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METHODS, TOOLS, AND TECHNOLOGIES

Integrating telemetry data at several scales with spatial capture–recapture to improve density estimates

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Abstract. Accurate population estimates are essential for monitoring and managing wildlife populations. Mark–recapture sampling methods have regularly been used to estimate population parameters for rare and cryptic species, including the federally listed Mojave desert tortoise (*Gopherus agassizii*); however, the methods employed are often plagued by violations of statistical assumptions, which have the potential to bias density estimates. By incorporating spatial information into conventional density estimation models, spatial capture–recapture (SCR) models can account for common assumption violations such as spatially heterogeneous detection probabilities and temporary emigration when animals leave plots during a survey. We conducted mark–recapture surveys at 10 1-km^2 plots in and adjacent to the Ivanpah Valley of California and Nevada from 2015 to 2019. Locality data were collected concurrently using radio-telemetry and GPS data loggers. GPS data demonstrated that desert tortoises frequently exhibited temporary emigration outside a plot during the survey periods, thereby complicating standard approaches for closed-model density estimation. We integrated mark–recapture survey data for subadults and adults at each plot with corresponding spatial capture locations and supplementary spatial data using a modified SCR model fitted in a Bayesian framework. We compared density estimates modeled with conventional non-spatial methods, as well as three SCR models based on symmetrical usage areas described by various levels and types of supplementary spatial data. The conventional model consistently resulted in inflated estimates of density while the SCR models allowed us to generate spatially corrected estimates for a species where detectability and densities are low. However, we found that if not properly specified, the temporal scale of supplementary data may result in an unintended source of bias in parameter estimates. Integrating spatial data over a larger temporal scale than mark–recapture surveys were conducted resulted in higher detection probabilities and lower density estimates, due to an overestimation of space use. Our results not only demonstrate the importance of accounting for spatial information but also the value of understanding the potential for bias when integrating multiple data sets at different temporal resolutions. The methods presented can be used to enhance monitoring efforts for the Mojave desert tortoise and other species where mark–recapture methods are used.

Key words: Bayesian; density estimation; *Gopherus agassizii*; GPS data loggers; mark–recapture surveys; Mojave desert tortoise; radio-telemetry; spatial capture–recapture.

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Introduction

Fundamental information for the conservation and management of wildlife populations includes reliable estimates of population density. Closed-population mark–recapture models are commonly used for population estimation and have long been an important wildlife management tool (Otis et al. 1978, Nichols 2014, Berry and Murphy 2019). These widely used methods rely on assumptions of population closure including geographically and demographically closed populations with no recruitment or losses, as well as assumptions about detection including homogeneous capture probability and retention and recognition of unique identification marks (Otis et al. 1978, Pollock et al. 1990, Pollock 2000). However, standard assumptions of mark–recapture models are often violated in practice (Begon 1983, Pollock 2000, Kendall and Bjorkland 2001). For instance, population density estimates are often derived from survey plots that are permeable to movement, thereby violating the geographic closure assumption and complicating standard approaches (Kendall and Bjorkland 2001, Royle and Young 2008). Plot-based density estimates also typically suffer from edge effects, where individuals occupying plot peripheries are less exposed to sampling than those in the center, resulting in spatial heterogeneity in detection probability (Efford 2004, Royle and Young 2008, Royle et al. 2018). Furthermore, the effective sampled area for plot-based density estimation is essentially unknown because neither the space use of individuals, nor the spatial dependency of capture probabilities, is explicitly acknowledged in conventional mark–recapture methods. These omissions result in an estimate of abundance over an undefined area and therefore cannot be used to reliably estimate population density (White et al. 1982, Anderson et al. 1983, Borchers and Efford 2008). Together, these violations can bias density estimates, potentially compromising critical management decisions (Freilich et al. 2000).

Spatial capture–recapture (SCR) methods have quickly gained popularity due to their ability to relax many of the standard capture–recapture assumptions and produce unbiased density estimates (Efford 2004, Royle and Young 2008, Efford and Fewster 2013, Royle et al. 2014). Relative to conventional capture–recapture models, basic SCR models require only one additional component: encounter locations, which are generally recorded as a part of mark–recapture surveys. SCR models are composed of an explicit individual-based spatial process model and an observation model that is conditional on the spatial process (Royle and Young 2008, Royle et al. 2014). Most SCR models assume that each individual in the population has a fixed activity center and that space use intensity drops off with distance from the activity center according to a spatial scale parameter (Efford 2004, Royle et al. 2018). The observation process then becomes conditional upon the spatial process such that individual detections are most likely where sampling effort (e.g., trap locations, survey plots, hair snares) coincides with high-intensity space use. Clearly, the additional complexity of SCR methods (relative to non-spatial capture–recapture models) can only be justified in cases where the space use of study animals can be usefully approximated on the basis of available data. By integrating additional individual locality data beyond the locations recorded during mark–recapture surveys (i.e., data from radio-telemetry or GPS loggers) to inform the spatial process model, further improvement of demographic parameter estimates (e.g., density, survival) and inferences regarding space use may be possible (Royle et al. 2013, Tenan et al. 2017, Linden et al. 2018, Paterson et al. 2019).

The Mojave desert tortoise (*Gopherus agassizii*) is a long-lived semi-fossorial species occurring in the Mojave Desert and western portion of the Sonoran Desert in the Southwestern United States. This species was listed as threatened under the U.S. Endangered Species Act in 1990 due to reports of declining populations (USFWS 1990). Desert tortoises spend the majority of their lives underground in excavated burrows, caliche caves, or other shelter sites (Nagy and Medica 1986, Bulova 1994, Nussear and Tracy 2007), and

this life-history trait often results in low and variable detection rates for this species (Anderson et al. 2001, Nussear et al. 2008). Regular and accurate population estimates are essential for monitoring the recovery of the species, and plot-based sampling has been a key component of monitoring efforts for the desert tortoise (USFWS 2011). Historically, conventional mark–recapture methods have been used to monitor density at permanent study plots based on 60-d search-encounter surveys consisting of a 30-d marking phase followed by a 30-d recapture phase, with 2.6-km^2 (1-mile^2) plots being covered by 1–2 persons over those time periods (Berry and Nicholson 1984, Berry 1986*a*). Tortoise activity is highly seasonal (Zimmerman et al. 1994, Nussear and Tracy 2007), driven by climate and resource availability, and changes widely over a 60-d window (Duda et al. 1999, Inman et al. 2009). Along with their cryptic nature, differences in detectability among size classes, and low and variable detection rates, desert tortoise populations are difficult to accurately quantify, and standard survey methods often violate closure and detection assumptions (Freilich et al. 2005, Nussear and Tracy 2007, Inman et al. 2009). Violations of assumptions of conventional methods, especially the presence of heterogeneity in detection probability and temporary emigration, have long been known to induce bias in density estimates (Otis et al. 1978) and were one of the main motivators behind the development of SCR models (Efford 2004, Royle et al. 2018). Adding additional layers of realism such as data on space use and movement should allow us to continue to refine estimates of density and other demographic parameters for the desert tortoise.

Our objective was to improve current methods for estimating density from plot-based surveys for desert tortoises by incorporating space use with mark–recapture survey data. We used desert tortoise mark–recapture data collected from 2015 to 2019 and supplementary locality data collected simultaneously with very high frequency (VHF) radio-telemetry and GPS data loggers at 10 1-km^2 study plots in and adjacent to the Ivanpah Valley of California and Nevada in the eastern Mojave Desert. We developed multiple candidate models of increasing complexity and data requirements to combine standard mark–recapture histories with corresponding spatial capture locations and, in some cases, additional spatial data (i.e., from radio-telemetry or GPS loggers) to describe space use and movement of individuals using a modified SCR model fitted in a Bayesian framework. Candidate models were compared using information-theoretic criteria. By incorporating spatial data, this research aims to reduce bias due to common assumption violations of conventional methods and provide accurate density estimates for the desert tortoise. These results have the potential to enhance the efficacy of long-term efforts to monitor population trends and inform recovery efforts for this and other species monitored with plot-based mark–recapture sampling.

Methods

Study area

In 2015, we established 10 1-km^2 long-term study plots in and adjacent to the Ivanpah Valley in the eastern Mojave Desert based on landform, connectivity, and potential influences of recently constructed solar facilities (Fig. 1). The Ivanpah Valley straddles the California–Nevada border and is located approximately 50 miles southwest of Las Vegas, Nevada, USA. The study plots and most of the surrounding area are managed by the U.S. Bureau of Land Management. Habitat characteristics and topography at the plots vary from creosote bush (*Larrea tridentata*) and white bursage (*Ambrosia dumosa*) as dominant shrubs in valley bottoms and lower alluvial fans to rocky mountain passes characterized by Mojave mid-elevation mixed desert scrub (Brown et al. 1979, Schulz et al. 2015). Since 2009, an increased commitment to reliance on renewable energy by multiple states in the southwestern United States has led to an increase in the number of utility scale renewable energy projects in the Ivanpah Valley, resulting in desert tortoise habitat loss and degradation (Lovich and Ennen 2011, USFWS 2011). Recent studies have identified the Ivanpah Valley as an area of high habitat suitability, a hotspot of genetic diversity, and important for range-wide connectivity for the desert tortoise (Nussear et al. 2009, Hagerty et al. 2011, Vandergast et al. 2013, Dutcher et al. 2020). Therefore, understanding and monitoring desert tortoise populations in this region is of great importance for informing recovery efforts.

