1 **Spatial Capture-Recapture: a Promising Method for Analyzing Data Collected Using**

2 **Artificial Cover Objects**

3 CHRIS SUTHERLAND[1,4], DAVID J. MUÑOZ[2], DAVID A. W. MILLER[2], AND EVAN H.

4 CAMPBELL GRANT[3]

5 [1] Department of Natural Resources, Cornell University, Ithaca, NY 14850, USA

6 [2] Department of Ecosystem Science and Management, Pennsylvania State University,

7 University Park, PA 16827, USA

8 [3] USGS Patuxent Wildlife Research Center, SO Conte Anadromous Fish Laboratory,

9 Turners Falls, MA 01360

10 [4] CORRESPONDENCE: e-mail, chrissuthy@gmail.com

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12 RRH: SCR FOR COVER OBJECT SURVEYS

13 ABSTRACT: Spatial capture-recapture (SCR) is a relatively recent development in

14 ecological statistics that provides a spatial context for estimating abundance and space use

15 patterns, and as a result improves inference about absolute population density. SCR has been

16 applied to individual encounter data collected non-invasively using methods such as camera

17 traps, hair snares and scat surveys. Despite the wide-spread use of capture based surveys to

18 monitor amphibians and reptiles, there are few applications of SCR in the herpetological

19 literature. We demonstrate the utility and promise of the application of SCR in studies of reptiles

20 and amphibians by analyzing capture recapture data from red-backed salamanders, *Plethodon*

21 *cinereus*, collected using artificial cover boards. Using SCR to analyze spatial encounter histories

22   of marked individuals, we found evidence that density differed little among 4 sites within the

23   same forest (on average 1.59 salamanders per m^2) and that salamander detection probability

24   peaked in early October (Julian day 278) reflecting expected surface activity patterns of the

25   species. The spatial scale of detectability, a measure of space use, suggests that the 95% fall

26   home range size for this population of red-backed salamanders was 16.89 m^2. Surveying reptiles

27   and amphibians using artificial cover boards regularly generates spatial encounter history data of

28   known individuals which can readily be analyzed using SCR methods, providing estimates of

29   absolute density and inference about the spatial scale of habitat use.

30   **Key words:** Artificial cover objects; Abundance; Amphibian; Density; Detection; Home

31   range; *Plethodon cinereus*; New York; Red-backed salamander; Spatially explicit capture-

32   recapture.

33   HERPETOFAUNA represent some of the most important components of many ecological

34   communities, and it is therefore of increasing concern that populations globally are in decline

35   (Gibbons et al. 2000; Stuart et al. 2004; Adams et al. 2013). However, the causes of these

36   declines are many and complex (Alford and Richards 1999; Beebee and Griffiths 2005; Hof et al.

37   2011), and monitoring herpetofauna is a non-trivial endeavor given that they are typically elusive

38   and cryptic species, occur at relatively low densities, and often have specific micro-habitat

39   preferences and narrow environmental thresholds (Grant et al. 1992; Gibbons et al. 2000; Weir et

40   al. 2005). As such, recommendations place increasing emphasis on the development and use of

41   standardized monitoring techniques and analytical methods for monitoring and assessing

42   populations (Parris 1999; Doan 2003; Mazerolle et al. 2007).

43   When individuals can be marked or can be recognized based on natural markings, capture

44   mark-recapture methods can be used to estimate abundance and well-established procedures

45   exist for both data collection and statistical analysis (Otis et al. 1978, Williams et al. 2002,

46   Amstrup et al. 2010). Trapping using drift nets, pitfall traps or cover object surveys are among

47   the most common methods advocated for monitoring amphibians and reptiles (Willson and

48   Gibbons 2009). In studies that employ multiple traps, or where animals are caught across a

49   relatively large study area, each observation of an individual occurs at a unique spatial location

50   so that trapping produces spatial encounter histories indicating both when and where each

51   individual was captured. Traditional capture-recapture approaches ignore the spatially explicit

52   individual-by-trap-by-occasion encounter information and uses only individual-by-occasion, i.e.,

53   non-spatial, encounter histories (Royle et al. 2014). The result is that, unless trapping occurs for

54   a discrete habitat unit such as a pond, the area being sampled is not well defined. The inability to

