estimates used in the split-plot, repeated measures ANOVA satisfied the Huynh-Feldt condition, verifying the covariate structure assumed in the split-plot design was appropriate (Littell et al. 1998).

The overall average estimate of temporary emigration (the probability of being absent from the study area) was high (0.87) and varied from 0.61 to

0.98 ($n = 50$ site-years). Random temporary emigration rates varied across habitat treatments and among years, and we found a habitat treatment × year interaction effect (Table 1, Fig. 1A). The model explained a high proportion of variation in the random temporary emigration estimates ($r^2 = 0.77$, $P = 0.017$). Low-elevation/disturbed/pine sites and high-elevation/undisturbed/deciduous sites showed temporal variation in temporary emigration estimates, likely driving the significant habitat × year interaction (Fig. 1A). Temporary emigration levels on other sites appeared to remain relatively stable over our 3-year study (Fig. 1A). In general, salamanders on low-elevation/disturbed/deciduous sites had higher temporary emigration rates (least-squares mean ± SE = $0.94 ± 0.02$, $n = 10$ site-years) than those on high-elevation/undisturbed/deciduous sites (least-squares mean ± SE = $0.77 ± 0.02$, $n = 10$ site-years; $F_{1,14} = 9.78$, $P = 0.0074$; Table 1, Fig. 1A). Vegetation type showed a significant effect among low-elevation/disturbed sites with deciduous sites having higher temporary emigration rates than pine sites ($F_{1,14} = 10.71$, $P = 0.006$; Table 1, Fig. 1A). We found no elevation effect among disturbed/deciduous sites, but mid-elevation/undisturbed/deciduous sites had higher temporary emigration rates than high-elevation sites (Table 1). We found no disturbance history effect among deciduous sites within an elevation class (Table 1).

Average conditional capture probability estimate was $0.30 ± 0.01$ ($\hat{p}(\cdot) ± SE(\hat{p}(\cdot))$; $n = 48$ site-years). The model explained a high proportion of the variability in this parameter estimate ($r^2 = 0.69$, $P = 0.176$). Habitat treatments and year appeared to have some influence on conditional capture probability (Table 2, Fig. 1B). Though not strictly significant, we also found an indication of a habitat treatment × year interaction, but no additional site effect (Table 2). Salamanders on low-elevation/disturbed/deciduous sites had the highest conditional capture probability (least-squares mean ± SE = $0.35 ± 0.03$, $n = 10$ site-years), while those on high-elevation/undisturbed/deciduous sites had the lowest estimates (least-squares mean ± SE = $0.20 ± 0.04$, $n = 9$ site-years). Elevation, and perhaps vegetation, appeared to have the strongest influence on conditional capture probability (Table 2). Disturbance history did not have a strong effect among mid-elevation/deciduous sites ($F_{1,14} = 0.29$, $P = 0.597$). The pattern of temporal conditional capture probability was different for low-elevation/disturbed/deciduous sites and high-elevation/