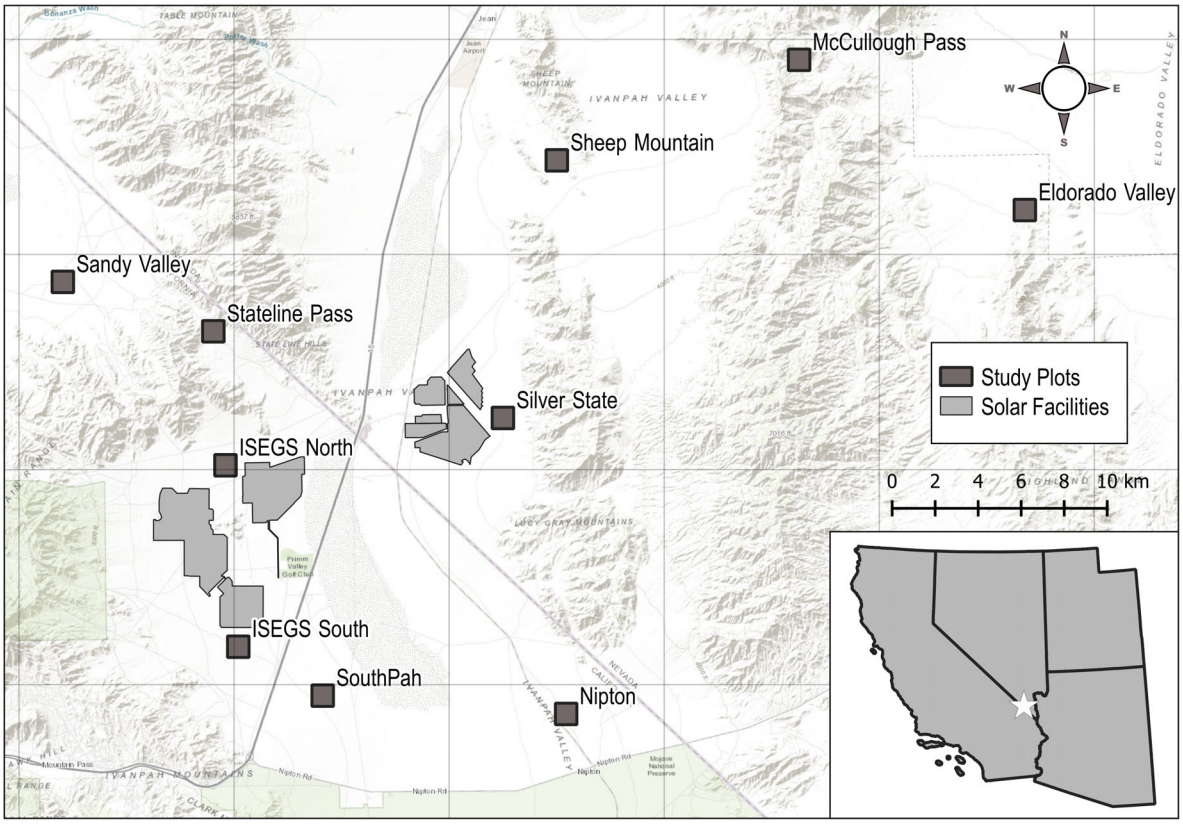

Fig. 1. Location of the 10 study plots in the Ivanpah Valley of California and Nevada, USA.

Mark–recapture surveys

We conducted closed-population mark–recapture surveys at the 10 study plots from 2015 to 2019. Sampling occurred at 3–4 of the 10 study plots in any given year resulting in each group of plots being surveyed every three years (Table 1). Each survey was conducted using a full coverage three-pass capture–recapture design where 20 experienced desert tortoise surveyors completed one full coverage pass of a plot each day over a three-day period. Surveyors divided into five crews of four people and alternated transects in a perpendicular direction (north–south, east–west) with crews changing search areas and covering new ground each day to alleviate surveyor bias due to previous knowledge of tortoise captures in a given area. Where physically possible, transects were spaced at 5-m intervals with each surveyor responsible for 2.5 m on either side of each 1-km transect; however, very rugged terrain comprises the McCullough Pass plot, and transects were spaced at 10-m intervals in order to complete the survey within the specified time period. In total, we conducted two complete surveys at six of the study plots and one full survey at each of the remaining four study plots.

All tortoises encountered during surveys were tagged with a unique identifier glued to a rear costal scute and given an inconspicuous temporary color mark to differentiate capture during the three sampling occasions so that we could score within-survey captures with minimal handling. Data collected for each capture included tortoise identification number, date and time of capture, spatial capture location (easting and northing, UTM NAD83 11 N), and demographic information including size in midline carapace length (MCL) and sex (male, female, or unknown).

Supplementary spatial data

Collection of desert tortoise locality data occurred concurrently during surveys and interim survey periods with the use of VHF

Table 1. Study plot names and survey dates.

Survey number	Plot name	Year surveyed	Survey dates
(1)	Eldorado Valley	2017	29 September–1 October
(2)	ISEGS North	2016	6–8 October
(3)	ISEGS North	2019	5–7 October
(4)	ISEGS South	2017	9–11 October
(5)	McCullough Pass	2015	15–17 October
(6)	McCullough Pass	2018	29 September–1 October
(7)	Nipton	2017	2–4 October
(8)	Sheep Mountain	2015	12–14 October
(9)	Sheep Mountain	2018	6–8 October
(10)	Stateline Pass	2016	9–11 October
(11)	Stateline Pass	2019	28–30 September
(12)	SouthPah	2017	6–8 October
(13)	Silver State	2015	18–20 October
(14)	Silver State	2018	3–5 October
(15)	Sandy Valley	2016	3–5 October
(16)	Sandy Valley	2019	2–4 October

Note: For any three-day survey at a plot, a unique survey number is designated.

radio-transmitters (Holohil Systems Ltd., Carp, Ontario, Canada RI-2B 15 g) and GPS data loggers (i-gotU GT-120; GPS error <10 m: Morris and Conner 2017) attached to the carapace of animals large enough to hold the equipment, generally greater than 160 and 180 mm MCL for VHF radio-transmitters and GPS data loggers, respectively. Tortoises were tracked on a monthly basis using VHF radio-telemetry, while GPS data loggers recorded positions hourly and were replaced with freshly charged units during monthly radio-tracking visits.

To reduce the effects of spatial and temporal bias inherent in movement data (Legendre 1993, Boyce et al. 2010), we eliminated telemetry locations collected between November and February from the data set. This coincides with a period of low to no activity when desert tortoises seek hibernacula to avoid cold temperatures and locations recorded are typically consistent throughout the winter (Bulova 1994, Nussear et al. 2007). Similarly, we reduced locality data from GPS loggers to data collected between mid-September and mid-October for each year used to inform model parameters. This time period coincides with the peak fall active season for the desert tortoise and data were reduced for consistency with survey conditions. GPS logger data were further subsampled to keep only locations recorded during what would be the length of a typical survey day, between 07:00 and 17:00 hours Pacific Standard Time.

Spatial capture–recapture

Model considerations and data formatting.—We estimated subadult and adult population density (tortoises larger than ≥160 mm MCL) separately for each closed three-day mark-recapture survey (hereafter, "survey"), including surveys conducted at the same study plot in different years; recaptures from prior-year surveys were considered to be new captures for our analyses. Due to lower encounter rates, juvenile desert tortoises (<160 mm MCL) were not considered in this study and not included in our models. To account for temporary emigration and plot-based edge effects, we designated extended "study areas" for each 1-km^2 plot (S; the area over which we infer population density for each survey plot) by adding an 800-m buffer around each plot (Fig. 2). The 800-m buffer width was determined to fully encompass an average home range radius for individuals in our study population. We verified that density estimates were not sensitive to buffer sizes above 800 m by running models with buffer sizes of 400, 800, and 1200 m.

We fitted models using data augmentation (Royle et al. 2007, Royle and Dorazio 2008), where the number of additional rows added to capture histories (possibly real, yet undetected individuals) was designated to enforce a maximum population density of 100 tortoises/km^2. Our designated maximum density is higher than the highest densities of adults historically recorded in the Ivanpah Valley (historical estimates represent all age classes: 86–106 km^{-2}, Berry 1978; 57–90 km^{-2}, Turner et al. 1982; 72–85 km^{-2}, Berry and Nicholson 1984). In this way, we were able to set a uniform prior distribution on population density N with a minimum of n_s/6.76 and a maximum of 100 individuals/km^2, where n_s represents the total number of individuals captured during a survey and 6.76 km^2 is the area of the extended study area S.