55   define the area sampled, makes it impossible to estimate relative densities of animals or to define

56   our sampled population, when in fact, most ecological and conservation oriented studies aim to

57   understand factors that affect relative density of animals in a habitat or population (Krebs 1994;

58   Buckland et al. 2005; Efford and Fewster 2013). Moreover, individual animals will also vary in

59   their proximity to traps and therefore the frequency with which they will be encountered. This

60   leads to heterogeneity among individuals in the rate at which they are captured that cannot

61   explicitly be accounted for when using encounter histories that are reduced to non-spatial

62   summaries. Failure to account for such heterogeneity will result in estimates of abundance being

63   negatively biased (Otis et al. 1978, Efford 2004).

64   These issues have been resolved, in part, by the recent development of spatial capture-

65   recapture models (SCR: Efford 2004; Borchers and Efford 2008; Royle and Young 2008). SCR

66   provides a spatial context for the estimation of abundance by first describing how individual's

67   activity centers (home range centers) are distributed across a prescribed area of known size, and

68   second, by modeling the probability an individual will be detected at any given trap as a

69   decreasing function of the distance between its activity center and the trap. Explicitly defining a

70   sampling region allows absolute density to be directly estimated (Borchers and Efford 2008), or

71   derived from spatially referenced estimates of abundance (Royle and Young 2008, Royle et al.

72   2014). The estimation of the spatial scale of detectability is analogous to a model of space use,

73   and in addition to accommodating location specific heterogeneity in encounter probabilities, can

74   provide information about patterns of space use and home range size (Royle et al. 2014).

75   Here we demonstrate the utility of SCR by analyzing spatially explicit individual

76   encounter history data collected during a survey of red-backed salamander *Plethodon cinereus* in

77   a forest in New York State. The data was collected using artificial cover boards, a particularly

78   appealing sampling method because it avoids destruction of habitat, is cost effective and requires

79   minimal maintenance, it minimizes observer bias, and importantly, has the potential to generate

80   relatively large sample sizes with little risk of mortality (Monti et al. 2000; Willson and Gibbons

81   2009; Hesed 2012). Although we focus on artificial cover board data from here, SCR is equally

82   applicable to any spatial sampling protocol in which individuals are uniquely identified

83   (Mazerolle and Bailey 2007). Analyzing spatially explicit encounter data collected from four

84   plots, we use a SCR model to estimate absolute salamander density and home range size.

85   Furthermore, we investigate whether salamander density varies across sampling plots within a

86   single woodland, and how surface activity patterns might influence detectability throughout a

87   single season. Finally, we compare spatially explicit estimates of salamander abundance to

88   estimates generated using traditional, non-spatial capture-recapture.

89   MATERIALS AND METHODS

90   Cover Board Surveys

91   In June 2014 four cover board arrays that were at least 20 m apart were established in the

92   Polson Nature Area, Ithaca, New York (42°25'26''N, 76°23'55''W, datum = North American

93   Datum 1983). Each cover board array was 5 x 10 m consisting of 50 pine cover boards (25 x 25 x

94   2.45 cm) spaced 1 m apart in a rectangular grid (Fig. 1). Each cover board was checked on

95   multiple occasions in the fall between 1st September and 9th of November 2014 (sites 1, 2, 3 and

96   4 were visited 7, 5, 6 and 4 times, respectively). We recorded the date of the survey and the

97   ambient air temperature immediately prior to checking under the cover boards. Each board was

98   then carefully lifted and all red-backed salamanders present on the surface under each of the

99   boards were collected, noting under which cover board each individual was found. On initial

100 capture, salamanders were given a unique individual mark by injecting visual implant elastomer

101 at up to four locations ventral and adjacent to each limb using combinations of up to 4 colors

102 making each individual uniquely recognizable (Fig. 2, see also Bailey 2004; Grant 2008). Such

103 marking over the course of the season generated binary encounter history for each animal

104 observed at least once, where y_{ijk}, indicates whether individual i was detected in trap j in

105 occasion k (y_{ijk} = 1 if detected and y_{ijk} = 0 otherwise).

