

SAMPLING PLETHODONTID SALAMANDERS: SOURCES OF VARIABILITY

ERIN J. HYDE, Cooperative Fish and Wildlife Research Unit, Department of Zoology, North Carolina State University, Raleigh, NC 27695, USA

THEODORE R. SIMONS,¹ Cooperative Fish and Wildlife Research Unit, Department of Zoology, North Carolina State University, Raleigh, NC 27695, USA

Abstract: Recent evidence of possible worldwide amphibian population declines has highlighted the need for a better understanding of species-specific habitat associations and methodologies for monitoring long-term population trends. Great Smoky Mountains National Park is committed to incorporating salamander population monitoring into the park's long-term inventory and monitoring program because of the large number of unique species in the park, and evidence that salamanders are finely tuned indicators of environmental quality. We present data on spatial and temporal patterns in salamander diversity and abundance in Great Smoky Mountains National Park and compare the bias and effectiveness of 4 common sampling techniques. We found that large-scale habitat characteristics, including disturbance history, proximity of streams, and elevation are useful to explain patterns of salamander distribution and abundance. With the exception of soil moisture, microhabitat variables were not helpful in understanding variations in salamander relative abundance. Data collected over 2 years suggest that common salamander sampling techniques vary significantly in their effectiveness, and they may often violate assumptions required for comparing salamander population indices over space or time. Salamander counts on our sites were highly variable. Neither sampling variability nor detectability were constant across habitat types or species. These characteristics reduce power for detecting long-term population trends and suggest that some common sampling methods may not provide indices suitable for long-term population monitoring.

JOURNAL OF WILDLIFE MANAGEMENT 65(4):624-632

Key words: *Desmognathus*, *Eurycea*, Great Smoky Mountains National Park, habitat associations, monitoring, *Plethodon*, Plethodontidae, salamanders, sampling.

Recent evidence of worldwide amphibian population declines has highlighted the need for a better understanding of species-specific habitat associations and methodologies for monitoring long-term population trends (Barinaga 1990, Blaustein and Wake 1990, Wake 1991, Lannoo 1996, Dodd 1997). The lack of long-term data, inadequate information about salamander habitat requirements, and a poor understanding of the precision and accuracy of sampling methods have hampered efforts to establish effective monitoring and conservation programs for salamanders. Most studies rely on relative abundance indices to compare population trends over time. However, few attempts have compared indices derived from different methods, to evaluate the underlying assumptions of these indices, or to examine the relationship of indices to the true population. Salamanders are inherently difficult to sample because their surface activity, and thus their detectability, varies with topography, season, humidity, climate, and other landscape variables. These variations in detectability may violate criti-

cal assumptions of the abundance indices produced by several common sampling methods.

Comparing 2 populations over time or space requires that $N_1/N_2 = [C_1/\beta_1]/[C_2/\beta_2] = C_1/C_2$, where N = population size, C = the number of individuals counted, and β = the detectability of individuals. Comparisons of count indices assume that $\beta_1 = \beta_2$, and that there is a linear relationship between counts (C) and population size (N), such that $E(C) = \beta N$ (Lancia et al. 1996).

The National Park Service (NPS) is committed to establishing long-term natural resource monitoring programs in approx. 250 national parks with significant natural resources (National Park Service 1992). As a prototype park in the NPS inventory and monitoring program, Great Smoky Mountains National Park (GRSM) is at the forefront of efforts to develop systematic approaches to inventory and monitor the composition and function of park ecosystems. Because of the large number of unique species in the park, and evidence that salamanders are finely tuned indicators of environmental quality (Duellman and Trueb 1986, Corn and Bury 1989), GRSM is committed to incorporating salamander population monitoring into the park's long-term inventory and monitoring program.

¹ E-mail: tsimons@ncsu.edu

We present data from GRSM on spatial and temporal patterns in salamander diversity and abundance, and associations of salamanders with large-scale habitat variables: disturbance history, proximity to streams, elevation, and 2 forest community types. We compare the bias and effectiveness of 4 salamander monitoring methodologies and present evidence that some common salamander sampling techniques may not produce reliable abundance indices, and therefore may not be suitable for long-term monitoring programs in the southern Appalachian mountains, and perhaps elsewhere.

STUDY AREA

Great Smoky Mountains National Park—205,665 ha of contiguous forest straddling the Appalachian Trail along the Tennessee–North Carolina border—is an internationally recognized refuge of temperate forest biodiversity. Geography and geology, combined with steep, complex topography, promote extreme gradients of temperature, moisture, and soil types across the park's environments. In many groups, including salamanders (Jackson 1989), these gradients produce levels of species diversity that are unmatched elsewhere in North America. Almost 20% of the world's salamander species are found in the southeastern United States, and half of these occur in the southern Appalachian mountains (Petranka 1998).

METHODS

During 1998 and 1999, we sampled salamanders at 104 sites between 500 m and 1,250 m above sea level within the Roaring Fork Watershed (Mt. LeConte USGS quadrangle) of Great Smoky Mountains National Park (Hyde 2000). We assigned each site to 1 of 5 150-m elevation classes. Access and topography precluded selecting sites at random. Sites were located adjacent to trails and were chosen by beginning at a random point at least 250 m from a trail head. Subsequent sites were spaced approx. 250 m apart to ensure independence with respect to individual salamanders. Two forest community types were considered based on the 7 community classification of 90 m Landsat imagery by MacKenzie (1993): mixed deciduous (cove hardwood, mixed mesic hardwood, tulip poplar, and mesic oak) and mixed pine (xeric oak, pine oak, and pine). Sites were scored as being adjacent (<50 m) to a stream, or not adjacent (>50 m) to a stream.

