

## Density Estimation in Terrestrial Chelonian Populations Using Spatial Capture–Recapture and Search–Encounter Surveys

J. ANDREW ROYLE<sup>1</sup> AND HALEY TURNER

*USGS Eastern Ecological Science Center, Laurel, Maryland, 20708, USA*

**ABSTRACT.**—Having an accurate estimate of population size and density is imperative to the conservation of chelonian species and a central objective of many monitoring programs. Capture–recapture and related methods are widely used to obtain information about population size of chelonians. However, classical capture–recapture methods have strict spatial sampling requirements and do not account for lack of geographic closure caused by movement of individuals in and out of the surveyed landscape. Newly developed spatial capture–recapture (SCR) models address these limitations by specification of explicit models for spatial sampling as well as the spatial distribution of individuals in the population. Spatial capture–recapture models have not yet been applied to the study of chelonian populations. Here we demonstrate their application to a population of box turtles in Maryland that has been studied for 75 yr. Results support dramatic declines in population size of box turtles since the 1940s.

Over 50% of all recognized turtle species are listed as globally threatened on the IUCN red list, with over 35% of species described as endangered or critically endangered (Rhodin et al., 2018). Turtles are facing increasing threats from anthropogenic activities, including habitat loss from development, road mortality, and illegal collection for the pet trade (Shepard et al., 2008; Erb, 2012). To prevent threatened species from slipping further toward extinction, many state and federal agencies support active monitoring programs for chelonian populations (Turtle Conservation Fund, 2002). Central to population monitoring and management of most species, including chelonians, is information about population size or density.

There are many techniques used to monitor abundance of terrestrial chelonians. For example, various studies have used occupancy models based on presence/absence data (Erb et al. 2015), distance sampling methods (Zylstra et al., 2010; O'Connor et al., 2015) and capture–mark–recapture (CMR) methods (Litzgus and Mousseau, 2004; Daigle and Jutras, 2005; Pittman et al., 2011). Verdon and Donnelly (2005) collected Florida Box Turtle data from visual searches and opportunistic encounters and used a mark–resight estimator of population size. Open population CMR models that include parameters describing recruitment and mortality rates have been used by Converse et al. (2005), Langtimm et al. (1996), and Tuberville et al. (2014).

Capture–recapture models assimilate information from encounter history data of individuals to estimate population size,  $N$ , and parameters that describe the observation process, namely, the probability of encounter of an individual during sampling, or detection probability,  $p$ , simultaneously. Closed population capture–recapture models require that repeated sampling be done, over time, under the assumption of a “closed population,” which is to say that individuals are not entering or leaving the population. A limitation of classical capture–recapture models is that the observation process is not spatially explicit;  $p$  does not depend explicitly on where sampling was done. Thus, when sampling is conducted within some geographic region there is usually an implicit assumption that the area is sampled more or less uniformly (there are “no holes” in the array; Otis et al., 1978). Such uniform sampling is almost impossible to do in practice and, when it is possible, it is usually

very impractical or inefficient. In practice, if a region is targeted for sampling by an observer walking on foot, there are two options that might produce uniform sample coverage: either the chosen area is small enough such that uniform coverage can be obtained by a reasonable number of observers or, for larger areas, uniform coverage can be achieved only by an extraordinary amount of effort. Even if small or large area sampling options can be employed, it is usually the case that organisms moving about in space will not always be available for encounter on the study area, no matter how large the study area is and regardless of the amount of effort used in sampling, because individual home ranges may only partially overlap the surveyed area. This induces the problem of temporary emigration and leads to ambiguity in the interpretation of population size estimates when it is not accounted for (Chandler et al., 2011).

It is advantageous to consider sampling designs that allow for a more flexible approach to sampling a landscape and accounting for the spatial structure of populations. In this article, we demonstrate the use of spatial capture–recapture (SCR; Royle et al., 2014) models applied to a study of box turtles in Maryland. We employ a flexible search–encounter (Royle et al., 2011) approach to spatial sampling in which one or more observers search a given study area in an unstructured manner, recording the GPS search path, and encounter locations of individuals, and their identity. Spatial capture–recapture models define detection probability to be spatially explicit in the sense that the probability of detection of an individual depends on both the search path and the location of individual turtles relative to that search path. In addition, SCR models provide an explicit characterization of how individuals are distributed across a landscape and their patterns of space use, which allow for population size and density to be estimated in a manner that accounts for temporary emigration because of the juxtaposition of individual home ranges with the surveyed area (Royle and Young, 2008). Spatial capture–recapture requires location information be collected on captured individuals to provide information about home range and activity centers of individuals in the sampled population (Royle et al., 2014). SCR has been widely applied to studies of mammals, in part because they can be effectively encountered by DNA sampling of hair snares or droppings (Kéry et al., 2011; Sollmann et al., 2012; Fuller et al., 2016) or through camera traps (Sollmann et al.,