106   Spatial Capture-Recapture

107   In SCR models, a spatial model of abundance and a spatial model of the detection process

108 are simultaneously fitted to the encounter history data **Y**. The abundance model describes the

109 distribution of animal activity centers which are typically assumed to be uniformly distributed

110 over a prescribed area of interest or state-space, S , i.e., $s_i \sim$ Uniform(S). For computational

111   convenience, S can be represented discretely as the center points of a fine grid, each of which is a

112   potential activity center (Fig. 1). The models requires that a state-space be defined by a buffer

113   around the trapping array that should be at least large enough to contain all of the activity centers

114   of individuals that have non-negligible probability of being detected in at least one of the traps,

115   or in other words, larger than the radius of a home range. The resolution of the discretization

116   should be fine enough to sufficiently approximate continuous space relative to the species'

117   movement, but should also be but coarse enough for computational tractability (Royle et al.

118   2014). For the salamanders, the state-space was generated using a buffer width of 5 m around

119   each cover board array (in excess of any published home range estimates), and discretized into

120   0.5 m x 0.5 m grid cells; the state-space for each of the four plots contained 981 point locations

121   and had an area of 245.25 m^2 (Fig. 1).

122   The second component is the observation model that relates the probability of detecting

123   an individual at a specific trap (artificial cover board) to the distance between the trap and the

124   animal's home range center. The use of a distance based detection model accounts for the

125   additional heterogeneity that arises from the variation in individual-to-trap distances in the

126   population, reducing the potential for biases in estimates of abundance and density (Otis et al.

127   1978, Efford 2004, Royle et al. 2014). The assumption is therefore that detection will be highest

128   for traps located near the as animals activity center and decline as distance from the activity

129   center increases. More formally, the model states that $p[\mathbf{x},\mathbf{s}]$, the probability of observing an

130   individual with an activity center $\mathbf{s}$ in a trap with known location $\mathbf{x}$, decreases with increasing

131   Euclidean distance, $d(\mathbf{x},\mathbf{s})$. The model has two parameters: p_0, the baseline detection probability,

132   or the probability that an individual would be detected at its activity center ($d(\mathbf{x},\mathbf{s}) = 0$), and σ, a

133   spatial scale parameter that characterizes the decline in detectability with distance from an

134   activity center. In fact, in some situations the parameter σ can be thought of as a movement

135   parameter, and as such, the model for encounter probability is analogous to a model of space use,

136   providing information about home range size during the period of sampling (Royle et al. 2014).

137   We refer to this formulation of the model, where the probability of detection depends solely on

138   the distance from an animal's activity center, as model SCR_0. However, as in non-spatial capture

139   recapture, other sources of detection heterogeneity need to be accounted for in order to avoid

140   biases (Otis et al. 1978). In SCR, variation in encounter rates can easily be incorporated using

141   standard logistic regression on the baseline detection probability p_0 and the parameters

142   simultaneously estimated, e.g.:

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

144   where β_0 is the intercept and β's are the regression coefficients relating detectability to any of the

145   R covariates of interest.

146   In this study, we were particularly interested in accounting for any temporal variation in

147   salamander detectability over the course of the sampling period that may reflect variation in

148   activity patterns of red-backed salamanders in the fall. We used both the day of survey (*time*),

149   and air temperature in °C (*temp*) as covariates to account for such variation. Moreover, we

150   suspected that there likely exists an optimal activity time or temperature during which activity

151   would be highest and salamanders would be most detectable. We therefore fitted models with

152   both linear *and* quadratic effects of both covariates on detection. Because time and temperature

153   are highly correlated we did not consider models in which both effects were present, i.e., models

154   could contain time *or* temperature, but not both.

155   Of course, the objective is to estimate the total population size, $\widehat{N}$, within the prescribed

156   area and so in addition to estimating the parameters of the detection model based on the spatial

157   encounter histories of the observed individuals (n_{obs}) the number of individuals that went

158   undetected (unobserved individuals: n_0) is also a parameter to be estimated. The estimated total

159   population size is therefore $\widehat{N} = n_{\mathrm{obs}} + \hat{n}_0$ and estimated density is derived as $\widehat{D} = \widehat{N} / |S|$, where

160    $|S|$ is the size of the state space S.