Land use history was determined from maps created by Pyle (1985) that describe 5 disturbance

history classes: undisturbed, settlement areas, and 3 types of logging disturbance: selective cut, light commercial cut, and industrial logging. For analysis, we combined land use history into 2 classes: disturbed (settled or logged) and undisturbed sites. Both disturbed and undisturbed sites are now completely forested because they have been protected since the park was established in 1934.

Because salamanders exhibit a variety of life histories, we used 4 sampling methods: searches of natural cover objects along transects (Jaeger 1970, 1994); night-time surface counts along transects (Ash and Bruce 1994); artificial cover boards (Fellers and Drost 1994, Jung et al. 1997); and leaf litter searches (Pauley 1995).

The sampling framework at each site was comprised of up to 4 parallel 50-m transects, 1 transect for each sampling method. Each site included all 3 diurnal transects whenever possible. However, impassable or unsafe terrain prohibited us from establishing all transects at some sites. The cover board transect consisted of 5 cover board stations each spaced 10 m apart. Each cover board station included 2 large (26 cm × 26 cm) and 3 small (13 cm × 26 cm) boards spaced 1 cm apart. All surface debris under the boards was removed so that each board lay flush against the topsoil. The leaf litter transect also consisted of 5 plots 10 m apart and approximately 1–2 m from the corresponding cover board plot. A flagged stick inserted into the ground marked the center of each leaf litter plot. The stick designated the intersection of 4 1-m × 1-m areas of leaf litter. At each plot, the leaf litter in 1 1-m × 1-m square was carefully removed, checked for salamanders, and replaced. A different 1-m × 1-m square was searched each time the plot was sampled to minimize disturbance to the plot. The natural cover transect was a 50-m × 3-m strip sampled by 2 observers walking side by side who turned (and replaced) all natural cover (sticks, logs, and rocks) within the transect. An additional 50-m × 3-m transect was used for opportunistic night surveys at a subset of sites. These transects were sampled by 2 observers who recorded all salamanders observed on the surface, or on herbs, ferns, or tree trunks. Night transects were only sampled when temperature and humidity conditions favored surface activity by terrestrial salamanders. Therefore, data from night transects were not directly comparable to data from other sampling methods, and they were excluded from some analyses.

We sampled all sites at least 3 times between 27 May and 5 August 1998 and 5 times between 5 April and 27 June 1999. All individuals observed on transects were counted and identified to species. We recorded snout-to-vent length (SVL), sex, substrate, and the presence of any injuries or parasites for each individual. Air and soil temperature, leaf litter depth, cloud cover, and canopy cover were recorded at all diurnal transects. We collected leaf litter samples and soil samples from each cover board and leaf litter station on each sampling occasion to determine soil moisture. We collected samples in cloth bags that were sealed in plastic in the field to prevent drying. Cloth sample bags were weighed at the end of each day, dried at a low temperature in a drying oven, and weighed again. Percent moisture was calculated as $1 - \text{dry weight}:\text{wet weight}$.

We used simple linear regression to determine the extent to which soil moisture was associated with salamander abundance, and to determine the extent to which natural cover estimates were correlated with salamander abundance. A non-parametric Kruskal-Wallis test expressed as a chi-square approximation (Zar 1996) was used to test for differences in capture frequencies related to soil moisture and salamander size. We visually estimated natural cover (logs, sticks, rocks) as the percent cover of 4 3-m \times 12.5-m plots along each natural cover transect. We used the Mann-Whitney nonparametric rank test (Zar 1996) and the Shannon Diversity Index (Magurran 1988) to compare salamander abundance and salamander species diversity across disturbance history, elevation, and forest type. We used 2-tailed *t*-tests to compare salamander diversity among habitats and sampling methods, to determine if the mean SVL of salamanders varied by sampling method, and to determine whether the size of artificial cover boards (26 cm \times 26 cm or 26 cm \times 13 cm) was associated with the size of salamanders captured.

To evaluate broad-scale patterns of salamander abundance and the variability among sampling methods, we summed our capture data for both years by site and modeled the log (mean abundance + 1) as a function of the 3 primary sampling methods, 2 site disturbance classes, 2 forest types, 2 stream proximity classes, and 5 elevation classes using a split-plot ANOVA (PROC GLM) in SAS (SAS Institute 1999). The model included disturbance, forest type, elevation, and stream proximity as whole plot treatment factors, and sampling method as the split plot treatment factor. We tested for main effects and for 2-way

interactions between sample method and disturbance, forest type, elevation, and stream proximity.

We examined capture rate variability to assess the effectiveness of the 4 sampling methods tested. We determined both spatial variation (variation among sites within a sampling period) and temporal variation (variation within sites over time) for 7 common species using 1999 count data. We estimated temporal variation by calculating the coefficient of variation (CV) of counts at each of the 104 sites over the 5 sampling periods in 1999 and used those values to calculate an average CV for the 104 sites. We estimated spatial variation by calculating the CV of all 104 sites within each of the 5 sampling periods and then calculated an average CV for the 5 periods.

