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Abstract: Spatial capture–recapture (SCR) is a relatively recent development in ecological statistics that provides a spatial context for estimating abundance and space use patterns, and improves inference about absolute population density. SCR has been applied to individual encounter data collected noninvasively using methods such as camera traps, hair snares, and scat surveys. Despite the widespread use of capture-based surveys to monitor amphibians and reptiles, there are few applications of SCR in the herpetological literature. We demonstrate the utility of the application of SCR for studies of reptiles and amphibians by analyzing capture–recapture data from Red-Backed Salamanders, *Plethodon cinereus*, collected using artificial cover boards. Using SCR to analyze spatial encounter histories of marked individuals, we found evidence that density differed little among four sites within the same forest (on average, 1.59 salamanders/m^2) and that salamander detection probability peaked in early October (Julian day 278) reflecting expected surface activity patterns of the species. The spatial scale of detectability, a measure of space use, indicates that the home range size for this population of Red-Backed Salamanders in autumn was 16.89 m^2. Surveying reptiles and amphibians using artificial cover boards regularly generates spatial encounter history data of known individuals, which can readily be analyzed using SCR methods, providing estimates of absolute density and inference about the spatial scale of habitat use.

Key words: Abundance; Amphibian; Cover boards; Density; Detection; Home range; *Plethodon cinereus*; New York; Red-Backed Salamanders; Spatially explicit capture–recapture

Herpetofauna represent some of the most important components of many ecological communities and there is increasing concern that populations globally are in decline (Gibbons et al. 2000; Stuart et al. 2004; Adams et al. 2013). The causes of these declines are many and complex, however, and monitoring herpetofauna is a nontrivial endeavor given that these organisms are cryptic, occur at relatively low densities, and often have specific microhabitat preferences and narrow environmental thresholds (Grant et al. 1992; Alford and Richards 1999; Beebee and Griffiths 2005; Weir et al. 2005; Hof et al. 2011). As such, recommendations place increasing emphasis on the development and use of standardized monitoring techniques and analytical methods for monitoring and assessing populations (Parris 1999; Doan 2003; Mazerolle and Bailey 2007).

When individuals can be recognized by marks (natural or anthropogenic), capture–recapture methods can be used to estimate abundance and well-established procedures exist for both data collection and statistical analysis (Otis et al. 1978; Williams et al. 2002; Amstrup et al. 2010). Trapping using drift nets, pitfall traps, or cover object surveys are common methods advocated for monitoring amphibians and reptiles (Willson and Gibbons 2009). In studies that employ multiple traps, or where animals are caught across a relatively large study area, each observation of an individual occurs at a unique spatial location so that trapping produces spatial encounter histories that indicate both when and where each individual was captured. Traditional capture–recapture approaches ignore the spatially explicit individual-by-trap-by-occasion encounter information and use only individual-by-occasion (i.e., nonspatial), encounter histories (Royle et al. 2013b). The result is that, unless trapping occurs within a discrete habitat unit such as a pond, the area being sampled is not well defined. The inability to define the area

sampled makes it impossible to estimate absolute densities of animals or to define the sampled population when, in fact, most ecological and conservation studies aim to understand factors that affect density of animals in a habitat or population (Krebs 1994; Buckland et al. 2005; Efford and Fewster 2013). Moreover, individual animals also vary in their proximity to traps and, therefore, the frequency with which they will be encountered. This leads to heterogeneity among individuals in their capture rates that cannot explicitly be accounted for when using encounter histories that are reduced to nonspatial summaries. Failure to account for such heterogeneity will result in estimates of abundance being negatively biased (Otis et al. 1978; Efford 2004).

These issues have been resolved, in part, by the recent development of spatial capture–recapture models (SCR; Efford 2004; Borchers and Efford 2008; Royle and Young 2008). SCR provides a spatial context for the estimation of abundance by (1) describing how an individual's activity centers (home range centers) are distributed across a prescribed area of known size and (2) modeling the probability an individual will be detected at any given trap as a decreasing function of the distance between its activity center and the trap. Explicitly defining a sampling region allows absolute density to be directly estimated (Borchers and Efford 2008), or derived from spatially referenced estimates of abundance (Royle and Young 2008; Royle et al. 2013b). The estimation of the spatial scale of detectability is analogous to a model of space use, and in addition to accommodating location-specific heterogeneity in encounter probabilities, can provide information about patterns of space use and home range size (Royle et al. 2013b).