Sex-specific differences in home range size are well documented for the desert tortoise with males having significantly larger home ranges than females (Berry 1986*b*, O'Connor et al. 1994, Duda et al. 1999, Franks et al. 2011). This was incorporated by modeling the spatial scale parameter σ as sex-dependent. Additionally, in

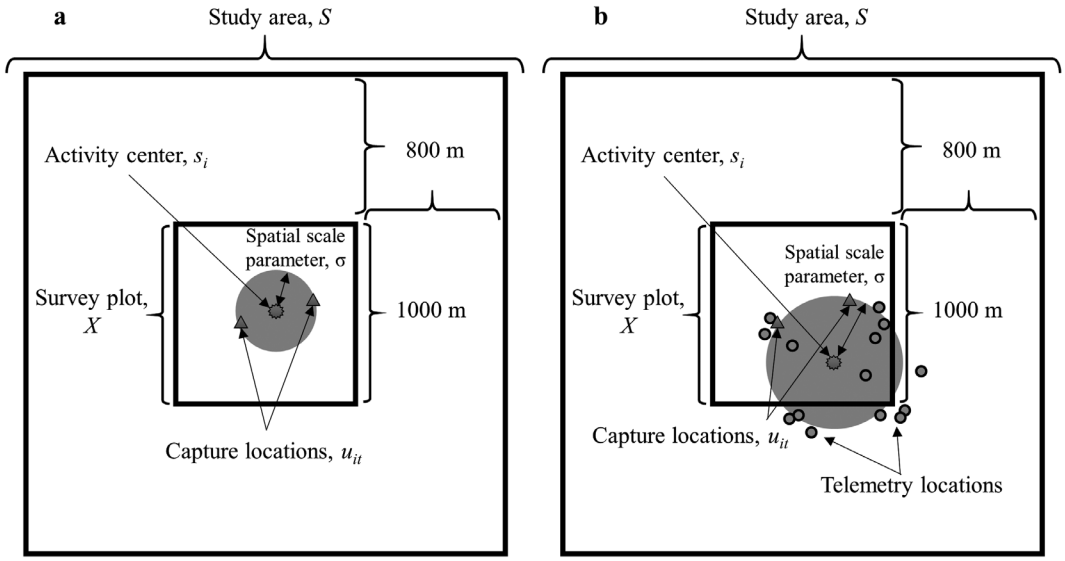

Fig. 2. Schematic representation of the extended study area, *S*, and relevant model parameters for (a) Model 2: Base SCR and (b) Model 3: SCR Three-day Locations and Model 4: SCR Complete Telemetry. For Model 3 and 4, corresponding activity areas will be at different scales due to the differences in the temporal scale of supplementary data. SCR, spatial capture–recapture.

many species one sex is more detectable (Nussear et al. 2008) and this was incorporated by modeling the baseline probability of detection p as a function of sex. We used Bayesian multiple interpolation to infer the sex of augmented individuals and individuals of unknown sex on the basis of empirical sex ratios for each survey. In order to account for differences in detectability among individuals, we also tested models with an individual-level random effect on capture probability.

Model variations and specification.—We built four model variations of increasing complexity with the intent to build in as much reality as possible by incrementally increasing the amount and type of information used to inform tortoise space use and movement (Table 2). The first model variation (Conventional Non-spatial) is a Bayesian closed-population model that does not explicitly account for spatial or movement processes. The second model (Base SCR) is a Bayesian SCR implementation that integrates spatial capture locations along with standard capture histories. The third model (SCR Three-day Locations) integrates hourly GPS logger and any VHF radio-telemetry data collected during the three-day surveys for each plot in addition to spatial capture locations. The fourth model (SCR Complete Telemetry) integrates on average four years of subsampled monthly VHF radio-telemetry data per individual (ranging from 2011 to 2019, depending on the study plot) in addition to spatial capture locations.

1. Model 1: Conventional Non-spatial.—In this model, the probability of detection p is estimated separately by sex and survey based on the proportion of occasions that each marked individual is detected. Space is not explicitly accounted for in this model, and therefore, the extent of the modeled area is equivalent to the survey area, X. Density, D, is then derived from the estimate of N divided by the area of X:

$$D = \frac{N}{A_X}$$

As an additional extension (Model 1b), we modeled variation in probability of detection among individuals as a logit-normal random effect with mean zero and an estimated variance term.

Model 2: Base SCR.—

1. Spatial process model.—In this model, each individual i in the population has an activity center, $s_i = (s_{xi}, s_{yi})$, located in two-dimensional space

Table 2. Model variations and descriptions.

Model	Description/data	Detection probability p	Male effect p	Spatial scale parameter σ	Male effect σ
(1) Conventional Non-spatial	Non-spatial capture histories	(a) By survey	Yes	N/A	N/A
		(b) By individual	Yes	N/A	N/A
(2) Base SCR	Spatial capture histories	(a) By survey	Yes	Survey-invariant	Yes
		(b) By individual	Yes	Survey-invariant	Yes
(3) SCR Three-day Locations	Spatial capture histories and GPS/telemetry data over the three-day survey	(a) By survey	Yes	By survey	Yes
		(b) By individual	Yes	By survey	Yes
(4) SCR Complete Telemetry	Spatial capture histories and all telemetry data representing full home ranges	(a) By survey	Yes	By survey	Yes
		(b) By individual	Yes	By survey	Yes

Note: SCR, spatial capture–recapture.

(with dimensions represented by x and y) and an activity use area represented by a Gaussian kernel with spatial scale parameter σ. Thus, the location for individual i (observed or unobserved) during sampling occasion t is:

$$u_{xit}|s_{xi} \sim \text{Normal}(s_{xi}, \sigma^2)$$

$$u_{yit}|s_{yi} \sim \text{Normal}(s_{yi}, \sigma^2)$$

where u_{xit} and u_{yit} represent the x- and y-coordinates, respectively, for spatial location u of individual i during sampling occasion t, s_{xi} and s_{yi} represent the x- and y-coordinates of activity center s for individual i, and σ is the spatial scale parameter. In the Base SCR model, spatial parameters are estimated solely based on the spatial capture locations during the three capture occasions in a single survey (Fig. 2a). We estimated σ separately for each sex but assumed that the baseline spatial scale parameter σ_0 was survey-invariant (small sample size prevented us from being able to estimate separate spatial scale parameters for each three-day survey). This model assumes that some captured individuals will have activity centers s_i outside of the surveyed area X, that individuals captured at capture occasion t may be located outside the survey area at occasion $t \pm 1$, and that some individuals within the extended study area S may be located outside the survey area X on all three capture occasions.

2. *Observation model.*—The observation model describes how the observed data are obtained conditional on the spatial process model. For individuals occurring within the survey area X (contained within the greater study area S) during sampling occasion t (i.e., the individual was available for capture), individual i is detected with probability of detection p, and for individuals occurring outside the survey area X, the model assumes that individual i is not available for capture for that occasion and $p = 0$:

$$p^* = \begin{cases} p_{it} & \text{Inside survey area } X \\ 0 & \text{Outside survey area } X \end{cases}$$

where p^* is the realized probability of detection. Mean probability of detection p_0 was estimated based on the proportion of occasions that each individual was captured on the plot and determined to be located within the surveyed area during missing captures. Probability of detection for each individual and plot was modeled as survey- and sex-dependent. Finally, capture histories were modeled as a set of Bernoulli outcomes:

$$y_{it}|u_{it}, z_i \sim \text{Bernoulli}(z_i \times p(u_{it}))$$

where y_{it} is the observed capture history for individual i during sampling occasion t at location u_{it}, conditional on whether it is determined to be a member of the population based on the zero-inflated model:

$$z_i \sim \text{Bernoulli}(\psi)$$

where z_i is the result of a set of Bernoulli outcomes based on Ψ, the inclusion probability, evaluating whether pseudo-individual i is a member of the population, N, and located within the extended study area S. The derived population estimate, N, is then the sum of z_i across all i. Density, D, is then computed as:

$$D = \frac{N}{A_S}$$

where A_S is the full area of the extended study area S. In addition, this model includes an extension of the observation model (Model 2b) by modeling individual heterogeneity in probability of detection using the same methods as described in Model 1b above.

Model 3: SCR Three-day Locations.—Specification of the SCR Three-day Locations observation model is equivalent to the Base SCR model; however, the spatial process model for this variation also integrates supplementary spatial data collected concurrently during the three-day surveys for each plot with the use of VHF radiotelemetry and GPS data loggers (Fig. 2b). In some occasions, supplementary data were not collected on the first or second day of a survey due to individuals being unknown prior to capture or GPS logger failure, and we substituted data collected on subsequent days when available. Additionally, we leveraged all available data collected at each plot during the three-day survey period by including location data for additional tortoises not in the capture histories (i.e., animals never captured during systematic mark-recapture surveys) to inform model parameters. These supplementary locations provided considerably more information on how tortoises use space at each plot (i.e., for estimating parameters s_i and σ), and for this model variation, we were able to model the baseline spatial scale parameter σ_0 as a function of survey as well as a function of sex. In addition, this model includes an extension of the observation model (Model 3b) by modeling individual heterogeneity in probability of detection using the same methods as described in Model 1b above.

Model 4: SCR Complete Telemetry.—Specification of the SCR Complete Telemetry observation model is equivalent to the SCR Three-day Locations model; however, the spatial process model for this variation integrates all available supplementary independent spatial data (after subsampling to reduce autocorrelation, see "*Supplementary spatial data*" above) collected on a monthly basis with the use of VHF radiotelemetry (Fig. 2b). As in the previous model, both supplementary data and spatial capture locations were used to inform model parameters s_i and σ and, depending on the duration and resolution of the integrated locations, are assumed to be biologically equivalent to the center and general size of individual i's home range. With the additional telemetry locations, we had sufficient data to model the baseline spatial scale parameter σ_0 as a function of survey as well as a function of sex. In addition, this model includes an extension of the observation model (Model 4b) by modeling individual heterogeneity in probability of detection using the same methods as described in Model 1b above.

Priors.—For all models, the sex effect on probability of detection was assigned an uninformative Uniform(−3, 3) prior on the logit-scale, and the sex effect on the baseline spatial scale parameter σ_0 was assigned a Normal(0, 0.1) prior on the log-scale. Activity center locations s_i were assigned a uniform prior over the study area S, and we assigned the baseline spatial scale parameter σ_0 a Uniform(0, 500) prior in meters. The inclusion parameter Ψ was assigned a Uniform(0, 1) prior. For models that include a variance term (1b, 2b, 3b, and 4b), we assigned an inverse Gamma(0.1, 0.1) prior.