We follow the classification described by Petranka (1998), and for closely related species that are difficult to separate in the field, we refer to 3 species complexes. The *glutinosus* complex is comprised of *Plethodon glutinosus* and *Plethodon oconluftee*. The *fuscus* complex is comprised of *Desmognathus conanti*, *Desmognathus santeetlah*, and *Desmognathus fuscus*. The *imitator* complex is comprised of *Desmognathus imitator* and *Desmognathus ocoee*.

We used program MONITOR (Gibbs 1996) to examine how our power to detect population trends over time was influenced by the number of sites sampled, the number of samples per site, the number of years of sampling, the timing of sampling within a year, and the mean and the variance of samples over time. We compared the power of different methods to detect 5% annual declines in salamander populations with 95% confidence. We determined power for populations of *Plethodon jordani*, *P. glutinosus* complex, and *P. serratus* using 10, 20, and 40 sites over 5, 10, 20, and 40 years of sampling. The sample means and standard deviations used for each analysis were derived from randomly selected 1999 sites. We conducted 500 replications for each analysis.

RESULTS

During 1998 and 1999, we collected 837 samples from artificial cover board transects, 700 samples from natural cover transects, 731 samples from leaf litter plots, and 97 samples from night transects which resulted in 6,110 salamander captures from 11 species. Percent total captures per species were *Plethodon jordani* (29.9%), *Desmognathus wrighti* (14.9%), *Plethodon glutinosus* complex (12.7%), *Plethodon serratus* (11.8%), *Desmognathus imitator* complex (11.5%), *Eurycea*

Table 1. Relative efficiency of 4 salamander sampling methods in Great Smoky Mountains National Park, 1998 and 1999. Number of samples = number of transects × number of visits per transect.

Method	Number of transects	Number of samples	Salamanders per transect	
			Salamander captures	\bar{x} SE
Cover boards	101	837	1,224	1.4 0.19
Natural cover	92	700	2,651	3.6 0.54
Leaf litter	97	731	566	0.8 0.14
Night	26	97	1,669	14.0 2.65
Total	316	2,365	6,110	

wilderae (10.1%), *Desmognathus fuscus* complex (6.7%), *Desmognathus quadramaculatus* (0.4%), *Desmognathus monticola* (0.3%), *Gyrinophilus porphyriticus* (0.2%), *Pseudotriton ruber* (<0.1%), unknown/hybrid (1.4%). We used only the 7 most common species (97% of all captures) for analyses.

Differences in the number of salamanders captured per transect indicate that night surveys and natural cover transects are more efficient for capturing salamanders than artificial cover boards or leaf litter searches (Table 1).

Sample Method.—Salamanders of all species except *Desmognathus fuscus* complex were more likely to be captured off of natural cover transects than under cover boards or leaf-litter plots (Fig. 1). Natural cover transects and cover boards per-

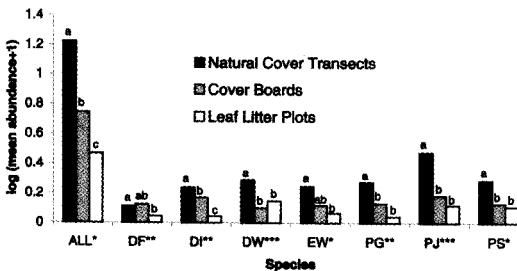


Fig. 1. The estimated relative abundance of salamander species depends on the sampling method used for all species combined (ALL), *Desmognathus fuscus* complex (DF), *Desmognathus imitator* complex (DI), *Desmognathus wrighti* (DW), *Eurycea wilderae* (EW), *Plethodon glutinosus* complex (PG), *Plethodon jordani* (PJ), and *Plethodon serratus* (PS). Analysis of variance (PROC GLM; SAS Institute 1999). Methods not sharing letter symbols were significantly different. Minimum significance levels denoted as: * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.

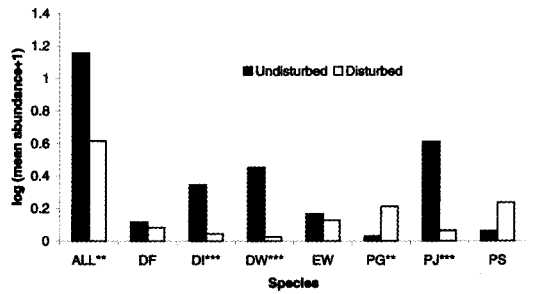


Fig. 2. Salamander abundance was higher on undisturbed sites for all species combined (ALL) and for *Desmognathus imitator* complex (DI), *Desmognathus wrighti* (DW), and *Plethodon jordani* (PJ). *Plethodon glutinosus* complex (PG) was more abundant on disturbed sites. Analysis of variance (PROC GLM; SAS Institute 1999). Minimum significance levels denoted as: * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.

formed equally well for *Desmognathus fuscus* complex. For all species except *Desmognathus imitator* complex, captures under cover boards were not significantly different from captures on leaf litter plots. We found significant interactions between habitat disturbance and sampling method for all species combined, as well as *Desmognathus wrighti*, *Plethodon glutinosus* complex, and *Plethodon jordani*. Significant interactions between elevation and sampling method were found for all species combined, *Desmognathus wrighti*, *Eurycea wilderae*, *Plethodon glutinosus* complex, and *Plethodon jordani*. We also found significant interactions between stream proximity and sampling method for all 3 species of *Desmognathus*. In every case, interactions were parallel to those of the main effects. Captures on natural cover transects tended to exaggerate the effect of stream proximity on *Desmognathus* species and the differences associated with disturbance and elevation found for the other species, but in no case did they change the qualitative conclusions derived from the main effects.

