USING COUNTS TO SIMULTANEOUSLY ESTIMATE ABUNDANCE AND DETECTION PROBABILITIES IN A SALAMANDER COMMUNITY

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ABSTRACT: A critical variable in both ecological and conservation field studies is determining how many individuals of a species are present within a defined sampling area. Labor intensive techniques such as capture-mark-recapture and removal sampling may provide estimates of abundance, but there are many logistical constraints to their widespread application. Many studies on terrestrial and aquatic salamanders use counts as an index of abundance, assuming that detection remains constant while sampling. If this constancy is violated, determination of detection probabilities is critical to the accurate estimation of abundance. Recently, a model was developed that provides a statistical approach that allows abundance and detection to be estimated simultaneously from spatially and temporally replicated counts. We adapted this model to estimate these parameters for salamanders sampled over a six year period in area-constrained plots in Great Smoky Mountains National Park. Estimates of salamander abundance varied among years, but annual changes in abundance did not vary uniformly among species. Except for one species, abundance estimates were not correlated with site covariates (elevation, soil and water pH, conductivity, air and water temperature). The uncertainty in the estimates was so large as to make correlations ineffectual in predicting which covariates might influence abundance. Detection probabilities also varied among species and sometimes among years for the six species examined. We found such a high degree of variation in our counts and in estimates of detection among species, sites, and years as to cast doubt upon the appropriateness of using count data to monitor population trends using a small number of area-constrained survey plots. Still, the model provided reasonable estimates of abundance that could make it useful in estimating population size from count surveys.

Key words: Abundance; Counts; *Desmognathus quadramaculatus*; Detection probability; Great Smoky Mountains National Park; Monitoring; *Plethodon jordani*; Salamanders

WIDELY reported declines in amphibian species in many regions of the world have necessitated the implementation of monitoring programs that are sufficiently robust to detect trends yet account for natural fluctuations in populations (Dodd, 2003; Hall and Langtimm, 2001; Heyer et al., 1994; Olson and Leonard, 1997; Pechmann, 2003). Aside from declines that appear to take place suddenly, status assessments usually are based on measured changes in abundance. The most commonly used method involves some form of a capture-mark-recapture (CMR) survey protocol. A population is sampled at variable time intervals (a *K*-sample capture-recapture model; Williams et al., 2002) and population size is estimated based on the subsequent capture history (Nichols, 1992; Williams et al., 2002). Abundance also can be estimated using removal sampling (Bruce, 1995; Petranka and Murray, 2001; Salvidio, 2001), although this method has not been used generally to assess

status. Individuals are continually removed from a defined study area until they are no longer captured. Regardless of method used, a species or population may be perceived as declining if abundance decreases through time during sampling.

Many problems exist when using such a simplistic interpretive approach (Alford and Richards, 1999; Marsh, 2001; Pechmann, 2003). For instance, the number of individual amphibians may fluctuate widely at a locality through time from natural causes (Green, 2003; Marsh, 2001; Pechmann et al., 1991; Pechmann and Wilbur, 1994). CMR is generally labor intensive; marking large numbers of small amphibians in such a way as to satisfy the model assumptions of CMR (Donnelly and Guyer, 1994; Pollock et al., 1990) is difficult or infeasible; and the recapture rates often are low (Jung et al., 2000; Smith and Petranka, 2000; Taub, 1961). Removal sampling is labor intensive and in extreme cases may alter the habitat, especially if rocks and debris are removed from a site in an attempt to reduce cover (Martof, 1962), although removal sampling

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need not be destructive (Bruce, 1995; Petranka and Murray, 2001; Salvidio, 2001). These factors combine to limit the number of sites that can be sampled and often result in large variances in derived population estimates. High amounts of variance in estimates result in low statistical power to detect population trends.

In addition to the considerations listed above, a great many biotic and abiotic factors exist that may influence the detection of a salamander at any particular point in time. Some of these variables include: the timing of annual reproductive cycles; seasonal events (cold, drought, heat, storms) that are usually unpredictable; diurnal versus nocturnal activity patterns; variation in air, water and substrate temperature; variation in soil moisture and rainfall; relative humidity; changes in barometric pressure; cloud cover/moon brightness; and prey availability. Dodd (2003) discusses ways in which these factors influence detection and provides illustrative examples. Each of these factors potentially introduces a sampling bias into the number of animals observed, a bias which may change hourly, daily, seasonally, or annually.

