

## ESTIMATING SITE OCCUPANCY AND SPECIES DETECTION PROBABILITY PARAMETERS FOR TERRESTRIAL SALAMANDERS

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**Abstract.** Recent, worldwide amphibian declines have highlighted a need for more extensive and rigorous monitoring programs to document species occurrence and detect population change. Abundance estimation methods, such as mark–recapture, are often expensive and impractical for large-scale or long-term amphibian monitoring. We apply a new method to estimate proportion of area occupied using detection/nondetection data from a terrestrial salamander system in Great Smoky Mountains National Park. Estimated species-specific detection probabilities were all  $<1$  and varied among seven species and four sampling methods. Time (i.e., sampling occasion) and four large-scale habitat characteristics (previous disturbance history, vegetation type, elevation, and stream presence) were important covariates in estimates of both proportion of area occupied and detection probability. All sampling methods were consistent in their ability to identify important covariates for each salamander species. We believe proportion of area occupied represents a useful state variable for large-scale monitoring programs. However, our results emphasize the importance of estimating detection and occupancy probabilities rather than using an unadjusted proportion of sites where species are observed where actual occupancy probabilities are confounded with detection probabilities. Estimated detection probabilities accommodate variations in sampling effort; thus comparisons of occupancy probabilities are possible among studies with different sampling protocols.

**Key words:** *amphibian; detection probability; Great Smoky Mountains National Park; monitoring; plethodontid salamanders; site occupancy.*

### INTRODUCTION

Evidence of global scale declines in amphibian populations has highlighted the need for more extensive and rigorous monitoring programs to document species occurrence and detect population changes. Numerous organizations are promoting long-term, large-scale studies to document, measure, and monitor amphibian populations (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), especially for species believed to be at risk. Among amphibians, plethodontid salamanders have been promoted as indicators of overall biodiversity and forest ecosystem integrity (Welsh and Droege 2001). Compared to most anurans, they are long-lived, slow to mature, and have relatively low fecundity (Petranka 1998). They also show susceptibility to a variety of natural and anthropogenic perturbations (see Welsh and Droege [2001] for a review).

Amphibian surveys have been initiated for several purposes, including (1) to establish baseline data and techniques for long-term monitoring programs (Gibbons et al. 1997, Corn 2000, Dodd et al. 2000, Hyde and Simons 2001), (2) to compare historical to current species distributions (Fisher and Shaffer 1996, Shaffer et al. 1998, Corser 2001) and (3) to identify and target hot spots of amphibian diversity and abundance for protection (Welsh and Lind 1988). Two important sources of variation, spatial variation and variation in detection probabilities, constrain the inferences drawn from these types of surveys (Yoccoz et al. 2001, Pollock et al. 2002). Studies often make inferences about large areas by collecting information from sample units selected by some probability-based sampling technique (e.g., stratified random sampling). Additionally, because not all species are detected in a sampled area, monitoring programs must estimate species detection probabilities (Pollock et al. 2002). Species detection probability is defined as the probability of detecting at least one individual of the species during a particular sampling occasion, given that individuals of the species are present in the area (Boulinier et al. 1998, MacKenzie et al. 2002). Although some salamander studies incorporate a spatial design (e.g., Welsh and Lind 1988, Hyde and Simons 2001), we know of no previous study that has estimated species detection probability. Most

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PLATE 1. (Left) Adult salamander of *Plethodon glutinosus* complex on a tree trunk in Great Smoky Mountains National Park. Photo credit: Theodore R. Simons. (Right) *Eurycea wilderae* perched on a May-Apple plant (*Podophyllum peltatum*). Photo credit: Chris Hagen.

salamander studies use a variety of sampling methods to document species occurrence and record the total number of individuals of each species seen at a given location. Individual counts (the total number of individuals seen of a species) are used as an estimate of abundance or relative abundance (Petranka et al. 1993, Hecnar and M'Closkey 1997, Aubry 2000). Likewise, the proportion of sites where a species was observed serves as an estimate of the proportion of area occupied (Hecnar and M'Closkey 1997, Pilliod and Peterson 2001). These state variables (abundance or relative abundance and the proportion of area occupied) are usually compared over time or space to make inferences about temporal changes in the communities' status, or the effects of environmental or anthropogenic factors (Petranka et al. 1993, Skelly et al. 1999, Pilliod and Peterson 2001).

Most amphibian studies that explore abundance, diversity, or community composition assume that either (1) all species are detected or (2) the detection probability of different species is the same for the times, locations, or sampling methods being compared (Boulinier et al. 1998). The assumption of complete or equal species detection probability is unlikely to be met for terrestrial salamanders. Few species are so conspicuous that they will be detected with 100% certainty. Unadjusted "observed" site occupancy rates contain an unknown negative bias unless detection probability is

one. Additionally, detection probability likely varies temporally due to seasonal behavioral patterns (Petranka 1998) and changing environmental conditions, or spatially due to site-specific habitat characteristics. Terrestrial salamander populations are believed to be largely subterranean, with only a small proportion of the population near the surface and available for capture on a given sampling occasion (Taub 1961, Heatwole 1962, Hairston 1987, Petranka and Murray 2001). Site-specific habitat characteristics influence the size of the available surface population (Bailey 2003). Some areas also support higher total populations of some species than others, creating clumped distributions of species throughout the landscape. Furthermore, different sampling techniques are likely to vary in their effectiveness at detecting species, making it difficult to compare results among studies with different sampling protocols (Barr and Babbitt 2001, Hyde and Simons 2001, Jenkins et al. 2002).

Recent theory has been developed to accommodate situations where species detection probability is less than one and where it varies among species or habitats (MacKenzie et al. 2002). This technique builds on traditional closed-population capture-recapture methods, but uses the proportion of area (or sites) occupied as a state variable to characterize ecosystem status. Briefly, the method involves visiting sites multiple times within a season where the target species is either de-

TABLE 1. ANOVA results testing the effects of species, year, and sampling method on proportion of area occupied estimates,  $\psi(\cdot)$ , using model,  $\psi(\cdot)p(\cdot)$  and all data combined.