Habitat Disturbance.—For all species combined, we detected more salamanders on undisturbed sites than on sites that were disturbed by settlement or logging prior to the creation of the park (Fig. 2). *Desmognathus imitator* complex, *Desmognathus wrighti*, and *Plethodon jordani* were significantly more abundant on undisturbed sites while *Plethodon glutinosus* complex showed a significant association with disturbed sites.

Forest Type.—We found no significant differences in salamander abundance on mixed deciduous (92 sites) or mixed pine (12 sites) forest

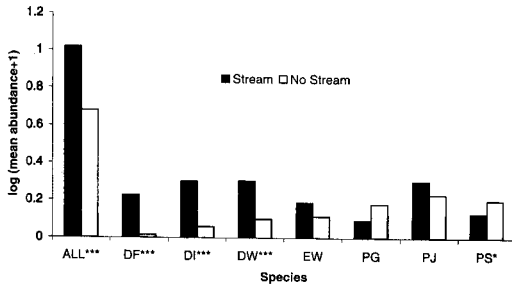


Fig. 3. Salamander abundance was higher on sites adjacent to streams for all species combined (ALL), *Desmognathus fuscus* complex (DF), *Desmognathus imitator* complex (DI), and *Desmognathus wrighti* (DW). *Plethodon serratus* (PS) was more abundant on sites away from streams. Analysis of variance (PROC GLM; SAS Institute 1999). Minimum significance levels denoted as: * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.

types, although *Plethodon serratus* tended to be more abundant on the somewhat drier mixed pine sites ($P < 0.07$). Power to detect associations with forest type was limited due to the small number of mixed pine sites.

Proximity to Streams.—Overall, the terrestrial salamanders we sampled tended to be more abundant on sites adjacent to streams (Fig. 3). *Desmognathus fuscus* complex, *Desmognathus imitator* complex, and *Desmognathus wrighti* showed highly significant associations with sites near streams, while *Plethodon serratus* tended to be associated with sites away from streams.

Elevation.—For all species combined, *Desmognathus wrighti*, *Plethodon glutinosus* complex, and *Plethodon serratus* abundance showed a significant association with elevation (Fig. 4). In most cases,

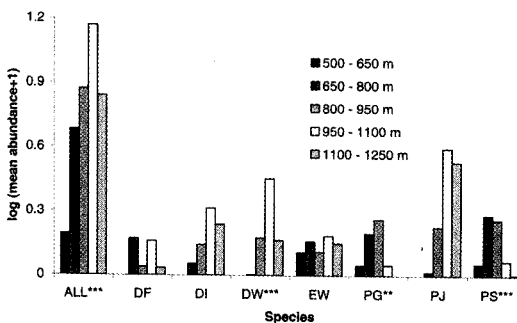


Fig. 4. Salamander abundance showed a significant association with elevation for all species combined (ALL), *Desmognathus wrighti* (DW), *Plethodon glutinosus* complex (PG), and *Plethodon serratus* (PS). Analysis of variance (PROC GLM; SAS Institute 1999). Minimum significance levels denoted as: * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.

the relationship was quadratic, with higher abundances on mid-elevation sites.

Shannon diversity indices were significantly higher on undisturbed sites than on disturbed sites for natural cover transects (undisturbed $\bar{x} = 0.86$, SE = 0.08; disturbed $\bar{x} = 0.68$, SE = 0.06, $t_{92} = 2.51$, $P = 0.01$), leaf litter searches (undisturbed $\bar{x} = 0.79$, SE = 0.08; disturbed $\bar{x} = 0.36$, SE = 0.06, $t_{95} = 4.66$, $P < 0.001$), and night transects (undisturbed $\bar{x} = 1.04$, SE = 0.11; disturbed $\bar{x} = 0.60$, SE = 0.11, $t_{37} = 2.56$, $P < 0.01$) and were nearly significant for artificial cover boards (undisturbed $\bar{x} = 0.86$, SE = 0.07; disturbed $\bar{x} = 0.68$, SE = 0.06, $t_{104} = 1.79$, $P = 0.07$).

Soil moisture explained a small amount of the variation in salamander relative abundance measured by artificial cover boards ($r^2 = 0.02$, $P = 0.001$), natural cover transects ($r^2 = 0.05$, $P < 0.001$), and leaf litter searches ($r^2 = 0.02$, $P < 0.001$). Soil moisture was significantly greater on undisturbed ($\bar{x} = 0.41$, SE = 0.02) and high-elevation ($\bar{x} = 0.41$, SE = 0.01) sites than on disturbed ($\bar{x} = 0.35$, SE = 0.01, $\chi^2_1 = 32.9$, $P < 0.01$) and low-elevation sites ($\bar{x} = 0.35$, SE = 0.01, $\chi^2_1 = 38.7$, $P < 0.01$), respectively. The other microhabitat variables measured (air temperature, soil temperature, canopy cover, cloud cover, and leaf litter depth) failed to explain a significant amount of the variation in salamander relative abundance. The quantity of natural cover at a site showed a positive association with salamander abundance using artificial cover boards ($r^2 = 0.11$, $P < 0.001$) and natural cover transects ($r^2 = 0.40$, $P < 0.001$).