A recent statistical approach to monitoring organisms uses an estimator based on whether animals are detected or not detected during repeated visits throughout a defined sampling area. These data then are used to derive the percent of area occupied (PAO) by members of a community which, through time, may give an estimate of status (MacKenzie et al., 2002; MacKenzie et al., 2003). In the past, the main hindrance to making reliable inferences about variation in species richness has been the inability to count all species present in an area during a survey. Weather conditions, the behavior of different species, cryptic coloration, and observer skill are just some factors affecting detection. Invariably, some species will be missed, thus biasing the estimates (Boulinier et al., 1998). Methods are now available which account for variation in detection probabilities, and which estimate species richness, standard error, and 95% confidence intervals (Nichols and Conroy, 1996). These methods have been extended to estimate several important vital rates in animal communities that are useful in assessing status, for example, rates of local species extinction, turnover, and colonization (MacKenzie et al.,

2003; Nichols et al., 1998a). These methods also have been used to test hypotheses concerning factors affecting temporal (Boulinier et al., 1998) and spatial variation (Nichols et al., 1998b) in species richness.

Despite new biometric approaches, many studies have used count surveys to track population status or implied that such counts could be used to monitor species' trends (Cooke, 1997; Davis, 1997; Houze and Chandler, 2002; Smith and Petranka, 2000; Welsh and Droege, 2001). Count surveys are employed routinely to sample many types of animal populations (Williams et al., 2002), including salamanders. In this survey method, pre-determined sites are visited repeatedly through time, and the number of animals observed or captured (via time- or area-constraint surveys, egg mass counts, coverboards, or traps) is tabulated. However, summaries of counts (e.g., averages) generally cannot provide accurate estimates of abundance of animals that are imperfectly detected (Hyde and Simons, 2001). Terrestrial salamanders usually are concealed beneath solid objects (rocks, logs) scattered throughout the forest litter or spend a considerable portion of their life cycle in underground habitats, and thus routinely are imperfectly detected. Likewise, stream-dwelling salamanders may be concealed among rocks and aquatic debris, and may retreat to moist inaccessible habitats as streams dry during droughts or decreased levels of surface flow.

A naïve approach regards count summaries as relative "indexes" of abundance (e.g., Hairston and Wiley, 1993; Smith and Petranka 2000); however, the comparison of such indexes (among locations or years) is valid only if detection rates are expected to have remained constant over the dimension of comparison, whether it be time, space or the number of species (Hyde and Simons, 2001; Thompson et al., 1998). Standardization of sampling protocols may help to moderate the variation in detectability, but much of this variation is often uncontrollable (e.g., weather, or habitat-related differences in detection). Therefore, a more statistically defensible approach is to develop a sampling design and inferential model that allow salamander abundance and detection to be estimated simultaneously from the counts. Recently, Royle (2004) has shown that count surveys with proper forms of spatial

and temporal replication may be used for this purpose. Here, we adapt Royle's approach to estimate the abundance and detection of salamanders at long-term census plots within the Great Smoky Mountains National Park. Our objectives are to derive population estimates for species in small stream and terrestrial salamander communities, to assess the uncertainty associated with count estimates of abundance and detection probabilities, and to explore correlations between abundance estimates and sampling covariates.

MATERIALS AND METHODS

Study Sites

Nine study sites were established in Great Smoky Mountains National Park, North Carolina and Tennessee: two sites along the Roaring Fork motor trail (at an elevation of 910–1040 m), two sites on the road between Newfound Gap and Clingmans Dome (1647–1745 m), three sites along Beech Flats Creek (1210–530 m), and two sites on Balsam Mountain between Soco Gap and the Heintooga overlook (1515–1685 m). These sites had been established previously by Smith and Petranka (2000), and criteria of site selection and a general overview of them are provided therein. Sites were accessible by road, and occurred in closed canopy old growth forest or forest regenerating from timber cutting prior to the establishment of the park in 1934. At higher elevations, the forest was dominated by red spruce (*Picea rubens*) and Fraser fir (*Abies fraseri*), whereas at lower elevations, eastern hemlock (*Tsuga canadensis*) and a mixed deciduous (primarily *Acer*, *Fagus*, *Betula*, *Cornus*, *Liriodendron*, *Liquidamber*) forest predominated.

Each site had a small stream or seepage area flowing through it along which study plots were established. Stream flow varied depending on rainfall, and on several occasions stream flow ceased or was negligible. Cessation of stream flow occurred especially at one high elevation site in mid- to late summer on Clingmans Dome (designated Clingmans Dome Upper) and at one low elevation site in spring near Roaring Fork (Roaring Fork Site 1). Slopes varied from nearly level to ca. 30 degrees. All sites contained an abundance of coarse woody debris, rocky stream bottoms, and other forms of cover for salamanders.