Source	df	Type III ss	F	P
Species	6	2.5518	75.80	<0.001
Year	2	0.0650	2.80	0.0066
Method	3	0.0795	4.72	0.0070
Species $\times$ Year	12	0.0958	1.42	0.2008
Year $\times$ Method	6	0.0694	2.06	0.0826
Species $\times$ Method	18	0.2214	2.19	0.0222
Error	36	0.2020		

Note: The tests of the effects of pairwise interactions are also reported.

tected, with probability  $p$ , or not detected. The goal is to estimate the proportion of sites that are occupied,  $\psi$ , knowing the species is not always detected, even when present. On any given sampling occasion, the species is either detected, which requires occupancy,  $\psi \times p$ , or not detected, which arises when either the species is present but not detected,  $\psi \times (1 - p)$ , or when it is not present,  $(1 - \psi)$ . In this paper, we describe the sampling requirements and assumptions of this new method. We then test a series of a priori hypotheses about proportion of area occupied estimates and species detection probabilities for seven salamander species that occur on sites in Great Smoky Mountains National Park (GSMNP) (see Plate 1 for photographs of two representative species). Specifically, we expected species detection probabilities to be less than one, and to vary among species. We tested whether the type of survey method, the number of sites sampled, or the number of sampling occasions per site affected estimates of proportion of area occupied or species detection probability. We expected that detection probabilities would change with these factors but that proportion of area occupied estimates would not. We explored the importance of time-specific covariates by estimating species detection probabilities among sampling occasions (within a season), and examined seasonal patterns between years. Finally, we investigated spatial variation in both proportion of area occupied and species detection probabilities associated with four large-scale habitat characteristics: prior disturbance history, vegetation type, elevation, and proximity to streams. Our previous research suggested that these factors might influence parameter estimates (Hyde and Simons 2001, Bailey 2003).

#### STUDY AREA

Great Smoky Mountains National Park (GSMNP) is at the forefront of efforts to develop long-term natural resource inventory and monitoring on U.S. Department of Interior lands. Located along the Tennessee–North Carolina border, the park's 205 665 ha of contiguous forest is internationally recognized for its rich temperate biodiversity. Geography and geology, along with

steep, complex topography, create temperature and moisture gradients that produce high levels of species diversity in many taxa, including salamanders. Approximately 10% of the world's salamander species are found in the southern Appalachian region (Petranka 1998). Salamanders are a high priority taxon for the park's inventory and monitoring program due to the large number of species and limited data on species distribution, abundance, and natural history.

#### METHODS

##### *Proportion of area occupied (PAO) estimation: methods and assumptions*

MacKenzie et al. (2002) describe a likelihood-based method for estimating proportion of area (or sites) occupied when species detection probabilities are less than 1. This work represents an extension of traditional closed-population capture–recapture theory, thus all estimation models assume that (1) the community of species is closed to additions (immigration or colonization), deletions (emigration or extinction), or other changes in occupancy during the study, (2) species are correctly identified, and (3) the probability of detecting a species at one site is independent of probability of detecting the species at all other sites (MacKenzie et al. 2002).

Sites must be visited a minimum of two times per sampling season and detection/nondetection information is recorded for a species at each location and sampling occasion. Estimable parameters include  $\psi_i$ , the probability that a species is present at site  $i$ , and  $p_{it}$ , the conditional probability that a species is detected at site  $i$  at time  $t$ , given presence. Both parameters may be expressed as a logit function of site-specific covariates (e.g., habitat type, elevation), and  $p_{it}$  may also include time-specific covariates (e.g., time, temperature, weather conditions) (MacKenzie et al. 2002). Presently, estimation methods also assume no heterogeneity among sites in either  $\psi$  or  $p$  not attributed to specified covariates. Species are analyzed separately, thus species-specific detection probabilities can be estimated. Computer software packages, ESOR or PRESENCE, are available online for parameter esti-

TABLE 2. ANOVA results testing the effects of species, year, and sampling method on species detectability estimates,  $\hat{p}(\cdot)$ , using model,  $\psi(\cdot)p(\cdot)$  and all data combined.

Source	df	Type III ss	F	P
Species	6	0.6949	16.99	<0.001
Year	2	0.3159	23.17	<0.001
Method	3	0.8547	41.81	<0.001
Species $\times$ Year	12	0.0979	1.20	0.3225
Year $\times$ Method	6	0.1204	2.94	0.0192
Species $\times$ Method	18	0.3401	2.77	0.0045
Error	36	0.2453		

Note: The tests of the effects of pairwise interactions are also reported.

mation,<sup>4</sup> and some methods have now been incorporated into program MARK (White and Burnham 1999).

#### Field methods

We extended work initiated by Hyde and Simons (2001), who sampled salamanders within the Roaring Fork Watershed, GSMNP during 1999 (Mt. LeConte USGS Quadrangle). These sites were located near trails, usually within 50 m, and spaced ~250 m apart, beginning at a random point at least 250 m from each trailhead. Sites were located in either disturbed (previously settled or logged prior to the establishment of the park in 1934) or undisturbed areas between the elevations of 670 m and 1060 m. Two forest community types were considered based on 90 m Landsat imagery (MacKenzie 1993): mixed deciduous (cove hardwood, northern hardwood, mixed mesic, and tulip poplar) and mixed pine (pine-oak and pine). Sites were either adjacent (<50 m), or not adjacent (>50 m), to a stream.

Relative abundance data were collected at 91 sites using two survey methods arranged as parallel transects: a natural cover transect (50 m long  $\times$  3 m wide) and five coverboard stations placed 10 m apart along a 50 m transect (see Hyde and Simons [2001] for details). Natural cover transects were sampled by two observers walking side by side who turned (and replaced) all natural cover (logs, sticks, and rocks) within the 50  $\times$  3 m area. Each coverboard station contained three large (26  $\times$  26 cm) and three small (13  $\times$  26 cm) boards space 1 cm apart (Hyde and Simons 2001). We continued to monitor a subset of 39 sites in 2000 and 2001. We collected data from each site during five sampling periods each year (1999–2001). Sampling occasions were spaced ~2 wk apart, from early April to late June. Sites were searched during the day when it was not raining. All individuals observed on each transect were identified to species, thus detection/nondetection information was obtained for each survey method, location, and sampling occasion.

