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Desert Tortoises, Density, and Violated Assumptions: Improving Estimates with Spatial Information

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by

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Abstract

Accurate population estimates are essential for monitoring the recovery of the federally listed Mojave desert tortoise (*Gopherus agassizii*), however, desert tortoise populations are difficult to accurately quantify due to a number of factors. Mark-recapture sampling methods have regularly been used to monitor this species, but the methods employed are often plagued by the violation 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 surveys. We conducted mark-recapture surveys separated by three years at 10 1-km^2 plots in and adjacent to the Ivanpah Valley of CA and NV from 2015-2019. Movement data were collected concurrently using radio-telemetry and GPS data loggers. GPS data demonstrated that desert tortoises frequently exhibited temporary emigration outside the plot during the three-day survey periods; thereby, complicating standard approaches for closed-model density estimation. We integrated mark-recapture survey data for adults (>160 mm MCL) 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 standard SCR models based on symmetrical usage areas described by various levels of supplementary spatial data, and a novel SCR model that integrates daily movement displacement quantified from fine-scale GPS data to define movement between sampling periods. The conventional model consistently resulted in inflated estimates of density while the standard SCR models allowed us to generate spatially corrected estimates for a species where detectability and abundance are low. However, we found that if not properly specified, the temporal scale of supplementary data may result in an unintended source of bias. Our results demonstrate the importance of accounting for spatial information as well was the value of understanding model specification when estimating density for the desert tortoise and have the potential to enhance the efficacy of long-term efforts to monitor population trends and inform recovery efforts.

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Introduction

A fundamental component of conservation and management of wildlife populations includes reliable estimates of population density, but rarely is it possible to obtain a complete direct count of all individuals in a population, thus methods for estimation are necessary. Closed-population mark-recapture models, which rely on detection estimation, have generally been considered the gold standard for population estimation and have become an important wildlife management tool, especially for secretive species that are notoriously difficult to detect (Otis et al. 1978, Willson et al. 2011, Daura-Jorge and Simões 2016). These widely used methods rely on statistical assumptions about detection probabilities of the species being modeled, including: geographically and demographically closed populations with no recruitment or losses, homogeneous capture probability and survival rates among individuals in the population, and retention and recognition of unique identification marks (Otis et al. 1978, Pollock et al. 1990, Pollock 2000). However, due to the inability to completely control experimental parameters when dealing with free-ranging wildlife, statistical assumptions of conventional mark-recapture models are often violated in the field or relaxed in analysis (Begon 1983, Pollock 2000, Kendall and Bjorkland 2001). For instance, plot based mark-recapture studies typically lack actual closure in the form of a physical barrier which can lead to temporary emigration, where individuals move on or off a plot during surveys, thereby violating the geographic closure assumption and complicating standard approaches (Kendall and Bjorkland 2001, Royle and Young 2008). Additionally, edge effects, where individuals on the periphery of the surveyed area are less exposed to sampling than those in the center, can result in spatial heterogeneity in detection probability (Efford 2004, Royle and Young 2008, Royle et al. 2018). These violations have the potential to cause bias in density estimates, which may impart error in the ability to accurately quantify demographic information used to make critical management decisions (Freilich et al. 2000). Furthermore, the effective sampled area is essentially unknown in these situations because neither the space use of individuals, nor the spatial nature of the sampling are included in conventional model parameters, and this omission of space results in an estimate of abundance over an undefined area and is not a true density estimate (White et al. 1982, Anderson et al. 1983, Borchers and Efford 2008).

Space use of individuals in the population has a direct effect on the probability of detection of those individuals, making it relevant to density estimation methods, but traditionally, measurement of these metrics have required distinct data sets and approaches. By incorporating an explicit process to describe how animals use space with conventional mark-recapture models, recently described spatial capture-recapture (SCR) models can account for some of the common assumption violations described above and have the potential to reduce bias in estimates of population size (Efford 2004, Royle and Young 2008, Efford and Fewster 2013, Royle et al. 2014). Furthermore, these methods require little extra effort on the behalf of the researcher and in their simplest form entail one additional component over conventional models: spatial encounter histories, which are generally recorded as an element of mark-recapture surveys. SCR models are hierarchical in the sense that they are comprised of an explicit spatial process model and an observation model, which is conditional on the spatial process (Royle and Young 2008, Royle et al. 2014). The spatial process describes how individuals are distributed in space and how they use space, elements that are not included in conventional models. The foundation of SCR is the assumption that each individual in the population has a latent activity center, which is centered in an activity use area and described by a spatial scale parameter (Efford 2004, Royle et al. 2018). The observation process then describes the imperfect detection of individuals during sampling based on their activity center and activity use area and is used to estimate abundance and derive density. It then follows suit that accurately described activity centers and use areas are necessary for accurately estimating density. Hence, by integrating movement data that are independent of mark-recapture sampling (i.e. movement data from radio-telemetry and GPS loggers) to inform model parameters, further improvement of estimates and inferences regarding space use are 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 that occurs in the Mojave Desert of the Southwestern U.S. This species was listed as threatened under the U.S. Endangered Species Act in 1990 due to reports of declining populations leading up to the listing (U.S. Fish and Wildlife Service 1990). The desert tortoise spends the majority of its life 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, when coupled with its cryptic nature, 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 federally listed desert tortoise, but due to their cryptic nature, differences in detectability between size classes, and fluctuations in activity driven by climate and resource availability, desert tortoise populations are difficult to accurately quantify, and conventional methods often violate spatial assumptions for this species (Freilich et al. 2005, Nussear and Tracy 2007, Inman et al. 2009). Historically, desert tortoise populations have been monitored using a variety of methods, and density metrics are currently estimated using distance sampling methods throughout the range (Allison and McLuckie 2018). However, distance sampling methods provide only coarse-scale estimates of density, and finer-scale knowledge of population metrics are also needed to properly manage this species (U.S. Fish and Wildlife Service 2011), thus methods for targeted monitoring at a smaller-scale such as mark-recapture models are necessary. Although, as described above, conventional mark-recapture methods often violate spatial assumptions for the desert tortoise, and the extent and effects of these violations on population parameter estimates have yet to be fully assessed.

Our objective was to improve upon current methods for estimating density for the desert tortoise by incorporating space use with mark-recapture survey data. We used desert tortoise search-encounter data collected from 2015-2019 and supplementary location data collected simultaneously with VHF-radio telemetry and GPS data loggers at ten 1-km^2 study plots in and adjacent to the Ivanpah Valley of California and Nevada in the eastern Mojave Desert. Since 2009, an increased commitment to reliance on renewable energy by multiple states in the southwestern U.S. has led to an increase in the number and scale of utility scale renewable energy projects in the Ivanpah Valley, resulting in desert tortoise habitat loss and degradation (U.S. Fish and Wildlife Service 2011, Lovich and Ennen 2011). Recent related studies have identified the Ivanpah Valley as an area of high habitat suitability, as well as a hotspot of genetic diversity and connectivity for the desert tortoise (Nussear et al. 2009, 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 for this species. We developed multiple candidate models of increasing complexity to combine standard mark-recapture histories with corresponding spatial capture locations and, in some cases, additional spatial data to describe space use and movement of individuals using a modified SCR model fitted in a Bayesian framework. We compared density estimates from the joint posterior distribution modeled with conventional non-spatial methods, as well as three standard SCR models based on symmetrical usage areas described by various levels of supplementary spatial data, and a novel SCR model that integrates daily movement displacement quantified from fine-scale GPS data to define movement between sampling periods. By incorporating spatial data, this research has the potential to reduce bias due to common assumption violations of conventional methods and provide unambiguous density estimates, and as a result has the potential to enhance the efficacy of long term monitoring efforts for this species.

Methods

Study Area

In 2015, we identified ten 1-km^2 long-term study plots in and adjacent to the Ivanpah Valley in the eastern Mojave Desert based on land form, connectivity, and potential influences of recently constructed solar facilities (Figure 1). The Ivanpah Valley straddles the California-Nevada border and is located approximately 50 miles southwest of Las Vegas, Nevada. 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 the dominant shrubs in valley bottoms and lower alluvial fans at the Nipton and SouthPah plots, to rocky mountain passes characterized by Mojave mid-elevation mixed desert scrub at the McCullough Pass and Stateline Pass plots (Brown et al. 1979, Schulz et al. 2015).

Mark Recapture Surveys

We conducted closed model mark-recapture surveys at the study plots from 2015-2019. Three to four of the ten study plots were sampled in any given year resulting in each group of plots being surveyed every three years (Table 1). Each primary 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. The surveyors were divided into five crews of four people, and transects were alternated in a perpendicular direction (North-South, East-West) with crews changing survey 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 meter intervals with each surveyor responsible for 2.5 meters on either side of each 1 kilometer transect; however, the McCullough Pass plot is comprised of very rugged terrain, and transects were spaced at 10 meter intervals at this plot in order to complete the survey within the specified time period. In total, two complete surveys were conducted at six of the study plots and one full survey was completed at each of the remaining four study plots.

All tortoises located during surveys were tagged with a unique identifier glued to a rear costal scute, and each animal encountered on the plot was given an inconspicuous temporary colored mark to differentiate capture during the three sampling occasions so that captures on previous occasions could be scored without having to remove animals from their burrows. 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 mean carapace length (MCL) and sex (male, female, or unknown).

Movement Data

Desert tortoise movement data were collected concurrently during surveys and during interim survey periods with the use of VHF radio-transmitters (Holohil Systems Ltd., 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 radio-telemetry, while GPS data loggers recorded positions hourly and were changed out and 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), the telemetry dataset was reduced to one location per month and locations collected between November and February were eliminated. This period coincides with a period of low to no activity when desert tortoises seek hibernacula to avoid cold temperatures and locations recorded during this time period are typically consistent throughout the winter (Bulova 1994, Nussear et al. 2007). Similarly, movement data from GPS loggers were reduced to data collected between mid-September and mid-October for each year that was 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 as desert tortoise movement varies throughout the year. GPS logger data were further subsampled to keep only locations recorded during what would be the length of a typical survey day, between 7 am and 5 pm Pacific Standard Time.

Spatial Capture-Recapture

Model Considerations and Data Formatting

Mark-recapture survey data were translated into capture histories y_{it}, for individuals $i = 1, 2, \ldots, n$, where each day of the three-day survey is equivalent to a sampling occasion t. Capture histories were tabulated in binary form where 0's and 1's indicate not captured ($y = 0$) or captured ($y = 1$) and include corresponding arrays of equal dimensions for spatial capture locations u_{it}, with one array for each coordinate axis (u_{xit}, u_{yit}). Due to lower encounters, juvenile desert tortoises (< 160 mm MCL) were not considered in this study and were removed from the capture histories and not included in our models.

We estimated adult population density (≥ 160 mm MCL) separately for each closed three-day mark-recapture survey, including surveys conducted at the same site in different years. Because we lacked sufficient data (i.e. three years of surveys) to estimate survival and recruitment (e.g., using a Jolly-Seber model analog; Jolly 1965, Seber 1965, Gardner et al. 2010), recaptures from prior-year surveys were considered to be new captures for our analyses. However, we estimated some movement parameters (see below) separately by site (instead of by survey), allowing us to borrow information from more than one year of telemetry and GPS logger data for estimating some key parameters for our SCR models.