Survey Protocol

We used the same basic survey protocol as described by Smith and Petranka (2000). Three 30 × 40 m plots (A, B, C) were established at each site. Plots were located in a gradient of increasing elevation, with plot A at the lowest point. The plots were arranged linearly along the stream in such a manner that the stream or seepage area paralleled the inside margin along one side of the plot (Dodd, 2003); plots were usually <30 m from one another. Parallel transect lines were established within a plot at 5 m intervals away from the stream and marked by survey flags. The stream or seepage area normally covered ca. 12% of a plot. Plots were surveyed diurnally once per month from 1993–1995 and 1998–2000 from June through August. Plot A was searched in June, plot B in July, and plot C in August. If sufficient searchers were available, one team searched the streambed and immediate streamside moving upstream, while a second team worked the parallel terrestrial transects. If only a few searchers were available, the streambed survey was finished prior to starting the terrestrial transects.

Searchers turned rocks and downed logs and branches, and rustled through surface litter to find salamanders. Surface debris was replaced in order to minimize disturbance. Salamanders were identified to species, and snout–vent length was measured to the nearest 5 mm; if a salamander escaped prior to measurement, it was estimated to be an adult or juvenile. Animals were released at the point of capture. Certain medium-sized desmognathines at some of these sites are impossible to identify with certainty because of extensive hybridization among sibling species (Petranka, 1998; Smith and Petranka, 2000; Tilley, 1981; Tilley and Mahoney, 1996). For this reason, we combined counts of *Demognathus imitator* and *D. ocoee* together to a *D. ochrophaeus* complex, and *D. santeetlah* and a low elevation *D. fuscus*-like animal, tentatively assigned to *D. conanti* (Dodd, 2004; Titus and Larson, 1996), to a *D. fuscus* complex, for analysis. Additional information on survey protocol is in Smith and Petranka (2000).

At the start of the surveys, we noted weather conditions and measured the air and water temperature (Atkins® K thermocouple

thermometer) and relative humidity (Nester Instruments® RH pen). The same measurements were repeated at the end of the survey and averaged to obtain a survey-specific covariate. We took three samples each of water and soil pH and conductivity at each site. Their measurements also were averaged to obtain a single survey-specific covariate. We used Hobo® temperature and relative humidity data loggers to examine variation in these variables and to identify possible unusual weather occurrences in 1998 and 2000 at various sites. Cool fronts were associated with the June surveys in both these years. Air and water temperatures were fairly constant otherwise. Relative humidity was >60% throughout the sampling period at Roaring Fork Site 1 in 1998, but no data were available at other sites and for other years.

Data Analysis

Our spatially- and temporally-replicated counts may be used to estimate both detection and site-specific abundance of salamanders, provided the abundance of salamanders at each site is assumed to remain constant in the time required to complete the survey (Royle, 2004). Three lines of evidence support this assumption. First, populations of terrestrial and stream-dwelling plethodontids are generally stable (Green, 2003; Hairston, 1987), and do not experience wide fluctuations in numbers over a short (3-month) time span, as may be expected for pond breeding species. Second, the timing of our surveys in early to mid-summer avoids the late summer influx of juveniles and larvae that might influence counts (life history data reviewed by Dodd, 2004; Petranka, 1998; Petranka and Murray, 2001). For example, the smallest *Desmognathus quadramaculatus* and *Plethodon jordani* were found from June to early July, suggesting a lack of new recruitment through the August survey. Third, both terrestrial and stream-dwelling salamanders tend to remain in rather small, circumscribed territories (Camp and Lee, 1996; Mathis et al., 1995; Merchant, 1972; Nishikawa, 1990), and do not randomly wander or migrate through an area.

We fitted Royle's model to the counts of 6 salamander species that were commonly observed in all 6 years of our study. Counts of one

species, *P. jordani*, appeared to be strongly correlated with elevation, which varies considerably among our sampling sites; therefore, we extended Royle's model to specify site-specific differences in mean abundance as a function of elevation. In particular, we let x_{jk} denote the number of salamanders observed at site j (= 1, ... , 9) and month k (= 1, ..., 3) and make 2 distributional assumptions:

$$[x_{jk} \mid N_j, \theta] \sim \text{Binomial}(N_j, \theta)$$

and

$$[N_j \mid \lambda_j] \sim \text{Poisson}(\lambda_j)$$

where θ is the probability of detection, N_j is the number of salamanders present at site j, and λ_j is the conditional mean abundance of salamanders at site j. The logarithm of the conditional mean abundance of salamanders at site j was modeled as a function of elevation w_j at that site as follows:

$$\log(\lambda_j) = \beta_0 + w_j\beta_1$$

where β_0 and β_1 denote the intercept and slope parameters in a Poisson-regression formulation. Thus, our estimates of spatial variation in abundance of *P. jordani* are related in part to differences in elevation among sites. We fitted the same model to the counts of the other 5 species, excluding elevation as a covariate (and β_1, of course), to estimate mean abundance among all 9 sites. We computed maximum-likelihood estimates of the model's parameters (θ, β_0, β_1) by maximizing the marginal likelihood function obtained by integrating over the possible values of N_j

$$L(\theta, \beta_0, \beta_1 \mid X)$$
$$= \prod_{j=1}^{9} \sum_{N_j=\max(x_{jk})}^{\infty} \frac{e^{-\lambda_j}\lambda_j^{N_j}}{N_j!} \prod_{k=1}^{3} \frac{N_j!}{x_{jk}!(N_j - x_{jk})!}$$
$$\times \theta^{x_{jk}}(1 - \theta)^{N_j - x_{jk}}$$

as described by Royle (2004).