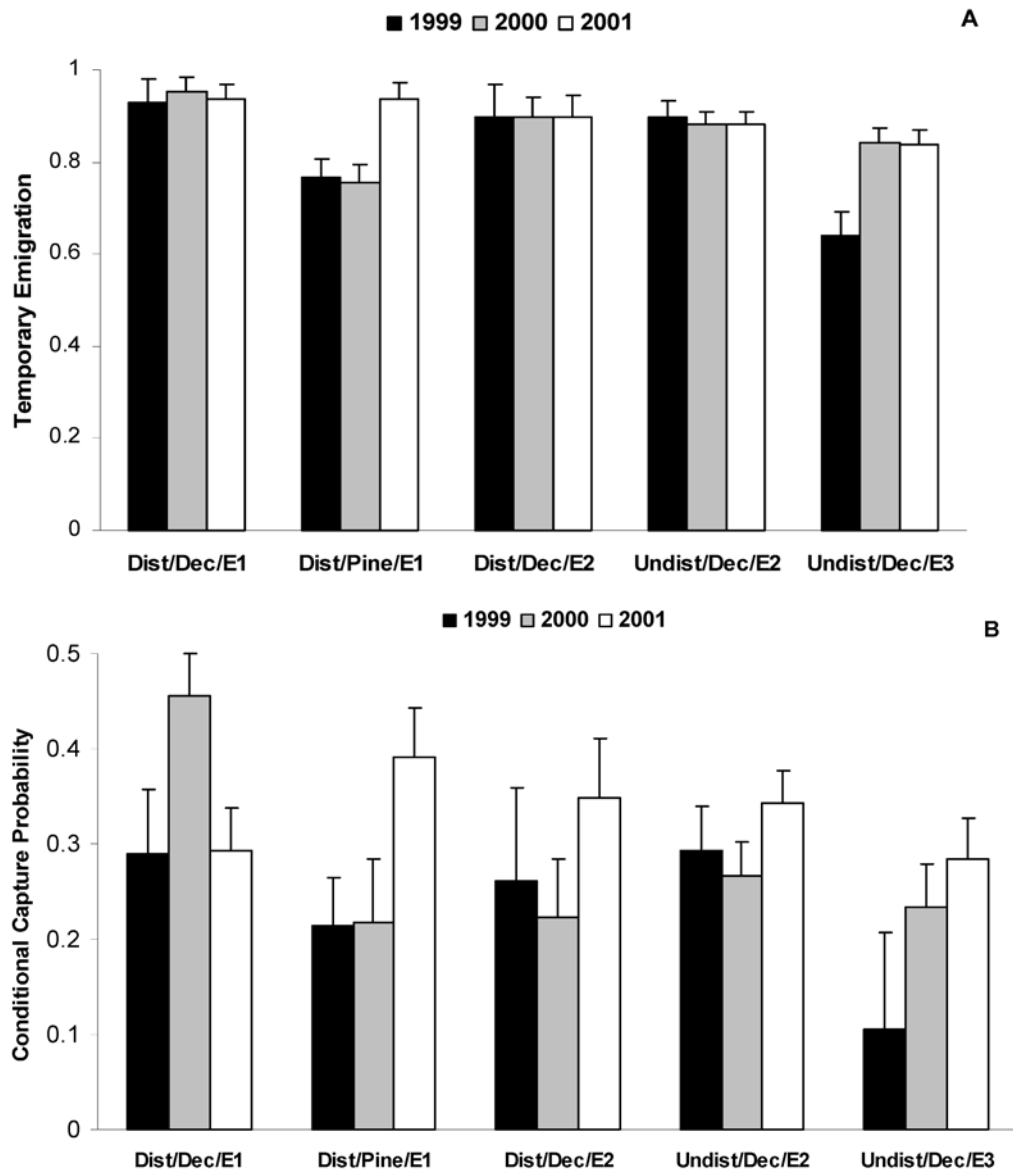


Fig. 1. Illustration of the habitat treatment \times year interaction and main effects from split-plot analysis of variance using parameter estimates as response variables: (A) temporary emigration and (B) conditional capture probability estimates for salamanders in Great Smoky Mountains National Park. Least squares mean (± 1 SE) are given for 5 habitat treatments and 3 years. Habitat treatments were combinations of disturbed (Dist) or undisturbed (Undist) forest, predominately Pine or deciduous (Dec) vegetation, and 3 elevation classes (lowest to highest: E1, E2, and E3). Parameter estimates were obtained using a model with seasonal invariant random temporary emigration, conditional capture probability, recapture probability, and average surface population size.

undisturbed/deciduous sites, and likely was the basis for the nearly significant habitat treatment \times year interaction effect (Table 2, Fig 1B). Average recapture probability ($\bar{c}(\dots) \pm SE(\hat{c}(\dots)) = 0.07 \pm 0.004$, $n = 50$ site-years) showed little spatial variation, but did vary across years ($F_{2,23} = 3.31$, $P = 0.056$). The model explained approximately 66%

of the variation in the recapture probability parameter ($P = 0.1830$). Elevation was the only factor that showed any influence on recapture probability, and only between mid- and high-elevation, undisturbed/deciduous sites; high-elevation sites had higher recapture probabilities ($F_{1,14} = 4.22$, $P = 0.059$).