161   We used maximum likelihood methods to jointly estimate each of the model parameters.

162   A key consideration in the methods outlined above is the treatment of the activity centers

163   because they are never known in practice. We adopt an integrated likelihood approach using a

164   function that evaluates the likelihood of the parameters of the SCR model integrated over all

165   possible (discrete) individual activity centers (Borchers and Efford 2008, Royle et al. 2014).

166   Maximum likelihood allows multiple competing models to be compared formally using AIC. We

167   obtain the maximum likelihood estimates using an integrated likelihood function (oSCR:

168   Sutherland, personal project), which is written and implemented in the **R** language (R Core Team

169   2012). We note that the **R** package **secr** can be used to implement the same suit of models

170   (Efford 2012).

171   Non-Spatial Comparison

172   Prior to the development of spatial capture-recapture, it would have been (and arguably

173   still is) conventional to estimate abundance using a suite of non-spatial closed population

174   capture-recapture methods (CR; e.g., those outlined in Otis et al. 1978). Although the inference

175   objective in CR is to estimate the size of the population, the spatial region to which N refers to is

176   often unclear. The traditional approach for converting CR abundance estimates to density is to

177   first create a convex hull around the trapping grid, and then apply a buffer to the convex hull

178   with a width based on either one-half the mean maximum distance ($^1/_2$ MMDM: Dice 1938) or

179   the full mean maximum distance moved (MMDM: Parmenter et al. 2003). The important point

180   here is that, although the estimate of abundance is fixed, density depends directly on which

181   buffer is chosen, and is thus to some degree arbitrary.

182   To emphasize the value of using spatial capture-recapture methods to obtain spatially

183   referenced estimates of abundance and therefore density, we collapsed the spatial encounter data

184   to non-spatial (individual-by-occasion) encounter histories for the salamanders and analyzed the

185   data using model M_h (Otis et al. 1978). Rather than assuming any specific structural between-

186   individual variation in detectability, model M_h accounts for individual heterogeneity using a

187   logit-normal model that assumes that the logit-transformation of individual detection

188   probabilities, p_i has a normal distribution with variance θ^2 (Coull and Agresti 1999, Dorazio and

189   Royle 2003):

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

191   Using site specific abundance under model M_h, density was computed for each site using

192   both the $^1/_2$MMDM and MMDM buffer areas and compared them to estimates of density from

193   the standard spatial capture-recapture model, SCR_0. Model M_h was applied to each site

194   separately and analyzed using the **R** code provided in Chapter 6 of Royle and Dorazio (2008).

195   RESULTS

196   In total, 299 red-backed salamanders were captured across the four cover board survey

197   plots (77, 60, 108 and 54). Of these, 134 were captured more than once (38, 18, 51, and 17,

198   respectively), and the maximum number of detections of a single individuals was 5. A total of 63

199   salamanders were observed under more than one cover board (19, 8, 29, and 7, respectively), and

200   the maximum number of boards a single individual was observed under was 4.

201   Red-backed salamander densities were generally similar across the four sites. Based on

202   AIC there was more support for constant density across sites than for between-site variability

203   (cumulative model weights = 0.67 and 0.33 respectively, Fig. 3b, Table 2). Although the

204   estimated number of unobserved individuals is constant in the most supported model ($n0 =$

205   152.94, 95 % CI: 126.26—185.26), site-specific differences in estimated abundance arises due to

206   the different numbers of observed individuals ($\widehat{N}_1 = 229.94$, $\widehat{N}_2 = 212.94$, $\widehat{N}_3 = 260.94$, $\widehat{N}_4 =$

207   206.94, see Table 2 for 95% CIs). In SCR, the area of interest is defined explicitly, which allows

208   for the formal conversion of abundance estimates ($\widehat{N}$) to absolute density ($\widehat{D}$) by dividing $\widehat{N}$ by

209   the size of the state-space, $|S|$: $\widehat{D} = \widehat{N} / |S|$. Estimated site specific salamander densities were $\widehat{D}_1 =$

210   1.62, $\widehat{D}_2 = 1.50$, $\widehat{D}_3 = 1.83$, and $\widehat{D}_4 = 1.45$ salamanders per m^2 (see Table 2 for 95 % CIs).