Here, we demonstrate the utility of SCR by analyzing spatially explicit individual encounter history data collected during a survey of Red-Backed Salamanders (*Plethodon cinereus*) in a forest in New York, USA. We collected data using artificial cover boards, an appropriate sampling method because, among other reasons, it (1) avoids destruction of
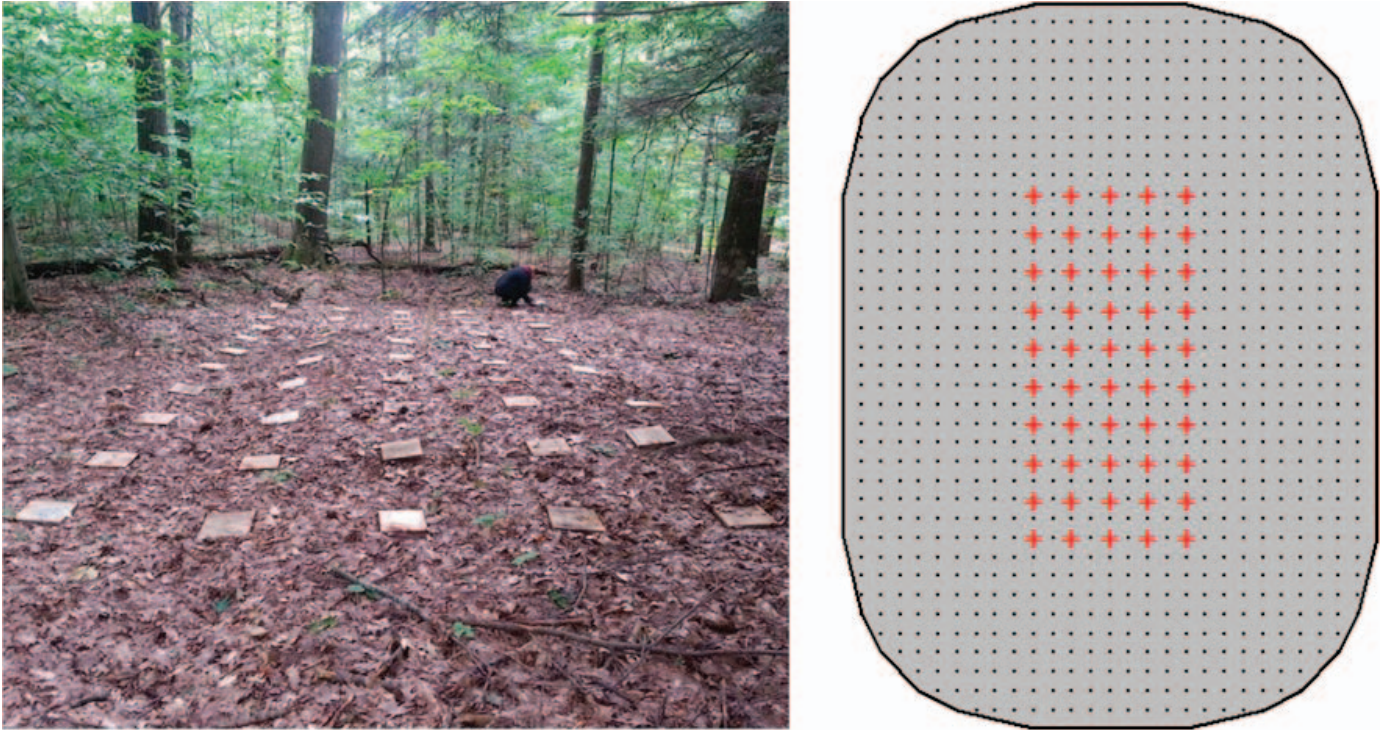
Fig. 1.—Left panel: a photograph of one of the artificial cover board arrays used in this study to capture Red-Backed Salamanders (*Plethodon cinereus*). Right panel: a schematic of the location data used in the spatial capture–recapture (SCR) models. The crosses represent the 50 cover boards located 1 m apart, the black points represent the center points of the discrete state-space (i.e., all possible activity center locations), and the gray area denotes the state-space S used in the SCR model. A color version of this figure is available online.