Table 2. Split-plot analysis of variance results testing the effects of 5 habitat treatments (combinations of disturbance history, vegetation type, elevation) and site on the conditional capture probability of salamanders in Great Smoky Mountains National Park. Conditional capture probability estimates were obtained at each site-year using a model with seasonal invariant random temporary emigration, conditional capture probability, recapture probability, and average surface population. Type III sums of squares (SS) and tests of the effects of the pairwise interaction involving year also are reported ($n = 48$ site-years).

Source	df	Type III SS	F	P
Habitat treatment	4	0.061	2.65	0.077
Site (Habitat treatment)	14	0.081	0.76	0.696
Year	2	0.051	3.38	0.056
Habitat treatment × Year	8	0.131	2.15	0.082
Error	19	0.145		
Contrasts	df	Contrast SS	F	P
Vegetation type within				
Disturbed/Low-elevation	1	0.019	3.35	0.089
Elevation level within				
Disturbed/Deciduous	1	0.013	2.18	0.162
Elevation level within				
Undisturbed/Deciduous	1	0.031	5.34	0.037
Disturbance type within				
Deciduous/Mid-elevation	1	0.002	0.29	0.597
Low-elevation/Disturbed vs. High-elevation/Undisturbed-Deciduous only	1	0.020	3.50	0.083

Average surface population size varied among habitat treatments and sites, but not among years (Table 3, Fig. 2). The model explained a high proportion of the variation in estimated surface populations ($r^2 = 0.87$, $P < 0.001$). Vegetation type and elevation both appeared to affect estimated surface populations and high-elevation/undisturbed sites supported higher surface populations than low-elevation/disturbed sites (Table 3, Fig. 2A). Estimated surface populations did not differ among disturbed and undisturbed, mid-elevation/deciduous sites ($F_{1,14} = 0.79$, $P = 0.389$). We estimated the average superpopulation size

$$(\hat{N}^o(.)) = \frac{\hat{N}(.)}{(1 - \hat{\gamma}(.))}$$

for each site, each year. The log ($\hat{N}^o(.)$) are shown in Fig. 2 for comparison with log ($\hat{N}(.)$).

The average estimate of our derived effective capture probability ($\hat{p}^o(.) = (1 - \hat{\gamma}(.))\hat{p}(.)$) was 0.03 ± 0.02 ($\hat{p}^o(.)$ SE($\hat{p}^o(.)$); $n = 48$ site-years). This parameter was invariant across habitat treatments and among years.

We found some species-specific differences in salamander population parameter estimates. Some evidence was found of species-specific differences among temporary emigration estimates

Table 3. Split-plot analysis of variance results testing the effects of 5 habitat treatments (combinations of disturbance history, vegetation type, elevation) and site on log ($\hat{N}(.)$), the estimated average surface population size of salamanders in Great Smoky Mountains National Park. Average surface population size estimates were obtained at each site-year using a model with seasonal invariant random temporary emigration, conditional capture probability, recapture probability, and average surface population size. Type III sums of squares (SS) and tests of the effects of the pairwise interaction involving year also are reported ($n = 49$ site-years).

Source	df	Type III SS	F	P
Habitat treatment	4	14.700	7.78	0.002
Site (Habitat treatment)	14	6.617	2.32	0.042
Year	2	0.483	1.19	0.326
Habitat treatment × Year	8	1.979	1.22	0.340
Error	20	4.071		
Contrasts	df	Contrast SS	F	P
Vegetation type within				
Disturbed/Low-elevation	1	3.250	8.68	0.020
Elevation level within				
Disturbed/Deciduous	1	0.392	0.83	0.378
Elevation level within				
Undisturbed/Deciduous	1	6.870	14.53	0.002
Disturbance type within				
Deciduous/Mid-elevation	1	0.274	0.58	0.459
Low Elevation/Disturbed vs. High Elevation/Undisturbed-Deciduous only	1	7.974	16.87	0.001