211   Based on AIC, models that allowed detection to vary across season as a function of

212   survey day (*time*) were overwhelmingly preferred to models using temperature (Table 2), and the

213   quadratic effect of day of survey was preferred to a linear effect. The quadratic effect suggests

214   that detectability is highest around Julian day 278, 5th October, and that detection was lowest at

215   the beginning and the end of the fall season (Fig. 3a). The estimated baseline encounter

216   probability was highest at the mean Julian Day (278) and was $p_0 = 0.09$ (95 % CI: 0.07—0.10)

217   and lowest on the first and last survey days $p_0 = 0.02$. The estimated regression coefficients for

218   the quadratic effect of Julian Day were $\beta_{day} = 0.004$ (95 % CI: -0.09—0.10) and $\beta_{day2} = -0.46$

219   (95 % CI: -0.56—-0.37).

220   The estimated spatial scale parameter that characterizes the decline in detection with

221   distance was $\sigma = 0.93$ (95 % CI: $0.83 - 1.08$). In the case of the standard SCR encounter model

222   (the bivariate normal model, Royle et al. 2014), the 95 % home range size can be computed by

223   first calculating the appropriate radius: $r = \sigma\sqrt{5.99}$ and then computing the area: $HR = \pi r^2$ (Royle

224   et al. 2014). For red-backed salamanders in this study, the estimated 95 % home range radius is

225   2.28 m (95 % CI: $2.03 - 2.64$ m) and the resulting estimated 95 % home range size is 16.28 m^2

226   (95 % CI: $12.96 - 21.94$ m^2).

227   Density derived from estimates of abundance using non-spatial capture-recapture were

228   computed using an assumed sampling area (½ MMDM and MMDM), and were calculated

229   independently of any CR based estimation of abundance. The effective sampling area using the

230   ½ MMDM and MMDM buffers were 84.69 m^2 and 148.77 m^2 respectively. Of course, the non-

231   spatial estimates of density depend on which buffer area is used; point estimates of density for

232   the four sites based on the ½ MMDM buffer were 1.43, 3.39, 1.84 and 1.20 salamanders per m^2,

233   and were always higher than when based on the MMDM buffer: 0.81, 1.93, 1.05, and 0.68

234   salamanders per m^2 respectively (see Table 2 for 95% CIs). For demonstrative purposes, we can

235   compare these results with estimates form the spatial model using SCR_0 as a reference point for

236   comparing spatial and non-spatial density estimates. Non-spatial estimates of density using ½

237   MMDM buffer area generate values that are more in line with the spatially explicit estimates.

238   However, between site variation in density under model M_0 is not consistent with estimates from

239   model SCR_0.

240   DISCUSSION

241   We have demonstrated that spatial capture-recapture models can be applied to the kinds

242   of data regularly collected in amphibian and reptile studies to obtain spatially explicit estimates

243   of abundance, and hence of absolute density. Moreover, SCR can be used to formally account for

244   the heterogeneity in detection probability arising from individual's distance-based differences in

245   exposure to traps, and that including a model for detection as a function of distance from the

246   capture location yields interesting insights about a species' space-use patterns and ranging

247   behavior which can otherwise be challenging, particularly in herpetological studies.

248   The analysis of spatial encounter history data, like that commonly collected in studies of

249   amphibians and reptiles, resolves some of the major criticisms of conventional non-spatial

250   capture-recapture. Specifically, estimates of abundance from SCR are specific to a prescribed

251   spatial region, removing the need to decide a priori on an effective sampling area for converting

252   abundance estimates to estimates of density. Moreover, the heterogeneity inherent in any non-

253   spatial capture-recapture analysis, i.e., individual differences in 'distance to trap', is formally

254   accommodated using a distance-based encounter probability model. This is demonstrated in our

255   study by the fact that, although spatial and non-spatial estimates of red-backed salamander

256   densities are similar, under a non-spatial model that attempts to account for individual

257   heterogeneity (model M_h), densities are sensitive to the choice of buffer used ($^1/_2$ MMDM or

258   MMDM). This decision of which buffer size to be used is not necessary in SCR and thus

259   uncertainty in which density estimate is appropriate is avoided.