#### PAO estimation and covariates

Data from our 39 sites were used to estimate  $\psi$  and  $p$  for the seven most common species using program PRESENCE. Our first set of analyses assume that species presence and detection probabilities were constant across time and sites,  $\psi(\cdot)p(\cdot)$ . While this constant model is not the best representation of the data for each of the species, our purpose was to compare the relative impacts of various sampling protocols and using parameter estimates from different models may introduce unknown biases that would have confounded our conclusions (Boulinier et al. 1998). We explored the effects of survey method and intensity on  $\hat{\psi}(\cdot)$  and  $\hat{p}(\cdot)$  estimates using information from four different “sampling methods”: (1) detections from natural cover and coverboard transects combined for five sampling occasions

per season (all data), (2) detections from natural cover transects only (NCT only), (3) detections from coverboard transects only (CBT only), (4) detections from natural cover and coverboard transects combined from only two sampling occasions per season (sampling occasions 3 and 5) (2 occs). We used point estimates of  $\hat{\psi}(\cdot)$  and  $\hat{p}(\cdot)$ , and the proportion of sites where the species was observed,  $\psi$  (obs), which is a naïve estimate of proportion of area occupied, as response variables in three separate ANOVAs to test for potential main effects and interactions of species, year, and sampling method. We used the three-way interaction as the error term in each ANOVA. To investigate how increasing the number of sites would affect parameter estimates, we analyzed data from our larger set of 91 sites in 1999 and compared  $\hat{\psi}(\cdot)$  and  $\hat{p}(\cdot)$  estimates to our subset of 39 sites in that same year.

We explored the importance of covariates by modeling parameters as a logit function of time (i.e., sampling occasion; for  $p$  only) or four large-scale habitat characteristics (previous disturbance history, vegetation type, elevation, and stream presence). Disturbance history, vegetation type, and stream proximity were treated as categorical covariates and elevation was standardized and used as a continuous variable. We tested the importance of each covariate separately for seven salamander species using variations in the basic model parameters:  $\psi_i$  and  $p_{it}$ . First, we held the proportion of sites occupied constant,  $\psi(\cdot)$ , and allowed species detection to vary with time and each covariate separately,  $p(t)$  and  $p(\text{Cov})$  (five models). Next, we held species detection probability constant,  $p(\cdot)$ , and varied  $\psi$  with each covariate separately,  $\psi(\text{Cov})$  (four additional models). We used our constant model,  $\psi(\cdot)p(\cdot)$ , as a reference. These 10 models were ranked according to AIC values (Akaike 1973, Burnham and Anderson 1998) calculated by program PRESENCE. The lowest ranked  $\psi(\cdot)p(\text{Cov})$  model and  $\psi(\text{Cov})p(\cdot)$  model for each species were combined in a  $\psi(\text{Cov})p(\text{Cov})$  model to explore if including covariates in both parameters improved model performance. We repeated this procedure for the four different sampling methods described above to investigate if the same covariate was chosen for all sampling methods. We stress that the models were chosen a priori to compare several factors we felt were likely to affect parameter estimates. The model selected “best” does not necessarily represent all of the environmental or biological processes that influenced the probability of occupancy or species detection probabilities.

#### RESULTS

Over three field seasons from 1999 to 2001, we captured a total of 2292 salamanders of 10 different “species” at 39 independent sites. The seven “species” used in our analysis included *Plethodon jordani* (PJ), *Plethodon serratus* (PS), *Desmognathus wrighti* (DW), *Eurycea wilderae* (EW; see Plate 1), and three species

<sup>4</sup> URL: (<http://www.mbr-pwrc.usgs.gov/software.html>)

TABLE 3. The 1999 example of parameter estimates using model,  $\psi(\cdot)p(\cdot)$ , from three sampling methods on 39 sites: natural cover transect data from five sampling occasions (NCT), coverboard transect data from five sampling occasions (CBT), and combined NCT and CBT data with two sampling occasions (2 occs).

Species	$\psi(\text{min})$	NCT			CBT		
		$\psi(\text{obs})$	$\hat{\psi}(\cdot)$ [1 SE]	$\hat{p}(\cdot)$ [1 SE]	$\psi(\text{obs})$	$\hat{\psi}(\cdot)$ [1 SE]	$\hat{p}(\cdot)$ [1 SE]
DF	0.41	<b>0.13</b>	<b>0.14 [0.06]</b>	0.36 [0.11]	0.33	0.37 [0.09]	0.40 [0.07]
DI	0.38	<b>0.26</b>	<b>0.27 [0.07]</b>	0.46 [0.08]	0.26	0.35 [0.11]	0.24 [0.08]
DW	0.26	0.26	0.26 [0.07]	0.57 [0.07]	0.26	0.31 [0.12]	0.20 [0.08]
EW	0.64	0.54	0.63 [0.10]	0.32 [0.05]	0.38	0.84 [0.33]	0.12 [0.05]
PG	0.77	0.69	0.73 [0.08]	0.45 [0.05]	<b>0.51</b>	<b>0.60 [0.09]</b>	0.41 [0.05]
PJ	0.46	0.44	0.44 [0.08]	0.67 [0.05]	<b>0.31</b>	<b>0.33 [0.08]</b>	0.46 [0.07]
PS	0.82	0.74	0.76 [0.07]	0.52 [0.04]	<b>0.54</b>	<b>0.60 [0.09]</b>	0.41 [0.05]

Notes: Results are given for seven salamander species: *Desmognathus fuscus* complex (DF), *Desmognathus imitator* complex (DI), *Desmognathus wrightii* (DW), *Eurycea wilderae* (EW), *Plethodon glutinosus* complex (PG), *Plethodon jordani* (PJ), and *Plethodon serratus* (PS). The proportion of sites where a species was observed using both NCT and CBT data is  $\psi(\text{min})$ ;  $\psi(\text{obs})$  is the proportion of sites where a species was observed for the given data set. Boldface entries indicate instances where  $\psi(\text{min})$  was not within the interval  $\hat{\psi}(\cdot) \pm 1 \text{ SE}$  (i.e., poor estimates). Results from both transects on 91 sites (five sampling occasions) are also listed but are not directly comparable because the proportions of habitat covariates different between the 39-site and 91-site data sets.

complexes described by Petranka (1998). The glutinosus complex (PG) includes *Plethodon glutinosus* and *Plethodon oconluftee* (see Plate 1). The fuscus complex (DF) includes *Desmognathus conanti*, *Desmognathus santeetlah*, and *Desmognathus fuscus*. The imitator complex (DI) is comprised of *Desmognathus imitator* and *Desmognathus ocoee*.