<sup>1</sup>Corresponding author. E-mail: aroyle@usgs.gov  
DOI: 10.1670/21-016

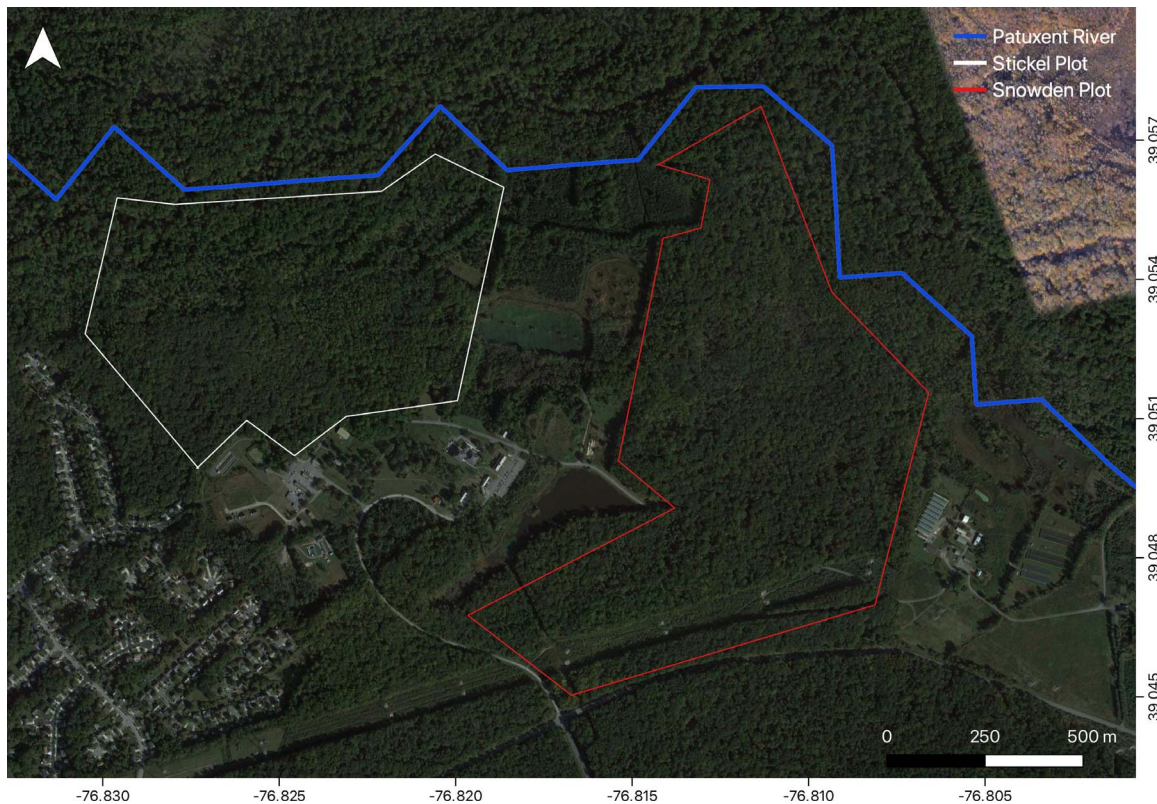


FIG. 1. The two study areas, Stickel (white) and Snowden (red), on the Patuxent Wildlife Research Center (PWRC) in Laurel, Maryland. The green line is the Patuxent River.

2011; Harmsen et al., 2020). However, SCR has been underutilized in studies of reptiles. Royle and Young (2008) applied SCR to a study of the elusive Flat-Tailed Horned Lizard, and Schmidt et al. (2017) used SCR to estimate the density of the Slow Worm, *Anguis fragilis*. In this article, we attempt to fill this methodological gap by offering a new approach for sampling and population estimation of terrestrial chelonian populations, based on SCR and a flexible search-encounter sampling method. We apply these methods to a field study of Eastern Box Turtles in Maryland.

#### MATERIALS AND METHODS

**Study Area.**—We conducted our study on Patuxent Wildlife Research Center (PWRC), a 12,841-acre center in southeastern Maryland that is restricted from public access. Most of the data were collected from two forest plots at PWRC, the Stickel plot (Fig. 1, white polygon) which is about 175 acres and includes the area surveyed historically by Lucille Stickel, and the Snowden plot (Fig. 1, red polygon) which is roughly 230 acres and borders Snowden pond (Stickel, 1950). Habitat in these plots included upland and bottomland primarily beech (*Fagus grandifolia*) forest that borders the southern bank of the Patuxent River.

**Survey Methods.**—We conducted visual search-encounter surveys (Royle et al., 2011) from June through October 2020. Surveyors walked arbitrary paths within the target survey area, visually searched for Eastern Box Turtles, and carried smart phones running the GAIA GPS application ([www.gaiagps.com](http://www.gaiagps.com)) to record the foot path of each individual surveyor. When a turtle was visually captured, the surveyor recorded the distance from the observer, as well as the coordinates of each turtle. Surveyors

recorded three readings of coordinates from each turtle's location using the app "My GPS Coordinates" (version 4.0 or greater) typically with an error range of 0–33 feet. We averaged the three recordings for each turtle for more accurate location data. We recorded the ID of each recaptured turtle, and permanently marked new turtles on the marginal scutes with a triangular file, according to a standardized numeral notching system (Buhlmann et al., 2008). When a turtle was encountered, we took morphological measurements, counted annuli (from the clearest dorsal scute), and recorded sex characteristics (eye color, hind toenail length, flaring of carapace, position of anal vent) for inclusion in the long-term collection of Eastern Box Turtle data at PWRC.

**Statistical Methods.**—Spatial capture-recapture (SCR) is a class of hierarchical models for estimating population density that allows for a flexible and spatially explicit characterization of both the sampling process (the "observation model") and a model component (the "ecological process model"), which describes the distribution of individuals in the population being sampled (Royle et al., 2018). As with classical (nonspatial) capture-recapture models, SCR models use individual encounter history data. However, in SCR models the encounter histories are three dimensional, describing not only the time (or occasion) of capture of each individual, but also its location of capture. In typical SCR studies, capture locations represent camera traps (Harmsen et al., 2020), baited hair snag stations (Linden et al., 2017) or cover boards for salamanders (Sutherland et al., 2016). However, in the sampling of terrestrial reptiles fixed trap locations are seldom used because of the impracticality or ineffectiveness of these methods for most species, especially turtles. Instead, survey sites are typically searched systematically or even haphazardly by observers or sniffer dogs. We call this search-encounter sampling



(from Royle et al., 2011). In the context of search–encounter surveys, such as that implemented in our box turtle project, we create a grid over the study area to define “effective traps.” In particular, let  $x_j$  represent the center point of the  $j$ th grid cell, and the encounter data are  $y_{ijk} = 1$  if individual  $i$  is encountered in grid cell  $j$  on sampling occasion  $k$ . Thus, the data structures for search–encounter data are analogous to that from camera trapping and related studies that produce individual–encounter history data, affording the ability to fit SCR models to these data.