Implementation.—All models were fitted in a Bayesian framework using Markov chain Monte Carlo (MCMC) routines implemented in the JAGS software, which was called from R using the "runjags" package (Denwood 2016, Plummer 2017, R Core Team 2020). See Appendix S1 for the original JAGS code for each model. We ran three independent parallel chains for 5000 iterations each, with a "burn-in" of 30,000 iterations that were discarded. Posterior summaries (posterior medians and Bayesian credible intervals) were computed from the remaining 15,000 MCMC samples. Credible intervals represent 90% highest posterior density (HPD) intervals.

Model convergence and performance.—Model convergence was inspected by visually examining trace and density plots and calculating the Gelman-Rubin diagnostic for each parameter (with values <1.1 indicating convergence on the posterior; Brooks and Gelman 1998, Gelman et al. 2013). We assessed model performance with the use of the widely applicable information criterion (WAIC), which was estimated in R using the "loo" package (Watanabe 2010, Gelman et al. 2014, Vehtari et al. 2020).

Results

Mark–recapture surveys

A total of 143 subadult and adult desert tortoises were captured during surveys at the 10 study plots from 2015 to 2019. Specific breakdowns by survey (1–16) are provided in Table 3 and corresponding capture histories are included in Appendix S2: Table S1. Total captures of unique individuals over a three-day survey period ranged from two adults encountered during Survey 13 (Silver State in 2015) to 26 adults during Survey 6 (McCullough Pass in 2018). Recaptures between subsequent primary surveys (every three years) at the same plot were low, with 24 individuals recaptured (25.26%; $n = 95$) among the six plots with two completed surveys (see Table 3). Sex distribution varied by plot and survey year, but overall, males were captured more frequently (51.7%) than females (39.9%). In total, there were 74 males, 57 females, and 12 tortoises of unknown sex captured. Tortoises of unknown sex were generally <200 mm MCL.

Supplementary spatial data

The number of individuals with supplementary location data differed based on model variation. Plot-specific information on individuals with telemetry and GPS data is provided in Table 3 with more detailed information provided in Appendix S2: Table S1. For the Three-day model, 119 (83.2%, $n = 143$) tortoises in the capture histories plus 34 auxiliary animals had locations collected with VHF radio-telemetry and/or GPS data loggers during corresponding survey periods resulting in 5955 total locations used to inform model parameters. Parameters from the Complete Telemetry model were informed based on data from 133 individuals (93.0%) in the capture histories with supplementary monthly VHF radio-telemetry data totaling 3819 occurrence records.

Spatial capture–recapture

Model convergence and performance.—Joint posterior samples for the individual effect on probability of detection from Model 3b, as well as two parameters from Model 4b, the male and individual effects on probability of detection, failed convergence diagnostics due to slow mixing. The Gelman-Rubin convergence diagnostic for all other parameters was <1.1 and therefore expected to have converged (Gelman et al. 2013).

Overall, the best performing model according to WAIC was Model 4a: SCR Complete Telemetry assuming constant probability of detection per primary survey (Table 4). Model selection results indicated that the models with higher levels of complexity and additional integrated spatial information performed better than those that incorporated less information and did not

Table 3. Tortoise sex breakdowns by survey number with corresponding model-based totals for VHF radio-telemetry and GPS logger data.

Survey	Total	Male	Female	Unk	Recapture during subsequent survey	Model 3: Individuals with GPS/telemetry	Model 4: Individuals with telemetry
(1)	7	5	2	0		7	7
(2)	8	2	5	1		4	7
(3)	5	2	3	0	3	15	5
(4)	6	3	1	2		6	4
(5)	19	9	8	2		15	16
(6)	26	12	13	1	11	25	26
(7)	17	10	6	1		17	16
(8)	12	7	5	0		10	12
(9)	9	3	5	1	4	6	9
(10)	3	2	1	0		3	3
(11)	8	7	1	0	1	8	8
(12)	18	12	6	0		20	18
(13)	2	0	2	0		6	2
(14)	12	5	4	3	1	18	9
(15)	6	2	3	1		6	6
(16)	9	5	4	0	4	10	9

Table 4. Model performance.

Model	WAIC	SE	ΔWAIC	WAICwt	pWAIC
4a: SCR Complete Telemetry	654.63	29.23	0	1	120.79
4b: SCR Complete Telemetry, *p* by individual	707.00	32.95	52.37	0	169.59
3a: SCR Three-day Locations	761.40	33.15	106.77	0	89.58
2a: Base SCR	779.57	32.58	124.94	0	95.67
3b: SCR Three-day Locations, *p* by individual	874.17	40.43	219.54	0	172.17
1a: Conventional Non-spatial	869.75	34.54	215.12	0	59.30
2b: Base SCR, *p* by individual	910.25	42.10	255.62	0	192.05
1b: Conventional Non-spatial, *p* by individual	1014.8	44.83	360.17	0	171.54

Notes: The WAIC column contains the calculated scores sorted from lowest to highest, the SE column represents the standard error for the WAIC computations, the ΔWAIC column is the relative difference in WAIC between the top-ranked model and each of the models, the WAICwt column represents the probability of each model given the data, and the pWAIC column lists the effective number of parameters which are used as a penalization term. SCR, spatial capture–recapture; WAIC, widely applicable information criterion.

explicitly account for space. However, model variations that incorporated heterogeneity in the probability of detection at the individual level resulted in higher uncertainty in estimates and did not perform as well as the respective models where probability of detection was assumed constant. We report all results hereafter for model variations (1a, 2a, 3a, 4a) where probability of detection was assumed constant across the primary survey period.

Model results.—Results from the joint posterior distributions for each of the candidate models are presented in Table 5 (see Appendix S2: Table S2 for Model 1b, 2b, 3b, and 4b results), and density estimates for all 16 primary surveys are visualized in Fig. 3. The Non-spatial model generally resulted in higher median estimates of density than the SCR models (Models 2–4), ranging from 2.88 to 29.8 subadults and adults/km^2. Integrating supplementary spatially referenced data resulted in a downward shift in median estimates. Density results for corresponding primary surveys based on the Base and Three-day models were similar and ranged from 2.81 to 26.18 and 3.70 to 27.66 subadults and adults/km^2, respectively. The Complete Telemetry model resulted in the lowest median estimates and ranged from 2.07 to 26.33 tortoises/km^2. However, results from the Complete Telemetry model were likely biased low due to the spatial scale parameter being biased high for this model (see *Discussion*). Uncertainty in density estimates, measured as differences in the width of the HPD intervals, was not consistent across models and varied based on primary survey. In general, density results from the Non-spatial model had smaller interval widths, but this is largely false precision as lower estimates were truncated based on the actual number of captured tortoises during a survey. However, for surveys where detection rates and recaptures were very low (i.e., Surveys 10 and 13), the Base and Complete Telemetry models resulted in less uncertainty than the Non-spatial model.

Posterior estimates for the spatial scale parameter σ varied based on model variation, as well as primary survey (Fig. 4, Table 5). For each survey, there was a noticeable increase in σ with an increase in the temporal scale of supplementary spatial data used to inform model parameters. For the Base model without supplementary telemetry data and the Three-day model, estimates of σ were lower by 15.97–71.03% and 29.82–81.33%, respectively, than the Complete Telemetry model as the latter integrated spatial data over a much larger temporal scale (years vs. days). For the Base model, σ was assumed to be survey-invariant and the global median estimate was 70.64 m, while for the Three-day model, median estimates of σ overlapped this estimate and ranged from 23.03 m for Survey 5 (McCullough Pass in 2015) to 97.15 m for Survey 4 (ISEGS S in 2017). For the Complete Telemetry model, median estimates of σ ranged from 84.37 m for Survey 6 to 244.73 m for Survey 3 (ISEGS N in 2019). In many cases, estimates of σ for subsequent surveys at the same study plot were similar, likely due to recaptures and similar patterns of space use at a plot (Fig. 4). Across all models that incorporated a sex effect on σ (Models 2–4), estimated use areas were larger for males. This resulted in use areas that were

Table 5. Joint posterior summaries of model parameters representing the median and 90% highest posterior density credible interval [5%, 95%].