Measures of abundance produced by different sampling methods were not strongly correlated. Weak relationships were found for results from cover boards and natural cover transects ($n = 636$, $r^2 = 0.11$, $P < 0.001$) and for cover boards and leaf litter searches ($n = 667$, $r^2 = 0.13$, $P < 0.001$). Natural cover transects and leaf litter searches were also weakly correlated ($n = 700$, $r^2 = 0.19$, $P < 0.001$).

The size of salamanders differed among capture methods (Fig. 5). Salamanders captured on natural cover or night transects were significantly larger than those captured by other methods. An exception was that individual *Plethodon serratus* captured on leaf litter plots were significantly larger than individuals captured by other methods. Cover board size also may cause a bias in the size of salamanders captured. For example, in *Desmognathus imitator* complex, individuals captured under small cover boards ($\bar{x} = 27.48$, SE = 0.65) were significantly smaller than individuals captured under large cover boards ($\bar{x} = 30.45$, SE

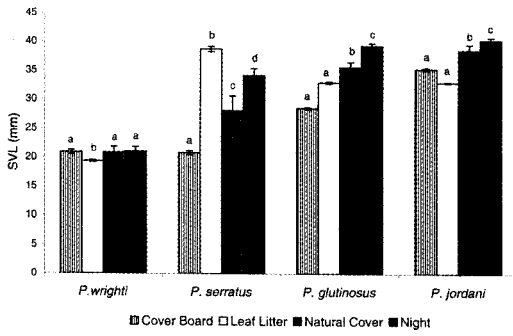


Fig. 5. Mean snout-to-vent length (SVL) of 4 *Plethodon* salamander species using 4 different sampling techniques in Great Smoky Mountains National Park. Error bars represent standard errors. Methods not sharing letter symbols were significantly different at $P < 0.05$ or less. *P. glutinosus* refers to *Plethodon glutinosus* complex.

= 0.79, $P < 0.004$). Similar patterns were observed for *Desmognathus fuscus* complex, *Eurycea wilderae*, and *Plethodon jordani*.

Sampling Variability

All sampling methods showed extremely high temporal and spatial variation in capture rates. For all methods and species, spatial variation was greater than temporal variation (Fig. 6). Natural cover transects had the lowest spatial and temporal variation of any diurnal method for all species except *D. wrighti*. Artificial cover boards had higher variation in capture rates than natural cover transects but considerably less variation than leaf litter searches. Although night transects had the lowest variation of any method, these figures are not directly comparable because night transects were only conducted under conditions that favored surface activity by salamanders. For combined species counts, temporal variation was significantly higher on disturbed sites than on undisturbed sites for artificial cover boards ($P = 0.04$), natural cover transects ($P < 0.001$), and leaf litter searches ($P < 0.001$; Fig. 7).

Power Analysis

The power to detect population trends using various sampling methods was similar for *Plethodon jordani*, *Plethodon glutinosus* complex, and *Plethodon serratus* (Table 2). No sampling method yielded adequate power (>90%) to detect population trends with 5 or fewer years of sampling. Leaf litter sampling had low power (from 0.07 to 0.25 for 20 sites) to detect long-term population

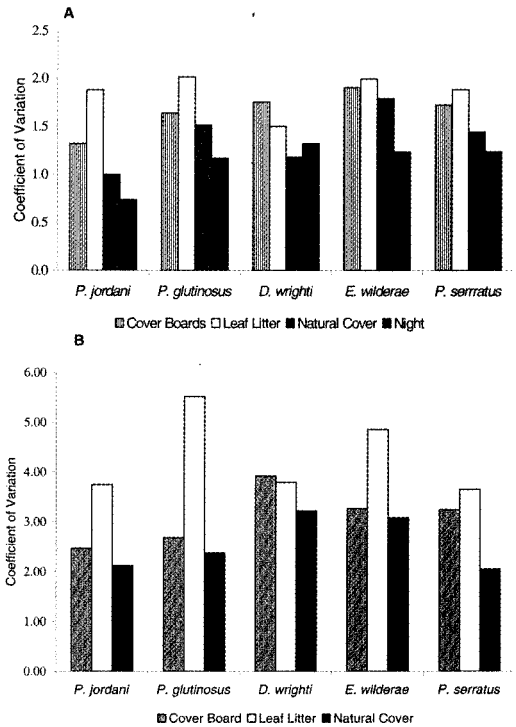


Fig. 6. (A) Temporal variation in salamander counts in 1999 in Great Smoky Mountains National Park. Temporal variation was estimated by calculating the coefficient of variation (CV) of counts at each of the 104 sites over the 5 sampling periods in 1999 and using those values to calculate an average CV for the 104 sites. (B) Spatial variation was estimated by calculating the CV of all 104 sites within each of the 5 sampling periods and then calculating an average CV for the 5 periods. *P. glutinosus* refers to *Plethodon glutinosus* complex.