**Ecological Process Model.**—Spatial capture–recapture models assume that a population of  $N$  individuals is sampled and that each individual has associated with it a spatial location that represents its activity center, or home range center, defined by its  $x$  and  $y$  coordinates as  $s_i = (s_{xi}, s_{yi})$ , about which its activities are concentrated. The important concept underlying SCR models is that the collection of activity centers  $s_1, \dots, s_N$  is regarded as a realization of a statistical point process (Efford, 2004; Illian et al., 2008), a class of probability models for characterizing the spatial pattern and distribution of points. To formalize the point process model it is necessary to describe the probability distribution function of the point locations. The simplest possible point process model, in common with classical distance sampling models, is to assume that each of the  $N$  individual activity center locations are distributed uniformly in space (the “uniformity assumption”):

$$s_i \sim \text{Uniform}(S), \quad (1)$$

where  $S$  is an explicit spatial region within which sampling takes place. The region  $S$  is referred to as the state-space of the point process and is an essential component of a probabilistic characterization of potential activity centers that represent individuals in the SCR framework. In practice, the state-space is chosen by buffering the area sampled such that individuals in the population near the edge of the buffer should have negligible probability of being captured in the surveyed area. For computational reasons related to likelihood evaluation (see Sutherland et al., 2019), the state-space is defined by a discrete mesh of points.

With SCR models, the goal is to estimate the population size of individuals ( $N$ ) within any region of the state-space  $S$ , or the density of individuals  $D$ , the number of individual activity centers per unit area of  $S$ . As implemented in the R package oSCR (Sutherland et al., 2019),  $D$  is an explicit parameter of the likelihood that arises under a Poisson point process model for the activity centers (see also Borchers and Efford, 2008) and  $N$  is estimated by multiplying the area of the state-space by the estimate of  $D$ .

**Observation Model.**—Formulation of the capture–recapture model in terms of an explicit model for the distribution of individuals in space (or their activity centers), leads naturally to two powerful extensions of classical capture–recapture that constitute the key elements of SCR. First, it allows us to describe the probability that an individual is encountered for each sample location  $x_j$  for  $j = 1, 2, \dots, J$ , conditional on its activity center. Thus, the encounter model is spatially explicit, unlike traditional capture–recapture. Second, by acknowledging the spatial structure of the sample locations, it is natural then to retain the spatial information in the encounter histories that then describe not only which individual is captured when, but also where that capture occurs. Thus, the encounter histories are three-dimensional structures, indexed by individual ( $i$ ), occasion ( $k$ ) and spatial location ( $j$ ), that is,  $y_{ijk}$ . A standard model, which we adopt here, assumes that the individual encounters are Bernoulli random

variables:

$$y_{ijk} \sim \text{Bernoulli}(p_{ijk}), \quad (2)$$

where  $p_{ijk}$  is the probability of encountering individual  $i$  in trap  $j$ , and occasion  $k$ . The encounter probability model depends on the distance between the trap location ( $x_j$ ) and the individual's activity center ( $s_i$ ). We used the half-normal encounter model in which

$$p_{ijk} = p_0 \times e^{-(1/2\sigma^2)d(x_j, s_i)^2}. \quad (3)$$

The parameter  $p_0$  is the baseline encounter probability, the probability of encountering an individual at its activity center, and it may be modeled to depend on covariates that vary by trap, occasion, or individual (e.g., sex). For example, in our analysis we have covariates “effort” and “day of survey” (we allowed for a quadratic response), and we evaluate whether those affect baseline detection probability using a logistic model:

$$\text{logit}(p_{0,j,k}) = \alpha_0 + \alpha_1 \text{Effort}_{j,k} + \alpha_2 \text{Day}_k + \alpha_3 \text{Day}_k^2.$$

In addition to baseline detection probability, the parameter  $\sigma$  describes the rate at which detection probability declines as a function of distance between the sample location ( $x_j$ ) and the individual's activity center ( $s_i$ ),  $d(x_j, s_i)$ . The parameters  $p_0$ ,  $\sigma$  can be modeled as a function of covariates, although we only consider covariates on  $p_0$  in our analysis of the box turtle data.

The GPS track data from each survey was processed to produce the necessary data for SCR models. We gridded the surveyed area into  $30 \times 30$  m cells and determined if a cell was sampled or not by whether a buffered search track intersected the grid cell. We buffered each track by 10 m, which is near the upper limit of detection distance from visual encounters (Fig. 2). The total amount of buffered search track area overlapping the grid cell during a survey occasion (i.e., summed over observers) was used as a search-effort covariate. The choices of buffer width and grid cell size are not critical, but should be chosen to enable a meaningful characterization of the distribution of search effort over the survey region. For human observers, our experience is that space within about 10 m of an observer is subject to some level of sampling effort (see Results). Therefore, we created a search-effort covariate for grid cells, say  $E_{j,k}$  for grid cell  $j$  and survey occasion  $k$ , by computing the total coverage of each track within each grid cell for all available search tracks. The grid cell search-effort coverage was summed over observers for each survey day. Thus, the effort covariate  $E_{j,k}$  is a numerical covariate between 0 (no observers' buffered tracks intersect the grid cell) and the number of observers for a given day, if the grid cell was fully covered by all observers' search tracks.

We used the R package oSCR (Sutherland et al., 2019) for model fitting and summarizing the output. We fit a set of SCR models including the null model with constant parameters and models in which baseline encounter rate varied by day of season (linear and quadratic effects were considered), or search effort per grid cell or both covariates. The six models were ranked by Akaike information criterion (AIC).