RESULTS

A total of 9766 salamanders of 13 species was recorded during the surveys. Most captures were of members of the *D. ochrophaeus* complex (3359), followed by *P. jordani* (1896), *D. quadramaculatus* (1457), *D. fuscus* complex (938), *D. wrighti* (526) and *Eurycea wilderae*

TABLE 1.—Maximum-likelihood estimates of mean abundance (salamanders per site) with 95% confidence limits (in parentheses). Na = not available because no salamanders observed in sample. Ne = not available because the model could not be fitted to the counts.

Year	D. ocrophaeus complex	D. fuscus complex	D. wrighti	D. quadramaculatus	E. wilderae
1993	132.5 (72.7, 241.3)	Na	Ne	85.2 (45.5, 159.7)	20.7 (4.4, 98.5)
1994	123.2 (83.4, 182.0)	Ne	13.8 (7.1, 26.8)	40.3 (24.9, 65.4)	12.6 (3.5, 45.3)
1995	57.1 (39.8, 82.0)	43.7 (22.9, 83.4)	5.1 (3.0, 8.7)	132.4 (45.4, 385.9)	12.7 (3.3, 49.3)
1998	47.9 (37.1, 62.0)	122.1 (28.9, 515.4)	40.1 (13.5, 119.3)	171.6 (70.3, 418.6)	34.1 (11.9, 97.2)
1999	182.5 (78.6, 424.0)	Ne	27.6 (8.0, 94.9)	18.3 (9.3, 36.1)	Ne
2000	104.3 (60.4, 180.1)	28.7 (15.4, 53.6)	31.4 (4.1, 244.1)	29.8 (11.9, 74.9)	36.6 (13.2, 101.3)

(502). The remaining species (*D. marmoratus*, *D. monticola*, *Gyrinophilus porphyriticus*, *P. glutinosus*, *P. metcalfi*, *P. oconaluftee*, *P. serratus*) were found in much lower numbers and were not used in analyses. Six hundred ten salamanders could only be identified to genus or escaped before a positive identification could be made; these were nearly all stream-dwelling desmognathines.

Estimates of salamander abundance varied among years, but annual changes in abundance did not vary uniformly among species (Table 1). Variances were rather large, and the widely overlapping 95% confidence intervals (CI) indicate that there were no statistical differences in the mean annual abundance estimates within a species at the localities sampled. Abundance estimates were not correlated with site covariates (elevation, soil and water pH, conductivity, air and water temperature) in most species; the uncertainty in the estimates was so large as to make correlations ineffectual in predicting which covariates might influence abundance. The only exception was the effect of elevation on the abundance estimates for *P. jordani*. In all years, elevation positively correlated in *P. jordani* (Fig. 1). The effect of elevation on estimates of abundance is clearly evident when specific sites are compared. At the relatively low elevation Roaring Fork Site 1 (930 m), the mean estimate of abundance for *P. jordani* was <20 salamanders in four of six years, and <50 salamanders in the other two years. Estimates were between 19 and 90 salamanders per year at middle elevation Beech Flats Lower (1210 m), and increased to between 90 and 450 salamanders per year at high elevation Clingmans Dome Lower (1740 m) (Fig. 2).

Detection probabilities varied among species and sometimes among years for the six species examined (Table 2), and did not seem to vary consistently among species from one year to the next. The more commonly observed species, such as *P. jordani* (except in 1995) and members of the *D. ochrophaeus* complex, had the highest mean detection probabilities (to 0.38), although with notable exceptions (*D. quadramaculatus* in 1999 at 0.36 and *D. wrighti* in 1995 at 0.41). The rarer species, *D. wrighti* and *E. wilderae*, had the lowest detection probabilities, although again there were notable exceptions (*P. jordani* in 1995 at 0.06 and *D. fuscus* complex in 1998 at 0.08). Probabilities were generally consistent only for *E. wilderae* in all years (Table 2). Visual examination of the 95% CI's suggest that detection probabilities were significantly different (1998 vs. 1999) or marginally so (2000 vs. 1998) only for members of the *D. ochrophaeus* complex compared with other years; CI's were not significantly different for *D. fuscus* complex, *D. wrighti*, *D. quadramaculatus*, *E. wilderae*, and *P. jordani* among years. The lowest detection probabilities were for *P. jordani* in 1995, and the highest probabilities were for *D. wrighti*, also in 1995 (Table 2). Taken together, the wide ranging CIs suggest a great degree of variation which is not consistent within or among species; no clear patterns are apparent.