PAO estimation: constant model with all sampling data combined

Both  $\hat{\psi}(\cdot)$  and  $\hat{p}(\cdot)$  estimates had good precision for each of the seven species ([SE (estimate)/estimate] never exceeded 30% for any species). All response variables varied among all main effects: species, year, and sampling method and there was a significant species  $\times$  method interaction (Tables 1 and 2). There was no consistent pattern of  $\hat{\psi}(\cdot)$  and  $\hat{p}(\cdot)$  among the different species (Fig. 1). *Desmognathus wrightii* had the lowest occupancy estimate ( $\hat{\psi}(\cdot) \pm 1 \text{ SE} = 0.26 \pm 0.01$ ,  $n = 3 \text{ yr}$ ), but relatively high probability of detection ( $\hat{p}(\cdot) \pm 1 \text{ SE} = 0.57 \pm 0.06$ ,  $n = 3 \text{ yr}$ ) (Fig. 1). *Eurycea wilderae* had the lowest probability of detection ( $\hat{p}(\cdot) \pm 1 \text{ SE} = 0.33 \pm 0.04$ ,  $n = 3 \text{ yr}$ ) but relatively high occupancy estimates ( $\hat{\psi}(\cdot) \pm 1 \text{ SE} = 0.60 \pm 0.05$ ,  $n = 3 \text{ yr}$ ). Detection probabilities decline over years for five of the seven species (DF, DW, EW, PJ, and PS), but this does not translate to  $\hat{\psi}(\cdot)$  declines for those same species (Fig. 1). In fact, the two species that showed declining  $\hat{\psi}(\cdot)$  estimates were the species with relatively constant  $\hat{p}(\cdot)$  estimates (DI and PG) (Fig. 1).

PAO estimation: constant model with different sampling methods

The all-data and NCT-only sampling methods produced  $\hat{\psi}(\cdot)$  estimates that were similar to  $\psi(\text{obs})$  values (all-data mean difference  $\pm 1 \text{ SE} = 0.03 \pm 0.01$ , NCT mean difference  $\pm 1 \text{ SE} = 0.05 \pm 0.01$ ,  $n = 21 \text{ species-years}$ ). However,  $\psi(\text{obs})$  values for both CBT-only and 2-occs methods were on average 12% lower than their

respective  $\hat{\psi}(\cdot)$  estimates (CBT mean difference  $\pm 1 \text{ SE} = 0.12 \pm 0.03$ , 2 occs mean difference  $\pm 1 \text{ SE} = 0.12 \pm 0.03$ ,  $n = 21 \text{ species-years}$ ). Furthermore, precision of  $\hat{\psi}(\cdot)$  and  $\hat{p}(\cdot)$  estimates were poor for the CBT-only and 2-occs methods (e.g., Table 3). The  $\psi(\text{obs})$  value from the all-data method can be viewed as a minimum known proportion of sites occupied,  $\psi(\text{min})$ . We investigated whether  $\psi(\text{min})$  was within the interval:  $\hat{\psi}(\cdot) \pm 1 \text{ SE}$  for the three other sampling methods (e.g., Table 3). The NCT-only failed to include  $\psi(\text{min})$  for *Desmognathus fuscus* complex (1999, 2001) and *Desmognathus imitator* complex (1999) (Table 3). The 2-occs

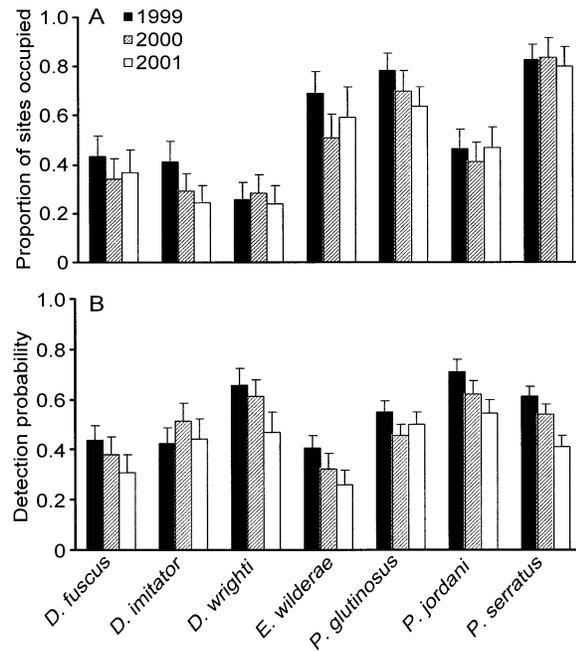


FIG. 1. Parameter estimates (mean + 1 SE) for (A) proportion of sites occupied,  $\psi(\cdot)$ , and (B) detection probability,  $p(\cdot)$ , for seven salamander species or species complexes.

TABLE 3. Extended.