We used the output from oSCR to estimate the population size by scaling the density estimate by the area of the state-space. To do this, we must know that oSCR parameterizes density in terms of the expected number of individual activity centers “per state-space grid cell” (Sutherland et al., 2019). The state-space for fitting the SCR models in oSCR was defined by a grid of 2,390 points, constructed by taking every other point of

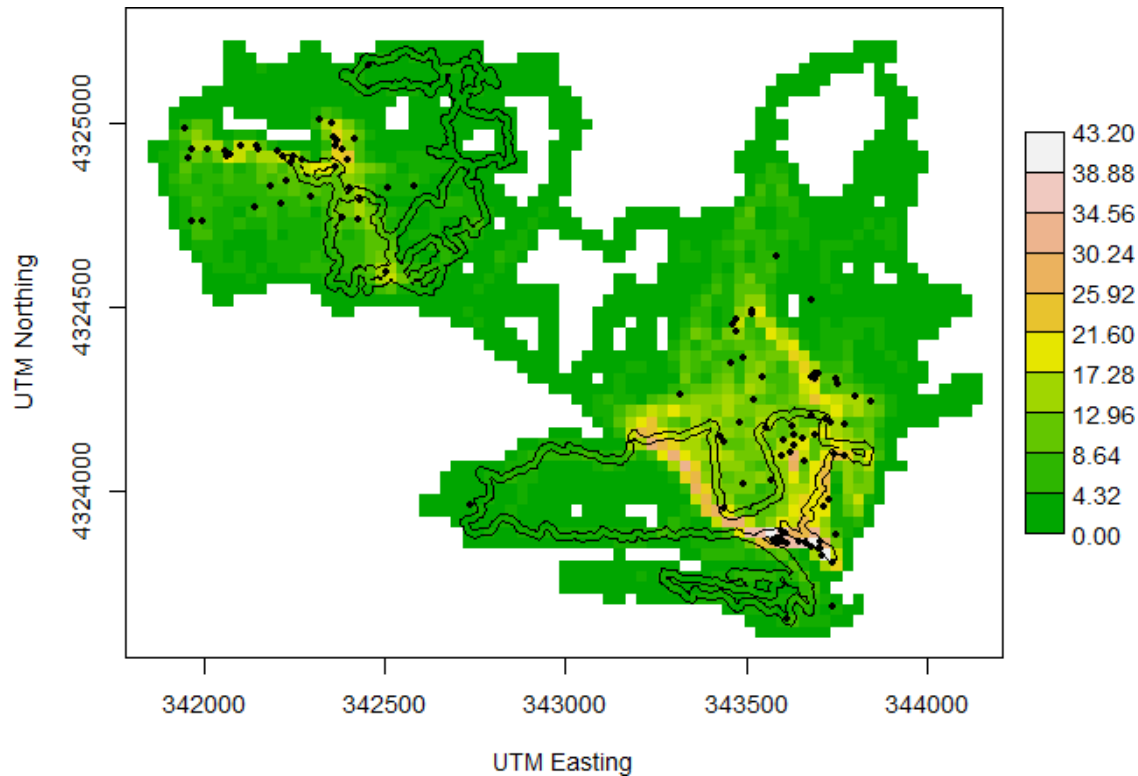


FIG. 2. Season total search effort. Numerical values are the total frequency of observer passes through the center of each grid cell during the 60 d of survey activity (1–4 surveyors each survey day). For example, a value of 40 would mean that a given grid cell was searched 40 times during the season. The buffered track lines, outlined in black, show the search path of one surveyor on Day 5 in the Stickel plot (northwest region) and Day 58 in the Snowden plot (southeast region). The black dots represent capture locations of box turtles over the season.

the  $30 \times 30$  m effort grid. A coarser grid improves the model run time and does not have material effect on the MLEs as long as the resolution of the state-space grid is finer than about one-fourth of an individual's home range area (Sutherland et al., 2019).

*Ordinary (Nonspatial) Capture–Recapture Analysis.*—Our data set is not well suited for ordinary capture–recapture models because of extreme spatial heterogeneity in sampling, as characterized by the spatial distribution of search effort per grid cell (see Results) which cannot be accounted for by ordinary capture–recapture models. Furthermore, it is not possible to assign a “sampled area” to the estimate of abundance produced by ordinary capture–recapture models because the landscape is not strictly closed. Nevertheless, we reduced our data set to a set of 73 ordinary encounter histories, a record of when each individual was captured during the 60 survey days. We accounted for temporal variation in sampling between the Snowden pond and historical Stickel sites because in most days only one or the other of those plots was surveyed. Therefore, the encounter history for a given individual was inferred to have a deterministic 0 on days in which the plot it belongs to was not surveyed. We considered fitting the standard suite of closed population capture–recapture models (Otis et al., 1978) to these data to compute the estimated population size for comparison to that of the SCR model.

## RESULTS

A total of 73 individual live turtles were captured 113 times over the span of 60 search days between 23 June 2020 and 15 October 2020. Most surveys occurred between 0800 h and 1300 h, and typically lasted 3–4 h, with between 1–4 surveyors

present. Out of these 60 search days, 34 surveys had 1 surveyor present, 17 had 2 surveyors present, 7 had 3 surveyors present, and 2 had 4 surveyors present. There was a cumulative total of 286.2 individual surveyor hours and 395.2 total miles covered during the 60-d search effort. The total effort per grid cell over the whole season is shown in Figure 2. The mean coverage of a grid cell was 4.51 passes (SD = 6.28), the maximum coverage was 43.2, and 2,687 out of 4,779 grid cells had no coverage (Fig. 2), highlighting the extreme heterogeneity in spatial search effort and hence the need for a spatially explicit estimation framework.

Of the 73 turtles captured, 50 were captured once, 14 were captured twice, 4 were captured on 3 occasions, 2 were captured on 4 occasions, and 3 were captured on 5 occasions. There is some indication that encounter probability varied over the season (Fig. 3). The average distance between observer and turtle encounter location was 4.27 m among 112 captures, with one capture lacking distance from observer data (Fig. 4).