($F_{3,37} = 2.39$, $P = 0.085$; Fig. 3A). Large salamanders had slightly lower temporary emigration rates than small salamanders ($F_{1,37} = 3.50$, $P = 0.069$; Fig. 3A). Conditional capture probabilities also showed some evidence of differences among species groups ($F_{3,37} = 2.46$, $P = 0.080$; Fig. 3A), with *Plethodon* species having higher estimates than *Desmognathus* species ($F_{1,37} = 5.93$, $P = 0.020$). We found a strong species effect on estimates of recapture probabilities ($F_{3,37} = 10.28$, $P < 0.001$). In general, recapture probability increased with increased species size (Fig. 3A). Temporal differences in estimates of species-specific parameters mimicked the trends detected in the species-combined analysis. Both conditional capture probability and recapture probability tended to increase over the 3-year study (Fig. 3B).

DISCUSSION

Parameters affecting estimates of salamander detection probability and abundance varied both spatially and temporally within 1 watershed in GSMNP. We found that temporary emigration varied spatially and was higher on low-elevation/disturbed/deciduous sites than high-elevation/undisturbed/deciduous sites. This result was expected because older, more mature forests

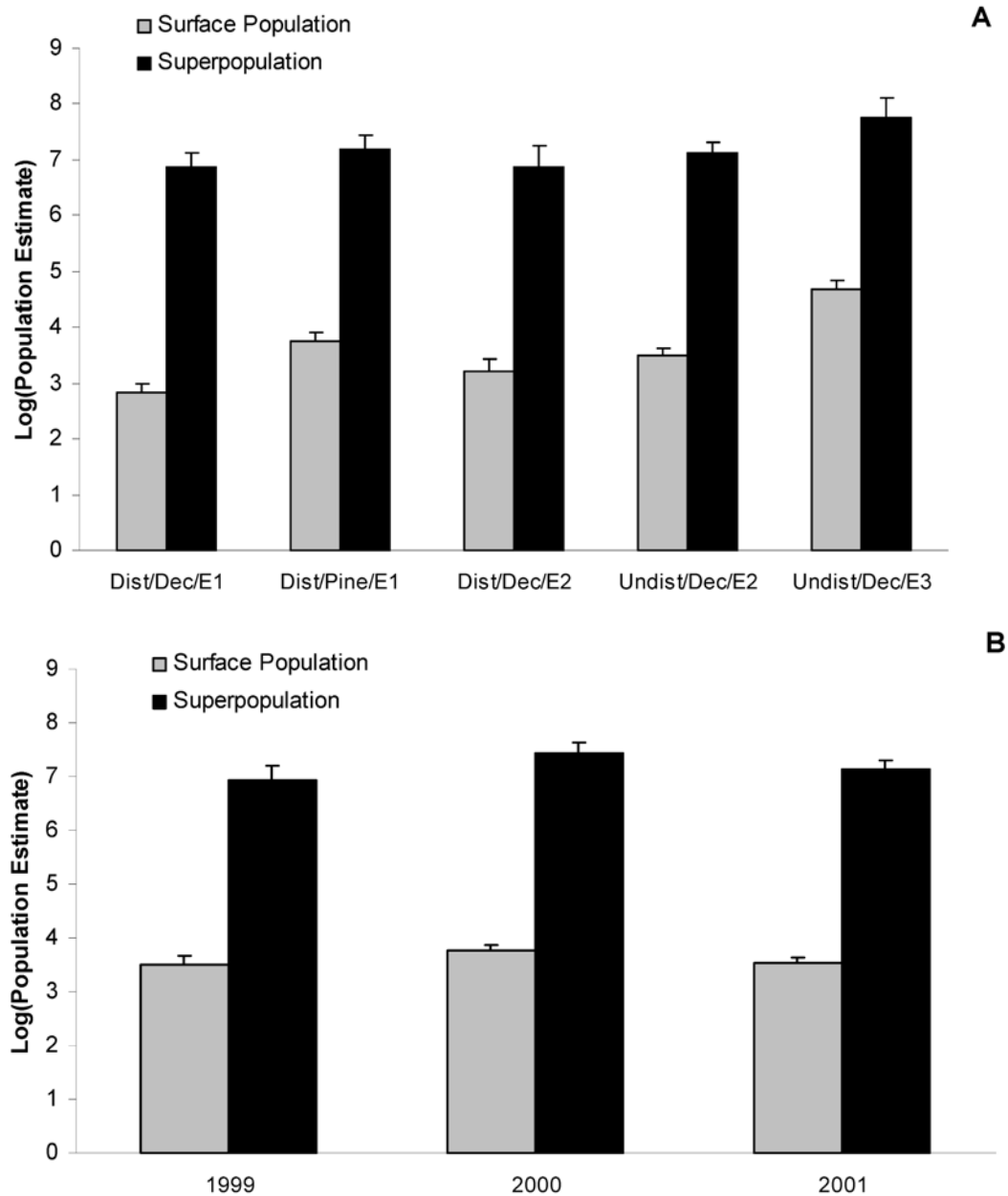


Fig. 2. Estimated average log (population sizes) \pm 1 SE for salamanders in Great Smoky Mountains National Park across (A) 5 habitat treatments and (B) 3 years. Habitat treatments were combinations of disturbed (Dist) or undisturbed (Undist) forest, predominately Pine or deciduous (Dec) vegetation, and 3 elevation classes (lowest to highest: E1, E2, and E3). Population size estimates were obtained using a model with seasonal invariant random temporary emigration, conditional capture probability, recapture probability, and average surface population size. Log (population size estimates) were different among habitat treatments but not among years.

often have less daily and seasonal microhabitat variability than younger forests (Harris 1984, Dupuis et al. 1995, Herbeck and Larsen 1999). We would expect salamanders in moist, stable

habitats to emigrate below the surface less often than salamanders found in areas with constantly changing microhabitat conditions. Temporary emigration estimates also seemed to vary between