2 occs			91 Sites		
$\psi(\text{obs})$	$\hat{\psi}(\cdot)$ [1 SE]	$\hat{p}(\cdot)$ [1 SE]	$\psi(\text{obs})$	$\hat{\psi}(\cdot)$ [1 SE]	$\hat{p}(\cdot)$ [1 SE]
0.29	0.37 [0.11]	0.53 [0.16]	0.26	0.27 [0.05]	0.48 [0.05]
0.28	0.30 [0.08]	0.78 [0.11]	0.40	0.41 [0.05]	0.47 [0.04]
0.23	0.23 [0.07]	0.87 [0.09]	0.31	0.31 [0.05]	0.63 [0.04]
0.49	0.58 [0.12]	0.59 [0.11]	0.56	0.62 [0.06]	0.37 [0.03]
<b>0.54</b>	<b>0.58 [0.09]</b>	0.73 [0.09]	0.53	0.54 [0.05]	0.52 [0.03]
0.44	0.46 [0.09]	0.79 [0.09]	0.46	0.46 [0.05]	0.73 [0.03]
0.67	0.87 [0.15]	0.51 [0.10]	0.66	0.68 [0.05]	0.51 [0.03]

method produced  $\hat{\psi}(\cdot)$  estimates with large standard errors, but still failed to include  $\psi(\text{min})$  for the *Plethodon glutinosus* complex (1999, 2000) and *Plethodon serratus* (2000). The CBT-only method performed worst, failing to include  $\psi(\text{min})$  for the three *Plethodon* species in most years (Table 3).

The significant species  $\times$  method interaction for all response variables ( $\psi(\text{obs})$ ,  $\hat{\psi}(\cdot)$ ,  $\hat{p}(\cdot)$ ), indicated an inconsistent efficacy of sampling methods for the different species. The *Plethodon* pattern is consistent with increasing  $\psi(\text{obs})$  and  $\hat{\psi}(\cdot)$  estimates in the following order: CBT only < 2 occs < NCT only < all data. *Desmognathus* species had more consistent  $\psi(\text{obs})$  and  $\hat{\psi}(\cdot)$  estimates across sampling methods, except for *Desmognathus fuscus* complex, which had low  $\psi(\text{obs})$  values using the NCT-only method. In general,  $\hat{p}(\cdot)$  increased across sampling methods in the following order: CBT only < NCT only < all data < 2 occs. Two species deviate from this pattern: *Plethodon serratus* (CBT only < NCT only < 2 occs < all data) and *Desmognathus fuscus* complex (NCT only < CBT only < 2 occs < all data).

Including more sites (91 total) in the 1999 analysis improved parameter precision, but showed similar trends to those observed in our subset of 39 sites (Table

3). Species detection probabilities did not change from those obtained with only the 39 sites, but  $\hat{\psi}(\cdot)$  estimates were slightly lower for three species (DF, PG, PS) (Table 3). This likely reflects differences in the proportion of important habitat characteristics between the 39-site and 91-site data sets (see *Discussion*).

*PAO estimation: time- and site-specific covariates*

Species-specific detection probabilities were consistent over our three-year study (no species  $\times$  year interaction, Table 2), but patterns of detection probability varied among species. By including a time-specific covariate (sampling occasion) in our estimates of detection probability,  $p(t)$ , we were able to examine the patterns of species-specific detection probability within the sampling season (Fig. 2). Four species (DF, DI, DW, PJ) had lower detection probabilities for the first sampling occasion and higher probabilities in the middle and late sampling rounds (Fig. 2). *Plethodon serratus* was the only species to show consistent and substantial declines in detection probabilities over the sampling season (Fig. 2).

We explored the importance of both time- and site-specific covariates in species-specific  $\psi$  and  $p$  estimates by comparing AIC values for 10 competing models. Disturbance history was an important covariate for the *Desmognathus imitator* complex, *Plethodon glutinosus* complex, and *Plethodon serratus* (Fig. 3). Occupancy probability,  $\psi(\text{dist})$ , and detection probability,  $p(\text{dist})$ , were higher on disturbed sites for *Plethodon glutinosus* complex and *Plethodon serratus*, but lower for the *Desmognathus imitator* complex (Fig. 3). Occupancy and detection probabilities were higher for *Desmognathus fuscus* complex and *Eurycea wilderae* on sites near streams (Fig. 3). *Plethodon jordani* estimates of  $\psi$  and  $p$  increased with increasing elevation.

While the significance of covariates varied among species, important covariates were identified by all sampling methods. For example, among competing  $\psi(\text{Cov})p(\cdot)$  models,  $\psi(\text{elevation})p(\cdot)$  had the lowest AIC values for *Plethodon jordani* data from all four sampling methods (Table 4). Two notable exceptions were: (1) analysis involving CBT-only data favored models that included stream proximity more often than anal-

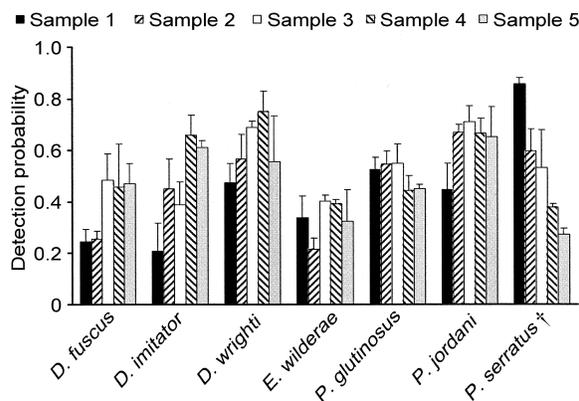


FIG. 2. Time-specific species detection probability estimates,  $\hat{p}(t)$  ( $t =$  five sampling occasions; values are mean + 1 SE,  $n = 3$  yr) for seven salamander species or species complexes. A dagger ( $\dagger$ ) denotes species for which the time covariate was included in the “best” model.

TABLE 4. AIC values for competing  $\psi(\cdot)p(\text{Cov})$  and  $\psi(\text{Cov})p(\cdot)$  models using *Plethodon jordani* data from 39 sites in 1999.