habitat; (2) minimizes maintenance and observer bias; (3) is cost effective; and, importantly, (4) has the potential to generate relatively large sample sizes with little risk of mortality (Monti et al. 2000; Willson and Gibbons 2009; Hesed 2012). Although we focus on artificial cover board data, SCR is equally applicable to any spatial sampling protocol in which individuals are uniquely identified (Mazerolle and Bailey 2007). Analyzing spatially explicit encounter data collected from four plots, we used SCR methods to estimate absolute salamander density and individual home range size. Furthermore, we investigated whether salamander density varies across sampling plots within a woodland, and how surface activity patterns might influence detectability throughout a season. Finally, we compared spatially explicit estimates of salamander abundance to estimates generated using traditional nonspatial capture–recapture.

Materials and Methods
Cover Board Surveys

In June 2014, four cover board arrays that were at least 20 m apart were established in the Polson Nature Area, Ithaca, New York (42°25′26″N, 76°23′55″W; datum = NAD83). Each cover board array was 5 × 10 m consisting of 50 pine cover boards (25 × 25 × 2.45 cm) spaced 1 m apart in a rectangular grid (Fig. 1). Each cover board was checked on multiple occasions in the fall between 1 September and 9 November 2014 (Sites 1, 2, 3, and 4 were visited 7, 5, 6, and 4 times, respectively). We recorded the date of the survey and the ambient air temperature immediately prior to checking under the cover boards. Each

board was then carefully lifted and all Red-Backed Salamanders present on the surface under each of the boards were collected, noting under which cover board each individual was found. On initial capture, salamanders were given a unique individual mark by injecting visual implant elastomer at up to four locations ventral and adjacent to each limb using combinations of up to four colors, making each individual uniquely recognizable (i.e., a total of 624 combinations; Bailey 2004; Grant 2008). Such marking over the course of the season generated a binary encounter history for individuals observed at least once, where y_{ijk}, indicates whether individual i was detected under board j in occasion k ($y_{ijk} = 1$ if detected and $y_{ijk} = 0$ otherwise).

Spatial Capture–Recapture

In SCR models, a spatial model of abundance and a spatial model of the detection process are simultaneously fitted to the encounter history data Y (Fig. 2). The abundance model describes the distribution of animal activity centers, which are typically assumed to be uniformly distributed over a prescribed area of interest or state-space, S, (i.e., $s_i \sim \text{Uniform}[S]$). For computational convenience, S can be represented discretely as the center points of a fine grid, each of which is a potential activity center (Fig. 1). The model requires that a state-space be defined by a buffer around the trapping array that should be at least large enough to contain all of the activity centers of individuals that have nonnegligible probability of being detected in at least one of the traps (i.e., larger than the radius of a home range). The resolution of the discrete representation of space should be fine enough to sufficiently approximate continuous
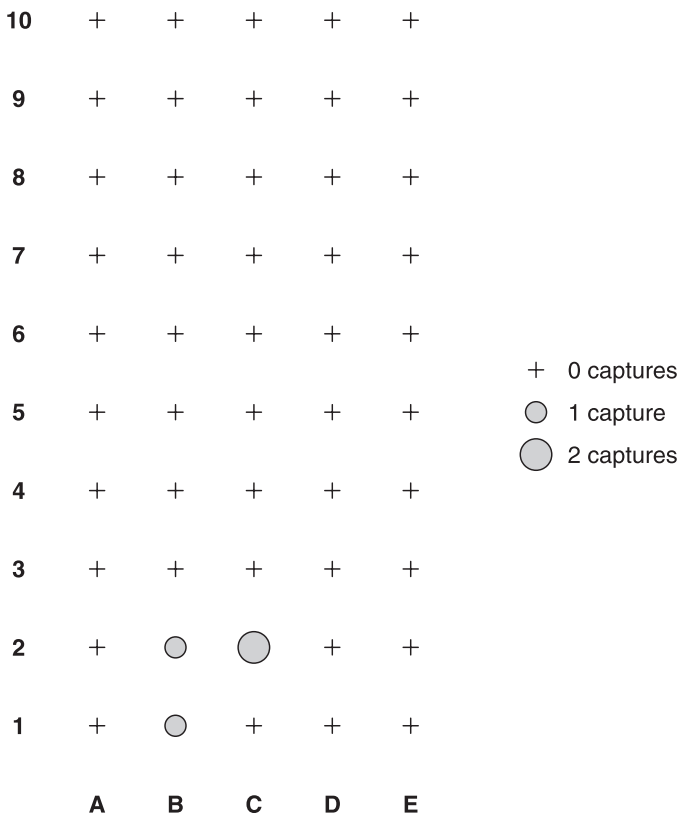
FIG. 2.—An example of spatial capture histories for Red-Backed Salamanders (*Plethodon cinereus*). The spatial locations and frequencies of capture locations are shown for an individual that was captured four times during the study period.