DISCUSSION

Surprisingly little information exists in the published literature on abundance or density estimates for terrestrial and aquatic plethodontid salamanders. Community estimates of salamander abundance, provided as the number of individuals per ha (density), differ by as much as 7 fold (Burton and Likens, 1975; Petranka and Murray, 2001). Undoubtedly, variation in estimates, both intraspecifically and among communities, reflects differences among sites, salamander assemblages, sampling
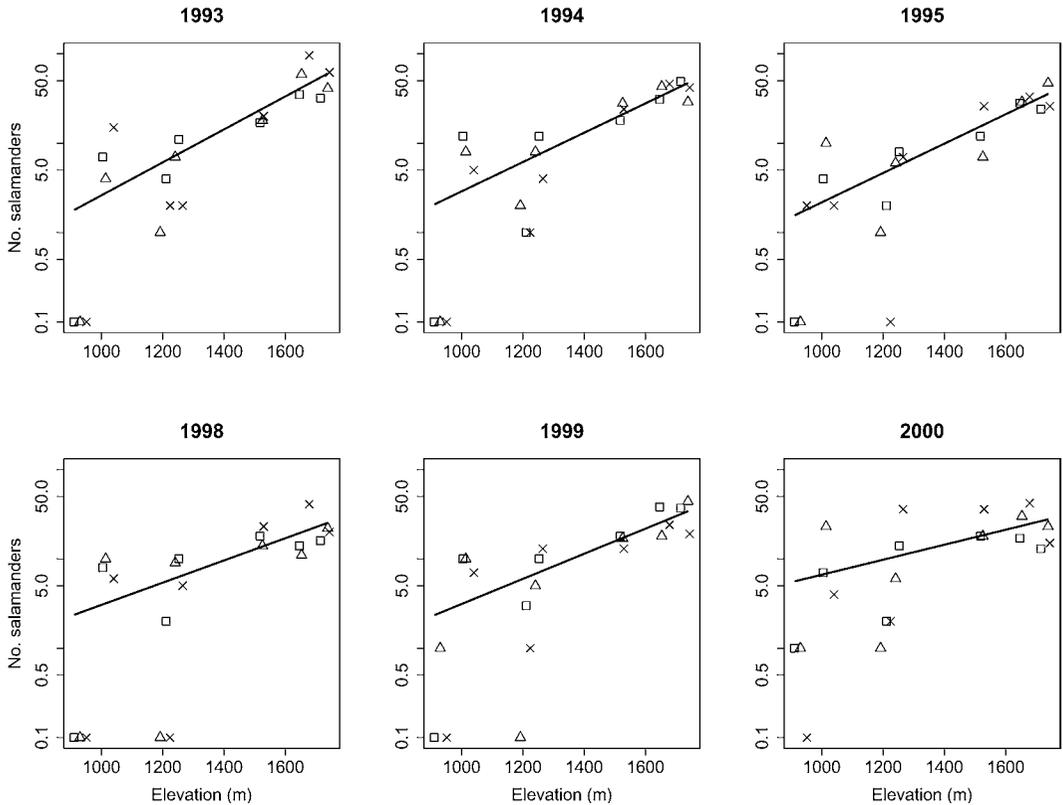
FIG. 1.—Relationship between estimated salamander abundance and elevation for *Plethodon jordani*, 1993–1995 and 1998–2000, at 27 plots in Great Smoky Mountains National Park. □ = June survey; △ = July survey; ✕ = August survey. The Y-axis is in logarithmic scale. Elevation in meters.

protocols, environmental conditions, and methods of analysis. Few assessments have been subject to rigorous analysis, especially with the biometrical models used increasingly by researchers working in other vertebrate groups (Williams et al., 2002). For these reasons, both inter- and intraspecific comparisons are difficult and fraught with uncertainty.

Royle's estimator provided a reasonable approximation of abundance of several species of salamanders in the Great Smoky Mountains. Our abundance estimates are generally similar to those obtained in the southern Appalachians for *P. jordani* (1300/ha, although this figure probably includes several members of the *P. jordani* complex rather than *P. jordani* sensu stricto; see Highton and Peabody, 2000) and the *D. ochrophaeus* complex (2500/ha, Smith and Petranka, 2000). One other estimate is available for *P. jordani*: 8600/ha at an unspecified location in the Great Smoky Moun-

tains (Petranka, 1998). At our highest elevation sites, *P. jordani* was estimated to have a mean abundance of between 866 salamanders/ha to as high as 4925 salamanders/ha. At the low elevations sites, *P jordani* was much less abundant, that is, from 42 to 372 salamanders/ha. At all locations, 1995 appeared to be a very good year for *P. jordani*. Examination of monthly rainfall and temperature data for both low and high elevation sites revealed no unusual patterns in the Smokies in 1995 relative to the other years.