Covariate	All-data models			NCT models		
	$\psi(\text{Cov})p(\cdot)$	$\psi(\cdot)p(\text{Cov})$	$\psi(\text{Cov})p(\text{Cov})$	$\psi(\text{Cov})p(\cdot)$	$\psi(\cdot)p(\text{Cov})$	$\psi(\text{Cov})p(\text{Cov})$
None	163.47	163.47	...	162.80	162.80	...
Time	...	168.47	...	...	167.28	...
Disturbance	145.83	160.00	...	143.50	159.05	...
Vegetation	161.61	160.75	...	161.48	161.11	...
Stream	165.09	165.42	...	164.67	164.14	...
Elevation	<b>142.51</b>	<b>134.35</b>	<b>125.16</b>	<b>141.62</b>	<b>136.28</b>	<b>128.42</b>

Notes: The four different sampling methods are: combined natural cover and coverboard transect data from five sampling occasions (all data), natural cover transect data from five sampling occasions (NCT), coverboard transect data from five sampling occasions (CBT), and combined natural cover and coverboard transect data with two sampling occasions (2 occs). Lowest AIC values are in bold type for each set of competing models. Combining consistently low-ranked  $\psi(\cdot)p(\text{Cov})$  and  $\psi(\text{Cov})p(\cdot)$  models in a  $\psi(\text{Cov})p(\text{Cov})$  model often improved model performance. "NA" indicates that the model was not fit or yielded nonsensical parameter estimate.

yses using data from other sampling methods, and (2) disturbance history and elevation covariates were occasionally interchanged, because these habitat characteristics are often correlated on our study sites with disturbed areas usually found at lower elevations. Among competing  $\psi(\text{Cov})p(\cdot)$  and  $\psi(\cdot)p(\text{Cov})$  models, usually one covariate fit the data much better than any

other covariate; rarely were there multiple competing models with  $\Delta$  AIC values  $< 2.0$  (e.g., Fig. 3, Table 4). On occasion, *Plethodon glutinosus* complex data was fit well by all competing models, thus favoring no distinct covariate. *Plethodon serratus* was the only species where the best combined model contained two different covariates,  $\psi(\text{dist})p(t)$ . Modeling detection prob-

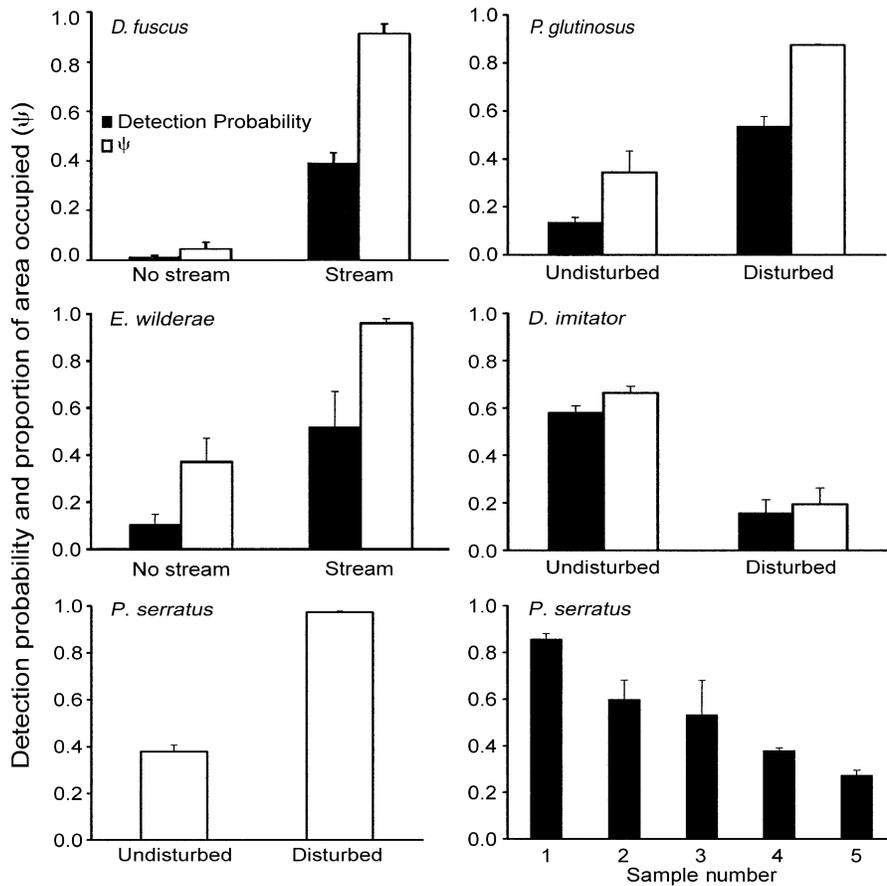


FIG. 3. Parameter estimates with species-specific habitat covariates (mean + 1 SE,  $n = 3$  yr) using  $\psi(\text{Cov})p(\cdot)$  and  $\psi(\cdot)p(\text{Cov})$  models with lowest AIC values. All sampling methods were capable and consistent at identifying important habitat covariates, and results using natural cover and coverboard transect data combined (all data) are presented here.

TABLE 4. Extended.

CBT models			2 occs models		
$\psi(\text{Cov})p(\cdot)$	$\psi(\cdot)p(\text{Cov})$	$\psi(\text{Cov})p(\text{Cov})$	$\psi(\text{Cov})p(\cdot)$	$\psi(\cdot)p(\text{Cov})$	$\psi(\text{Cov})p(\text{Cov})$
132.26	132.26	...	87.81	87.81	...
...	138.24	...	...	89.14	...
119.83	134.17	...	NA	72.33	...
132.93	129.81	...	86.50	84.45	...
130.94	<b>124.15</b>	...	89.69	88.50	...
<b>111.26</b>	127.03	<b>100.85</b>	<b>63.33</b>	<b>51.64</b>	<b>53.64</b>

ability as a linear function of time (sampling occasion) would likely fit *Plethodon serratus* data even better (Fig. 2). The inclusion of more sites in 1999 (91 sites) produced similar results to those found using only 39 sites. Combining the best  $\psi(\text{Cov})p(\cdot)$  and  $\psi(\cdot)p(\text{Cov})$  models, in a  $\psi(\text{Cov})p(\text{Cov})$  model, often improved model fit (i.e., resulted in lower AIC values) emphasizing the importance of including covariates in both parameter estimates (e.g., Table 4). However, fitting the more complex model,  $\psi(\text{Cov})p(\text{Cov})$ , was difficult for the CBT-only and 2-occs methods, which had reduced amounts of detection data.