Parameter	Model 1a Non-spatial	Model 2a Base SCR	Model 3a SCR Three-day Locations	Model 4a SCR Complete Telemetry
Male effect: p (logit-scale)	0.09 [−0.3, 0.5]	0.35 [−0.13, 0.84]	0.45 [0, 0.93]	1.18 [0.54, 1.85]
Individual effect: p (logit-scale)	. . .	. . .	. . .	. . .
Male effect: σ (log-scale)	. . .	0.28 [0.13, 0.43]	0.74 [0.71, 0.76]	0.4 [0.37, 0.43]
Global σ (m)	. . .	70.64 [63.15, 78.98]	. . .	. . .
(1) p	0.53 [0.32, 0.74]	0.77 [0.54, 1]	0.76 [0.54, 0.96]	0.76 [0.5, 1]
σ (m)	. . .	. . .	56.22 [52.49, 60.2]	145.29 [135.07, 156.68]
Ψ	0.08 [0.04, 0.14]	0.06 [0.03, 0.1]	0.06 [0.03, 0.1]	0.05 [0.02, 0.08]
Density	7.68 [6.72, 9.61]	6.06 [3.11, 9.61]	5.92 [2.81, 9.32]	4.88 [2.22, 7.54]
(2) p	0.76 [0.61, 0.9]	0.86 [0.71, 0.99]	0.88 [0.74, 0.99]	0.91 [0.75, 1]
σ (m)	. . .	. . .	68.71 [64.71, 72.96]	185.33 [176.47, 194.05]
Ψ	0.08 [0.04, 0.13]	0.07 [0.03, 0.11]	0.07 [0.03, 0.11]	0.05 [0.02, 0.08]
Density	7.69 [7.69, 8.65]	6.8 [3.7, 10.36]	6.66 [3.7, 10.36]	5.18 [2.66, 7.69]
(3) p	0.5 [0.26, 0.74]	0.58 [0.29, 0.87]	0.63 [0.35, 0.91]	0.75 [0.43, 1]
σ (m)	. . .	. . .	66.45 [63.53, 69.31]	244.73 [231.79, 257.64]
Ψ	0.06 [0.02, 0.11]	0.05 [0.02, 0.09]	0.05 [0.02, 0.09]	0.03 [0.01, 0.06]
Density	5.77 [4.81, 7.69]	5.18 [1.92, 9.02]	4.73 [1.78, 8.14]	3.25 [1.33, 5.77]
(4) p	0.59 [0.37, 0.8]	0.81 [0.57, 1]	0.87 [0.64, 1]	0.86 [0.62, 1]
σ (m)	. . .	. . .	97.15 [82.52, 113.63]	138.43 [131.48, 145.27]
Ψ	0.07 [0.03, 0.11]	0.05 [0.02, 0.09]	0.05 [0.02, 0.08]	0.04 [0.02, 0.07]
Density	5.77 [5.77, 7.69]	5.18 [2.51, 8.58]	4.44 [1.92, 6.95]	4.14 [1.92, 6.66]
(5) p	0.38 [0.23, 0.52]	0.38 [0.22, 0.53]	0.35 [0.2, 0.5]	0.27 [0.13, 0.43]
σ (m)	. . .	. . .	23.03 [22.27, 23.79]	92.7 [89.55, 95.95]
Ψ	0.25 [0.16, 0.35]	0.22 [0.13, 0.32]	0.24 [0.14, 0.35]	0.23 [0.13, 0.36]
Density	24.03 [19.22, 31.72]	21.6 [13.02, 31.21]	23.67 [14.05, 34.32]	23.08 [13.31, 35.8]
(6) p	0.45 [0.33, 0.57]	0.47 [0.34, 0.61]	0.46 [0.33, 0.59]	0.39 [0.25, 0.53]
σ (m)	. . .	. . .	27.9 [26.85, 28.94]	84.37 [81.89, 86.87]
Ψ	0.3 [0.21, 0.4]	0.26 [0.18, 0.36]	0.28 [0.19, 0.38]	0.26 [0.17, 0.37]
Density	29.8 [24.99, 35.56]	26.18 [18.2, 35.5]	27.66 [19.23, 36.98]	26.33 [17.6, 35.95]
(7) p	0.5 [0.35, 0.65]	0.58 [0.4, 0.75]	0.52 [0.35, 0.69]	0.65 [0.45, 0.85]
σ (m)	. . .	. . .	46.7 [44.54, 48.77]	141.96 [134.54, 149.46]
Ψ	0.19 [0.12, 0.27]	0.16 [0.1, 0.22]	0.16 [0.1, 0.23]	0.12 [0.08, 0.18]
Density	18.26 [16.34, 22.11]	15.53 [9.32, 21.15]	16.27 [10.06, 22.63]	12.28 [7.99, 17.01]
(8) p	0.68 [0.53, 0.82]	0.7 [0.53, 0.86]	0.68 [0.51, 0.84]	0.78 [0.59, 0.97]
σ (m)	. . .	. . .	40.97 [39.65, 42.3]	164.29 [156.73, 171.77]
Ψ	0.12 [0.07, 0.18]	0.11 [0.06, 0.15]	0.11 [0.06, 0.16]	0.08 [0.04, 0.12]
Density	11.53 [11.53, 13.46]	10.5 [6.51, 15.53]	10.8 [6.21, 15.53]	7.99 [4.73, 11.39]
(9) p	0.79 [0.64, 0.91]	0.76 [0.6, 0.89]	0.76 [0.61, 0.9]	0.77 [0.59, 0.94]
σ (m)	. . .	. . .	62.36 [58.97, 65.93]	140.36 [131.89, 148.75]
Ψ	0.09 [0.05, 0.14]	0.08 [0.04, 0.12]	0.08 [0.04, 0.12]	0.07 [0.03, 0.1]
Density	8.65 [8.65, 9.61]	7.84 [4.44, 11.98]	7.69 [3.99, 11.39]	6.51 [3.4, 9.62]
(10) p	0.05 [0, 0.22]	0.04 [0, 0.2]	0.04 [0, 0.21]	0.04 [0, 0.24]
σ (m)	. . .	. . .	78.98 [64.15, 95.07]	149.85 [131.57, 168.29]
Ψ	0.23 [0.01, 0.75]	0.22 [0.01, 0.73]	0.21 [0.01, 0.73]	0.16 [0.01, 0.67]
Density	22.11 [2.88, 74.97]	21.45 [1.18, 73.08]	21.01 [1.18, 73.37]	15.68 [0.59, 67.46]
(11) p	0.26 [0.06, 0.45]	0.25 [0.06, 0.47]	0.21 [0.04, 0.4]	0.21 [0.02, 0.51]
σ (m)	. . .	. . .	28.95 [26.86, 31.08]	205.29 [193.56, 217.62]
Ψ	0.14 [0.05, 0.27]	0.12 [0.04, 0.25]	0.13 [0.04, 0.28]	0.09 [0.02, 0.2]
Density	12.5 [7.69, 24.99]	12.13 [3.99, 24.7]	13.17 [4.73, 28.25]	8.65 [2.81, 20.12]
(12) p	0.53 [0.39, 0.68]	0.58 [0.42, 0.75]	0.64 [0.48, 0.81]	0.74 [0.54, 0.93]
σ (m)	. . .	. . .	71.94 [69.79, 74.2]	198.4 [191.27, 206.2]
Ψ	0.2 [0.13, 0.27]	0.16 [0.1, 0.23]	0.15 [0.09, 0.21]	0.11 [0.07, 0.16]

(Table 5. Continued.)

Parameter	Model 1a Non-spatial	Model 2a Base SCR	Model 3a SCR Three-day Locations	Model 4a SCR Complete Telemetry
Density	19.22 [17.3, 22.11]	16.42 [10.65, 22.49]	14.79 [10.06, 20.56]	11.09 [7.25, 14.94]
(13) *p*	0.3 [0.01, 0.62]	0.5 [0.03, 0.89]	0.34 [0.01, 0.67]	0.61 [0.19, 1]
σ (m)	. . .	. . .	25.62 [24.64, 26.59]	193.6 [176.16, 211.45]
Ψ	0.04 [0, 0.16]	0.03 [0, 0.09]	0.04 [0, 0.13]	0.02 [0, 0.06]
Density	2.88 [1.92, 14.42]	2.81 [0.3, 9.17]	3.70 [0.3, 12.28]	2.07 [0.3, 5.47]
(14) *p*	0.53 [0.36, 0.69]	0.63 [0.43, 0.82]	0.7 [0.5, 0.87]	0.78 [0.56, 1]
σ (m)	. . .	. . .	62.61 [60.56, 64.81]	176.02 [165.98, 186.29]
Ψ	0.14 [0.08, 0.2]	0.11 [0.06, 0.16]	0.1 [0.06, 0.16]	0.08 [0.04, 0.12]
Density	12.5 [11.53, 15.38]	10.95 [5.92, 15.53]	10.36 [6.07, 14.94]	7.84 [4.59, 11.39]
(15) *p*	0.6 [0.4, 0.81]	0.59 [0.37, 0.82]	0.59 [0.37, 0.82]	0.7 [0.43, 0.97]
σ (m)	. . .	. . .	59.71 [56.15, 63.37]	218.76 [202.62, 235.08]
Ψ	0.07 [0.03, 0.11]	0.06 [0.02, 0.1]	0.06 [0.02, 0.1]	0.04 [0.02, 0.07]
Density	5.77 [5.77, 7.69]	5.92 [2.66, 9.91]	5.92 [2.51, 9.62]	4.14 [1.92, 6.95]
(16) *p*	0.6 [0.42, 0.78]	0.62 [0.42, 0.82]	0.61 [0.41, 0.8]	0.74 [0.5, 0.99]
σ (m)	. . .	. . .	42.09 [39.26, 45.15]	225.45 [206.71, 243.42]
Ψ	0.1 [0.05, 0.15]	0.08 [0.04, 0.13]	0.09 [0.05, 0.14]	0.06 [0.03, 0.09]
Density	8.65 [8.65, 10.57]	8.43 [3.99, 12.43]	8.58 [4.88, 13.46]	5.62 [3.11, 8.58]

Notes: Primary surveys are identified by numbers (1–16), which correspond to the primary survey numbers listed in Table 1. See Appendix S2: Table S2 for Model 1b, 2b, 3b, and 4b results. SCR, spatial capture–recapture; . . ., not significant.

approximately 1.3 times larger for males than females for the Base SCR model, 2.09 times larger for the Three-day model, and 1.49 times larger for the Complete Telemetry model.