Our corresponding mean estimates were between 399 and 1521 salamanders/ha for individuals of the *D. ochrophaeus* complex. However, it is likely that the actual density for this species complex is much higher in optimal habitat. At our sites, most salamanders of the *D. ochrophaeus* complex were concentrated in and along stream margins, whereas the density estimates were based on an entire plot which
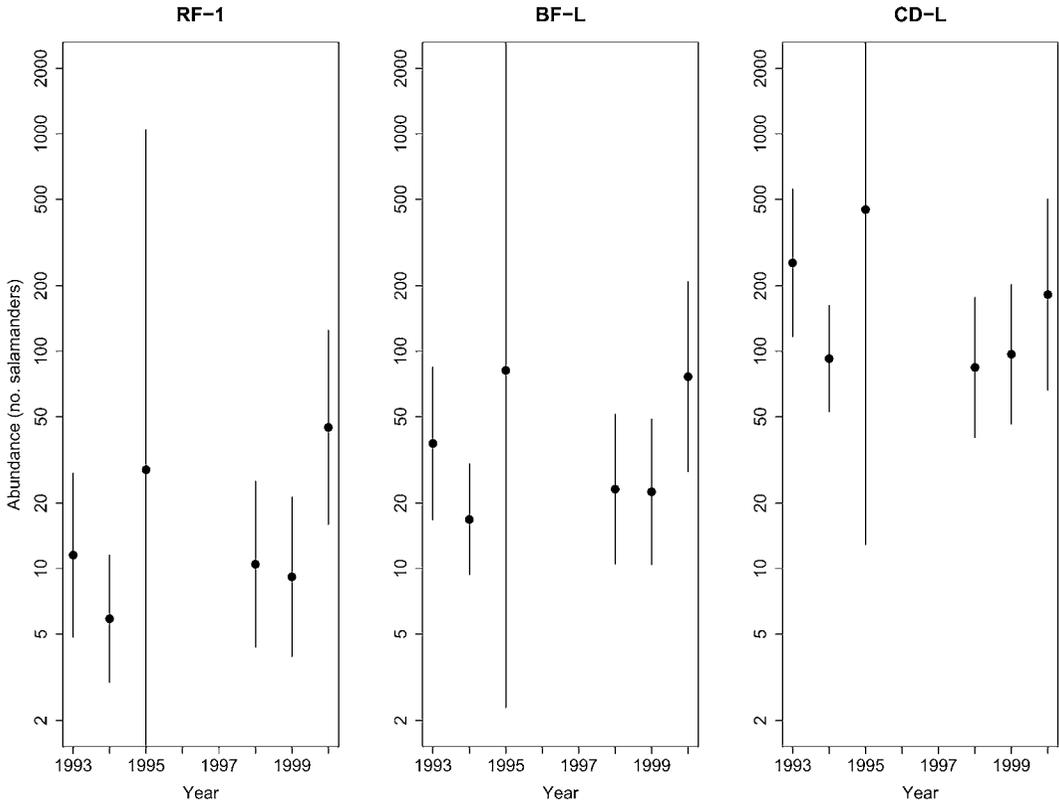
FIG. 2.—Relationship between salamander abundance and elevation at a low elevation site (RF-1, 930 m), a middle elevation site (BF-L, 1210 m), and a high elevation site (CD-L, 1740 m) for *Plethodon jordani* in Great Smoky Mountains National Park. The error bars give 95% confidence intervals around a mean (●). The Y-axis is in logarithmic scale. Estimates of site-specific abundance $\hat{\lambda}_j$ were computed on a logarithmic scale ($\hat{\phi}_j = \log(\hat{\lambda}_j)$); therefore, 95% confidence limits of abundance were computed in the usual way by transforming back to an arithmetic scale: $\exp(\hat{\phi}_j \pm z_{0.025}SE(\hat{\phi}_j))$. These confidence limits are therefore asymmetrically positioned about the estimate of abundance $\hat{\lambda}_j$.

included much terrestrial habitat. Assuming that the stream and its margins occupied 37.5% of a plot (that is, a stream corridor 15 m wide by 30 m in length), then density estimates for this species would increase to between 1064 and 4056 salamanders/ha (or between 2.4 and 9 salamanders/m^2), depending on year.