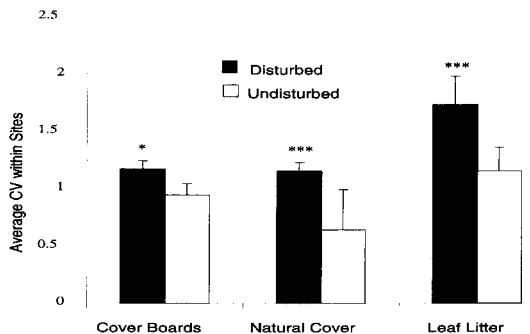


Fig. 7. Average temporal variation in pooled salamander samples at disturbed and undisturbed sites in Great Smoky Mountains National Park. Each site was sampled 8 times. Cover boards: $n = 55$ disturbed, 33 undisturbed sites. Natural cover: $n = 59$ disturbed, 30 undisturbed sites. Leaf litter: $n = 49$ disturbed, 31 undisturbed sites. Error bars indicate 1 standard error.

trends even after 20 years of sampling. Natural cover transects had higher power (from 0.29 to 1.0 for 20 sites) than any other diurnal method. With few exceptions, 40 sites were necessary to achieve greater than 90% power even after 20 to 40 years of sampling. Although power was greater for night transects than any other method, these results are not directly comparable with other methods as discussed above.

DISCUSSION

Patterns of salamander distribution and abundance in Great Smoky Mountains National Park reflect the influence of numerous habitat factors. Salamanders were more abundant on undisturbed, mid-elevation sites adjacent to streams, and on sites with higher soil moisture and more ground cover. These results should not be surprising to those familiar with the natural history of plethodontid salamanders. They are, nevertheless, significant with regard to our ability to measure the relative abundance of these species. Even within a single watershed, habitat factors introduce significant variability in terrestrial salamander abundance. This variability can be a major influence on the detectability of species, and thus our ability to make inferences about abundance. Individual species on our sites varied in their response to habitat factors, presumably reflecting species-specific habitat preferences or interspecific competition for resources (Jaeger 1979; Jaeger et al. 1982; Mathis 1990, 1991).

Our findings suggest that differences in salamander diversity and abundance associated with habitat disturbance may persist for more than 60 years. The effects of habitat disturbance on salamander populations have been debated in the literature without agreement (Ash and Bruce 1994, Duffy 1994, Johnson et al. 1993, Petranka et al. 1993). More recently, Aubry (2000) reported a positive association between stand age and amphibian species richness, biomass, and total abundance in managed Douglas-fir forests in the Pacific Northwest. Our results suggest that habitat disturbance associated with logging or agriculture may have long-term effects on salamander communities in the southern Appalachian mountains.

Understanding patterns in salamander abundance and habitat associations is essential for managers planning salamander monitoring or conservation programs. Because spatial and temporal patterns of distribution and abundance are species-specific, salamander population data should be considered on a species-by-species basis. In partic-

Table 2. Power to detect 5% annual population declines with 95% confidence for *Plethodon glutinosus* complex, *Plethodon jordani*, and *Plethodon serratus* in Great Smoky Mountains National Park with 3 samples per site per year.

Taxon	Method	Number of sites	Power			
			5 yr	10 yr	20 yr	40 yr
<i>P. glutinosus</i> complex	Cover boards	10	0.040	0.090	0.150	0.420
		20	0.110	0.290	0.770	0.990
		40	0.210	0.740	1.000	1.000
	Leaf litter	10	0.006	0.028	0.072	0.386
		20	0.022	0.054	0.192	0.632
		40	0.056	0.084	0.318	0.918
	Natural cover	10	0.048	0.092	0.124	0.132
		20	0.062	0.144	0.286	0.368
		40	0.178	0.784	1.000	1.000
	Night	10	0.134	0.566	1.000	1.000
		20	0.358	1.000	1.000	1.000
		40	0.514	1.000	1.000	1.000
<i>P. jordani</i>	Cover boards	10	0.056	0.088	0.274	0.732
		20	0.082	0.236	0.580	0.964
		40	0.162	0.624	0.992	1.000
	Leaf litter	10	0.022	0.054	0.110	0.498
		20	0.078	0.212	0.562	0.913
		40	0.106	0.324	0.856	1.000
	Natural cover	10	0.216	0.844	1.000	1.000
		20	0.278	0.890	1.000	1.000
		40	0.672	1.000	1.000	1.000
	Night	10	0.340	0.964	1.000	1.000
		20	0.692	1.000	1.000	1.000
		40	0.840	1.000	1.000	1.000
<i>P. serratus</i>	Cover boards	10	0.010	0.094	0.144	0.010
		20	0.030	0.266	0.316	0.030
		40	0.056	0.394	0.482	0.056
	Leaf litter	10	0.022	0.054	0.112	0.430
		20	0.024	0.078	0.248	0.742
		40	0.068	0.206	0.630	0.996
	Natural cover	10	0.058	0.176	0.402	0.574
		20	0.150	0.554	0.984	1.000
		40	0.216	0.854	1.000	1.000
	Night	10	0.192	0.768	0.998	1.000
		20	0.312	0.980	1.000	1.000
		40	0.598	1.000	1.000	1.000

ular, the unique habitat preferences of endemic or rare species should be considered when selecting methods for long-term population monitoring.