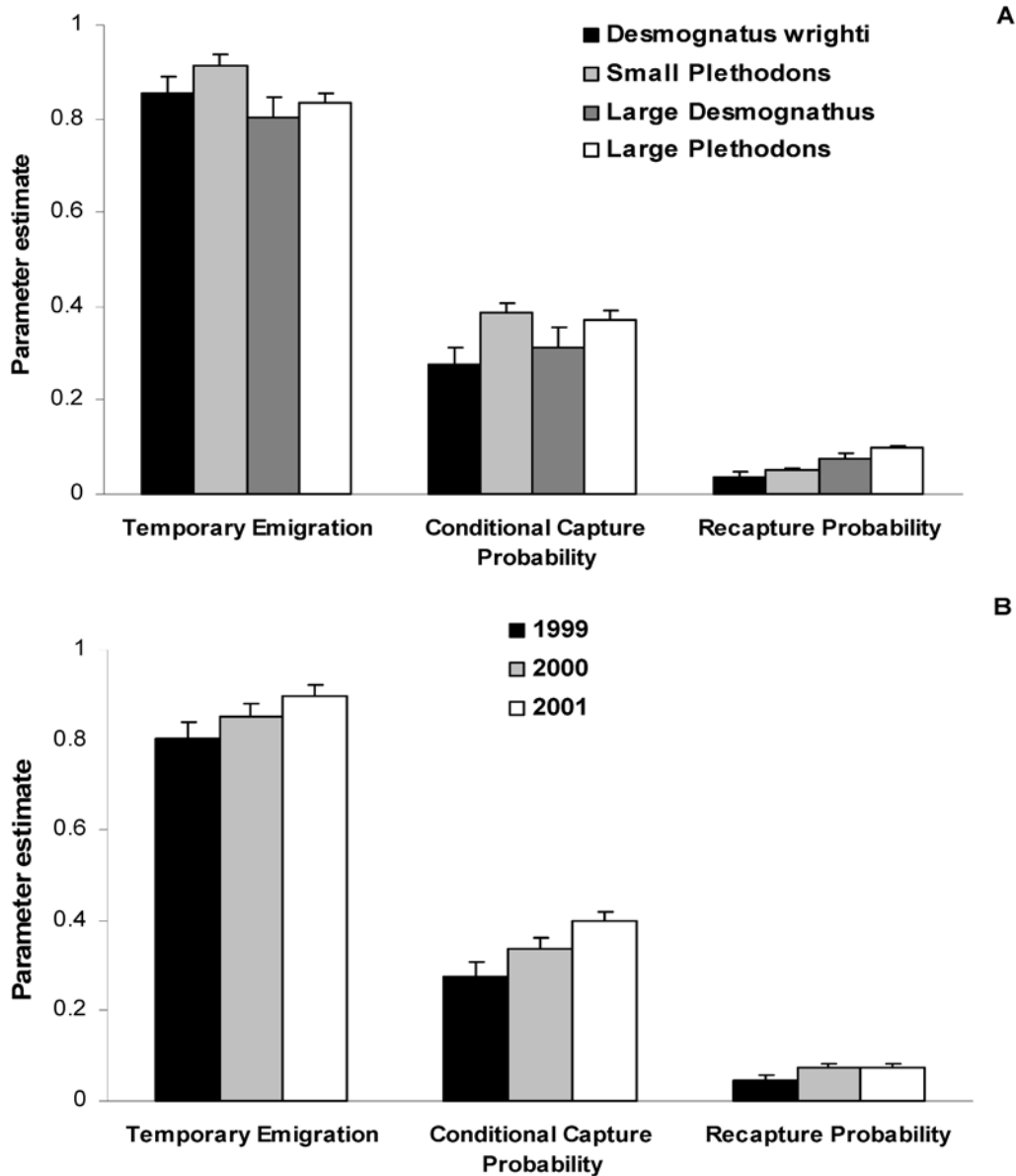


Fig. 3. Population parameter estimates (least squares mean \pm 1 SE) for salamanders in Great Smoky Mountains National Park across (A) 4 species groups and (B) 3 years. Parameter estimates were obtained using a model with seasonal invariant random temporary emigration, conditional capture probability, recapture probability, and average surface population size. We found evidence for species-specific differences for all parameter estimates, especially recapture probability. Conditional capture probability and recapture probability estimates varied among years, mimicking trends from analyses where all species were combined.

species with larger salamanders having lower estimates than smaller salamanders. We might have lacked adequate sample sizes to provide strong evidence, but biologically we expect smaller species to dehydrate more rapidly than larger salamanders due to larger surface-to-volume

ratios (Grover 2000). These smaller species may therefore retreat below the surface more often than larger species.

Conditional capture probabilities govern our ability to detect salamanders at a given location. Conditional capture probabilities varied both spa-

tially and temporally at our study sites. Salamanders on low-elevation/disturbed/deciduous sites had higher conditional capture probabilities than those at high-elevation or pine-dominated sites. Environmental factors and surface population sizes likely affect conditional capture probability. Count-based studies often have shown a relationship between number of salamanders captured and the amount of woody debris (studies in Szaro et al. 1988). Conditional capture probability had a positive relationship with the variability in natural cover on our sites in GSMNP (Bailey 2002). Natural cover on low-elevation/disturbed sites possibly was more clustered, which concentrated salamanders and made them easier to capture. Furthermore, high-elevation/undisturbed/deciduous sites had the highest estimates of surface populations while low-elevation/disturbed/deciduous sites had the lowest estimates. In general, individual capture probabilities tend to decrease as population sizes increase, especially if sampling effort is comparable across populations. Salamander surface population estimates were higher and conditional capture probabilities were lower on high elevation/undisturbed sites that presumably have relatively constant soil moisture conditions and adequate cover distribution. Sites with variable soil moisture conditions or patchily distributed natural cover had smaller surface populations and higher conditional capture probabilities.