Typical of plot-based mark-recapture surveys, the boundaries of our 1-km^2 study plots do not represent true physical boundaries and animals are not constrained to the plot. To account for temporary emigration and edge effects in our SCR framework, we designated 'study areas' for each site (S; the area over which we infer population density for each site) that extended beyond our 1-km^2 survey plots (X; the surveyed area) (Figure 2). Specifically, we defined study areas (S) by adding an 800 m buffer around our 1-km^2 plots (i.e., each study area covered a 6.76-km^2 area centered on the survey plot), with the specific buffer width determined to fully encompass the average home-range radius for individuals in our study population. In addition, we ran SCR models with buffers of 400, 800, and 1200 m and verified that density estimates were not sensitive to buffer sizes above 800 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 for each site (possibly real, yet undetected individuals, or 'pseudo-individuals') was designated to enforce a maximum population density of 100 tortoises/km^2. Our designated maximum density is approximately four times higher than the highest number of observed adults at any site, and is in line with the highest densities historically recorded in the Ivanpah Valley (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 individuals per km^2 and a maximum value of 100 individuals per km^2, where n_s represents the total number of individuals captured at each site.

Gender specific differences in home range size are well documented for the desert tortoise with males having significantly larger home ranges than females (Berry 1986a, O'Connor et al. 1994, Duda et al. 1999, Franks et al. 2011). This was incorporated into our models by modeling the spatial scale parameter σ, which describes the spatial scale of activity, as a function of whether or not an individual was male. Additionally, in many species one sex is more detectable and this was incorporated by modeling probability of detection p as a function of sex. The sex effect in our model was assigned as a male based effect based on *a priori* knowledge and field experience suggesting that males are more likely to be captured than females (Nussear et al. 2008). In order to account for differences in detectability between size classes and behavior we also tested models where the probability of detection varied at the individual level. 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.

Model Variations & Specification

We built five 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 conventional Bayesian closed-population model, and does not explicitly account for spatial or movement processes. The second model (Base SCR) is a standard Bayesian SCR model that integrates capture locations along with standard capture histories. The third model (SCR Three-day Locations) integrates GPS and VHF radio-telemetry data collected concurrently during the three-day surveys for each plot with the Base SCR model to estimate activity centers and the parameter σ. The fourth model (SCR Complete Telemetry) integrates multiple years of VHF radio-telemetry data with the Base SCR model to estimate activity centers and the parameter σ. The fifth model (SCR Daily Movement) uses averaged daily movement distance data from GPS loggers to inform tortoise movements and models daily movements as an uncorrelated random walk.

Model 1: Conventional Non-spatial

The first variation is not a spatial model and was constructed and analyzed within the same Bayesian framework using data augmentation in order to facilitate comparisons between estimates from the conventional and spatial models. For density estimation, this model implicitly assumes that all individuals are located within the survey plot boundaries, and are therefore always available for capture. The probability of detection p is estimated separately by sex and primary 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 surveyed area, X. Density, D, is then derived from the estimate of N divided by the area of X:

$$D = N/A_X$$

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. The variance term was assigned an inverse gamma prior with shape and rate (0.1, 0.1).

Model 2: Base SCR

Spatial Process Model

The basis of the spatial process model is the assumption that each individual in the population has an activity center, $s_i = (s_{xi}, s_{yi})$, which represents a fixed location in two-dimensional space, and an activity use area represented by a Gaussian kernel centered at the activity center s_i such that the area around the activity center s_i with a radius of 1.96 x σ represents a 95% utilization distribution. Thus, the location for individual i (observed or unobserved) during sampling occasion t is conditional on the latent activity center s_i and the spatial scale parameter σ, and is sampled according to the model:

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

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

Estimation of the activity center and spatial scale parameter is context dependent and for the Base SCR model is estimated solely based on the actual capture locations during the three capture occasions in a single survey (Figure 2a). 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 $t\pm1$, and that some individuals within the study area S may be located outside the surveyed area X on all three capture occasions. For the Base SCR model 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):

$$log(\sigma_{survey,ind}) = \sigma_0 + Male.effect_\sigma \times is.male_{survey,ind}$$

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 prior distribution with limits (0, 200) in meters.

Observation Model

The observation model describes how the observed data are obtained conditional on the spatial process model. For individuals with capture locations within the survey area X (i.e., the individual was available for capture), individual i is detected with probability of detection p, and for individuals with locations outside the survey area the model assumes that individual i is not available for capture for that occasion and $p = 0$. 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 site was modeled as survey- and sex-dependent:

$$p^* = \begin{cases} p_{survey,ind} & Inside\ survey\ area \\ 0 & Outside\ survey\ area \end{cases}$$

$$logit(p_{survey,ind}) = p_{0survey} + Male.effect_p \times is.male_{survey,ind}$$

Male effect was assigned an uninformative prior based on a uniform distribution with limits of (-3, 3) on the logit-scale.

Finally, capture histories were modeled as a set of Bernoulli outcomes:

$$y_{it}|u_i, z_i \sim Bernoulli(z_i * p(u_{it}))$$

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:

$$z_i \sim Bernoulli(\Psi)$$

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*. When z_i is equal to one, individual *i* considered as a member of the population and not included when z_i is equal to zero. The inclusion parameter Ψ is assumed uniformly distributed with limits of (0, 1). The derived population estimate, *N*, is then the sum of observed individuals, *n*, and the pseudo-individuals determined to be part of the population (where $z_i = 1$). Density, *D*, is derived from the resulting parameter estimate of *N*, which represents the number of individuals located within the extended sampled area, *S*:

$$D = N/A_S$$

Where A_s is the full area of the extended sampled area.

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

The SCR Three-day Locations model is equivalent to the Base SCR model, but it also integrates supplementary spatial data collected concurrently during the three-day surveys for each plot with the use of VHF radio-telemetry and GPS data loggers (Figure 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 failure, and we substituted data collected on subsequent days when available. Additionally, we leveraged all available data collected at each site during the three-day survey period by including location data for auxiliary tortoises not in the capture histories (i.e. known animals captured on a previous survey) to inform model parameters. In this model, supplementary data are used, in addition to capture locations, to inform model parameters s_i and σ. The supplementary locations provided considerably more information on how tortoises use space at each site, and for this model variation we were able to model the baseline spatial scale parameter σ_0 as a function of the primary survey as well as a function of sex:

$$log(\sigma_{survey,ind}) = \sigma_{0survey} + Male.effect_{\sigma} \times is.male_{survey,ind}$$

We assumed a larger spatial scale in this model given that the integrated telemetry and GPS data include all locations for animals collected over the survey period. We assume σ_0 is uniformly distributed with limits (0, 500) in meters.

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

The SCR Complete Telemetry model is equivalent to the SCR Three-day Locations model, however, this model integrates all available supplementary independent spatial data (after subsampling to reduce autocorrelation, see above) collected with the use of VHF radio-telemetry (Figure 2b). As in the previous model, both supplementary data and capture locations are 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. As in the previous model, the telemetry locations provided considerably more information on how tortoises use space at each site and for this model variation we were able to model the baseline spatial scale parameter σ_0 as a function of primary survey as well as a function of sex. Given that the integrated telemetry data were collected at a larger temporal scale (years vs. days), we assumed a larger spatial scale as an individual is likely to be recorded using more of its home range so it would follow suit that σ_0 is larger in this model variation. Here we assume σ_0 is uniformly distributed with limits (0, 500) in meters.

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.

Model 5: SCR Daily Movement

The fifth model variation is described by a unique spatial process model, where movement of individuals between capture occasions is described based on a distribution of daily movement. Daily movement distances used to inform the model were calculated from subsampled movement data collected with the use of GPS data loggers (see Movement Data section above). We fit the distribution based on average distance moved by an individual over a 24 hour period during the fall active season, and assume a gamma distribution on movement distances. Additionally, we leveraged all available data collected at each site during the fall active season by also including daily movement distances for tortoises not in the capture histories (i.e. known animals captured on a previous survey) to inform model parameters. The shape parameter of the daily movement distribution was assigned a prior based on a gamma distribution with shape and rate (0.001, 0.001), while the rate parameter was computed from the mean movement distance (*meandist*) and shape as:

$$rate_{survey,ind} = shape \div meandist_{survey,ind}$$

Where mean movement distance (*meandist*) is modeled as a function of primary survey and sex according to the model:

$$meandist_{survey,ind} = meandist_0 + site.effect_{survey} + male.effect_{dist} \times is.male_{survey,ind}$$

The movement process assumes an uncorrelated random walk process and unknown locations for individual i (observed or unobserved) were interpolated based on any known locations and the fitted movement process. For augmented individuals we assigned an initial location randomly with in the study area.

Implementation

Population parameters were estimated by fitting the models using a Bayesian framework implemented in R with BUGS (Bayesian Using Gibbs Sampling) using the JAGS software (Plummer 2017, R Core Team 2019). Estimation of the joint posterior distributions of the parameters was carried out using a Gibbs sampler, which is a Markov Chain Monte Carlo algorithm, and obtains a sample of the model parameters from the posterior distribution by Monte Carlo simulation after discarding a “burn-in” sample. To monitor convergence it is recommended that several independent chains are generated for each model parameter. Therefore, we ran three independent parallel chains for 5000 iterations each, with a "burn-in" of 30,000 iterations that were discarded. Posterior summaries were computed from the 15,000 total iterations from the three chains. We compare the posterior median and the 90% Bayesian credible interval based on the highest posterior density (HPD) for each of the candidate models.

Model Convergence and Performance

Model convergence was inspected by visually examining the trace plots and density plots, and calculating the Gelman-Ruban convergence diagnostic for each parameter. The Gelman-Rubin diagnostic analyzes the difference between independent chains for each of the estimated parameters and convergence is expected when the scale reduction factor for parameters is < 1.1 (Brooks and Gelman 1998, Gelman et al. 2013).

Model performance was assessed with the use of the Widely Applicable Information Criterion (WAIC) (Watanabe 2010). WAIC methods are comparable to other information criterion based methods including Akaike information criterion (AIC) and Deviation information criterion (DIC), however, WAIC is considered a more fully Bayesian and, therefore, preferable method for estimating out-of-sample prediction accuracy for fitted Bayesian models. As opposed to DIC methods which are based on a point estimate, WAIC uses the entire posterior distribution. Using WAIC methods, the expected log predictive density is estimated based on the log pointwise predictive density and a penalization term for the effective number of parameters in order to adjust for over-fitting (Gelman et al. 2014).

Results

Mark-Recapture Surveys

A total of 143 adult desert tortoises (>160 mm MCL) were captured at the ten study plots from 2015-2019. Specific breakdowns by primary survey (1-16) are provided in Table 3 and corresponding capture histories are included in Appendix 1. 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 twenty-four individuals recaptured (25.26%; n=95) between 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.

Movement Data

The number of individuals with supplementary location data varied based on model variation. Site specific information on individuals with telemetry and GPS data are provided in Table 3 with more detailed information provided in Appendix 1. The telemetry and GPS data were reduced using methods outlined above and model specific totals are provided in Table 4. For the Three-day model, 117 (81.1%, n=143) tortoises in the capture histories plus 10 auxiliary animals had locations collected with VHF-radio telemetry and/or GPS data loggers during corresponding survey periods resulting in 5825 total locations used to inform model parameters. Parameters from the Telemetry model were informed based on data from a total of 135 individuals (94.4%) in the capture histories with supplementary radio-telemetry data totaling 3890 occurrence records. For the Movement model, data from GPS loggers attached to 113 (79%) individuals in the capture histories as well as 47 auxiliary tortoises resulted in 10,757 locations recorded over the fall active season that were used to inform the daily movement model.

Spatial Capture Recapture

Model Convergence and Performance

The Gelman-Ruban convergence diagnostic for all relevant parameters was < 1.1, and therefore expected to have converged (Gelman et al. 2013). Additionally, trace plots of model parameters were heteroscedastic and where expected, density plots converged on a single peak. However, 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.