Our data from GRSM suggest that commonly used salamander sampling techniques may violate assumptions required to make valid comparisons of population indices over space or time. We found species-specific biases in capture probabilities for different sampling methods, unequal

sample variances across habitat types, and a lack of linearity among our sampling methods. These biases violate several critical assumptions of abundance indices, which limits our ability to interpret field data and to detect changes in populations over time.

The assumptions of relative abundance indices can be violated in a number of ways. The detectability of salamanders (β) may vary across habitats, over time, because of differences in salamander behavior, or because of differences in the ability of people to detect salamanders (because some people are more skilled, or because sampling is more difficult on steep terrain or in heavy vegetation). Differences in the quantity of ground cover, density of underground burrows, soil moisture, soil temperature, or other habitat characteristics may alter the surface activity of salamanders, and thus their detectability among sites. Short-term movements that occur when salamanders move between cover objects, leaf litter, and underground refugia in response to changing humidity levels (Heatwole 1962, Jaeger 1980) are likely to change the detectability of salamanders sampled with a particular method. Differences in climate or weather patterns over time also are likely to affect the activity patterns of salamanders and thus the detectability of salamanders with a given sampling method.

Unequal detectability may occur across both space and time. For example, if an open habitat type is more susceptible to drying than a more protected habitat (perhaps due to differences in canopy cover, ground cover, etc.) salamanders may take refuge in underground burrows on the open habitats, and be less detectable than on protected sites that remain consistently cooler and moister. In this case, the 2 habitats may have equal detectability during moist periods but different detectability during dry periods. Such differences in detectability greatly reduce power to detect population trends. More research is needed to determine the factors that influence detectability for different species over space and time.

Power analyses indicate that natural cover transects may be the most effective method for detecting long-term population trends at our study sites. The lower power associated with artificial cover boards compared to natural cover transects is probably related to the low mean capture rate associated with cover boards. Future work should examine the feasibility of increasing cover board capture rate by using additional boards per site. Higher capture rates will in-

crease the power of cover board sampling while meeting the objectives of standardization, minimal site disturbance, and efficiency.

Increased sampling variation on disturbed sites may reflect differences in surface cover, soil organic matter, or moisture at disturbed and undisturbed sites. Because increased sampling variability decreases our ability to detect population trends, salamander population declines may be most difficult to detect on disturbed habitats, the very regions that are most likely to suffer declines in salamander diversity or abundance. Catch-per-unit effort, variability among counts, practicality, and disturbance caused by sampling all must be considered when choosing a sampling method. We found natural cover transects and artificial cover board transects to be the most effective sampling techniques for detecting long-term salamander population trends because of their lower sampling variability, reasonable capture success, and ease of use. However, the extreme variation inherent in all the methods we examined ($CV > 100\%$) severely limits their utility for population monitoring. The sampling variability reported by Smith and Petranka (2000) on 30-m \times 40-m natural cover plots was substantially lower than the variability from our 3-m \times 50-m plots. This difference is not unexpected, and it illustrates the trade-offs inherent to intensive and extensive monitoring objectives. The higher capture rates and lower variability associated with fewer but larger plots increases power to detect changes in abundance. Reducing plot size and expanding the geographic scope of a monitoring program will inevitably reduce power to detect population change. The feasibility of monitoring terrestrial salamander populations over large geographic areas using current methodologies remains suspect.

The development of reliable sampling methods for a range of salamander species and habitats is essential before extensive monitoring programs are established. Field and laboratory studies using marked animals will be necessary to understand if the behavior, movement, and survival of salamanders is consistent with the assumptions of abundance indices. Without such information, considerable resources could be wasted gathering unreliable data.

ACKNOWLEDGMENTS

Funding for this research was provided by Friends of Great Smoky Mountains National Park and the U.S. Geological Survey. We thank the staff of GRSM, in particular K. Langdon and D.

Soehn, for their logistic and administrative assistance. L. Bailey, G. Brown, G. Farnsworth, K. Pollock, J. Petranka, S. Shriner, P. Simons, and 2 anonymous reviewers made valuable contributions to the manuscript.