In general, estimated probability of detection per primary sampling period within the surveyed area was lower based on the Non-spatial model and median estimates ranged from 4.86% for Survey 10 (Stateline Pass in 2016) to 78.61% for Survey 9 (Sheep Mountain in 2018). This trend was expected as this model contains no explicit process to account for temporary emigration and assumes that every individual is available for capture during every occasion. The Base, Three-day, and Complete Telemetry models all resulted in higher estimated probability of detection within the plot boundaries. However, the Complete Telemetry model resulted in the highest median estimates of detection probability due to larger posterior estimates of σ, which account for more space use. Estimates from this model ranged from 4.11% for Survey 10 to 90.85% for Survey 2 (ISEGS N in 2016) with upper bounds for multiple surveys (Surveys 1, 2, 3, 4, 13, and 14) reaching 100% detection rates within the surveyed area. Additionally, the median sex effect across all model variations indicated that males typically had a higher probability of being detected than females at the study plots.

Estimated activity centers from the posterior distribution of the Three-day and Complete Telemetry models were visualized for each encountered tortoise and compared with 95% utilization distributions quantified externally (based on adehabitatHR package in R: Calenge 2006) using the same supplementary spatial data used to inform each model (Fig. 5). Estimated activity centers were visually representative of the center of an individual's home range for the corresponding spatial data. For the Complete Telemetry model, there was little variation in home range centers for individuals that were recaptured on subsequent surveys as these were based on the same supplementary data. However, estimated home range centers for individuals varied considerably between the Three-day and Complete Telemetry models due to the different temporal scales of supplementary spatial data, thus demonstrating the importance of matching the temporal scale of supplementary spatial data to the temporal scale of surveys for this species.

Discussion

In this study, we developed four model variations of increasing complexity that integrate different levels of information, and we compare estimates of density from each of these models

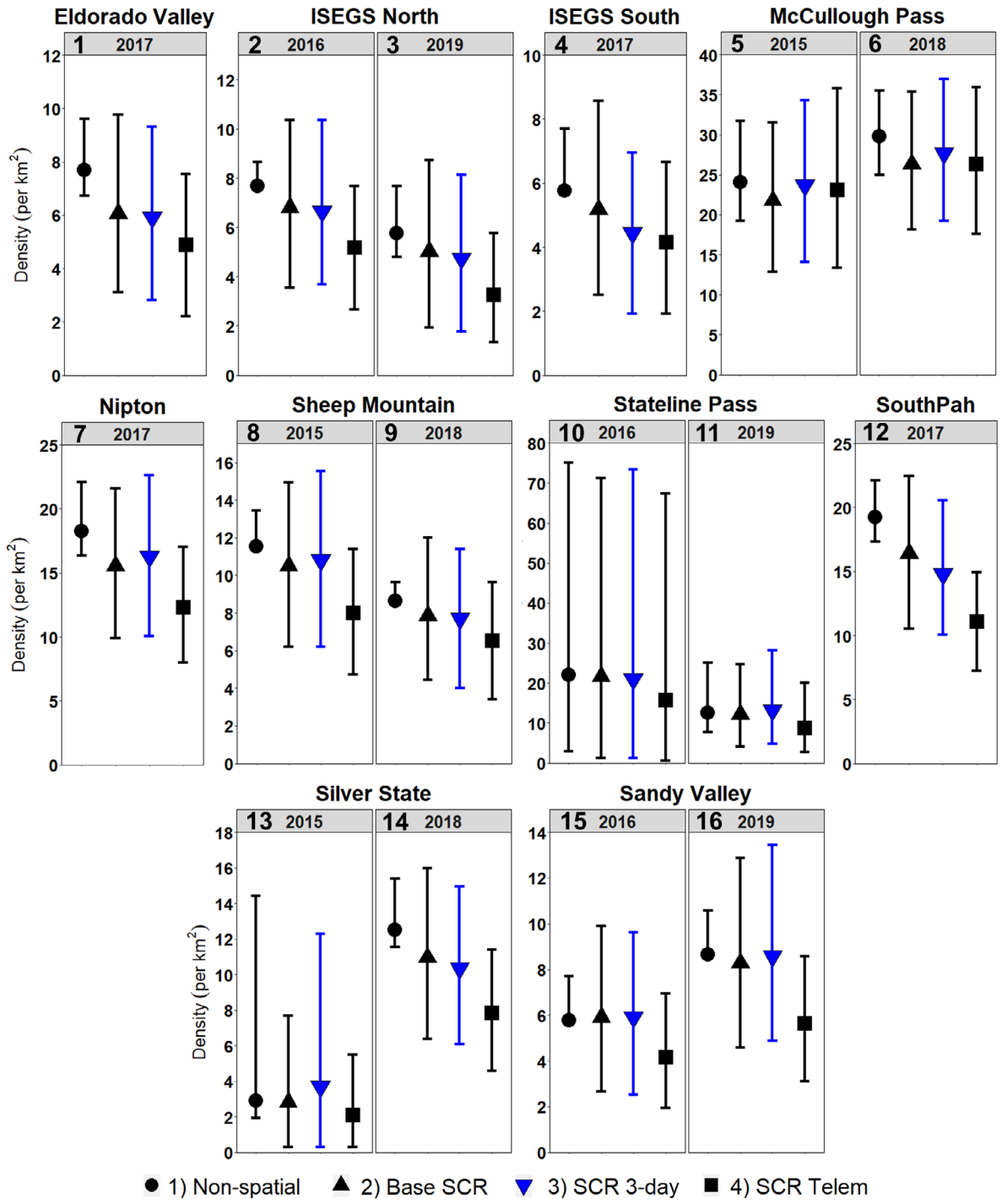

Fig. 3. Joint posterior estimates of density representing the median and 90% highest posterior density credible interval. Results are grouped by study plot and survey year with different model variations displayed from left to right for each year as follows: (1) Model 1a: Conventional Non-spatial, (2) Model 2a: Base SCR, (3) Model 3a: SCR Three-day Locations, and (4) Model 4a: SCR Complete Telemetry. The preferred model, SCR Three-day Locations, is highlighted in blue. Primary surveys are identified by numbers (1–16), which correspond to the primary survey numbers listed in Table 1. SCR, spatial capture–recapture.

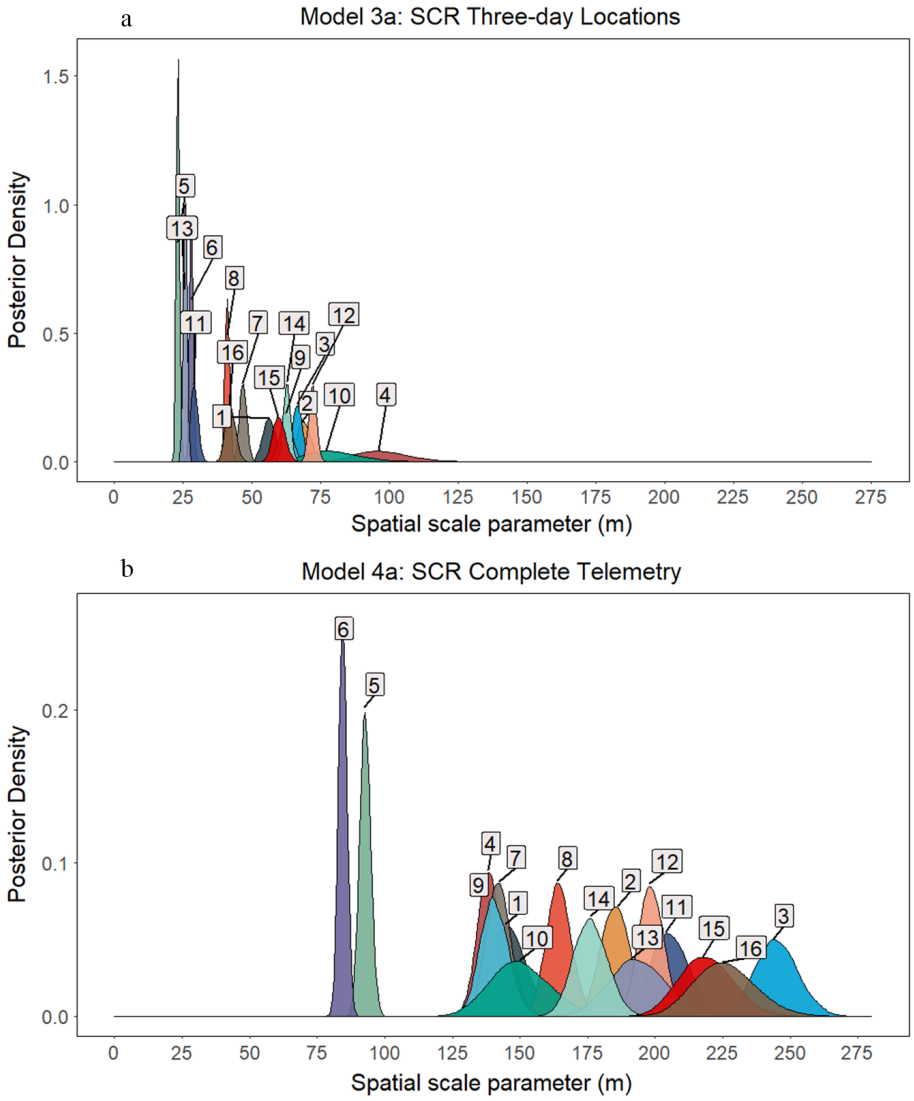

Fig. 4. Joint posterior estimates of sigma for a female desert tortoise for each primary survey based on (a) Model 3: SCR Three-day locations and (b) Model 4: SCR Complete Telemetry. Primary surveys are identified by numbers (1–16), which correspond to the primary survey numbers listed in Table 1. SCR, spatial capture–recapture.

for a species where detectability and abundance are low. Our results demonstrate that conventional non-spatial approaches consistently result in inflated estimates of density for desert tortoise populations and can lead to false precision by not explicitly accounting for space use. In general, model performance improved with increasing complexity and higher levels of integrated spatial information. Additionally, by integrating various temporal levels of supplementary spatial data to inform model parameters, our study highlights that the temporal scale of such data has a direct effect on density estimates and, if not properly specified, can result in a source of unintended bias. For this species, our results indicate that integrating spatial data over a larger temporal scale than mark-recapture surveys are conducted can bias the spatial scale parameter σ high, leading to bias in detection probabilities and density estimates, resulting in higher and

lower estimates, respectively. This research demonstrates the importance of understanding the implications of study design and model choice when estimating density using SCR methods, especially when estimates may have management implications for a threatened species such as the Mojave desert tortoise.