Overall, the best performing model according to WAIC was Model 4a: SCR Complete Telemetry assuming constant probability of detection per primary survey. WAIC scores and associated metrics for each candidate model are reported in Table 5. 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 didn’t 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 equivalent model variation where probability of detection was assumed constant. We report all results hereafter for model variations (1a, 2a, 3a, 4a, & 5) 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 6 (see Appendix 2 for Model 1b, 2b, 3b, & 4b results), and density estimates for all 16 primary surveys are visualized in Figure 3. The Non-spatial model generally resulted in higher median estimates of density than the standard SCR models (Models 2-4), while median estimates from the Non-spatial and Movement models were similar (Figure 3), ranging from 2.88 to 29.8 and 3.55 to 28.4 adults per km^2, respectively. 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 26.33 and 3.55 to 27.66 adults per km^2, respectively. While the Telemetry model resulted in the lowest median estimates and ranged from 2.07 to 26.33 tortoises per km^2. However, results from the Telemetry model were biased low due to positive bias in the estimated spatial scale parameter for this model (see below). Uncertainty in density estimates, measured as differences in the width of the HPD intervals, were 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 Telemetry models resulted in less uncertainty than the Non-spatial model. The Movement model generally resulted in the most uncertainty in density estimates.

Posterior estimates for the spatial scale parameter σ varied based on model variation, as well as primary survey (Figure 4; Table 6). 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 7.28-86.27%, respectively, than the 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 70.90 m, while for the Three-day model median estimates of σ overlapped this estimate and ranged from 24.27 m for Survey 5 (McCullough Pass in 2015) to 226.92 m for Survey 3 (ISEGS N in 2019). For the Telemetry model, median estimates of σ ranged from 84.37 m for Survey 5 to 244.73 m for Survey 3. 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 (Figure 4). Across all models that incorporated a male effect on σ (Models 2, 3, & 4), estimated use areas were larger for males. This resulted in use areas that were approximately 1.3 times larger than females for the Base model, 1.99 times larger for the Three-day model, and 1.49 times larger for the Telemetry model.

For the Movement model median estimates of the *meandist* parameter were 47.17 m and the male effect on movement was 49.4 m, indicating that males move more than females at the study plots. Median site effects ranged from -27 m for Survey 5 to 24.39 m for Survey 8 (SouthPah in 2017). Fitted gamma distributions based on median posterior estimates for each primary survey are visualized in Figure 5. There is slight variation between surveys but in general all distributions are heavily skewed toward zero to very short average daily movement distances. Only the surveys with the two lowest site effects (Surveys 5 and 6) followed similar trends to the posterior estimates of σ above, signifying a consistent use of space across individuals and temporal scales for this site (McCullough Pass). Differences for the other surveys are likely due to the larger number of auxiliary animals used to estimate these parameters for this model (Table 4; Appendix 1).

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 Telemetry models all resulted in higher estimated probability of detection within the plot boundaries. However, the 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, & 14) reaching 100% detection rates within the surveyed area. Additionally, the median male 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 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 that were used to inform each model (Figure 6). Estimated activity centers were visually representative of the center of an individual's utilization distribution for the corresponding spatial data. For the 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 Telemetry models due to the different temporal scales of supplementary spatial data, thus demonstrating the importance of matching the temporal scale of supplementary data to the temporal scale of surveys for this species.

Discussion

In this study we developed five model variations of increasing complexity that integrate different levels of information, and we compare estimates of density from each of these models 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 in estimates by not explicitly accounting for space use of this species. In general, model performance improved with increasing complexity and higher levels of integrated spatial information; however, the model that incorporated the highest level of supplementary data, Model 5: SCR Daily Movement, did not follow this trend, which we discuss below.

Additionally, by integrating various temporal levels of supplementary spatial data to inform model parameters, our study highlights that the temporal scale of supplementary spatial 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 lead to positively biased estimates of the spatial scale parameter σ, which in turn lead to positively biased detection probabilities and negatively biased density estimates. 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, which is especially true for a threatened species such as the Mojave desert tortoise.

Historically, conventional mark-recapture methods have been used to monitor density for the desert tortoise at permanent study plots based on 60-day search-encounter surveys consisting of a 30-day marking phase followed by a 30-day recapture phase, with 1 mi^2 (2.6 km^2) plots being covered by 1-2 persons over those time periods (Berry and Nicholson 1984, Berry 1986b). Tortoise activity is highly seasonal (Zimmerman et al. 1994, Nussear and Tracy 2007), being driven by climate and resource availability and changes over a 60-day window (Duda et al. 1999, Inman et al. 2009), thereby complicating the homogeneous capture probability assumption. Natural history, and extensive field experience suggest that this species (as do many species) violates additional assumptions of conventional mark-recapture models. This includes geographic closure due to temporary emigration and lack of physical boundaries to surveyed areas, as well as homogeneous detection probability due to edge effects where individuals on the periphery of the surveyed area are less likely to be detected than those in the center (Figure 6; 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). For the desert tortoise these violations complicate standard mark-recapture approaches and often translate to positively biased density estimates. This occurs because conventional non-spatial models do not include an explicit process to account for space use on or off a survey plot, and thereby assume that any individual captured on any occasion but missed on another should have been available for capture, resulting in negatively biased detection probabilities, and ultimately a higher number of estimated undetected individuals. Our results confirm this (Figure 3; Table 6), demonstrating that in most cases conventional methods result in inflated estimates of density for this species because every encountered individual is “confined” to the area surveyed, while GPS data collected over the same period show that tortoises violate geographic closure assumptions by crossing arbitrary plot boundaries (Figure 6). However, we found that at sites 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; Figure 4), conventional non-spatial methods result in similar estimates of density to the standard SCR models (Figure 3; Table 6) because the geographic closure assumption is being met in this instance. Although, 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 (Figure 4).

Population density and space use are both important measures that are used to make informed decisions regarding conservation and management of a species in question and arguably, both metrics are highly correlated. SCR combines concepts of employing space use to determine the probability of detection based on location data from individuals in the population, and in doing so can provide spatially corrected density estimates (Efford 2004, Royle and Young 2008, Efford and Fewster 2013, Royle et al. 2014). Increasingly, studies have demonstrated that SCR models outperform their conventional non-spatial counterparts in terms of accuracy and precision by taking into account space use of study animals and can provide unambiguous estimates of density, especially for rare and elusive species (Efford 2004, Royle and Young 2008, Royle et al. 2009, Kéry et al. 2010, Romairone et al. 2018). The foundation of these models is the assumption that each individual has an activity center around which their movements are centered as defined by a spatial scale parameter, and for a species like the desert tortoise that demonstrates high site fidelity this assumption is easily met (Freilich et al. 2000). In line with previous studies, our standard SCR models generally resulted in spatially corrected estimates of density by taking into account where and how tortoises use space, and in doing so ultimately provide a more accurate estimate (Royle and Young 2008, Royle et al. 2014).

Additional studies have extended SCR models and demonstrated that integrating supplementary location data to further inform how individuals use space can lead to additional improvements of model performance and accuracy of estimates (Sollmann et al. 2013b, Royle et al. 2013, Tenan et al. 2017). To date these results have been based on trapping studies and simulations carried out over extend periods of time (months vs.

days) and have relied on supplementary locality data from a few individuals to extrapolate space usage for the entire population (2 individuals in Tenan et al. 2017; 3 in Sollmann et al. 2013a and Royle et al. 2013; 4-8 in Paterson et al. 2019; 6-8 in Linden et al. 2018 44 in Sollmann et al. 2013b). 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 94.4% (n=135), and GPS data for as much as 79% (n=113) of all tortoises in our capture histories to inform space use as a function of primary survey and sex. Activity centers and space use in our SCR models were calculated based on locations collected over various time periods. This included only spatial capture locations in the Base model, spatial capture locations and telemetry/GPS data collected concurrently during the three-day survey period in the Three-day model, and spatial capture locations and telemetry data collected over multiple years in the Telemetry model, resulting in estimated activity centers and use areas that are more representative of true space use for individuals at our study plots. However, more data are not necessarily better, and our results indicate that if not properly specified, the temporal scale of supplementary data used to inform SCR models has the potential to introduce an unintended source of bias (Figure 6). Based on model performance metrics (i.e. WAIC; Table 5) the Telemetry model appears to be the best model resulting in lower median densities and more precision (Figure 3; Table 6), but we contend that this model ultimately resulted in negatively biased density estimates. By incorporating supplementary telemetry data collected over multiple years to describe activity areas and define the spatial scale parameter, those areas may equate to an actual home range, but are based on how a tortoise uses space at a much larger temporal scale than for the three-day period that our mark-recapture surveys were conducted over. Desert tortoises do not use the entirety of their home range over a three day period, and in fact are not known to be very active, spending approximately 98% of their life inactive underground (Marlow 1979, Nagy and Medica 1986, Nussear and Tracy 2007). GPS data collected during the fall active season at our plots indicates that approximately 70% of the time tortoises do not move from day to day, so even during the time of year that is considered an "active period" tortoises are not likely to move much, if at all. Hence, by incorporating home range scale data the Telemetry model overestimated the spatial scale parameter and in doing so biased probability of detection within the plot boundaries high by accounting for missed captures off the plot too frequently. This resulted in negatively biased estimates of undetected individuals and overall density. For a species characterized by low activity, such as the desert tortoise, 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.

In the Movement model we stepped away from the activity center assumption and missing capture locations were estimated based on how far a tortoise is likely to move in a day by drawing a movement distance from a fitted gamma distribution of average daily movements collected during the fall active season so as to align with the timing of our surveys (Figure 5). The goal of this novel model variation was to fit a distribution that could be applicable range-wide for the desert tortoise, thereby eliminating the need to monitor movement of individuals and reducing the time and associated cost of doing so. However, not surprisingly, this distribution of daily movements is heavily skewed towards zero to very short movements for this species (Figure 5), and this model essentially equates to the Non-spatial model in that tortoises are most often estimated to not move between captures and remain on the plot (Figure 3). While this model allowed for differences in activity as a function of sex and site, this approach assumed that individuals act similarly throughout the fall active season from year to year as the distribution of daily movements was estimated from data collated from multiple years. Not only are tortoise activity and movement affected by variations in climate and resource availability from year to year in the Mojave Desert (Duda et al. 1999, Freilich et al. 2000, Nussear and Tracy 2007), they are also driven by daily fluctuations in temperature and precipitation (Medica et al. 1980, Ruby et al. 1994, Zimmerman et al. 1994, Freilich et al. 2000). Given this variability, an approach that mutes variance in movements through averaging across years is likely not effective, and in this case, results in an additional source of unmodeled heterogeneity in probability of detection for this species. By focusing on location data collected over the same time period as the surveys are conducted, the Base and Three-day models account for fluctuations in activity at the daily level and we argue, reduce bias in estimates. However, for a species that is less prone to daily changes in environmental conditions and doesn’t meet the activity center assumption of standard SCR models, such as some mammal populations (Beisiegel and Mantovani 2006, Edwards et al. 2009, Nandintsetseg et al. 2019), the Movement model could be a good alternative to a standard SCR model and once a representative distribution of movement is complied, has the potential to be applied to describe movement of unmarked individuals.