LITERATURE CITED

- ASH, A. N., AND R. C. BRUCE. 1994. Impacts of timber harvesting on salamanders. *Conservation Biology* 8:300–301.
- AUBRY, K. B. 2000. Amphibians in managed, second-growth Douglas-fir forests. *Journal of Wildlife Management* 64:1041–1052.
- BARINAGA, M. 1990. Where have all the froggies gone? *Science* 247:1033–1034.
- BLAUSTEIN, A. R., AND D. B. WAKE. 1990. Declining amphibian populations: a global phenomenon? *Trends in Ecology and Evolution* 5:203–204.
- CORN, P. S., AND R. B. BURY. 1989. Logging in western Oregon: responses of headwater habitats and stream amphibians. *Forest Ecology and Management* 29:39–57.
- DODD, C. K., JR. 1997. Imperiled amphibians: a historical perspective. Pages 165–200 in G. W. Benz and D. E. Collins, editors. *Aquatic fauna in peril: the southeastern perspective*. Southeastern Aquatic Research Institute Special Publication 1. Lenz Design & Communications, Decatur, Georgia, USA.
- DUPELLMAN, W. E., AND L. TRUEB. 1986. *Biology of amphibians*. McGraw-Hill, New York, USA.
- DUFFY, D. C. 1994. Seeing the forest for the trees—response. *Conservation Biology* 7:436–439.
- FELLERS, G. M., AND C. A. DROST. 1994. Sampling with artificial cover. Pages 146–150 in W. R. Heyer, M. A. Donnelly, R. W. McDiarmid, L. C. Hayek, and M. S. Foster, editors. *Measuring and monitoring biological diversity: standard methods for amphibians*. Smithsonian Institution Press, Washington, D.C., USA.
- GIBBS, J. P. 1996. Sampling requirements for detecting trends in amphibian populations. Presentation given at the Third Annual Meeting of the North American Amphibian Monitoring Program. <http://www.im.nbs.gov/naamp3/naamp3.html>
- HEATWOLE, H. 1962. Environmental factors influencing local distribution and activity of the salamander, *Plethodon cinereus*. *Ecology* 43:460–472.
- HYDE, E. J. 2000. Assessing the diversity and habitat associations of salamanders in Great Smoky Mountains National Park. Thesis, North Carolina State University, Raleigh, USA.
- JACKSON, L. E. 1989. Mountain treasures at risk: the future of the southern Appalachian national forests. The Wilderness Society, Washington, D.C., USA.
- JAEGER, R. G. 1970. Potential extinction through competition between two species of terrestrial salamanders. *Evolution* 24:632–642.
- . 1979. Seasonal spatial distributions of the terrestrial salamander *Plethodon cinereus*. *Herpetologica* 35:90–93.
- . 1980. Density-dependent and density-independent causes of extinction of a salamander population. *Evolution* 34:617–621.
- . 1994. Transect sampling. Pages 103–107 in W. R. Heyer, M. A. Donnelly, R. W. McDiarmid, L. C. Hayek, and M. S. Foster, editors. *Measuring and monitoring biological diversity: standard methods for amphibians*. Smithsonian Institution Press, Washington, D.C., USA.
- , D. KALVARSKY, AND N. SHIMIZU. 1982. Territorial behaviour of the red-backed salamander: expulsion of intruders. *Animal Behaviour* 30:490–496.
- JOHNSON, A. S., W. M. FORD, AND P. E. HALE. 1993. The effects of clearcutting on herbaceous understories are still not fully known. *Conservation Biology* 7:433–435.
- JUNG, R. E., S. DROEGE, AND J. R. SAUER. 1997. DISPro amphibian project: standardized monitoring methods for amphibians in national parks and associations in time and space between amphibian abundance and environmental stressors. Project Proposal from Patuxent Wildlife Research Center to Environmental Protection Agency. Patuxent Wildlife Research Center, Laurel, Maryland, USA.
- LANCIA, R. A., J. D. NICHOLS, AND K. H. POLLOCK. 1996. Estimating the number of animals in wildlife populations. Pages 215–253 in T. A. Bookhout, editor. *Research and management techniques for wildlife and habitats*. The Wildlife Society, Bethesda, Maryland, USA.
- LANNOO, M. J. 1996. *Okoboji wetlands: a lesson in natural history*. Iowa City Press, Iowa, USA.
- MACKENZIE, M. D. 1993. The vegetation of Great Smoky Mountains National Park: past, present, and future. Dissertation, University of Tennessee, Knoxville, USA.
- MAGURRAN, A. E. 1988. *Ecological diversity and its measurement*. Princeton University Press, New Jersey, USA.
- MATHIS, A. 1990. Territoriality in a terrestrial salamander: the importance of resource quality and body size. *Behaviour* 112:162–175.
- . 1991. Territories of male and female terrestrial salamanders: costs, benefits, and intersexual spatial associations. *Oecologia* 86:433–440.
- NATIONAL PARK SERVICE. 1992. *Natural resources inventory and monitoring guideline*. National Park Service NPS-75, Washington, D.C., USA.
- PAULEY, T. K. 1995. Aquatic salamanders. Pages 14–22 in R. C. Reardon, coordinator. *Effects of diflufenuron on non-target organisms in broadleaf forested watersheds in the northeast*. National Center of Forest Health Management, FHM-NC-05-95. U.S. Department of Agriculture, Washington, D.C., USA.
- PETRANKA, J. W. 1998. *Salamanders of the United States and Canada*. Smithsonian Institution Press, Washington, D.C., USA.
- , M. E. ELDRIDGE, AND K. E. HALEY. 1993. Effects of timber harvesting on southern Appalachian salamanders. *Conservation Biology* 7:363–370.
- PYLE, C. 1985. Vegetation disturbance history of Great Smoky Mountains National Park: an analysis of archival maps and records. U.S. National Park Service Research/Resources Management Report SER-77.
- SAS INSTITUTE. 1999. SAS/STAT[®]. Version 8. SAS Institute, Cary, North Carolina, USA.
- SMITH, C. K., AND J. W. PETRANKA. 2000. Monitoring terrestrial salamanders: repeatability and validity of area-constrained cover object searches. *Journal of Herpetology* 34:547–557.
- WAKE, D. B. 1991. Declining amphibian populations. *Science* 253:860.
- ZAR, J. H. 1996. *Biostatistical analysis*. Prentice-Hall, Upper Saddle River, New Jersey, USA.

Received 15 March 2000.

Accepted 31 May 2001.

Associate Editor: Sullivan.