260   Reptiles and amphibians pose particular challenges for population assessments (Gibbons

261   et al. 2000). This is particularly true for red-backed salamanders; despite their large range across

262   much of the eastern United States and Canada, surface counts often reflect only a subset of the

263   population because many remain underground, even during high activity periods (Smith and

264   Petranka 2000). Our results are suggestive of this and indicate that throughout the fall sampling

265   period, peak salamander detectability, which we associate with peak surface activity, occurred

266   around mid-autumn and was lower and the beginning and end of the sampling period (i.e.,

267   described by the quadratic effect of 'day of the survey' on detection probability). These findings

268   are consistent with previous studies that show peak autumn activity in early-mid October that

269   coincide with optimal foraging conditions and reduced activity in the earlier warmer summer

270   months and colder winter months either side of the optimum (see Monti et al. 2000, Leclair et al.

271   2008).

272   Using the standard encounter model (the bivariate normal model, Royle et al. 2014), the

273   parameter estimate of the 'movement' parameter, σ, can be converted to an estimate of the 95%

274   home range size (see Results). It is encouraging that our SCR based estimates of home ranges are

275   consistent with previously published values of between 10 and 30 m^2 using intensive sampling

276   (Kleeberger and Werner 1982). In fact, in their study, Kleeberger and Werner (1982) found that

277   *P. cinereus* home range sizes varied according to sex and age class (juvenile vs. adult). Although

278   not the focus of this study, SCR can easily accommodate individual covariates such as group

279   membership (Royle et al. 2015) and be used to formally compare structure in parameter σ (i.e., in

280   the scale of movement). The apparent agreement of our findings based on SCR, and other home

281   range size estimators based on detailed sampling of fewer individuals further highlights the value

282   of using spatially explicit encounter history data to estimate movement parameters and thus

283   account for individual heterogeneity in detection.

284   Comparing published red-backed salamander density estimates is more difficult, largely

285   due to the variability in methodologies used to collect data and to produce estimates of density at

286   different locations throughout their range. In their classic study of red-backed salamanders at

287 Hubbard Brook Forest and their importance to forest ecosystem function, Burton and Likens

288 (Burton and Likens 1975) estimated red-backed salamander densities of 0.24 per m^2. While

289 showing that salamander dry biomass for their estimate is nearly 2 times greater for this one

290 species than all breeding birds combined in the forest, they note that their number is undoubtedly

291 an underestimate due to missed individuals. Our density estimates were > 6 times those of

292 Burton and Likens and further demonstrates the importance of this species in NE forest

293 ecosystems. Our estimates of density of around 1.6 salamanders per m^2 are similarly greater than

294 other previously reported densities in both New York (0.37 salamnders per m^2: Wyman and

295 Jancola 1992) and in other parts of Northeastern USA (e.g., 0.33 and 0.39 salamanders per m^2:

296 Mathewson 2009), although, notably, both did not formally account for imperfect detection. In

297 fact, these, and many other studies of red-back salamanders, account for the undetected portion

298 of the population using *ad hoc* adjustments to surface counts, limiting the use of such smaller

299 scale studies to make region-wide comparisons. When detectability has been formally account

300 for, for example using mark-recapture analysis, reported density estimates are somewhat higher,

301 and more in line with our findings (e.g., 2.82 salamnders per *m*: Mathis 1991; and 0.73 to 1.29

302 salamnders per m^2: Semlitsch 2014), although these abundance estimates are based on non-

303 spatial capture-recapture and are thus subject to heterogeneity induced bias (Otis et al. 1978,

304 Efford 2004) and a dependence on the choice of effective sampling area (Royle et al. 2014).

305   We focus here on the use of artificial cover boards (ACOs) for generating individual

306 encounter histories based on the capturing of uniquely identifiable individuals. However, we

307 stress that the application of SCR is not limited to ACO surveys. In fact, many reptile and

308 amphibian sampling methodologies require an explicit spatial design in the form of transects,

309 area searches or physical trapping lines/arrays, and in many situations, it is feasible to either

310   identify individuals based on unique marks and or by physically marking individuals (Blomberg

311   and Shine 2006). Therefore, the vast majority of studies that generate capture-recapture data and

312   are used to estimate abundance can also be used to estimate density, arguably a more apply

313   spatial capture recapture methods (Royle et al. 2014).