Natural history and extensive field experience suggest that this species regularly violates assumptions central to conventional mark-recapture models including homogeneous detection probability and geographic closure due to temporary emigration and "edge effects" (Fig. 5; Freilich et al. 2005, Nussear and Tracy 2007, Inman et al. 2009). These violations have long been known to induce bias, especially when estimates are calculated with naïve density estimators, where density is inferred based on the actual size of the trapped or surveyed area, and not on the effective sampled area (which is generally unknown) (Anderson et al. 1983, Wilson and Anderson 1985). Our results demonstrate that in most cases, conventional methods result in inflated density estimates for this species because every encountered individual is "confined" to the area surveyed (Fig. 3, Table 5), while GPS logger data collected over the same period showed that tortoises in our study population regularly violate geographic closure assumptions by crossing arbitrary plot boundaries (Fig. 5). As such, historical estimates of density for the desert tortoise based on conventional mark-recapture surveys are undoubtedly biased high.

Previous work has focused on attempting to correct for temporary emigration and "edge effects" in conventional methods by integrating a boundary strip around the trapping grid or survey plot and extending the area over which to infer density (Wilson and Anderson 1985, Parmenter et al. 2003). In fact, results of this work have been incorporated in protocols for density estimation of the Sonoran desert tortoise (*Gopherus morafkai*), a closely related species (Averill-Murray 2000). These approaches have been based on buffers calculated using various metrics, including trap intervals and home range size, as well as mean maximum distance moved between captures. However, Parmenter et al. (2003) found that estimates are significantly affected by the size of the (sometimes arbitrarily) chosen boundary estimator, resulting in density estimates biased high when boundary strips are under-specified and biased low when over-specified. Further, they caution that these metrics often require a large number of theoretical assumptions that may not be met. Adding a boundary strip essentially changes the survey area in an attempt to account for space use by study animals outside the plot and this concept is closely related to the extended study area incorporated in our SCR models. By inferring density over an extended study area of sufficient size and fitting models with the use of data augmentation, our SCR models explicitly acknowledge space use on and off the plot as well as the spatial dependency of capture probabilities, ultimately achieving the goal of these previous efforts.

Population density and space use are both important measures that are used to make informed decisions regarding conservation and management of species generally, and arguably, both metrics are highly correlated. SCR combines these concepts, employing space use to determine the probability of detection based on spatial location data from individuals in the population, and can provide more accurate density estimates (Efford 2004, Royle and Young 2008, Efford and Fewster 2013, Royle et al. 2014). In line with previous studies, our modified SCR models resulted in spatially corrected estimates of density by taking into account where and how tortoises in our population use space (Royle and Young 2008, Royle et al. 2014). However, we found that at study plots where tortoises use considerably less space and are mostly concentrated away from the edges of the plot (i.e., Surveys 5 and 6 at McCullough Pass; Fig. 4), conventional non-spatial methods resulted in similar estimates of density to the SCR models (Fig. 3, Table 5), presumably because the geographic closure assumption was sufficient in this instance. In our study, this was generally the exception, as space use by individuals at the McCullough Pass plot was considerably lower than other study plots (Fig. 4).

Recent studies have extended standard SCR models and demonstrated that integrating supplementary spatial data to further inform how individuals use space can lead to additional improvements of model performance and accuracy (Royle et al. 2013, Sollmann et al. 2013*b*, Tenan et al. 2017). To date, these results have

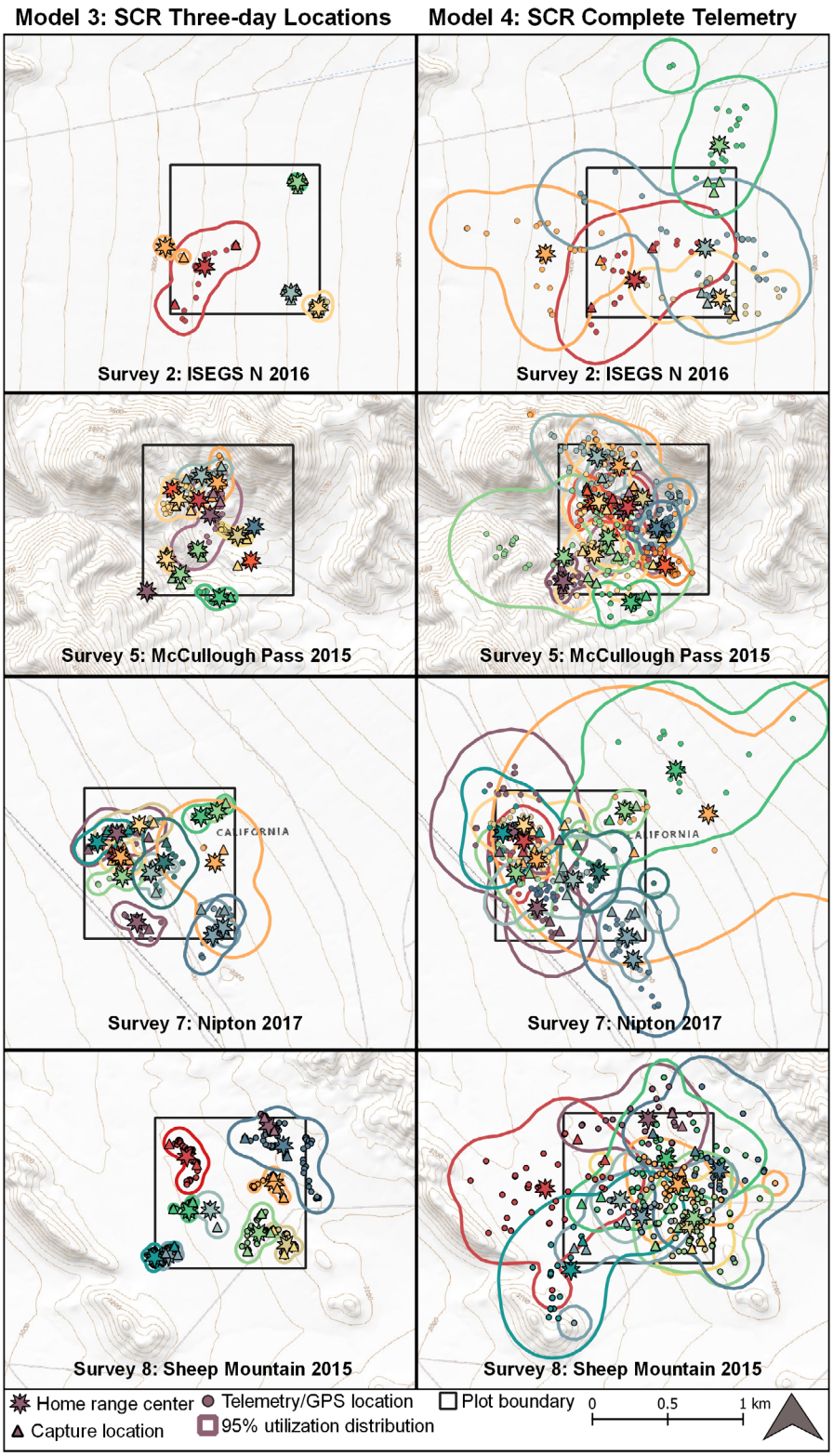

Fig. 5. Actual capture locations (triangles), supplemental telemetry/GPS locations used to inform model

(Fig. 5. *Continued*)
parameters (points), and estimated home range centers from the joint posterior distribution (stars) based on Model 3: SCR Three-day Locations on the left and Model 4: SCR Complete Telemetry on the right for tortoises located during representative surveys. Estimated 95% utilization distributions (based on adehabitatHR package in R: Calenge 2006) are visualized as corresponding colored outlines. SCR, spatial capture–recapture.

been largely based on trapping studies and simulations carried out over extended periods of time (months vs. days) and have relied on supplementary data from few individuals to extrapolate space usage for the entire population (two individuals in Tenan et al. 2017; three in Sollmann et al. 2013*a* and Royle et al. 2013; 4–8 in Paterson et al. 2019; 6–8 in Linden et al. 2018; and 44 in Sollmann et al. 2013*b*). In this study, we integrated supplementary data for a much larger proportion of the population than most previous studies, including telemetry data for as much as 93% (n = 133) of all tortoises in our capture histories. However, in many cases, the individuals in a capture–recapture study may not have supplemental telemetry data at the time of the survey. In the Three-day model, we leveraged additional spatial data from auxiliary individuals separate from those in the captured population, demonstrating that supplemental spatial data from similar populations can be used to inform SCR model parameters when available.