space relative to the species' movement, but should also be but coarse enough for computational tractability (Royle et al. 2013b). In our study, the state-space was generated using a buffer width of 5 m around each cover board array (exceeding any published home range estimates for the species), and divided into discrete 0.5 × 0.5–m grid cells; the state-space for each of the four plots contained 981 point locations and had an area of 245.25 m^2 (Fig. 1).

The second component is the observation model that relates the probability of detecting an individual at a specific cover board (trap) to the distance between the board and the animal's home range center. The use of a distance-based detection model accounts for the additional heterogeneity that arises from the variation in individual-to-trap distances in the population, reducing the potential for biases in estimates of abundance and density (Otis et al. 1978; Efford 2004; Royle et al. 2013b). Therefore, the assumption is that detection will be highest for boards located near the subject's activity center, and decline as distance from the activity center increases. The model states that $p[x,s]$, the probability of observing an individual with an activity center s, in a trap with location x, decreases with increasing Euclidean distance, $d[x,s]$. The model has two parameters: p_0, the baseline detection probability, or the probability that an individual would be detected at its activity center ($d[x,s] = 0$); and σ, a spatial scale parameter that characterizes the decline in detectability with distance from an activity center. In some situations the parameter σ can be thought of as a movement parameter, and as such, the model for

encounter probability is analogous to a model of space use, providing information about home range size during the period of sampling (Royle et al. 2013b). We refer to this formulation of the model, where the probability of detection depends solely on the distance from an animal's activity center, as model SCR$_0$. As in nonspatial capture–recapture models, however, other sources of detection heterogeneity need to be accounted for in order to avoid biases (Otis et al. 1978). In SCR, variation in encounter rates can easily be incorporated using standard logistic regression on the baseline detection probability p_0 and the parameters simultaneously estimated:

$$\log(p_0/(1-p_0)) = \beta_0 + \beta_1 X_1 + \ldots + \beta_R X_R,$$

where β_0 is the intercept and β's are the regression coefficients relating detectability to the R covariates of interest.

We were particularly interested in accounting for any temporal variation in salamander detectability over the course of the sampling period that might reflect variation in activity patterns of Red-Backed Salamanders in the fall. We used both the day of survey, and air temperature (°C) as covariates to account for such variation. Moreover, we suspected that there likely exists an optimal activity time or temperature during which activity would be highest and salamanders would be most detectable. We therefore fitted models with both linear and quadratic effects of both covariates on detection. Because time and temperature are highly correlated we did not consider models in which both effects were present (i.e., models could contain time or temperature, but not both).

Our objective was to estimate the total population size, $\hat{N}$, within the prescribed area. Thus, we not only estimated the parameters of the detection model based on the spatial encounter histories of the observed individuals (n_{obs}) (Fig. 2), but also the number of individuals that went undetected (unobserved individuals: n_0). The estimated total population size is therefore $\hat{N} = n_{obs} + \hat{n}_0$ and estimated density is derived as $\hat{D} = \hat{N}/|S|$, where $|S|$ is the size of the state-space S.