The AIC ranking of SCR models (Table 1) indicates the top model includes both effects of effort and day (quadratic) on detection probability. The second-best model, by two AIC units, includes effort and only a linear day effect, and the third-best model includes effort only. The parameter estimates for all six models are shown in Table 2. For the baseline (intercepts) of each parameter, there were no large differences in parameter estimates among the six models, so we focus interpretation here on those from the top model, containing effects of both day and effort on detection probability. The model shows an estimated density of  $-1.521$  on the log scale, so back-transforming yields  $\exp(-1.521) = 0.2185$ . To interpret this, note that oSCR parameterizes density in terms of individuals “per state-space

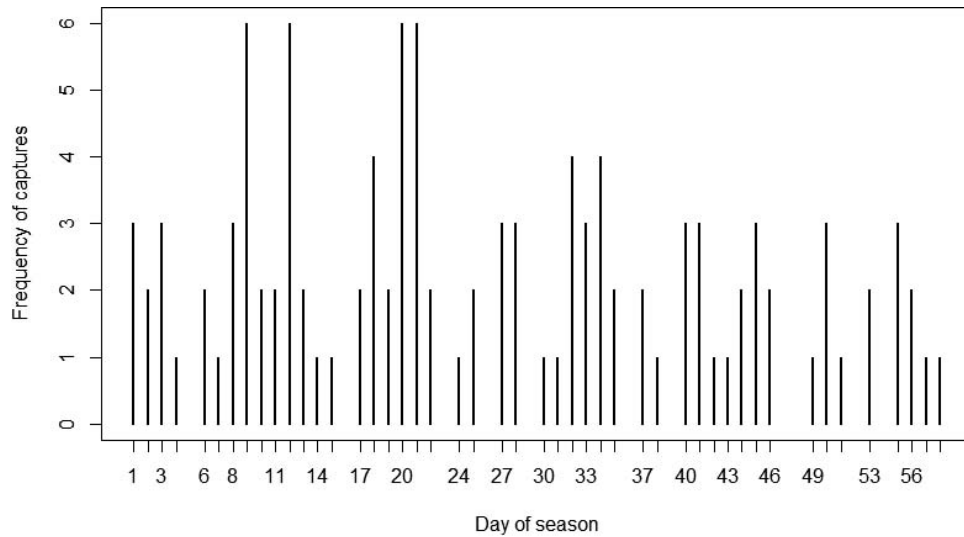


FIG. 3. Daily frequency of box turtle encounters over the 60-d search effort.

grid cell" (Sutherland et al., 2019). The state-space consisted of 2,390 (created by thinning the  $30 \times 30$  m sample grid by two) and therefore  $\exp(-1.521) = 0.2185$  turtles per  $1,800 \text{ m}^2$  or about 1.2139 turtles per hectare, or 0.552 turtles per acre. Applying this to the two delineated plots in Figure 1 results in population sizes of approximately  $0.552 \times 175 = 96.6$  (delta method SE = 15.3) and  $0.552 \times 230 = 127$  (SE = 20.1) individuals in Stickel and Snowden plots, respectively.

The top model indicates a highly significant positive effect of "effort," the more coverage a grid cell received by surveyor effort, the higher is the probability of encounter of a turtle in that grid cell. If we fail to account for spatial heterogeneity in this search-effort covariate (compare Model 1 to Model 4) we found that estimated density is reduced slightly ( $\exp[-1.521] = 0.2185$  vs.  $\exp[-1.578] = 0.2064$ ). Our observation is consistent with the effects of unmodeled heterogeneity in detection probability (Dorazio and Royle, 2003) although, in this instance, not modeling the search-effort heterogeneity only leads to a small downward shift in the estimated density. The estimated scale parameter from the SCR encounter probability model (i.e.,  $\sigma$  from Eq. 3) under the best model is  $\hat{\sigma} = \exp(4.148) = 63.3$  m (delta method SE = 5.74). Thus, the 95% home-range radius (Royle et al., 2014:p. 136), the radius from the home-range center

within which we expect 95% of an individual's locations to lie, is  $\sqrt{5.99} \times 63.3 = 155$  m.

We used the `get.real()` function in oSCR to estimate baseline encounter probability by setting the effort covariate to 1.0 (i.e., one individual observer passing through a grid cell), resulting in an estimate of  $\hat{p} = 0.004$  (SE = 0.00009). Baseline detection probability is the probability of detecting an individual when sampling precisely at the individual's activity center, which is not comparable to the "per sample occasion" encounter probability of ordinary capture-recapture models.

*Ordinary Capture-Recapture Model Estimates.*—We were able to fit the standard models M0 (constant  $p$ ) and Mh (heterogeneous  $p$ , described by a two-point finite mixture). Models Mt (time-specific  $p$ ) and Mb (behavioral response) were not identifiable. Model M0 produced a total population size estimate of the two survey areas of 78 (95% confidence interval [CI]: 72–84) and model Mh produced an estimate of 80 (78–81). These are vastly different from the estimate produced by the SCR model which is to be expected given the extreme heterogeneity in spatial sampling intensity over the study area which cannot be accounted for using ordinary CR models. In essence, we believe the standard closed population models are providing estimates of population size that represent the core surveyed area which is much smaller than the extent of the study area surveyed over the season. Although this explanation is not precise, we note that SCR and ordinary CR models are simply not comparable in the absence of strict design constraints.