The integration of multiple data sets to study demographic processes is an increasing trend in ecology. Recently developed integrated population models provide a framework for a unified analysis of data sets collected at differing temporal and spatial scales (Schaub and Abadi 2011, Zipkin and Saunders 2018), including capture–recapture survey data and telemetry data (Fieberg et al. 2010, Johnson et al. 2010). While the use of integrated models can result in more precision in estimates (Abadi et al. 2010) and provides the ability to estimate additional parameters beyond those explicitly sampled, based on our results we caution that even subtle differences in scale among integrated data sets have the potential to result in bias in parameter estimates. Based on model performance metrics (i.e., WAIC; Table 4), the Complete Telemetry model appears to be the best model, resulting in lower median densities and more precision (Fig. 3, Table 5), but we contend that this model ultimately biased density estimates low. By incorporating supplementary telemetry data collected over multiple years to describe activity areas and define the spatial scale parameter, those areas equate to an actual home range, but are based on how a tortoise uses space at a much larger temporal scale than the three-day period of our surveys. Desert tortoises do not use the entirety of their home range over a three-day period and GPS data collected during the fall active season at our plots indicate that approximately 70% of the time tortoises do not move from day to day. Hence, by incorporating home range scale data the Complete Telemetry model overestimated the spatial scale parameter and biased probability of detection within plot boundaries high by accounting for missed captures off the plot too frequently. This resulted in low estimates of undetected individuals and overall density. For a species characterized by low activity, our results indicate that the temporal scale of supplementary location data should be equivalent to the temporal scale of sampling, as in the Base and Three-day models, especially for a succinct sampling period such as our three-day surveys.

With advancements in VHF radio-transmitters and GPS data logger technology, researchers now have the ability to quantify movement data and space use of individuals and populations on a much finer scale (Tomkiewicz et al. 2010). While traditionally cost prohibitive and restricted to large animals, recent size reductions in GPS loggers have made this technology applicable to the desert tortoise and other turtle and tortoise species (Forin-Wiart et al. 2015). However, the cost and time associated with undertaking a long-term study of animal movement can be high and therefore is not always feasible. While a long-term data set can be valuable for numerous reasons (Hebblewhite and Haydon 2010), this research demonstrates that it is not necessary in order to obtain accurate and meaningful estimates of density for this species. Based on our study design, we suggest the Three-day model resulted in the least bias by considering how individuals use space over the same time

period as surveys occur. However, obtaining movement data even at a three-day resolution comes with some cost as purchasing and attaching/removing equipment can be expensive not to mention stressful for animals (Murray and Fuller 2000, Withey et al. 2001, Thomas et al. 2011). The Base model was restricted to estimating σ as a global variable across all surveys due to data limitations, but even so, resulting posterior distributions of density estimates overlapped those from the Three-day model (Fig. 3) and median estimates between the two models were similar (Table 5). A longer survey period resulting in additional recaptures would likely permit estimation of σ as a function of survey and further improve estimates for the Base model, but would result in much larger personnel costs. We suggest this model could be a suitable alternative when a small loss in accuracy (median estimates differed by 0–2.07 tortoises/km^2) is not worth the high cost and time commitment associated with collecting supplementary spatial data.

We ran into additional data limitations due to low rates of detection and recaptures during some surveys (Survey 13: Silver State in 2015, Survey 10: Stateline Pass in 2016), and this resulted in high levels of uncertainty in estimates for these surveys (especially Survey 10). In the case of Survey 13, two individuals were detected over the three-day survey with only one being recaptured on a second occasion, and during Survey 10, three individuals were detected with no recaptures. In both instances, SCR methods did not provide an improvement in parameter estimation over conventional methods as there was very little information about space use to inform model parameters. Unfortunately, for a species like the desert tortoise where detection and abundance are often low (Anderson et al. 2001, Nussear et al. 2008, Allison and McLuckie 2018), this is a potential problem that will likely persist regardless of the model approach. However, during subsequent surveys, additional animals were detected at these plots and recapture rates increased resulting in less uncertainty in estimates (Fig. 3, Table 5). While closed-population methods resulted in high levels of uncertainty, we expect that estimates generated under an open-population "robust" design model would improve based on these results (Pollock et al. 1990). The majority of "new" animals detected on the second round of surveys were large adults (see Appendix S2: Table S1), and this increase in estimated density was likely not due to recruitment but a factor of differences in detectability and varying patterns of space use. These two plots (Silver State and Stateline Pass) are characterized by similar habitat types consisting of large incised washes where caliche caves are commonly used as refugia. Caliche excavations are generally much deeper than soil burrows making detection more difficult (Riedle et al. 2008, Mack et al. 2015). Differences in detectability between shelter site types further emphasize that this species regularly violates statistical assumptions of mark–recapture methods, which complicates standard approaches. Future studies are needed to evaluate and incorporate the effects of habitat level characteristics into population modeling efforts.

Another potential confounding factor in our models includes sources of unmodeled heterogeneity due to behavioral response to capture. Trap response is common in mark-recapture studies where animals are disturbed which can lead to an increase ("trap-happy") or decrease ("trap-shy") in recaptures resulting in negatively or positively biased estimates, respectively (Nichols et al. 1984, Pollock et al. 1990). A "trap-happy" response is typically due to animals being enticed to enter traps or approach scratch posts by being baited and is common among studies of small mammals (Nichols et al. 1984) and, consequently, not relevant in the context of our study. However, the potential does exist for a tortoise to exhibit a behavioral response leading to a decrease in probability of recapture including retreating deep into a shelter site or making a long-distance movement after being handled. However, Hinderle et al. (2015) did not detect differences in net displacement between handling and control groups of desert tortoises, suggesting that prolonged handling events do not have an effect on movement behavior for this species. Additionally, Averill-Murray (2002) found that recapture rates of Sonoran desert tortoises in Arizona were not affected when tortoises exhibited signs of distress by voiding their bladders during handling events, and Pike et al. (2005) found no difference between recapture rates for gopher tortoises (*Gopherus polyphemus*) in Florida that were handled and not handled.

Visualizations of GPS data over the three-day survey period (Fig. 5) and estimates of the spatial scale parameter from the Three-day model based on those data (Fig. 4, Table 5) indicate that behavior of tortoises was likely not affected as most did not move large distances after being handled in our study.

Turtle and tortoise species worldwide are in danger of extinction and reliable methods for measuring population parameters are crucial for assessing and monitoring these species (Ernst and Lovich 2009, Stanford et al. 2020). This is especially true for the Mojave desert tortoise, where recovery is contingent on regular and accurate estimates of population density (Nussear and Tracy 2007, USFWS 2011). With respect to the entirety of this species' range, our plots were concentrated in the same general area yet our results indicated considerable spatial differences in density among plots. Spatial patchiness in density has been well documented for this species (Krzysik 2002, Tracy et al. 2004, U.S. Fish and Wildlife Service 2011), but current monitoring of desert tortoise populations is occurring at a much larger spatial scale. Since 1999, density metrics for the desert tortoise have been estimated using distance sampling methods in Tortoise Conservation Areas (TCAs) throughout the range (Anderson et al. 2001, Allison and McLuckie 2018). While they provide range-wide summaries of population trends, these methods result in coarse-scale estimates of density as they are extrapolated over a much larger area than is surveyed due to low encounter rates on transects. Our study plots are located between two TCAs (Ivanpah and Eldorado Valley), and the majority of our surveys resulted in estimates that were significantly higher than reported densities (Allison and McLuckie 2018). This disparity emphasizes the need for focused demographic monitoring to complement current range-wide monitoring, as outlined in the 2011 Revised Recovery Plan (Recovery Criterion 1b; USFWS 2011). Identifying fine-scale changes in population parameters requires monitoring at a finer scale, and our findings highlight the importance of focused sampling for this and other species with variable densities across their distributions.

Spatial capture–recapture models are increasingly being used to estimate spatially explicit population parameters for a variety of taxa, including birds (Schaub and Royle 2014), small mammals (Romairone et al. 2018), large mammals (Sollmann et al. 2013*a*, Tenan et al. 2017, Paterson et al. 2019), and herpetofauna (Royle and Young 2008, Muñoz et al. 2016), among others, based on a variety of capture–recapture sampling designs and model extensions, including the integration of supplementary spatial data from multiple data sets. As the use and approaches of these models and the collection and integration of supplemental information increase, it is pertinent to consider and examine the effects that study design and model specification may have on the reliability of resulting estimates. In this study, we found that while integrating all available telemetry data led to a higher ranking model, it ultimately resulted in an unintended source of bias and skewed density estimates downward. However, this finding is likely specific to the study species and sampling design presented here. Our results suggest that for species that use the entirety of their home range over the course of sampling or sampling conducted over an extended period of time (months vs. days), integrating home range scale locality data (i.e., matching that of sampling) may result in more reliable estimates. The integration of supplemental spatial data within the SCR framework has the potential to improve estimates, but our results indicate there is not a "one size fits all" approach to generating reliable estimates using these methods. Fortunately, the flexibility of these models means that they can be tailored to study species and specific research needs; however, our findings underscore that basic knowledge of how a species uses space is critical in this process.

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Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3689/full