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 (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 not always feasible. While a long-term dataset on movement can be valuable for numerous reasons (Hebblewhite and Haydon 2010), this research demonstrates that it is not necessary in order to obtain accurate and unambiguous estimates of density for the desert tortoise. Based on our study design the Three-day model resulted in the least bias in estimates by taking into account how individuals use space over the same three-day period as surveys. By integrating supplementary locality data collected over the three-day period the spatial scale parameter σ was estimated separately for each primary survey. This provided an accurate and precise estimate of space use by individuals during each primary survey (Figure 4a), which was used to estimate density with more accuracy. Previous studies have demonstrated that not only does space use by desert tortoises vary by sex but there is also high variability among populations (Berry 1986a), and our results corroborate this (Figure 4). However, obtaining movement data even at a three-day resolution comes with some cost as purchasing and attaching/removing equipment can be expense and also 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 (Figure 3) and median estimates between the two models were similar (Table 6); hence, this model could be a suitable alternative when a small loss in accuracy (median estimates differed by 0-1.77 adult per km^2) isn't worth the high cost and time commitment associated with collecting movement 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 a very low rate of recapture, 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 (Figure 3; Table 6). The majority of "new" animals detected on the second round of surveys were large adults (see Appendix 1) 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 is comprised of hard calcium carbonate and due to its high integrity excavations typically consist of multiple tunnels and are generally much longer than soil burrows making detection more difficult (Riedle et al. 2008, Mack et al. 2015). Differences in detectability between shelter site types further emphasizes that this species regularly violates statistical assumptions of mark-recapture methods, which complicates standard approaches.

Another potential confounding factor in our models includes sources of unmodeled heterogeneity due to behavioral response to capture. Trap response is a behavioral response common in mark-recapture studies where animals are disturbed and physically handled and 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. Although, the potential does exist in our study 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 (*Gopherus morafkai*) 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 (Figure 6) and estimates of the spatial scale parameter from the Three-day model based on those data (Figure 4; Table 6) indicate that behavior of tortoises was likely not affected as most did not move large distances after being handled in our study.

Median densities based on the preferred model, the Three-day model, at our plots ranged from 3.55 adults per km^2 for Survey 13 (Silver State in 2015) to 27.66 for Survey 6 (McCullough Pass in 2018) (Table 6). With respect to the entirety of this species' range our plots are concentrated in the same general area yet our results indicate considerable spatial differences in density between 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 methods for monitoring desert tortoise populations are occurring at a much larger spatial scale. Since 1999, density metrics for the desert tortoise have been estimated using distance sampling methods throughout the range (Allison and McLuckie 2018). These surveys are conducted in designated Tortoise Conservation Areas (TCAs) and estimates are calculated based on encounter rates and adjusted post hoc for imperfect detection of individuals located farther from the transect centerline (Buckland et al. 2001, Anderson et al. 2001). While they do 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. 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 densities reported from these TCAs (Allison and McLuckie 2018). Our findings highlight the importance of focused sampling for this species as identifying fine-scale changes in population parameters requires monitoring at a fine-scale level.

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, Allison and McLuckie 2018, Stanford et al. 2018). 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, U.S. Fish and Wildlife Service 2011). Based on our results, conventional mark-recapture approaches lead to inflated estimates of density and false precision in estimates for this species due to complications from violated assumptions such as unmodeled spatial heterogeneity in capture probability and temporary emigration. By incorporating spatial capture histories and supplementary location data, SCR methods can account for these violations and provide more reliable estimates of desert tortoise density (Efford, 2004; Royle & Young, 2008). However, if not properly specified, the temporal scale of supplementary location data used to inform model parameters may result in an additional unintended source of bias. Incorporating spatial data at the same scale as surveys resulted in accurately described space use and ultimately, less bias in estimates in the Three-day model. Although, our results demonstrate that for a three-day survey for the desert tortoise, a species characterized by low activity levels (Marlow 1979, Nagy and Medica 1986, Nussear and Tracy 2007) and short distance movements (Figure 5; Duda et al. 1999), the Base model generally resulted in similar estimates to the preferred model. Thus, we suggest that the Base model can provide a cost efficient solution to calculating spatially corrected densities for this species as the only additional components necessary are spatial capture histories, which are generally recorded as an element of mark-recapture surveys. These results not only demonstrate the importance of accounting for spatial information, but also the value of understanding model specification when estimating density for the desert tortoise, and have the potential to enhance the efficacy of long-term efforts to monitor population trends and inform recovery efforts.

TABLE 1. Survey numbers, plot names, years surveyed, and survey dates. For any three-day survey at a plot a unique survey number is designated.

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

TABLE 2. Model variations and descriptions.

Model	Description/Data		Detection Probability *p*	Male effect *p*	Spatial scale parameter *σ/meandist*	Male effect *σ/meandist*
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
5) **SCR Daily Movement**	Spatial capture histories and averaged daily GPS movement data		By survey	Yes	By survey	Yes

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	Model 5: Individuals with GPS
(1)	7	5	2	0		7	7	10
(2)	8	2	5	1		4	7	20
(3)	5	2	3	0	3	14	5	20
(4)	6	3	1	2		14	4	6
(5)	19	9	8	2		15	16	27
(6)	26	12	13	1	11	24	26	27
(7)	17	10	6	1		17	16	17
(8)	12	7	5	1		10	12	12
(9)	9	3	5	1	4	6	8	12
(10)	3	2	1	0		3	3	6
(11)	8	7	1	0	1	7	8	6
(12)	18	12	6	0		18	18	25
(13)	2	0	2	0		6	2	17
(14)	12	5	4	3	1	18	9	17
(15)	6	2	3	1		8	6	6
(16)	9	5	4	0	4	7	9	6

TABLE 4. Supplementary location data by model variation. Overall, there were 143 unique tortoises captured.

	Model 3: Individuals with GPS/ telemetry	Model 4: Individuals with telemetry	Model 5: Individuals with GPS
Captured individuals	117	135	113
Auxiliary tortoises	10	0	47
Supplementary locations	5825	3890	10757
Average locations per individual	46	29	67

TABLE 5. Model performance. 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.

Model	WAIC	SE	ΔWAIC	WAICwt	*p*WAIC
4a: SCR Complete Telemetry	654.63	29.23	0	1	120.79
4b: SCR Complete Telemetry, heterogeneous detection probability	707.00	32.95	52.37	0	169.59
3a: SCR Three-day Locations	750.16	32.75	95.53	0	89.61
2a: Base SCR	779.57	32.58	124.94	0	95.67
5: Daily Movement	801.07	33.92	146.44	0	96.22
3b: SCR Three-day Locations, heterogeneous detection probability	863.51	39.89	208.88	0	171.66
1a: Non-spatial	869.75	34.54	215.12	0	59.30
2b: Base SCR, heterogeneous detection probability	910.25	42.10	255.62	0	192.05
1b: Non-spatial, heterogeneous detection probability	1014.8	44.83	360.17	0	171.54

TABLE 6. Joint posterior summaries of model parameters representing the median and 90% highest posterior density credible interval [5%, 95%]. Primary surveys are identified by numbers (1-16), which correspond to the primary survey numbers listed in Table 1. See Appendix 2 for Model 1b, 2b, 3b, and 4b results.

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, 0.83]	0.49 [0.01, 0.97]	1.18 [0.54, 1.85]
Individual effect: p *(logit-scale)*	------------------	------------------	------------------	------------------
Male effect: σ *(log-scale)*	------------------	0.27 [0.12, 0.42]	0.69 [0.66, 0.71]	0.4 [0.37, 0.43]
Global σ (m)	------------------	70.9 [63.64, 78.32]	------------------	------------------
(1) p	0.53 [0.32, 0.74]	0.78 [0.54, 1]	0.76 [0.53, 0.96]	0.76 [0.5, 1]
σ (m)	------------------	------------------	57.83 [53.95, 61.83]	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, 9.76]	5.92 [2.66, 9.17]	4.88 [2.22, 7.54]
(2) p	0.76 [0.61, 0.9]	0.86 [0.71, 1]	0.88 [0.73, 0.99]	0.91 [0.75, 1]
σ (m)	------------------	------------------	68.67 [64.54, 72.68]	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 [3.55, 10.36]	6.66 [3.55, 10.06]	5.18 [2.66, 7.69]
(3) p	0.5 [0.26, 0.74]	0.59 [0.32, 0.9]	0.81 [0.53, 1]	0.75 [0.43, 1]
σ (m)	------------------	------------------	226.92 [217.3, 236.77]	244.73 [231.79, 257.64]
Ψ	0.06 [0.02, 0.11]	0.05 [0.02, 0.09]	0.03 [0.01, 0.06]	0.03 [0.01, 0.06]
Density	5.77 [4.81, 7.69]	5.03 [1.92, 8.73]	3.25 [1.33, 5.47]	3.25 [1.33, 5.77]
(4) p	0.59 [0.37, 0.8]	0.81 [0.57, 1]	0.87 [0.63, 1]	0.86 [0.62, 1]
σ (m)	------------------	------------------	97.86 [83.45, 114.51]	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 [0.23, 0.54]	0.34 [0.2, 0.49]	0.27 [0.13, 0.43]
σ (m)	------------------	------------------	24.27 [23.48, 25.12]	92.7 [89.55, 95.95]
Ψ	0.25 [0.16, 0.35]	0.22 [0.13, 0.32]	0.24 [0.15, 0.36]	0.23 [0.13, 0.36]
Density	24.03 [19.22, 31.72]	21.75 [12.87, 31.51]	23.52 [14.2, 34.17]	23.08 [13.31, 35.8]
(6) p	0.45 [0.33, 0.57]	0.47 [0.34, 0.61]	0.45 [0.33, 0.59]	0.39 [0.25, 0.53]
σ (m)	------------------	------------------	28.69 [27.61, 29.77]	84.37 [81.89, 86.87]

Parameter	**Model 5 SCR Daily Movement**
Male effect: p *(logit-scale)*	0.43 [-0.07, 0.9]
meandist (m)	47.17 [39.69, 54.37]
Male effect: movement (m)	49.4 [46.82, 51.82]
Global shape	0.53 [0.52, 0.54]
(1) p	0.65 [0.39, 0.9]
site effect (m)	11.9 [1.54, 22.89]
Ψ	0.07 [0.03, 0.11]
Density	6.8 [3.11, 10.65]
(2) p	0.8 [0.63, 0.96]
site effect (m)	-5.3 [-13.48, 2.81]
Ψ	0.08 [0.04, 0.12]
Density	7.54 [3.7, 11.39]
(3) p	0.58 [0.28, 0.88]
site effect (m)	-5.48 [-13.89, 2.47]
Ψ	0.06 [0.02, 0.1]
Density	5.47 [2.07, 9.62]
(4) p	0.77 [0.52, 1]
site effect (m)	-4.03 [-15.06, 7.94]
Ψ	0.06 [0.02, 0.1]
Density	5.77 [2.81, 9.62]
(5) p	0.35 [0.21, 0.51]
site effect (m)	-27 [-34.53, -19.41]
Ψ	0.24 [0.14, 0.35]
Density	23.52 [14.05, 34.02]
(6) p	0.46 [0.33, 0.59]
site effect (m)	-26.73 [-34.39, -19.35]