## DISCUSSION

Capture-recapture models are widely used for estimating population size of terrestrial chelonian populations. However, classical capture-recapture methods such as those in widespread use do not acknowledge the spatial structure inherent in sampling animal populations. Individuals moving freely about their home range may not always be available for capture, and this can lead to difficulty interpreting estimates of  $N$  from closed population models and ambiguity in converting population size estimates to density estimates because effective sample area is usually not known precisely, because of movement of individuals in space and imprecise characterization of surveyor efforts. In addition, closed CR models do not account for spatial

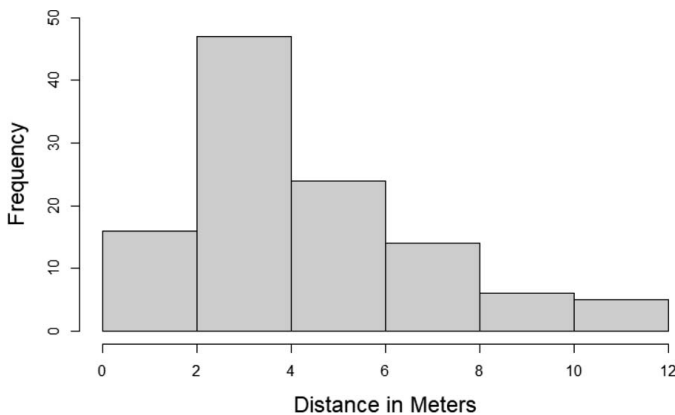


FIG. 4. The distribution of distances between observer and location of turtle upon capture.

TABLE 1. AIC table for the four SCR models fit to the box turtle data.

Model	logL	K	AIC	dAIC	Weight	CumWt
D(~1) p(~effort + day + day2) sig(~1)	724	6	1,460	0.0	7.2e-01	0.72
D(~1) p(~effort + day) sig(~1)	726	5	1,462	2.0	2.7e-01	0.99
D(~1) p(~effort) sig(~1)	730	4	1,467	7.8	1.5e-2	1.00
D(~1) p(~day+day2) sig(~1)	805	5	1,621	161.3	0	1.00
D(~1) p(~day) sig(~1)	807	4	1,621	161.5	0	1.00
D(~1) p(~1) sig(~1)	811	3	1,628	168.4	0	1.00

heterogeneity in sampling, because encounter probabilities are not spatially explicit. On the other hand, using SCR models, we can both account for spatial heterogeneity in sampling and also nonclosure of the population because of individual movements about their home range. SCR is an ideal analytic framework for studying terrestrial chelonian populations because this taxon is widely studied using visual search methods, and, using this method, there will necessarily be spatial heterogeneity in search effort, which can be accommodated explicitly using SCR models.

Motivated by the recent development of SCR methods, we applied SCR to a population of box turtles at Patuxent Research Refuge in Maryland that was first studied in the 1940s (Stickel, 1950). We used human observers to survey the landscape in an unstructured or haphazard manner, while recording their GPS search track during sampling. The GPS search tracks were used to compute an effort covariate related to the amount of coverage of each  $30 \times 30$  m grid cell. Conceptually, SCR regards surveyed grid cells in a manner analogous to classical catch traps, or camera traps, and models the probability of detection as a function of an individual's home range center and a given, searched grid cell.

The long-term nature of data collection on the Eastern Box Turtle population at PWRC presents a unique opportunity to contrast population demography of box turtles over a period of 75 yr (Stickel, 1978; Hall et al., 1999). Lucille Farrier Stickel initiated the first box turtle study on the plot in 1945, for a much smaller area (approximately 11.8 ha of searched area) than was surveyed by our effort. Hall et al. (1999) evaluated long-term trends in box turtles at the historical Stickel site using counts of detected individuals based on intensive searches over multiple days with multiple surveyors. Based on count indices, the population at PWRC has evidently been decreasing since the 1940s (Hall et al., 1999:Table 1), a trend that is supported by our results. We spent 286 h in the field and captured 73 unique turtles a total of 113 times. Our efficiency (turtles/hour = 0.26) is comparable to the 1985 and 1995 surveys reported by Hall et al. (1999), but dramatically lower than 1945–1975 surveys (maximum of  $291/172 = 1.69$  turtles/h in 1955, minimum  $117/75 = 1.56$  turtles/h in 1975). Because earlier surveys did not use SCR methods, and locations of sampling and detections are not available for the historical data, it is difficult to compare population density directly. However, using an informal

method based on dividing turtles caught two or more times in 1945 by the total acreage of the study site (a 42.6-acre area meant to include all turtle home ranges), Stickel estimated that there were between 4 and 5 adult turtles per acre, for a total population of 191.7 box turtles (Stickel, 1950). Although our results suggest a higher overall population, they represent the population for an area roughly 362 acres larger than Stickel's, thereby explaining our much lower density estimate of approximately 0.55 turtles per acre. Additionally, unlike Stickel, we used both juveniles and adults in our analyses. Though Hall et al. (1999) suggested the declines might be caused by changes in hydrology, the decline could be because of road mortality and habitat loss, as PWRC is surrounded by busy roads and increasingly developed landscape. Given the longevity of the species, the loss of even a few adults may result in negative population growth rates. Further studies are required to determine if box turtle population declines on the center are caused by one of these factors, or even some alternative such as disease. We aim to continue the current survey for a number of years in hopes of estimating both survival and recruitment probabilities for these populations, thus allowing for an explicit estimate of the population growth rate and an assessment of potential threats.

Spatial capture–recapture models provide an estimate of space use by individuals in the sampled population. Our estimate for the 95% home range radius of 155 m (see Results) is slightly larger than reported by Stickel (1950) who reported about 108 m (average of males and females) based on her ingenious device constructed by affixing a thread spool to the carapace of turtles. Stickel's estimate of 108 m was the average of the maximum distance moved among individuals over a variable period of time (10 turtles tracked for 1–44 d and 1 for 161 d). Because our estimate is based on movements of individuals over nearly a full season, the larger estimate might be expected.

We believe that SCR models show great promise for monitoring populations of terrestrial turtles and reptiles in general because SCR allow for a very flexible approach to spatial sampling in which observers or even sniffer dogs can wander around space haphazardly to detect specimens. Furthermore, not having to navigate to stay on transects or delineate quadrats to sample is a substantial time savings in the field and makes sampling accessible to lesser-trained individ-

TABLE 2. Coefficients (standard errors) for the four models fitted to the box turtle data.