Petranka and Murray (2001) calculated density estimates of 3700 *D. wrighti* and 1490 *E. wilderae* individuals/ha based on removal sampling from two 30 × 30 m plots during 22 consecutive nightly searches in the Great Craggy Mountains. We estimated that there was an annual mean of between 43 and 334 *D. wrighti*/ha, and between 105 and 305 *E. wilderae*/ha, at our sampling sites. Using our 95% CIs extends the range considerably, to 2034 *D. wrighti* and 844 *E. wilderae* individuals/ha. Burton and Likens (1975) estimated

that there were 400 adult *E. bislineata*, a sister species of *E. wilderae*, per hectare in a New Hampshire watershed. For *D. quadramaculatus*, stream densities are reported to be 5.6 to 11.7 individuals (adults, juveniles, larvae)/m^2 in one population in western North Carolina at ca. 1040 m (Davic and Orr, 1987). Our mean estimates ranged from 537 to 2288 salamanders per ca. 90 m^2 (6 to 25.4 individuals/m^2), depending on year. Our estimate assumes that all *D. quadramaculatus* were captured within a stream corridor 3 m wide by 30 m in length, and it also includes all life stages.

The advantage of the Royle model is that the abundance estimates are based solely on counts at fixed sampling locations over the course of a multi-year inventory, thus providing a relatively simple way to track abundance without the necessity to mark individuals. At the same

TABLE 2.—Maximum-likelihood estimates of detection probability with 95% confidence limits (in parentheses). Na = not available because no salamanders were observed in the sample. Ne = not available because the model could not be fitted to the counts.

Year	*D. ocrophaeus* complex	*D. fuscus* complex	*D. wrighti*	*D. quadramaculatus*	*E. wilderae*	*P. jordani*
1993	0.18 (0.10, 0.31)	Na	Ne	0.20 (0.10, 0.35)	0.11 (0.02, 0.42)	0.17 (0.07, 0.34)
1994	0.23 (0.15, 0.33)	Ne	0.23 (0.11, 0.42)	0.29 (0.17, 0.45)	0.19 (0.05, 0.52)	0.38 (0.20, 0.59)
1995	0.28 (0.19, 0.39)	0.16 (0.08, 0.29)	0.41 (0.23, 0.62)	0.10 (0.03, 0.28)	0.19 (0.04, 0.56)	0.06 (0.001, 0.73)
1998	0.38 (0.29, 0.47)	0.08 (0.02, 0.29)	0.12 (0.04, 0.32)	0.12 (0.05, 0.27)	0.12 (0.04, 0.31)	0.24 (0.11, 0.46)
1999	0.11 (0.05, 0.24)	Ne	0.13 (0.03, 0.37)	0.36 (0.17, 0.62)	Ne	0.27 (0.12, 0.51)
2000	0.17 (0.10, 0.29)	0.20 (0.10, 0.35)	0.09 (0.01, 0.47)	0.18 (0.06, 0.41)	0.13 (0.04, 0.33)	0.13 (0.04, 0.32)

time, the analysis provides estimates of detection probabilities with associated confidence intervals that are necessary to prevent biases across sites and sampling methods (Hyde and Simons, 2001; Jung et al., 2000; Schmidt, 2003).

We found such a high degree of variation in our counts and detection probabilities among species, sites, and years as to cast doubt upon the appropriateness of using count data to assess population trends when relatively small numbers of sampling sites are monitored; these results are in agreement with conclusions drawn from other studies (Hyde and Simons, 2001; Jung et al., 2000). Smith and Petranka (2000) argued that area-constrained searches that provide count data generate valid indices to monitor trends of plethodontid salamanders. We used data from Smith and Petranka (2000) for 1993–1995 on the exact same plots to examine abundance and detection probabilities; both varied significantly at these sites (Tables 1, 2). This result suggests that a comparison of counts among plots is invalid. We noted a similar effect among species, years, and sites from 1998–2000. The reason for variation in detection probabilities is not readily apparent. However, one way to reduce the uncertainty would be to sample a much larger number of sites over the course of a year, for example, by using a less labor intensive sampling protocol such as 30 minute time-constrained surveys. In this manner, counts with associated detection probabilities might yield abundance estimates that are much more useful and informative for monitoring purposes.

In any case, Marsh (2001) noted that coefficients of variation of abundance estimates could vary 2 to 10-fold even with time series in excess of five years of sampling. The power to detect small, negative ($<-5\%$) population trends in Appalachian salamanders increases with the number of years (minimum of 10–40) and sites sampled (Hyde and Simons, 2001; Smith and Petranka, 2000). Small population changes, however, may have nothing to do with the question of immediate threats to amphibians, and surveying many populations intensively for a long time in order to detect trends is impractical. It is thus unlikely that count surveys based on a relatively small number of area-constrained sampling plots will be effective at monitoring population changes in terrestrial and aquatic plethodontids, regardless of estimator used. This is especially true when detection probabilities are absent (Schmidt, 2003).