Parameter		Model 1a Non-spatial	Model 2a Base SCR	Model 3a SCR Three-day Locations	Model 4a SCR Complete Telemetry
	Ψ	0.3 [0.21, 0.4]	0.26 [0.18, 0.36]	0.28 [0.18, 0.37]	0.26 [0.17, 0.37]
	Density	29.8 [24.99, 35.56]	26.33 [18.2, 35.35]	27.66 [18.93, 36.83]	26.33 [17.6, 35.95]
(7)	*p*	0.5 [0.35, 0.65]	0.58 [0.41, 0.76]	0.52 [0.34, 0.68]	0.65 [0.45, 0.85]
	σ (m)	------------------	------------------	47.93 [45.84, 50.17]	141.96 [134.54, 149.46]
	Ψ	0.19 [0.12, 0.27]	0.16 [0.1, 0.22]	0.16 [0.1, 0.24]	0.12 [0.08, 0.18]
	Density	18.26 [16.34, 22.11]	15.53 [9.91, 21.6]	16.42 [10.5, 23.08]	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)	------------------	------------------	42.02 [40.62, 43.37]	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 [6.21, 14.94]	10.8 [6.36, 15.53]	7.99 [4.73, 11.39]
(9)	*p*	0.79 [0.64, 0.91]	0.76 [0.6, 0.9]	0.76 [0.6, 0.9]	0.77 [0.59, 0.94]
	σ (m)	------------------	------------------	62.73 [59.14, 66.17]	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, 0.19]	0.04 [0, 0.24]
	σ (m)	------------------	------------------	79.15 [64.93, 95.19]	149.85 [131.57, 168.29]
	Ψ	0.23 [0.01, 0.75]	0.22 [0.01, 0.71]	0.23 [0.01, 0.76]	0.16 [0.01, 0.67]
	Density	22.11 [2.88, 74.97]	21.67 [1.18, 71.15]	23.22 [1.04, 76.18]	15.68 [0.59, 67.46]
(11)	*p*	0.26 [0.06, 0.45]	0.25 [0.05, 0.46]	0.21 [0.04, 0.42]	0.21 [0.02, 0.51]
	σ (m)	------------------	------------------	44.97 [36.6, 53.95]	205.29 [193.56, 217.62]
	Ψ	0.14 [0.05, 0.27]	0.12 [0.04, 0.25]	0.13 [0.04, 0.27]	0.09 [0.02, 0.2]
	Density	12.5 [7.69, 24.99]	12.13 [4.14, 24.7]	12.57 [4.44, 26.92]	8.65 [2.81, 20.12]
(12)	*p*	0.53 [0.39, 0.68]	0.58 [0.41, 0.74]	0.63 [0.46, 0.8]	0.74 [0.54, 0.93]
	σ (m)	------------------	------------------	72.79 [70.54, 75.04]	198.4 [191.27, 206.2]
	Ψ	0.2 [0.13, 0.27]	0.17 [0.1, 0.23]	0.15 [0.09, 0.21]	0.11 [0.07, 0.16]
	Density	19.22 [17.3, 22.11]	16.42 [10.5, 22.49]	14.94 [9.91, 20.56]	11.09 [7.25, 14.94]
(13)	*p*	0.3 [0.01, 0.62]	0.5 [0.08, 0.93]	0.34 [0.01, 0.68]	0.61 [0.19, 1]
	σ (m)	------------------	------------------	26.58 [25.58, 27.64]	193.6 [176.16, 211.45]
	Ψ	0.04 [0, 0.16]	0.03 [0, 0.08]	0.04 [0, 0.13]	0.02 [0, 0.06]
	Density	2.88 [1.92, 14.42]	2.81 [0.3, 7.69]	3.55 [0.44, 13.17]	2.07 [0.3, 5.47]
(14)	*p*	0.53 [0.36, 0.69]	0.63 [0.43, 0.82]	0.69 [0.51, 0.87]	0.78 [0.56, 1]
	σ (m)	------------------	------------------	64.29 [62.07, 66.46]	176.02 [165.98, 186.29]
	Ψ	0.14 [0.08, 0.2]	0.11 [0.06, 0.17]	0.1 [0.06, 0.15]	0.08 [0.04, 0.12]
	Density	12.5 [11.53, 15.38]	10.95 [6.36, 15.98]	10.21 [6.07, 14.94]	7.84 [4.59, 11.39]

Parameter		Model 5 SCR Daily Movement
	Ψ	0.28 [0.19, 0.38]
	Density	28.4 [19.67, 37.72]
(7)	*p*	0.54 [0.37, 0.72]
	site effect (m)	-19.54 [-27.2, -11.95]
	Ψ	0.17 [0.11, 0.25]
	Density	17.16 [10.65, 23.67]
(8)	*p*	0.69 [0.51, 0.86]
	site effect (m)	24.39 [14.05, 34.37]
	Ψ	0.11 [0.06, 0.16]
	Density	10.8 [6.36, 15.53]
(9)	*p*	0.77 [0.61, 0.9]
	site effect (m)	21.85 [11.88, 31.71]
	Ψ	0.08 [0.04, 0.13]
	Density	8.14 [4.14, 11.98]
(10)	*p*	0.04 [0, 0.2]
	site effect (m)	7.76 [-5.5, 22.36]
	Ψ	0.23 [0.01, 0.73]
	Density	23.08 [1.18, 73.37]
(11)	*p*	0.23 [0.04, 0.44]
	site effect (m)	6.53 [-6.28, 20.2]
	Ψ	0.13 [0.04, 0.26]
	Density	12.43 [4.14, 25.74]
(12)	*p*	0.6 [0.43, 0.78]
	site effect (m)	10.33 [2.03, 18.98]
	Ψ	0.17 [0.11, 0.24]
	Density	16.86 [10.65, 22.78]
(13)	*p*	0.36 [0.01, 0.71]
	site effect (m)	3.3 [-5.57, 12.61]
	Ψ	0.04 [0, 0.14]
	Density	3.55 [0.3, 13.46]
(14)	*p*	0.57 [0.38, 0.78]
	site effect (m)	3.97 [-5.16, 13.11]
	Ψ	0.12 [0.07, 0.18]
	Density	11.83 [7.1, 17.46]

Parameter	Model 1a Non-spatial	Model 2a Base SCR	Model 3a SCR Three-day Locations	Model 4a SCR Complete Telemetry
(15) *p*	0.6 [0.4, 0.81]	0.6 [0.36, 0.82]	0.59 [0.35, 0.8]	0.7 [0.43, 0.97]
σ (m)	------------------	------------------	60.78 [57.23, 64.55]	218.76 [202.62, 235.08]
Ψ	0.07 [0.03, 0.11]	0.06 [0.03, 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 [2.81, 9.91]	4.14 [1.92, 6.95]
(16) *p*	0.6 [0.42, 0.78]	0.62 [0.43, 0.82]	0.64 [0.43, 0.84]	0.74 [0.5, 0.99]
σ (m)	------------------	------------------	55.46 [50.58, 60.41]	225.45 [206.71, 243.42]
Ψ	0.1 [0.05, 0.15]	0.08 [0.04, 0.13]	0.08 [0.04, 0.13]	0.06 [0.03, 0.09]
Density	8.65 [8.65, 10.57]	8.28 [4.59, 12.87]	8.14 [4.44, 12.43]	5.62 [3.11, 8.58]

Parameter	Model 5 SCR Daily Movement
(15) *p*	0.6 [0.36, 0.82]
site effect (m)	1.09 [-10.21, 11.64]
Ψ	0.06 [0.02, 0.11]
Density	6.21 [2.81, 10.36]
(16) *p*	0.61 [0.39, 0.81]
site effect (m)	0.98 [-9.84, 12.07]
Ψ	0.09 [0.04, 0.14]
Density	8.88 [4.59, 13.46]

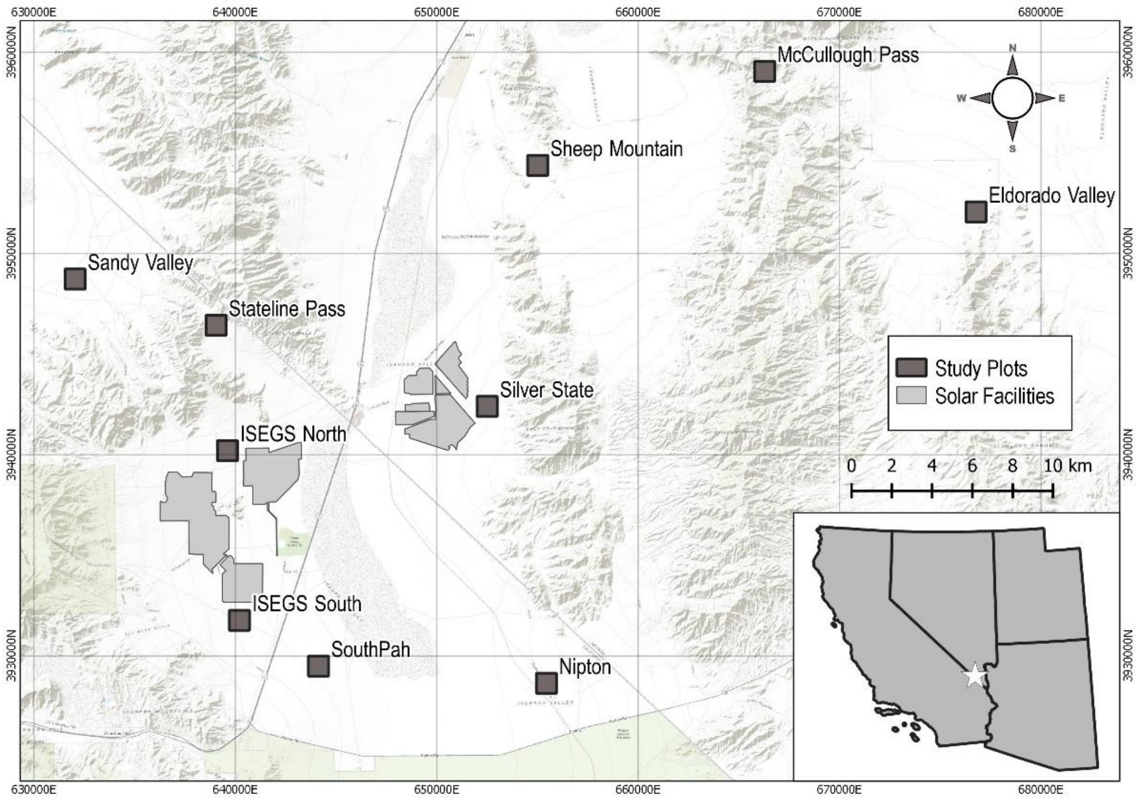

FIGURE 1. Location of the ten study plots in the Ivanpah Valley of CA and NV, U.S.A.

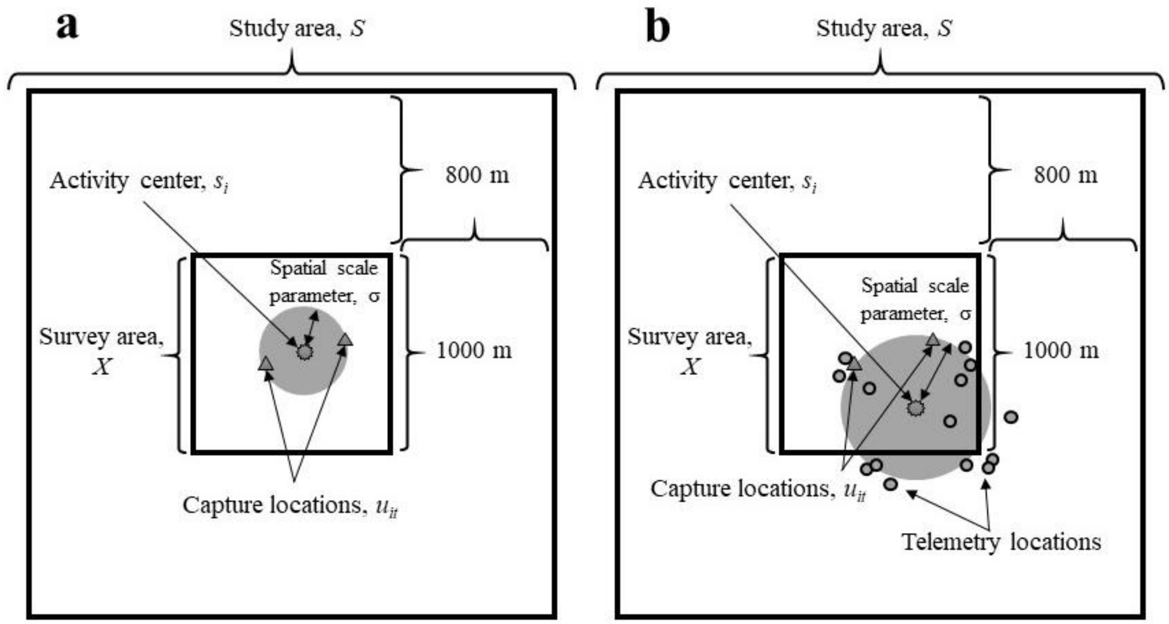

FIGURE 2. Schematic representation of the extended sampled area, *S*, and relevant model parameters for (a) Model 2: Base SCR and (b) Model 3: SCR Three-day Locations and Model 4: SCR Complete Telemetry. For Model 3 and 4 corresponding activity areas will be at different scales due to the differences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