We used maximum likelihood methods to jointly estimate each of the model parameters. Because the position of individual activity centers cannot be known, we adopted an integrated likelihood approach using a function that evaluates the likelihood of the parameters of the SCR model integrated over all possible (discrete) individual activity centers (Borchers and Efford 2008; Royle et al. 2013b). Maximum likelihood allows multiple competing models to be compared formally using Akaike information criteria (AIC). We obtained the maximum likelihood estimates using an integrated likelihood function (oSCR), which was implemented in R (R Core Team 2012; see Supplemental Material). We note that the R package secr can be used to implement the same suite of models (Efford 2014).

Non-Spatial Comparison

Among other reasons, nonspatial closed population capture–recapture methods differ from SCR in that the estimate of abundance is fixed and the conversion to density depends directly on which buffer is chosen, and is thus to some degree arbitrary (Otis et al. 1978; Parmenter et al. 2003). To emphasize the value of using SCR methods to

obtain spatially referenced estimates of abundance, and therefore density, we collapsed the spatial encounter data to nonspatial (individual-by-occasion) encounter histories for the salamanders and analyzed the data using model M_h (Otis et al. 1978). Rather than assuming any specific structural between-individual variation in detectability, model M_h accounts for individual heterogeneity using a logit-normal model that assumes that the logit-transformation of individual detection probabilities, p_i, has a normal distribution with variance θ^2 (Coull and Agresti 1999; Dorazio and Royle 2003):

$$\text{logit}(p_i) \sim \text{Normal}(\mu, \theta^2).$$

Using site-specific estimates of abundance under model M_h, density was computed for each site using two buffer areas based on the mean maximum distance moved (MMDM; see Dice 1938; Parmenter et al. 2003) and compared to estimates of density from the standard SCR model, SCR_0. Model M_h was applied to each site separately and analyzed using the R code provided in Chapter 6 of Royle and Dorazio (2008).

RESULTS

In total, 299 Red-Backed Salamanders were captured across the four cover board survey plots (77, 60, 108, and 54 in Plots 1, 2, 3, and 4, respectively). Of these, 134 were captured more than once (38, 18, 51, and 17, respectively), and the maximum number of detections of a single individuals was 5. A total of 63 salamanders were observed under more than one cover board (i.e., had spatial recaptures: 19, 8, 29, and 7, in Plots 1 to 4, respectively), and the maximum number of boards a single individual was observed under was four.

Densities of Red-Backed Salamanders were generally similar across the four sites. Based on AIC there was more support for constant density across sites than for between-site variability (cumulative model weights = 0.52 and 0.48, respectively; Fig. 3b, Table 1). Although the estimated number of unobserved individuals is constant in the most supported model (n_0 = 152.94, 95% confidence interval [CI] = 126.26–185.26), site-specific differences in estimated abundance arise on account of the different numbers of observed individuals ($\hat{N}_1$ = 229.94, $\hat{N}_2$ = 212.94, $\hat{N}_3$ = 260.94, $\hat{N}_4$ = 206.94; see Table 2 for 95% CIs). In SCR, the area of interest is defined explicitly, which allows for the formal conversion of abundance estimates ($\hat{N}$) to absolute density ($\hat{D}$) by dividing $\hat{N}$ by the size of the state-space, $|S|$: $\hat{D} = \hat{N}/|S|$. Estimated site-specific salamander densities were $\hat{D}_1$ = 1.62, $\hat{D}_2$ = 1.50, $\hat{D}_3$ = 1.83, and $\hat{D}_4$ = 1.45 salamanders/m^2 (see Table 2 for 95% CIs).