#### DISCUSSION

The choice of an appropriate state variable for a monitoring program depends on the program's objectives, scale, and resources. Most large-scale monitoring programs seek to determine the status of a system and periodically assess changes in the system over time (Olsen et al. 1999, Yoccoz et al. 2001). Monitoring population abundance usually involves costly capture-recapture methods. Site occupancy is a metric that is often used to assess changes in amphibian systems (Fisher and Shaffer 1996, Gibbons et al. 1997, Shaffer et al. 1998) and appropriate detection/nondetection data can be collected with much less effort. Although site occupancy may be a crude surrogate for actual population size, it represents an alternative for investigators involved in large-scale, multispecies monitoring programs. We feel that proportion of area occupied has good potential as a state variable for large-scale amphibian monitoring programs, but our results emphasize the importance of estimating detection probabilities rather than using unadjusted observed occupancy information.

Values of  $\psi(\text{obs})$  based on only one or two sampling occasions are likely to grossly underestimate true  $\psi$  values because species detection probabilities are not 1, nor are they constant across species, time, space, or sampling method. There are multiple factors that could affect detection probability for a given species including: local density, seasonal or behavioral patterns, size of the species, weather and environmental variations, or sampling effort in terms of number of sampling occasions or amount of area surveyed. Our findings suggest that nearly all of these factors are important in the detection of different terrestrial salamander species.

Body size was the only factor that did not appear to affect our ability to detect different species. Our smallest species, *Desmognathus wrighti*, had detection probabilities comparable to our largest species, *Plethodon glutinosus* complex.

Local density is likely to affect the detection probability of most species and is probably the most important source of heterogeneity among sites (Royle and Nichols 2003). As the density of a given species increases, so does the probability of detecting a single individual of that species. For example, *Desmognathus wrighti* is locally abundant when it occurs in our study area; often exceeding over 100 individuals in a  $15 \times 15$  m plot (L. L. Bailey, unpublished data). In contrast, *Eurycea wilderae* is a widespread species, but is never found in high abundances (>10 individuals) on the same terrestrial plots (L. L. Bailey, unpublished data). We cannot directly explore the relationship between the probability of detection and population sizes because we did not estimate abundances on our sites. However, recent simulation studies show that detection of (patch) occupancy is a good index of abundance in metapopulation studies (Lopez and Pfister 2001). In addition, methods have recently been developed to estimate abundance from repeated presence/absence data using the relationship between local abundance and species detection probability (Royle and Nichols 2003).

Estimated salamander detection probabilities reflect species-specific, seasonal behavioral patterns. Many salamander species including *Desmognathus wrighti*, members of the *Desmognathus fuscus* complex, and *Plethodon jordani* are known to disperse from winter retreats in early spring (Organ 1961, Petranka 1998) and then remain active on the surface during the warmer months of the year (Petranka 1998). Seasonal behavior was most prominent in *Plethodon serratus* whose detection probabilities consistently declined throughout the sampling season for all years and all sampling methods. *Plethodon serratus* adult surface activity is known to decline throughout April and juveniles often disappear beneath the ground by mid-May (Petranka 1998). This pattern explains why parameter estimates using 2-occs data for this species had higher standard errors than other *Plethodon* species whose detection probabilities for sampling occasions 3 and 5 were relatively high. It is important to note that detection probability is conditional, thus higher species de-

tection probabilities do not always translate to increased precision or accuracy in  $\psi$  estimates. For example, species detection probability estimates were often highest for the 2-occs sampling method, but both detection probabilities and  $\psi$  estimates via this method lacked precision and in some cases  $\psi$  estimates were inaccurate (not near  $\psi$  (min) values).

Environmental conditions may account for some of the variability in detection probabilities, but  $\psi$  should be less sensitive to these factors than estimates of population size or relative abundance, because even during unfavorable environmental conditions a few individuals of a species are likely to be detected at occupied sites. However, persistent drought may result in lower species detection rates and this may be why we see yearly declines in detection probabilities for five of our seven species. Total precipitation in April through June declined over the three years of our study and in 2001 was  $\sim 20$  cm below rainfall levels achieved in the four preceding years (Mt. LeConte National Weather Station). Another possibility for detection probability declines is a disturbance effect incurred by sampling transects five times per year. There are few studies that rigorously explore cumulative sampling effects, but investigators have cautioned against using natural cover searches because of perceived disturbance effects (Heyer et al. 1994). If disturbance were a factor in our study, we would have expected detection probabilities to decline throughout the sampling season, but only *Plethodon serratus* showed such a decline, which as discussed probably reflects normal seasonal activity patterns.

Variations in species-specific detection probability alone does not explain differences in  $\psi$  estimates among sampling methods unless some methods were unable to detect certain species ( $p = 0$ ). If  $p > 0$  for all sampling methods and variations in  $p$  were the only factor responsible for differences in  $\psi$ (obs) values among methods, then  $\psi$  estimation methods should incorporate these differences in detection probabilities and produce consistent species-specific  $\psi$  estimates across methods; there should be no significant interaction terms in our ANOVA for  $\hat{\psi}(\cdot)$ . Incorporating species-specific detection probabilities in  $\hat{\psi}(\cdot)$  estimates does remove the species  $\times$  year and method  $\times$  year interactions, but not the species  $\times$  method interaction. Estimates of  $\hat{\psi}(\cdot)$  were more consistent across sampling methods than  $\psi$ (obs) values for all seven species, still there were unaccountable differences among methods resulting in a significant species  $\times$  method interaction. We can think of three possible explanations for this interaction. First, our survey techniques may be unable to detect certain species. For example, average CBT detection probabilities were low ( $\hat{p}(\cdot) \leq 0.20$ ) for *Desmognathus wrighti* and *Eurycea wilderae*, suggesting that this method could be ineffective at detecting these species at some of the sites. Second, NCT and CBT were located several meters apart and may be sampling slightly