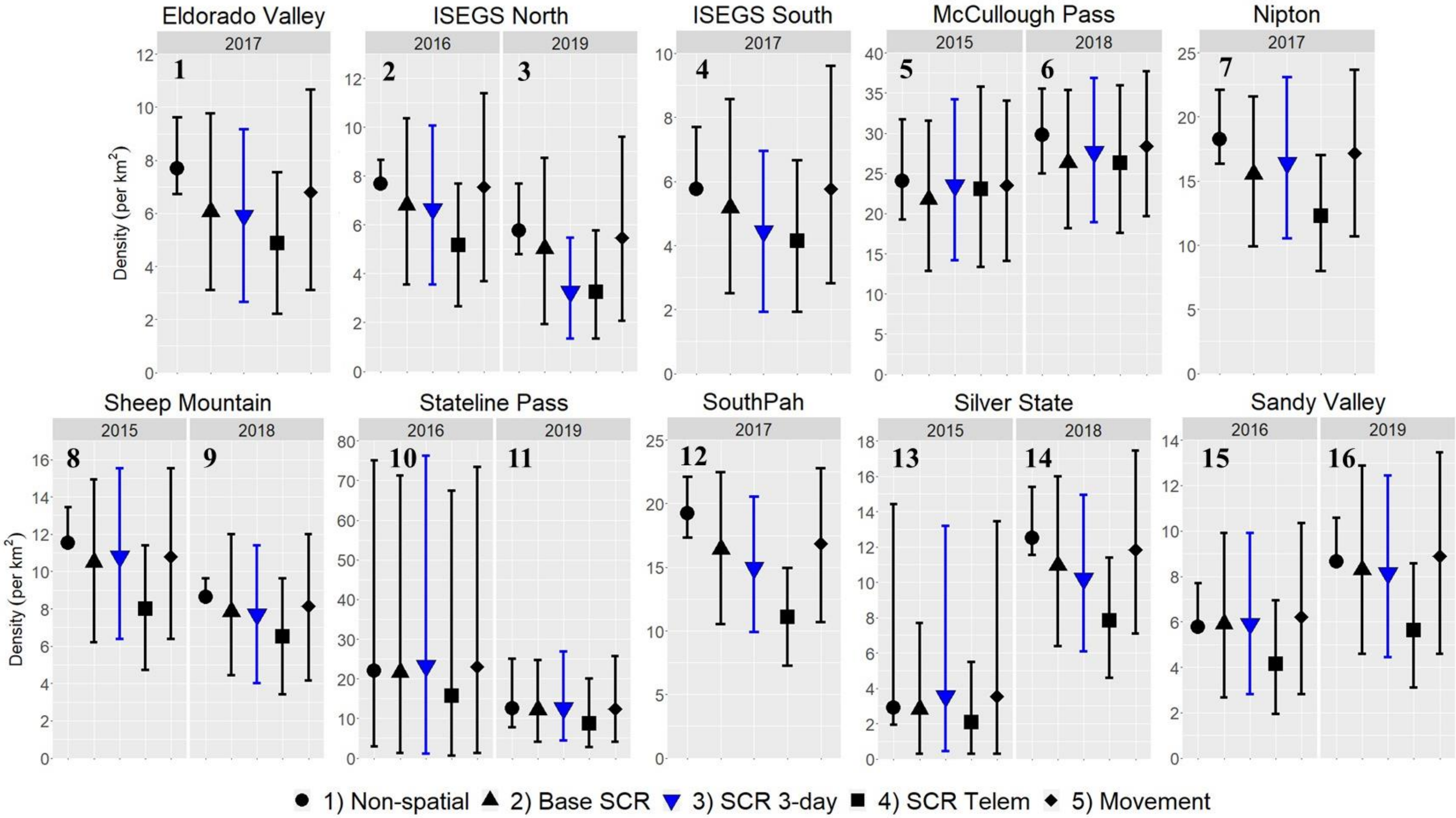

FIGURE 3. Joint posterior estimates of density representing the median and 90% highest posterior density credible interval. Results are grouped by site and survey year with different model variations displayed from left to right for each year as follows: 1) Model 1a: Conventional Non-spatial, 2) Model 2a: Base SCR, 3) Model 3a: SCR Three-day Locations, 4) Model 4a: SCR Complete Telemetry, and 5) Model 5: SCR Daily Movement. 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.

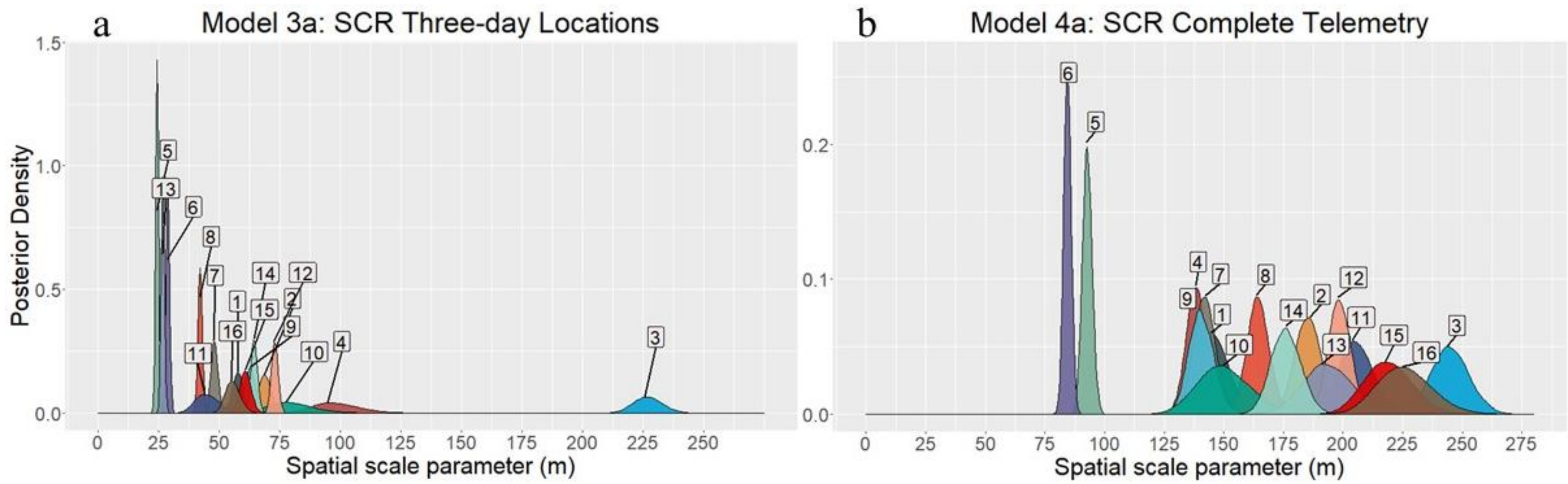

FIGURE 4. Joint posterior estimates of sigma for a female desert tortoise for each primary survey based on (a) Model 3: SCR Three-day locations and (b) Model 4: SCR Complete Telemetry. Primary surveys are identified by numbers (1-16), which correspond to the primary survey numbers listed in Table 1.

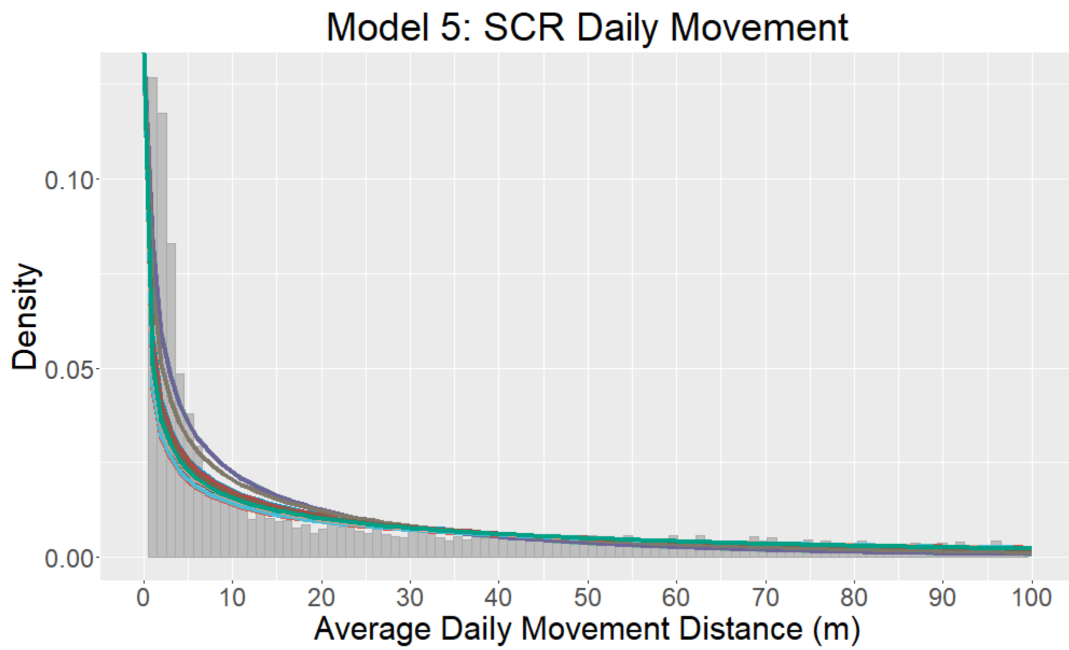

FIGURE 5. Fitted gamma distributions representing fall active season daily movement distances for a female desert tortoise for each primary survey based on joint posterior estimates from Model 5: SCR Daily Movement. Distributions are overlaid on all subsampled desert tortoise average daily movement distances collected with GPS-data loggers that were used to inform model parameters.