Based on AIC, models that allowed detection to vary across season as a function of survey day (time) were preferred to models using temperature (Table 1), and the quadratic effect of time was preferred to a linear effect. The quadratic effect indicates that detectability is highest around Julian day 278, 5 October, and that detection was lowest at the beginning and the end of autumn (Fig. 3a). The estimated baseline encounter probability was highest at the mean Julian day (278) and was p_0 = 0.08 (95% CI = 0.07–0.10) and lowest on the first and last survey days p_0 = 0.02. The estimated regression coefficients for the quadratic effect
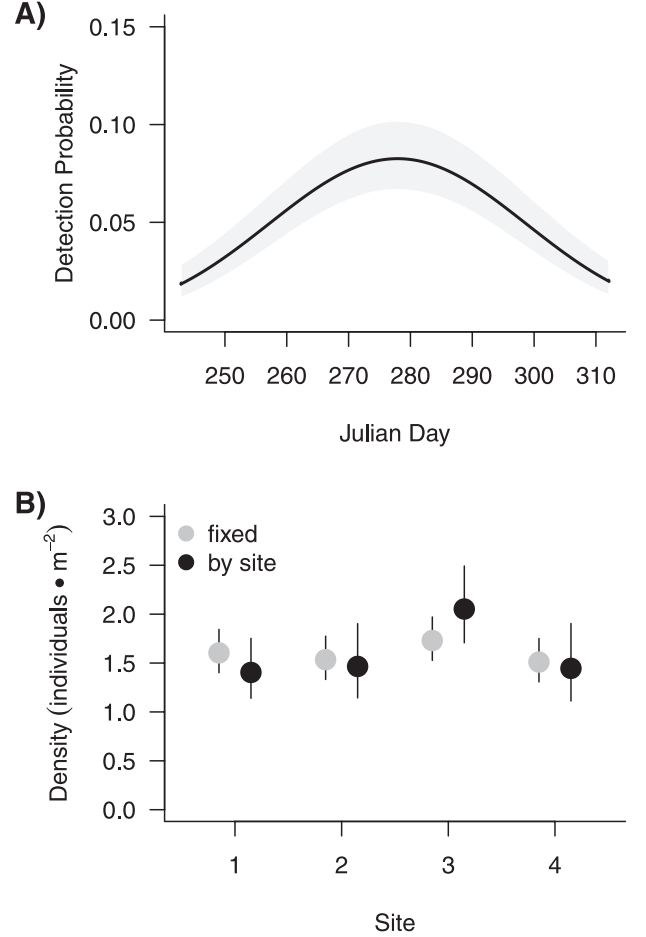

A)

B)

FIG. 3.—(A) Model estimates of the quadratic relationship between the baseline detection probability and Julian day for Red-backed Salamanders (*Plethodon cinereus*). The line represents the modelled relationship and the gray shaded area is the bootstrapped 95% confidence interval (CI). (B) Site-specific estimates of salamander density from the model with constant (fixed) density (gray points), and with density allowed to vary by site (black points). Solid black lines represent 95% CI.

of Julian day were β_{day} = 0.004 (95% CI = −0.09 to 0.10) and β_{day2} = −0.47 (95% CI = −0.56 to −0.37).

The estimated spatial scale parameter that characterizes the decline in detection with distance was σ = 0.94 (95% CI = 0.87–1.03). The standard SCR encounter model (the bivariate

TABLE 1.—Output summaries for 10 competing spatial capture–recapture models of Red-Backed Salamanders (*Plethodon cinereus*) generated in 2014 from four sites in a forest in New York, USA. Density (D) and detection (p_0) models are shown with their associated Akaike information criterion score, ΔAIC value, and the AIC weight (Ω). The "~1" notation represents null or intercept-only models, which are models with no covariate effects. The superscript "2" denotes the quadratic effect of day and/or temperature.

Density (D)	Detection (p_0)	AIC	ΔAIC	Ω
~1	~day + day^2	3387.09	0.00	0.52
~Site	~day + day^2	3387.22	0.13	0.48
~Site	~temp + temp^2	3429.34	42.26	0.00
~1	~temp + temp^2	3435.58	48.49	0.00
~Site	~temp	3477.36	90.27	0.00
~Site	~1	3478.44	91.35	0.00
~Site	~day	3478.48	91.39	0.00
~1	~1	3482.19	95.10	0.00
~1	~temp	3482.44	95.35	0.00
~1	~day	3483.11	96.02	0.00

TABLE 2.—A comparison of density estimates generated for Red-Backed Salamanders (*Plethodon cinereus*) at four forest sites using the standard/null spatial capture–recapture model (SCR0) and nonspatial methods. For the nonspatial model (M_h), we defined the sampling area as either the 1/2 or full mean maximum distance moved (MMDM). Site-specific density estimates (individuals/m^2) are given with 95% confidence interval (CI) in parentheses. See Methods for the formulation process for each model.