different areas or communities, which could account for the unexplainable differences of  $\hat{\psi}(\cdot)$  estimates. Third, the most likely reason for the species  $\times$  method interaction is the nonrandom placement of transects with respect to stream presence. On sites near streams, coverboard stations were always placed between the stream and the NCT. This nonrandom placement of transects explains the low CBT detection probabilities for terrestrial species, such as *Desmognathus wrighti*, and the unusually high detection probabilities for stream-side species of the *Desmognathus fuscus* complex. All other species, except *Desmognathus fuscus* complex, had higher detection probabilities using the NCT method because of the larger area sampled by NCT compared to CBT. We believe the species  $\times$  method interaction for  $\hat{\psi}(\cdot)$  estimates were the result of a flaw in our sampling design rather than a true species-specific affinity to either of our two survey techniques. Using PAO estimation allowed us to identify this design flaw that otherwise could have gone unnoticed.

Parameter estimates were also capable of revealing differences in species' distribution types (clumped or widespread) as well as potentially important species-specific habitat characteristics. Our findings suggest that *Desmognathus wrighti* has the most restricted distribution of salamander species in the Roaring Fork Watershed while *Plethodon serratus*, *Plethodon glutinosus* complex, and *Eurycea wilderae* were the most widespread. Analysis of data from all sampling methods consistently identified important covariates. If determining habitat associations were the main objectives of a monitoring study, our results suggest NCT and CBT represent overlapping effort and only one of these sampling methods would be necessary.

Including more sites in our 1999 analysis decreased  $\psi$  estimates for three species: *Desmognathus fuscus* complex, *Plethodon glutinosus* complex, and *Plethodon serratus*. All three species, especially *Plethodon glutinosus* complex and *Plethodon serratus*, have higher occupancy and detection probabilities on previously disturbed sites. Seventy-four percent of our 39 sites were previously disturbed compared to only 66% of the 91 sites. This finding emphasizes the importance of having a good spatial sampling design to insure that the chosen sample sites are representative of the entire area from which inferences are to be drawn.

Although  $\psi$  may be a useful state variable for a variety of monitoring studies, there are three caveats we would like to mention. First, current estimation methods only allow spatial heterogeneity attributed to specified covariates; current theory does not allow unexplained heterogeneity among sites, but more general models are being developed (D. MacKenzie and J. Nichols, *personal communication*). Second, models that include covariates only in the detection probability parameter,  $\psi(\cdot)p(\text{Cov})$  models, often yield unreasonable  $\psi(\cdot)$  estimates when detection probabilities were less than 0.15. MacKenzie et al. (2002) also encountered

this problem in their simulation study, concluding that the model has difficulty distinguishing between sites with low detection probability and sites where the species is truly absent (MacKenzie et al. 2002). Therefore,  $\psi$  estimation may not be useful for rare species, if detection probabilities are very low. However, if detection probabilities are greater than 0.15, but occurrence is low (e.g., *Desmognathus wrighti* species), then estimation methods should perform well. These methods may be extremely important in monitoring programs for species like *Eurycea wilderae* that have relatively low detection probabilities (provided  $p > 0.15$ ) but are widely distributed. Values of  $\psi(\text{obs})$  for this type of species are inclined to have strong negative bias. *Eurycea wilderae* is a management indicator species for the southern region of the National Forest Service and as such, populations of *Eurycea wilderae* will be monitored to assess the effects of forest management actions. Occupancy estimation may be one way to effectively monitor *Eurycea wilderae* populations in this region.

There are obvious trade-offs between sampling a large number of sites one or two times per season vs. multiple visits to fewer sites. Remote sites may be difficult and costly to sample multiple times within a season. Researchers are currently working on occupancy estimation methods directed at optimal allocation of sampling effort (see MacKenzie et al. 2002, Pollock et al. 2002). It may be beneficial to implement a "split-panel" (McDonald 2003) or double sampling design (Pollock et al. 2002) where occupancy data are collected a large number of sites, but multiple visits are made to a subset of these sites within a single sampling season.

#### CONCLUSIONS AND RECOMMENDATIONS

Our study is one of the first to apply recent theoretical developments (MacKenzie et al. 2002) to estimate proportion of area (or sites) occupied in a valid way. This state variable has historically been the most convincing metric in studies of amphibian declines, but has not been estimated correctly. Our results indicate that species detection probabilities for terrestrial salamanders are  $< 1$  and vary across time, space, species, and sampling methods. Simple occupancy information (i.e., the proportion of sites where a species was observed) is undoubtedly negatively biased by some unknown quantity. It is unreasonable and inefficient to standardize protocols for all factors that could possibly affect detection probabilities for different species. Instead, we recommend estimating occupancy probabilities for each species by repeatedly sampling sites within a season. Investigators concerned about disturbance effects caused by repeated sampling might consider randomly varying the exact location of sample units within an area or site. For example, a "site" may define an area in which a different randomly chosen subplot is sampled for each sampling occasions. In our terres-

trial salamander case, natural cover transects could have proceeded along different, randomly chosen compass heading for each sample occasion.

Using  $\psi$  estimation in combination with a good sampling design is essential. Investigators should clearly define an appropriate sample frame and use probability-based spatial sampling to insure that the chosen sample sites are representative of the entire area from which inferences are to be drawn. Investigators might consider stratifying sample units according to site-specific habitat characteristics important for both  $\psi$  and  $p$  estimation, but only if these characteristics are static for the duration of the study or monitoring program (e.g., elevation).

Occupancy estimation methods presented here may not be useful for rare species, if detection probabilities are very low. Survey methods should be able to detect the target species at least 15% of the time, given the species is present. Provided detection probability requirements are met,  $\psi$  estimation would allow researchers and managers to establish reliable baseline data for multiple species, compare species-specific  $\psi$  estimates over time or among different studies from various regions, and identify habitat characteristics important for species presence (occurrence).

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