Salamander surface activity is known to be influenced by environmental conditions such as temperature, humidity, soil acidity, and rainfall (Grover, 1998; Taub, 1961; Wyman and Hawksley-Lescault, 1987). Direct one-to-one correlations are sometimes difficult to establish without long-term data on both the activity and the variable in question immediately during and preceding sampling. For example, the amount of surface activity may depend on the timing and amount of rainfall, soil moisture, whether a threshold amount of rainfall occurs, or on a combination of these and other factors. Not surprisingly, we were unable to establish direct correlations between estimated salamander abundance and certain microhabitat variables which we recorded only at the time of sampling. In addition, low inter-site sample sizes probably inhibited our ability to establish possible correlations of abundance with the fixed-site variable (that is, elevation) for species such as *D. wrighti* and *E. wilderae*. The use of site-specific data loggers to continuously monitor environmental variables

may help clarify the influence of certain microclimatic effects on surface counts.

On the other hand, we demonstrated that elevation is correlated positively with abundance in *P. jordani*. Elevation is a particularly important variable in relation to salamander distribution because of its influence on life history parameters, such as age and size at metamorphosis and sexual maturity (Bruce, 2003). *Plethodon jordani* occurs most frequently at the highest elevations in the Smokies, where it is common under forest floor coarse woody debris. The lowest elevation that the species has been recorded in Great Smoky Mountains National Park is 775 m (Dodd, 2004). At lower elevations, the species hybridizes with *P. oconaluftee* (Highton, 1989), possibly because individuals are unable to differentiate important chemical cues during courtship between conspecifics and other members of the *Plethodon glutinosus* complex (Dawley, 1987). Optimal environmental conditions and a lack of intraspecific competitors probably are reflected in optimal abundance of this species at different elevations.

Using intensive sampling over a much smaller area of the Great Smokies, Hyde and Simons (2001) showed that abundance was highest for *D. wrighti* on mid-level slopes, although all of their study sites were <1250 m. *Plethodon jordani* was least abundant at the lowest elevations, whereas *E. wilderae* showed no effects of elevation on abundance. Although soil moisture explained a small amount of the observed variation in salamander abundance, a variety of other microhabitat covariate variables failed to explain any significant amount of variation. Our results concur with those of Hyde and Simons (2001), and exemplify the difficulty of correlating salamander abundance with individual microhabitat variables.

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A MORPHOLOGICALLY DISTINCT NEW SPECIES OF *PSEUDOEURYCEA* (CAUDATA: PLETHODONTIDAE) FROM THE SIERRA MADRE ORIENTAL OF PUEBLA, MÉXICO

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ABSTRACT: A new species of *Pseudoeurycea* is described from cloud forests of the Sierra Madre Oriental of Puebla, México. The new species is distinguished from all other *Pseudoeurycea* by its small size, stout body, short tail, large nostrils, presence of characteristic glandular convergent ridges on the pelvic region and the tail, and by its distinctive limb structure, with very small hands and feet that are extensively webbed and bear prominent but short and pointy middle digits. The only apparent close relative of this species is *P. praecellens*, from which it differs by the position and distribution of the dorsal and caudal glands, body proportions, nostril size and coloration. All specimens of the new species were found in cloud forest, under a canopy of *Liquidambar*, *Quercus*, and *arborescent* ferns, as well as in a coffee grove. The elevational range for the species is narrow, between 905 and 1400 m, unusually low elevations for *Pseudoeurycea*.

Key words: Caudata; Mexico; New species; North America; Plethodontidae; *Pseudoeurycea*; Taxonomy

INTRODUCTION

The genus *Pseudoeurycea*, with 37 described species, of which all but three are endemic to Mexico, is one of the largest assemblages of neotropical salamanders. The taxon was proposed by Taylor (1944) and has been fully stable since its initial diagnosis. The addition of new species, mostly based on morphological grounds (Adler, 1996; Bogert, 1967; Canseco-Márquez and Parra-Olea, 2003; Lynch and Wake, 1989; Lynch et al., 1983; Parra-Olea et al., 2001; Parra-Olea et al., 2004; Pérez-Ramos and Saldaña-de la Riva,

2003; Wake and Campbell, 2001), has not changed the basic phylogenetic structure of the genus. However, the transfer of *Pseudoeurycea parva* to *Ixalotriton* (Parra-Olea, 2002), and the transfer of *Parvimolge praecellens* to *Pseudoeurycea* (Wake and Elias, 1983), represent important modifications affecting the diagnosis of *Pseudoeurycea*. The recent use of molecular techniques has shown that a dramatic reorganization of *Pseudoeurycea* is needed. Mitochondrial DNA (mtDNA) data support inclusion of the morphologically distinctive species of *Lineatriton* within *Pseudoeurycea* (Parra-Olea and Wake, 2001). Otherwise, these complex results render *Pseudoeurycea* paraphyletic. A comprehensive

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