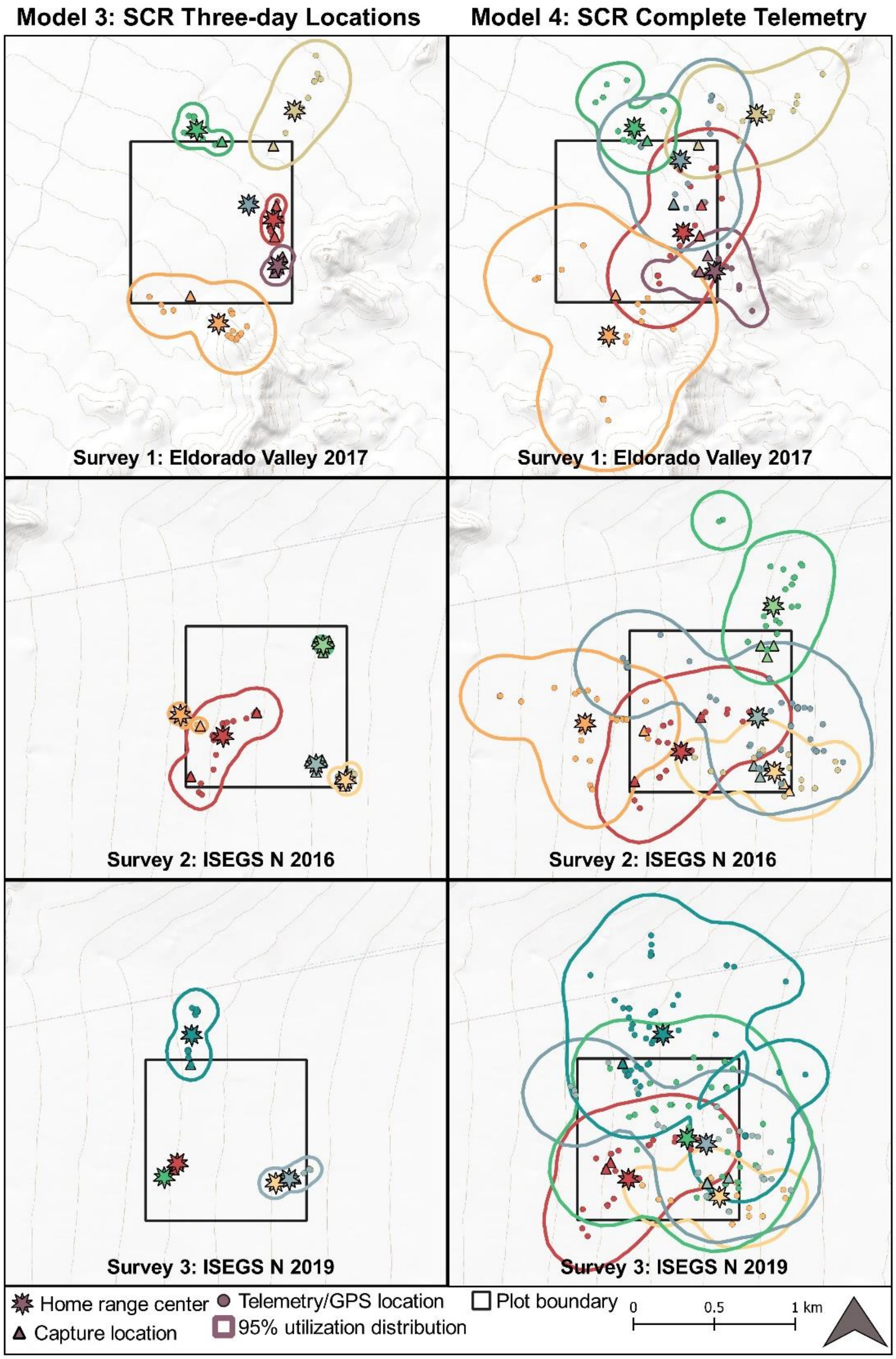

FIGURE 6. Actual capture locations, supplemental telemetry/GPS locations used to inform model parameters, and estimated home range centers from the joint posterior distribution based on Model 3: SCR Three-day Locations on the left and Model 4: SCR Complete Telemetry on the right with corresponding estimated 95% utilization distributions for tortoises located during representative surveys.

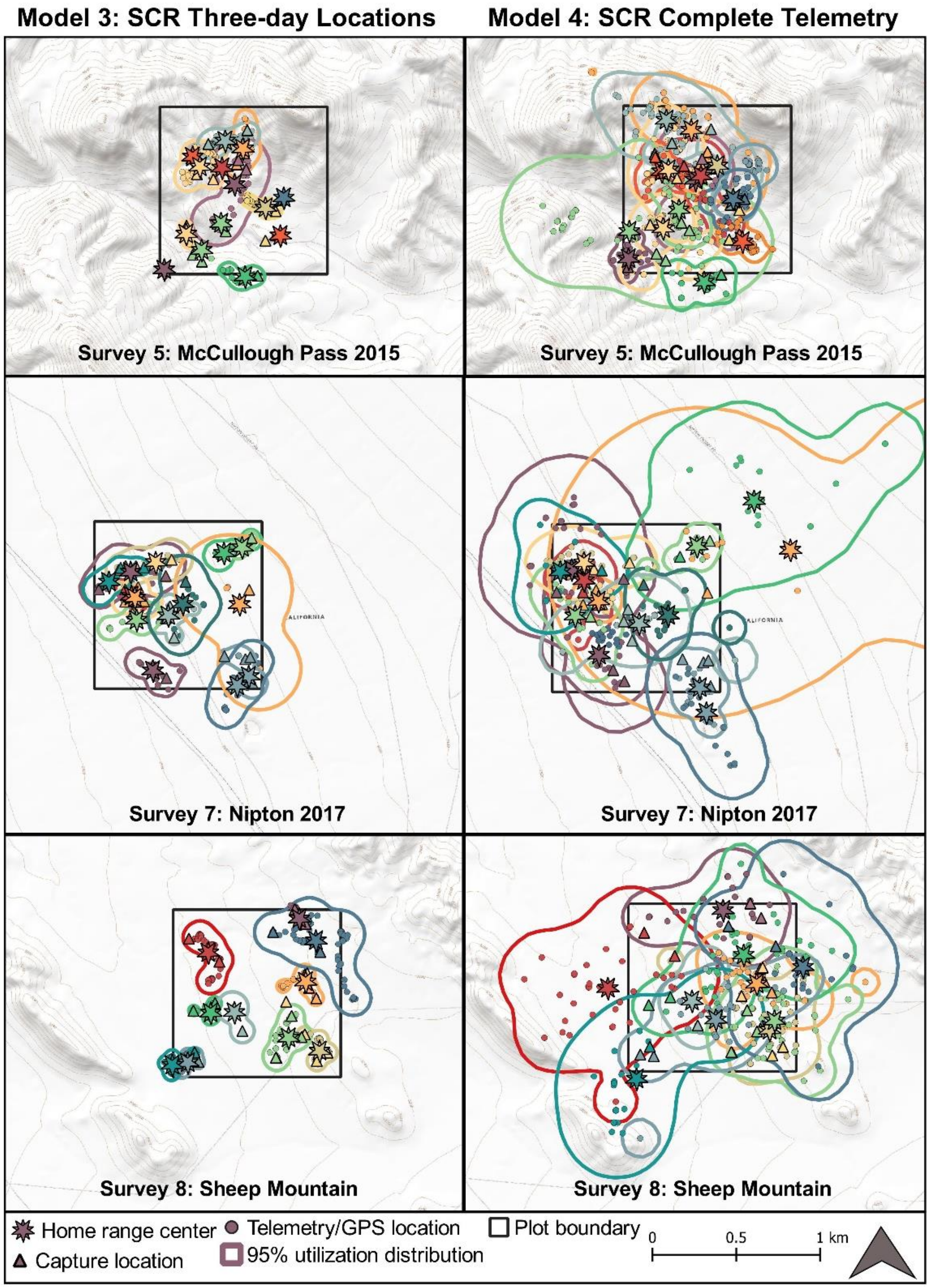

FIGURE 6 Continued. Actual capture locations, supplemental telemetry/GPS locations used to inform model parameters, and estimated home range centers from the joint posterior distribution based on Model 3: SCR Three-day Locations on the left and Model 4: SCR Complete Telemetry on the right with corresponding estimated 95% utilization distributions for tortoises located during representative surveys.

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Appendix 1: Capture Histories

(1) Eldorado Valley 2017: 9/29/2017-10/1/2017

	T1	T2	T3	Sex	MCL		Supplementary location data Model 3	Model 4	Model 5
CN100	1	1	0	Female	197		✓	✓	✓
CN101	1	0	1	Female	212		✓	✓	✓
CN105	0	1	1	Male	269			✓	✓
CN111	0	1	1	Male	259		✓	✓	✓
CN122	0	0	1	Male	239		✓	✓	✓
CN123	1	1	1	Male	253		✓	✓	✓
CN125	0	1	0	Male	231		✓	✓	✓
Total	**3**	**5**	**5**				**6**	**7**	**7**
Auxiliary tortoises							**1**	**0**	**3**

(2) ISEGS North 2016: 10/6/2016-10/8/2016

	T1	T2	T3	Sex	MCL		Supplementary location data Model 3	Model 4	Model 5
BS165	1	1	1	Male	257			✓	✓
CN600	1	0	1	Female	202		✓	✓	✓
CN602	1	0	0	Female	241		✓	✓	✓
CN615	1	1	0	Female	243		✓	✓	✓
CN617	1	1	1	Female	223		✓	✓	✓
SL419	1	1	1	Male	275			✓	✓
SL431	1	1	0	Female	218			✓	✓
UNK1	1	1	1	Unknown	Unknown				
Total	**8**	**6**	**5**				**4**	**7**	**7**
Auxiliary tortoises							**0**	**0**	**13**

(3) ISEGS North 2019: 10/5/2019-10/7/2019

	T1	T2	T3	Sex	MCL	Recap	Supplementary location data Model 3	Model 4	Model 5
CN600	1	0	1	Female	202	✓	✓	✓	✓
CN615	1	1	1	Female	243	✓	✓	✓	✓
SL410	1	0	0	Male	272			✓	
SL419	0	1	1	Male	275	✓	✓	✓	✓
SL427	1	0	0	Female	231		✓	✓	✓
Total	**4**	**2**	**3**			**3**	**4**	**5**	**4**
Auxiliary tortoises							**10**	**0**	**16**

(4) ISEGS South 2017: 10/9/2107-10/11/2017									
							Supplementary location data		
	T1	T2	T3	Sex	MCL		Model 3	Model 4	Model 5
BS139	1	0	0	Male	270		✓	✓	✓
BS140	1	1	1	Female	208		✓	✓	✓
BS142	0	1	1	Male	260		✓	✓	✓
BS148	1	1	1	Male	267		✓	✓	✓
UnkA1	0	1	1	Unknown	Unknown				
UnkA2	0	0	1	Unknown	Unknown				
Total	**3**	**4**	**5**				**4**	**4**	**4**
Auxiliary tortoises							**10**	**0**	**2**

(5) McCullough Pass 2015: 10/15/2015-10/17/2105									
							Supplementary location data		
	T1	T2	T3	Sex	MCL		Model 3	Model 4	Model 5
CN804	1	0	1	Male	273		✓	✓	✓
CN809	0	1	0	Female	209		✓	✓	✓
CN815	0	1	0	Female	230		✓	✓	✓
CN816	1	0	1	Female	233		✓	✓	✓
CN820	1	0	0	Female	231		✓	✓	✓
CN823	1	1	0	Male	270		✓	✓	✓
CN824	1	1	1	Male	275		✓	✓	✓
CN835	1	0	0	Male	227		✓	✓	✓
CN847	0	1	1	Male	278		✓	✓	✓
CN866	1	0	1	Female	230		✓	✓	✓
CN867	1	0	1	Male	212		✓	✓	✓
CN869	0	1	0	Female	242		✓	✓	✓
CN870	0	1	0	Male	233		✓	✓	✓
CN871	0	0	1	Female	214			✓	
CN880	0	0	1	Male	257			✓	✓
CN898	1	0	0	Female	221		✓	✓	✓
UMM	1	1	1	Male	Unknown				
UMT	0	1	0	Unknown	Unknown				
UMTW	1	0	0	Unknown	Unknown				
Total	**11**	**9**	**9**				**14**	**16**	**15**
Auxiliary tortoises							**1**	**0**	**17**

(6) McCullough Pass 2018: 9/29/2015-10/1/2015									
							Supplementary location data		
	T1	T2	T3	Sex	MCL	Recap	Model 3	Model 4	Model 5
CN802	1	1	1	Female	221		✓	✓	✓