Model	logD	logp0	logsig	Day	Day 2	Effort
D(~1) p(~effort + day + day2) sig(~1)	-1.521 (0.159)	-7.441 (0.278)	4.148 (0.091)	-0.097 (0.065)	-0.083 (0.048)	1.855 (0.138)
D(~1) p(~effort + day) sig(~1)	-1.516 (0.159)	-7.678 (0.257)	4.150 (0.091)	-0.084 (0.0595)	—	1.846 (0.138)
D(~1) p(~effort) sig(~1)	-1.524 (0.159)	-7.664 (0.256)	4.150 (0.091)	—	—	1.850 (0.136)
D(~1) p(~day+day2) sig(~1)	-1.58 (0.157)	-5.96 (0.237)	4.148 (0.089)	-0.178 (0.061)	-0.057 (0.039)	—
D(~1) p(~day) sig(~1)	-1.577 (0.157)	-6.121 (0.214)	4.126 (0.089)	-0.168 (0.057)	—	—
D(~1) p(~1) sig(~1)	-1.591 (0.159)	-6.101 (0.214)	4.128 (0.089)	—	—	—



uals, including volunteers of all skill levels. Spatial capture–recapture is more data intensive, however, because one must record locations of specimens as well as the GPS search track of the human or dog-team observer. In practice it might be the case that a search track is missing for a given observer and survey occasion. In fact, in our 2020 field study this occurred two times and those records were deleted from the data set (and not used in analyses here). The flexibility and extensibility of SCR is also advantageous for population studies of reptiles. The SCR model itself is also very flexible and can be extended to include many specific elements of spatial population ecology, for example, including explicit models of spatial variation in density (Borchers and Efford, 2008), resource selection to be integrated into SCR models (Royle et al., 2013), as well as notions of landscape connectivity (Fuller et al., 2016), and fully open models that allow for movement dynamics such as dispersal (Ergon and Gardner, 2014; Schaub and Royle, 2014).

**Acknowledgments.**—We gratefully acknowledge the help of the following contributors: S. Kimble for his survey and radio-tracking efforts and for his knowledge and advice; P. Henry for her dedication to the organization of the long-term collection on Eastern Box Turtle data at PWRC; L. Erb for reviewing a draft manuscript; S. Spencer for her administrative help and support; and S. Lilienthal, A. Royle, and W. Huang, who volunteered their time to conduct turtle surveys. This work was conducted under Patuxent’s Animal Care and Use Committee permit 2019-02. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