	Density (95% CIs)		
Site	SCR0	M_h: 1/2 MMDM	M_h: MMDM
1	1.41 (1.15–1.76)	1.43 (1.39–1.47)	0.81 (0.79–0.84)
2	1.33 (1.05–1.72)	3.39 (3.30–3.48)	1.93 (1.88–1.98)
3	2.16 (1.79–2.62)	1.84 (1.80–1.88)	1.05 (1.03–1.07)
4	1.39 (1.07–1.82)	1.20 (1.17–1.24)	0.68 (0.66–0.71)

normal model; Royle et al. 2013b) estimates the 95% home range size by first calculating the appropriate radius ($r = \sigma\sqrt{5.99}$) and then computing the area: home range $= \pi r^2$ (Royle et al. 2013b). For Red-Backed Salamanders in this study, the estimated 95% home range radius was 2.31 m (95% CI = 2.13–2.53 m), and the resulting estimated 95% home range size was 16.90 m^2 (95% CI = 14.22–20.09 m^2).

Salamander densities derived from estimates of abundance using capture–recapture models were computed using an assumed sampling area (1/2 MMDM and MMDM), and were calculated independently of any capture–recapture-based estimation of abundance. The effective sampling area using the 1/2 MMDM and MMDM buffers were 84.69 m^2 and 148.77 m^2, respectively. The nonspatial estimates of density depend on which buffer area is used; point estimates of density for the four sites based on the 1/2 MMDM buffer were 1.43, 3.39, 1.84, and 1.20 salamanders/m^2, and were always higher than when based on the MMDM buffer: 0.81, 1.93, 1.05, and 0.68 salamanders/m^2, respectively (see Table 2 for 95% CIs). When compared to those using MMDM buffer area, nonspatial estimates of density using 1/2 MMDM buffer area generated values that are more similar to the spatially explicit estimates (SCR$_0$). However, between-site variation in density under model M_0 is not consistent with estimates from model SCR$_0$.

DISCUSSION

We have demonstrated that SCR models can be applied to the kinds of data regularly collected in amphibian and reptile studies to obtain spatially explicit estimates of abundance, and hence of absolute density. SCR was developed as a model of space use that has two distinct benefits: (1) it resolves the issue of unmodeled, distance-dependent heterogeneity in encounter probabilities that traditional capture–recapture methods suffer from and (2) it yields insights about patterns of space use and ranging behavior that can otherwise be challenging to ascertain, particularly in herpetological studies.

The analysis of spatial encounter history data, such as that commonly collected in studies of amphibians and reptiles, resolves some of the major criticisms of conventional nonspatial capture–recapture. In particular, the estimate of abundance from SCR data is specific to a prescribed spatial region, removing the need to decide on an arbitrarily defined effective sampling area for converting abundance estimates to estimates of density. Moreover, the heterogeneity in-

herent in any nonspatial capture–recapture analysis (i.e., individual differences in distance to trap) is formally accommodated using a distance-based encounter probability model. Although spatial and nonspatial estimates of Red-Backed Salamander densities were similar, densities are sensitive to the choice of buffer used in a nonspatial model that attempts to account for individual heterogeneity. The decision of which buffer size to be used is not necessary in SCR and, thus, uncertainty in which density estimate is appropriate is avoided.

Reptiles and amphibians pose particular challenges for population assessments (Gibbons et al. 2000). This is particularly true for Red-Backed Salamanders; despite their large range across much of the eastern United States and Canada, surface counts often reflect only a subset of the population because many remain underground, even during high-activity periods (Smith and Petranka 2000; Bailey et al. 2004). Our results indicate that throughout the autumn sampling period, peak salamander detectability (which we associate with peak surface activity) occurred around midautumn, and was lower at the beginning and end of the sampling period. These findings are consistent with previous studies that show peak autumn activity in early–mid-October, which coincides with optimal foraging conditions, and reduced activity in the earlier warmer summer months and colder winter months either side of that peak (see Monti et al. 2000; Leclair et al. 2008).