Temporary emigration and conditional capture and recapture probabilities increased during the 3 years of our study. This could indicate real differences or an increase in the efficiency of our catching and marking techniques. We had large yearly turnover in our field personnel and believe the estimated variation in capture probabilities was not the result of increased observer abilities over time. Recent elastomer-marking studies have shown good mark retention and appear to meet all capture–recapture assumptions (i.e., no mark-induced mortality, marks are not overlooked; Davis and Ovaska 2001, Bailey in press). Therefore, lower capture probabilities early in the study likely are not caused by mark loss or observer misidentification. Low-elevation/disturbed/pine and high-elevation/undisturbed sites showed higher temporal variation in temporary emigration and conditional capture probabilities. These sites may be more sensitive to environmental changes than sites found in other habitats.

Temporary emigration and conditional capture probability are confounded in most capture–recap-

ture models, and the confounded variable is often referred to as an effective capture probability (Kendall et al. 1997, Kendall 1999). We used our temporary emigration and conditional capture probability estimates to calculate an effective capture probability that could be compared to other salamander studies. Our overall estimate (0.03) is within the range of similar studies on terrestrial salamanders (Kramer et al. 1993, Jung et al. 2000, Smith and Petranka 2000). Interestingly, temporary emigration and conditional capture probabilities often were inversely related such that effective capture probabilities showed little spatial or temporal variation. This finding may encourage investigators to use counts as indices of population size, but we would discourage this practice because we have demonstrated that the processes governing effective capture probabilities vary both spatially and temporally.

Our study represents the first time that temporary emigration models have been applied to salamander populations. Additional studies are needed to determine how salamander detection probabilities vary across larger geographic areas. Recent studies in the southern Appalachians support our findings and indicate that effective capture probabilities vary spatially (Jung et al. 2000) and among species (Petranka and Murray 2001). Studies in Europe indicate that conditional capture probabilities vary spatially and temporarily, but not among age classes (Salvidio 2001). These results suggest that investigators should be cautious about drawing inferences based on count indices unless detection probabilities are estimated.

MANAGEMENT IMPLICATIONS

What are the implications of our findings for the development of monitoring strategies? Assume, for example, that our low-elevation/disturbed/deciduous sites represent poor-quality or fringe habitat for salamanders in the southern Appalachians. Relatively high conditional capture probabilities might encourage monitoring these sites for population decline. However, the combination of high levels of temporary emigration, low recapture probabilities, and low proportions of surface/superpopulation size would make precise population estimates nearly impossible on these poor-quality areas. Moreover, these factors would produce imprecise count indices that cannot accurately measure population change (Hyde and Simons 2001). Sampling a larger number of low-quality sites for presence–absence data and using “proportion of

area occupied” as a state variable reflecting population status may be more efficient (see MacKenzie et al. 2002 for details).

In contrast, assume that undisturbed/high-elevation/deciduous sites represent high-quality habitat in the southern Appalachians. Relatively low levels of temporary emigration, high recapture probability, and high surface/superpopulation ratios might encourage the use of simple count indices to document population change. Variability of counts likely is lower on high-quality sites (Smith and Petranka 2000, Hyde and Simons 2001, and see Welsh and Droege 2001 for review), and high surface/superpopulation ratios on these sites suggest that changes in the superpopulation should be reflected by the count indices. However, even on these high-quality sites, the surface population represents <20% of the superpopulation, and conditional capture probabilities are also relatively low. Thus, superpopulations may decline considerably before declines are seen in count indices. The sudden disappearance of amphibians from pristine habitats may reflect this phenomenon (Carey 1993, Berger et al. 1998, Lips 1999). Admittedly, most of these declines have affected aquatic amphibians (Laurance et al. 1996, Lips 1998, Carey et al. 1999) and the declines have been attributed to synergistic effects between pathogens and environmental conditions (Carey et al. 1999, Kiesecker et al. 2001). Nevertheless, these cases represent situations in which count indices in high-quality habitats went from high to low very quickly. Capture–recapture methods are likely to yield reliable, less variable surface and superpopulation estimates in habitats with low temporary emigration rates and high recapture probabilities.

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