## LITERATURE CITED

- BORCHERS, D. L., AND M. G. EFFORD. 2008. Spatially explicit maximum likelihood methods for capture–recapture studies. *Biometrics* 64:377–385.
- BUHLMANN, K., T. TUBERVILLE, AND J. W. GIBBONS. 2008. *Turtles of the Southeast*. University of Georgia Press, USA.
- CHANDLER, R. B., J. A. ROYLE, AND D. I. KING. 2011. Inference about density and temporary emigration in unmarked populations. *Ecology* 92:1429–1435.
- CONVERSE, S. J., J. B. IVERSON, AND J. A. SAVIDGE. 2005. Demographics of an ornate box turtle population experiencing minimal human-induced disturbances. *Ecological Applications* 15:2171–2179.
- DAIGLE, C., AND J. JUTRAS. 2005. Quantitative evidence of decline in a southern Québec Wood Turtle (*Glyptemys insculpta*) population. *Journal of Herpetology* 39:130–132.
- DORAZIO, R. M., AND J. A. ROYLE. 2003. Mixture models for estimating the size of a closed population when capture rates vary among individuals. *Biometrics* 59:351–364.
- EFFORD, M. 2004. Density estimation in live-trapping studies. *Oikos* 106:598–610.
- ERB, L. 2012. Conservation plan for the Eastern Box Turtle in Massachusetts. Massachusetts Division of Fisheries and Wildlife, Natural Heritage and Endangered Species Program. <https://doi.org/10.13140/RG.2.1.4469.6404>.
- ERB, L. A., L. L. WILLEY, L. M. JOHNSON, J. E. HINES, AND R. P. COOK. 2015. Detecting long-term population trends for an elusive reptile species. *The Journal of Wildlife Management* 79:1062–1071.
- ERGON, T., AND B. GARDNER. 2014. Separating mortality and emigration: modelling space use, dispersal and survival with robust-design spatial capture–recapture data. *Methods in Ecology and Evolution* 5:1327–1336.
- FULLER, A. K., C. S. SUTHERLAND, J. A. ROYLE, AND M. P. HARE. 2016. Estimating population density and connectivity of American mink using spatial capture–recapture. *Ecological Applications* 26:1125–1135.
- HALL, R. J., P. F. P. HENRY, AND C. M. BUNCK. 1999. Fifty-year trends in a box turtle population in Maryland. *Biological Conservation* 88:165–172.
- HARMSSEN, B. J., R. J. FOSTER, AND H. QUIGLEY. 2020. Spatially explicit capture recapture density estimates: robustness, accuracy and precision in a long-term study of jaguars (*Panthera onca*). *PLoS One* 15:e0227468.
- ILLIAN, J., A. PENTTINEN, H. STOYAN, AND D. STOYAN. 2008. *Statistical Analysis and Modelling of Spatial Point Patterns*. Wiley, USA.
- KÉRY, M., B. GARDNER, T. STOECKLE, D. WEBER, AND J. A. ROYLE. 2011. Use of spatial capture–recapture modeling and DNA data to estimate densities of elusive animals. *Conservation Biology* 25:356–364.
- LANGTIMM, C. A., C. K. DODD, AND R. FRANZ. 1996. Estimates of abundance of Box Turtles (*Terrapene carolina bauri*) on a Florida Island. *Herpetologica* 52:496–504.
- LINDEN, D. W., A. K. FULLER, J. A. ROYLE, AND M. P. HARE. 2017. Examining the occupancy–density relationship for a low-density carnivore. *Journal of Applied Ecology* 54:2043–2052.
- LITZGUS, J. D., AND T. A. MOUSSEAU. 2004. Demography of a southern population of the Spotted Turtle (*Clemmys guttata*). *Southeastern Naturalist* 3:391–400.
- O’CONNOR, K., C. D. RITTENHOUSE, J. J. MILLSPAUGH, AND T. A. G. RITTENHOUSE. 2015. Demographics and density estimates of two three-toed box turtle (*Terrapene carolina triunguis*) populations within forest and restored prairie sites in central Missouri. *PeerJ* 3:e1256.
- OTIS, D. L., K. P. BURNHAM, G. C. WHITE, AND D. R. ANDERSON. 1978. Statistical inference from capture data on closed animal populations. *Wildlife Monographs* 62:3–135.
- PITTMAN, S. E., T. L. KING, S. FAURBY, AND M. E. DORCAS. 2011. Demographic and genetic status of an isolated population of bog turtles (*Glyptemys mühlenbergii*): implications for managing small populations of long-lived animals. *Conservation Genetics* 2:1589–160.
- RHODIN, A. G. J., C. B. STANFORD, P. P. VAN DIJK, C. EISEMBERG, L. LUISELLI, R. A. MITTERMEIER, R. HUDSON, B. D. HORNE, E. V. GOODE, G. KUCHLING, ET AL. 2018. Global conservation status of turtles and tortoises (Order Testudines). *Chelonian Conservation and Biology* 17:135–161.
- ROYLE, J. A., AND K. V. YOUNG. 2008. A hierarchical model for spatial capture–recapture data. *Ecology* 89:2281–2289.
- ROYLE, J. A., A. J. MAGOUN, B. GARDNER, P. VALKENBURG, AND R. E. LOWELL. 2011. Density estimation in a wolverine population using spatial capture–recapture models. *The Journal of Wildlife Management* 75:604–611.
- ROYLE, J. A., R. B. CHANDLER, C. C. SUN, AND A. K. FULLER. 2013. Integrating resource selection information with spatial capture–recapture. *Methods in Ecology & Evolution* 4:520–530.
- ROYLE, J. A., R. B. CHANDLER, R. SOLLMANN, AND B. GARDNER. 2014. *Spatial Capture–Recapture*. Academic Press, USA.
- ROYLE, J. A., A. K. FULLER, AND C. SUTHERLAND. 2018. Unifying population and landscape ecology with spatial capture–recapture. *Ecography* 41:444–456.
- SCHAUB, M., AND J. A. ROYLE. 2014. Estimating true instead of apparent survival using spatial Cormack–Jolly–Seber models. *Methods in Ecology and Evolution* 5:1316–1326.
- SCHMIDT, B. R., A. MEIER, C. SUTHERLAND, AND J. A. ROYLE. 2017. Spatial capture–recapture analysis of artificial cover board survey data reveals small scale spatial variation in slow-worm *Anguis fragilis* density. *Royal Society Open Science* 4:1–8.
- SHEPARD, D. B., A. R. KUHN, M. J. DRESLIK, AND C. A. PHILLIPS. 2008. Roads as barriers to animal movement in fragmented landscapes. *Animal Conservation* 11:288–296.
- SOLLMANN, R., M. M. FURTADO, B. GARDNER, H. HOFER, A. T. A. JÁCOMO, N. M. TÔRRES, AND L. SILVEIRA. 2011. Improving density estimates for elusive carnivores: accounting for sex-specific detection and movements using spatial capture–recapture models for jaguars in central Brazil. *Biological Conservation* 144:1017–1024.
- SOLLMANN, R., B. GARDNER, AND J. L. BELANT. 2012. How does spatial study design influence density estimates from spatial capture–recapture models? *PLoS One* 7:e34575.
- STICKEL, L. F. 1950. Populations and home range relationships of the box turtle, *Terrapene c. carolina* (Linnaeus). *Ecological Monographs* 20:351–378.
- STICKEL, L. F. 1978. Changes in a Box Turtle population during three decades. *Copeia* 1978:221–225.
- SUTHERLAND, C., D. J. MUÑOZ, D. A. MILLER, AND E. H. C. GRANT. 2016. Spatial capture–recapture: a promising method for analyzing data collected using artificial cover objects. *Herpetologica* 72:6–12.

- SUTHERLAND, C., J. A. ROYLE, AND D. W. LINDEN. 2019. oSCR: a spatial capture–recapture R package for inference about spatial ecological processes. *Ecography* 42:1459–1469.
- TUBERVILLE, T. D., B. D. TODD, S. M. HERMANN, W. K. MICHENER, AND C. GUYER. 2014. Survival, demography, and growth of Gopher Tortoises (*Gopherus polyphemus*) from three study sites with different management histories. *The Journal of Wildlife Management* 78:1151–1160.
- TURTLE CONSERVATION FUND. 2002. A global action plan for conservation of tortoises and freshwater turtles. Strategy and Funding Prospectus 2002–2007. Conservation International and Chelonian Research Foundation, Washington, DC.
- VERDON, E., AND M. A. DONNELLY. 2005. Population structure of Florida Box Turtles (*Terrapene carolina bauri*) at the southernmost limit of their range. *Journal of Herpetology* 39:572–577.
- ZYLSTRA, E. R., R. J. STEIDL, AND D. E. SWANN. 2010. Evaluating survey methods for monitoring a rare vertebrate, the Sonoran desert tortoise. *The Journal of Wildlife Management* 74:1311–1318.

Accepted: 6 January 2022.

Published online: 26 September 2022.