Using the standard encounter model (the bivariate normal model; Royle et al. 2013b), the estimate of the movement parameter, σ, can be converted to an estimate of the 95% home range size (see Results). It is encouraging that our SCR-based estimates of home ranges are consistent with previously published values of between 10 and 30 m^2 using intensive sampling. Kleeberger and Werner (1982) reported that the home range sizes of *P. cinereus* varied according to sex and age class. Although not the focus of our study, SCR can easily accommodate individual covariates such as group membership (Royle et al. 2015) and be used to formally compare structure in parameter σ (i.e., in the scale of movement). The apparent agreement of our findings based on SCR and other home range size estimators based on detailed sampling of fewer individuals further highlights the value of using spatially explicit encounter history data to estimate movement parameters and thus account for individual heterogeneity in detection.

We used the binomial encounter model in our analysis, which is the most general formulation of the SCR model. For cover board surveys, where many individuals can be encountered under a single board, but individuals can be observed under a single board only during a single visit, the more complex multinomial or multi-catch encounter model is the correct model to use. When detection probabilities and encounter frequencies are low, however, as is the case here, the binomial and multi-catch models are statistically equivalent. As such, we adopted the more familiar binomial formulation of the SCR model.

Comparing published density estimates for Red-Backed Salamanders is more difficult, because of the variability in methodologies used to collect data and to produce estimates of density at different locations throughout their range (cf. Wyman and Jancola 1992; Mathewson 2009). In their classic study of this species, Burton and Likens (1975) estimated

densities of Red-Backed Salamanders at 0.24 individuals/m^2. They noted that their number is undoubtedly an underestimate because of missed individuals. Our density estimates were more than six times those of Burton and Likens (1975), and further demonstrate the importance of this species in forest ecosystems of the northeastern United States. Like other studies of Red-Backed Salamanders, these researchers account for the undetected portion of the population using ad hoc adjustments to surface counts, limiting the use of such smaller-scale studies to make region-wide comparisons (Burton and Likens 1975; Wyman and Jancola 1992; Mathewson 2009). When detectability has been accounted for, for example using mark–recapture analysis, reported density estimates are somewhat higher, and more in line with our findings (e.g., 2.82 individuals/m^2 in Mathis 1991; 1.29 individuals/m^2 in Semlitsch 2014). These abundance estimates are based on nonspatial capture–recapture (subject to heterogeneity-induced bias; Otis et al. 1978; Efford 2004) and a dependence on the choice of effective sampling area (Royle et al. 2013b).

We used artificial cover boards for generating individual encounter histories based on the capturing of identifiable individuals. The application of SCR is not limited to artificial cover board surveys, however, and many reptile and amphibian sampling methodologies require an explicit spatial design in the form of transects, area searches, or physical trapping lines/arrays (Blomberg and Shine 2006). Given that capture location is recorded in many studies that generate capture–recapture data to estimate abundance, these studies can also be used to estimate density using SCR methods (Royle et al. 2013b).

There is evidence that both reptile and amphibian populations are in decline worldwide (Gibbons et al. 2000; Houlahan et al. 2000; Böhm et al. 2013). The ability to monitor and assess the status of these populations is paramount, and requires the development of efficient field sampling protocols and well-developed analytical methods for producing estimates of density across space and time (Scott and Seigel 1992; Stuart et al. 2004; Böhm et al. 2013). The scope of this study was to illustrate the use of SCR in herpetological studies as a promising basis of data collection and analytical framework for generating repeatable and comparable estimates of population density. SCR methodology can be used for investigating many aspects of spatial ecology, including resource selection (Royle et al. 2013c), landscape connectivity (Royle et al. 2013a; Sutherland et al. 2014), spatial variation in density (Borchers and Efford 2008; Royle et al. 2013b), and movement or dispersal (Ergon and Gardner 2013; Schaub and Royle 2013). We encourage other researchers to adopt SCR as an informative analytical tool for monitoring herptofauna across both space and time.

SUPPLEMENTAL MATERIAL

Supplemental material associated with this article can be found online at http://doi.org/10.1655/HERPETOLOGICA-D-15-00027.S1.

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