314   There is evidence that both reptile and amphibian populations are in decline worldwide

315   (Burton and Likens 1975, Gibbons et al. 2000, Houlahan et al. 2000). The ability to monitor and

316   assess the status of these populations is thus paramount and requires the development of efficient

317   field sampling protocols, and well-developed analytical methods for producing estimates of

318   density that can be related to natural or anthropogenic environmental variation across space and

319   time (Scott and Seigel 1992, Stuart et al. 2004, Böhm et al. 2013). The scope of this study was to

320   provide, by way of demonstration, motivation and support for the use of SCR in herpetological

321   studies as a promising basis of data collection and analytical framework for generating

322   repeatable and comparable estimates of population density. Spatial capture-recapture methods

323   provide a suite of methods that can be used for directly investigating many aspects of spatial

324   ecology including resource selection or space usage (Royle et al. 2013b), landscape connectivity

325   (Royle et al. 2013a, Sutherland et al. 2014), spatial variation in density (Borchers and Efford

326   2008, Royle et al. 2014), and movement or dispersal (Schaub and Royle 2013; Royle et al. in

327   review, Ergon and Gardner 2013). SCR therefore offers great potential for monitoring

328   herptofauna across both local and range-wide scales, and over time, in a meaningful and

329   informative way.

333   Amphibian Research and Monitoring Initiative (ARMI) of the US Geological Survey. Approval

334   for the collection of data, and the handling and marking of animals was obtained from the

335   Patuxent Wildlife Research Center Animal Care and Use Committee (ACUC).

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508   TABLES

509   TABLE 1.—In total, we fit 10 competing spatial capture-recapture models to the

510 individual encounter histories generated from the four sites in a forest in New York. The table

511 shows parameterization of the density (*D*) and detection (*p*0) models and the associated AIC

512 scores, the ΔAIC which is the difference in AIC score between that model and model with the

513 lowest AIC, and the AIC weight for each model (Ω). The '~1' notation represents 'null' or

514 'intercept only' models, which are models with no covariate effects.

Density (D)	Detection (p0)	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
~ 1	~ 1	3477.36	90.27	0.00
~ site	~ temp	3478.44	91.35	0.00
~ site	~ 1	3478.48	91.39	0.00
~ site	~ day	3482.19	95.10	0.00
~ 1	~ temp	3482.44	95.35	0.00
~ 1	~ day	3483.11	96.02	0.00

515

516   TABLE 2.—To compare density estimates from spatial-capture models with those

517   generated using non-spatial methods, we fitted M_h, a non-spatial CR model that allows for

518   individual heterogeneity using a logit-normal random effects formulation of the model.

519   Converting non-spatial abundance estimates to density requires the definition of an effective

520   sampling area and, as is customary, we used the ½ and full 'mean maximum distance moved'

521   buffer widths. For comparison, we report site specific density estimates (salamanders per m^2)

522   with their associated 95 % confidence intervals in parentheses for the 'null' spatial capture-

523   recapture model (SCR_0), model M_h based on the ½ MMDM (M_h: 1/2 MMDM), and model M_h

524   based on the ½ MMDM (M_h: MMDM).

Site	Density (95% CIs)		
	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)

525

FIGURE CAPTIONS

526

527   FIG. 1.—A photograph of one of the artificial cover board arrays used in this study to

528   capture red back salamanders. On the right is a schematic of the spatial location data used in the

529   spatial capture recapture models: the red crosses are the 50 cover boards located 1m apart, the

530   black points are the center points of the discrete state-space (i.e., all possible activity center

531   locations), and the grey area denotes the state space S used in the SCR model.

532

533

534   FIG. 2.—An example of a salamander uniquely marked with injected colored elastomer

535   (front left: yellow, front right: red, back right: orange, and back left: blue). The right hands side

536   panel shows the spatially reference capture locations for this individuals that was captured four

537   times in under three unique cover boards.

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539

540   FIG. 3.—Model estimates of A) the quadratic relationship between the baseline detection

541   probability and Julian day. Detection, which is most likely linked to activity patterns, is highest

542   around Julian day 278 (October 5th). The blue line is the modelled relationship and the grey

543   shaded area is the bootstrapped 95 % confidence interval. B) Site specific estimates of

544   salamander density from the model with constant density (fixed, grey points), and density

545   allowed to vary by site (black points). Solid black lines are 95 % confidence intervals.