CN804	1	0	0	Male	273	✓	✓	✓	✓
CN805	0	1	1	Female	218		✓	✓	✓
CN808	1	0	1	Female	258		✓	✓	✓
CN815	0	0	1	Female	230	✓	✓	✓	✓
CN816	1	0	0	Female	233	✓	✓	✓	✓
CN823	1	1	1	Male	270	✓	✓	✓	✓
CN824	1	0	1	Male	275	✓	✓	✓	✓
CN827	1	1	1	Female	236		✓	✓	✓
CN830	0	1	0	Female	237		✓	✓	✓
CN835	1	1	0	Male	227	✓		✓	✓
CN846	0	1	0	Male	251		✓	✓	✓
CN847	1	0	0	Male	278	✓		✓	✓
CN856	1	0	1	Male	283		✓	✓	✓
CN866	0	0	1	Female	230	✓	✓	✓	✓
CN870	1	0	0	Male	233	✓	✓	✓	✓
CN877	1	1	1	Male	252		✓	✓	✓
CN878	0	0	1	Male	265		✓	✓	✓
CN880	1	1	0	Male	257	✓	✓	✓	✓
CN881	1	0	1	Female	237		✓	✓	✓
CN883	0	0	1	Female	209			✓	✓
CN887	1	0	0	Male	183		✓	✓	
CN888	1	0	0	Unknown	199		✓	✓	
CN889	1	1	0	Female	238			✓	
CN893	0	0	1	Female	233			✓	✓
CN898	1	1	0	Female	221	✓	✓	✓	✓
Total	**18**	**11**	**14**			**11**	**21**	**26**	**23**
Auxiliary tortoises							**3**	**0**	**9**

(7) Nipton 2017: 10/2/2017-10/4/2017

							Supplementary location data		
	T1	**T2**	**T3**	**Sex**	**MCL**		**Model 3**	**Model 4**	**Model 5**
BS503	0	1	1	Male	241		✓	✓	✓
BS512	1	1	1	Male	282		✓	✓	✓
BS513	1	1	0	Female	230		✓	✓	✓
CN002	1	0	0	Female	187		✓	✓	
CN003	1	0	0	Male	213		✓	✓	✓
CN004	1	1	1	Female	213		✓	✓	✓
CN005	1	1	1	Female	213		✓	✓	✓
CN007	0	0	1	Unknown	178			✓	✓
CN009	0	0	1	Female	222		✓	✓	✓
CN014	1	0	0	Male	207		✓	✓	✓
CN015	1	0	0	Male	264		✓	✓	✓

CN016	1	1	1	Male	208		✓	✓	✓
CN017	1	1	1	Female	237		✓	✓	✓
CN020	0	1	0	Male	237		✓	✓	✓
CN023	0	0	1	Male	197				
CN024	0	1	1	Male	270		✓	✓	✓
CN026	0	0	1	Male	197		✓	✓	✓
Total	**10**	**9**	**11**				**15**	**16**	**15**
Auxiliary tortoises							**2**	**0**	**3**

(8) Sheep Mountain 2015: 10/12/2015-10/14/2015

							Supplementary location data		
	T1	**T2**	**T3**	**Sex**	**MCL**		**Model 3**	**Model 4**	**Model 5**
CN900	1	0	1	Female	222		✓	✓	✓
CN901	1	0	1	Male	236		✓	✓	✓
CN903	1	1	1	Male	297			✓	✓
CN905	1	1	1	Female	229		✓	✓	✓
CN906	0	1	1	Male	274			✓	✓
CN907	1	1	1	Female	246		✓	✓	✓
CN908	1	1	1	Male	236		✓	✓	✓
CN909	1	1	0	Male	225		✓	✓	✓
CN910	1	0	0	Female	164		✓	✓	
CN914	1	0	1	Male	265		✓	✓	✓
CN916	0	1	1	Male	213		✓	✓	✓
CN919	0	1	0	Female	240		✓	✓	✓
Total	**9**	**8**	**9**				**10**	**12**	**11**
Auxiliary tortoises							**0**	**0**	**2**

(9) Sheep Mountain 2018: 10/6/2018-10/8/2018

							Supplementary location data		
	T1	**T2**	**T3**	**Sex**	**MCL**	**Recap**	**Model 3**	**Model 4**	**Model 5**
148	1	1	1	Female	230		✓	✓	✓
CN900	1	1	1	Female	222	✓	✓	✓	✓
CN907	0	1	1	Female	246	✓	✓	✓	✓
CN908	1	1	1	Male	236	✓	✓	✓	✓
CN909	1	1	1	Male	225	✓	✓	✓	✓
CN912	1	1	1	Female	188			✓	
CN918	1	1	0	Unknown	167				
CN934	1	1	0	Male	242		✓	✓	✓
CN953	0	1	0	Female	200			✓	
Total	**7**	**9**	**6**			**4**	**6**	**8**	**6**
Auxiliary tortoises							**0**	**0**	**7**

(10) Stateline Pass 2016: 10/9/2016-10/11/2016									
							Supplementary location data		
	T1	**T2**	**T3**	**Sex**	**MCL**		**Model 3**	**Model 4**	**Model 5**
CN746	1	0	0	Male	191		✓	✓	✓
CN748	0	1	0	Male	277		✓	✓	
CN749	0	0	1	Female	164			✓	
Total	**1**	**1**	**1**				**2**	**3**	**1**
Auxiliary tortoises							**1**	**0**	**6**

(11) Stateline Pass 2019: 9/28/2019-9/30/2019									
							Supplementary location data		
	T1	**T2**	**T3**		**MCL**	**Recap**	**Model 3**	**Model 4**	**Model 5**
CN704	1	0	1	Male	282		✓	✓	✓
CN706	1	0	0	Male	224			✓	✓
CN707	0	1	0	Male	216		✓	✓	
CN709	0	1	0	Male	252		✓	✓	✓
CN720	0	1	1	Male	300		✓	✓	✓
CN749	0	0	1	Female	164	✓	✓	✓	
CN751	1	1	0	Male	317		✓	✓	
CN767	0	0	1	Male	300			✓	
Total	**3**	**4**	**4**			**1**	**6**	**8**	**4**
Auxiliary tortoises							**1**	**0**	**3**

(12) SouthPah 2017: 10/6/2017-10/8/2017									
							Supplementary location data		
	T1	**T2**	**T3**	**Sex**	**MCL**		**Model 3**	**Model 4**	**Model 5**
BS586	1	1	1	Male	280		✓	✓	✓
BS590	1	1	1	Male	280		✓	✓	✓
BS602	1	0	0	Male	218		✓	✓	✓
BS609	1	1	0	Male	252		✓	✓	✓
CN202	1	0	0	Male	258		✓	✓	✓
CN203	1	0	1	Female	242		✓	✓	✓
CN205	0	1	0	Male	268		✓	✓	✓
CN212	1	0	1	Male	196		✓	✓	✓
CN214	1	0	0	Male	263		✓	✓	✓
CN215	1	1	1	Male	285		✓	✓	✓
CN216	1	1	0	Female	240		✓	✓	✓
CN219	0	1	0	Female	239		✓	✓	✓
CN220	0	1	1	Female	229		✓	✓	✓
CN221	0	0	1	Male	221		✓	✓	✓
CN225	1	0	0	Male	192		✓	✓	

CN228	1	1	1	Female	210		✓	✓	✓
CN229	1	0	0	Male	221		✓	✓	✓
CN230	1	1	1	Female	209		✓	✓	✓
Total	**14**	**10**	**9**				**18**	**18**	**17**
Auxiliary tortoises							**0**	**0**	**8**
(13) Silver State 2015: 10/18/2015-10/20/2015									
							Supplementary location data		
	T1	**T2**	**T3**	**Sex**	**MCL**		**Model 3**	**Model 4**	**Model 5**
SS1143	0	1	0	Female	224		✓	✓	✓
SS1321	1	1	0	Female	200		✓	✓	✓
Total	**1**	**2**	**0**				**2**	**2**	**2**
Auxiliary tortoises							**4**	**0**	**18**
(14) Silver State 2018: 10/3/2018-10/5/2018									
							Supplementary location data		
	T1	**T2**	**T3**	**Sex**	**MCL**	**Recap**	**Model 3**	**Model 4**	**Model 5**
SS1024	1	0	0	Male	235		✓	✓	✓
SS1049	1	0	1	Male	281		✓	✓	✓
SS1143	0	1	1	Female	224	✓	✓	✓	✓
SS1175	0	1	0	Female	220		✓	✓	✓
SS1300	1	0	0	Unknown	163				
SS1301	1	1	0	Female	223		✓	✓	✓
SS1302	1	1	1	Male	229		✓	✓	✓
SS1312	1	0	1	Unknown	166				
SS1314	1	0	0	Female	234		✓	✓	✓
SS1317	1	1	0	Unknown	164				
SS1326	0	1	1	Male	240		✓	✓	✓
SS1334	1	1	1	Male	242		✓	✓	✓
Total	**9**	**7**	**6**			**1**	**9**	**9**	**9**
Auxiliary tortoises							**9**	**0**	**11**
(15) Sandy Valley 2016: 10/3/2016-10/5/2016									
							Supplementary location data		
	T1	**T2**	**T3**	**Sex**	**MCL**		**Model 3**	**Model 4**	**Model 5**
CN501	1	1	0	Female	234		✓	✓	✓
CN504	1	0	0	Unknown	183		✓	✓	✓
CN506	0	1	1	Female	252		✓	✓	✓
CN507	0	1	1	Male	281		✓	✓	✓
CN508	0	1	1	Male	237		✓	✓	✓
CN521	1	1	1	Female	165		✓	✓	
Total	**3**	**5**	**4**				**6**	**6**	**5**
Auxiliary tortoises							**2**	**0**	**4**

(16) Sandy Valley 2019: 10/2/2019-10/4/2019									
							Supplementary location data		
	T1	T2	T3	Sex	MCL	Recap	Model 3	Model 4	Model 5
CN506	0	1	1	Female	252	✓		✓	✓
CN507	1	1	1	Male	281	✓	✓	✓	✓
CN508	0	0	1	Male	237	✓		✓	✓
CN511	1	1	0	Male	198		✓	✓	
CN512	1	0	1	Female	224		✓	✓	
CN519	1	0	0	Female	225			✓	
CN521	1	1	1	Female	165	✓	✓	✓	
CN526	1	1	1	Male	272		✓	✓	✓
CN528	0	1	0	Male	284		✓	✓	✓
Total	**6**	**6**	**6**			**4**	**6**	**9**	**5**
Auxiliary tortoises							**1**	**0**	**4**

Appendix 2: Additional results

Joint posterior summaries of model parameters representing the median and 90% highest posterior density credible intervals [5%, 95%]. Primary surveys are identified by numbers (1-16), which correspond to the primary survey numbers listed in Table 1.

Parameter		Model 1b Non-spatial, heterogeneous *p*	Model 2b Base SCR, heterogeneous *p*	Model 3b SCR Three-day Locations, heterogeneous *p*	Model 4b SCR Complete Telemetry, heterogeneous *p*
Male effect: *p* *(logit-scale)*		-0.71 [-1.87, 0.32]	-0.75 [-2.26, 0.67]	0.06 [-1.46, 1.27]	1.1 [-0.65, 2.77]
Individual effect: *p* *(logit-scale)*		2.02 [1.43, 2.64]	2.46 [1.8, 3.1]	2.03 [1.17, 2.9]	2.44 [1.07, 3.47]
Male effect: σ *(log-scale)*		------------------	0.27 [0.12, 0.42]	0.69 [0.66, 0.71]	0.4 [0.37, 0.43]
Global σ (m)		------------------	70.6 [63.32, 78.04]	------------------	------------------
(1)	*p*	0.36 [0.03, 0.7]	0.62 [0.2, 1]	0.66 [0.26, 1]	0.63 [0.19, 1]
	σ (m)	------------------	------------------	57.82 [53.99, 61.86]	145.3 [134.61, 155.8]
	Ψ	0.14 [0.04, 0.29]	0.09 [0.03, 0.19]	0.08 [0.03, 0.15]	0.06 [0.02, 0.13]
	Density	12.49 [6.72, 26.9]	9.17 [2.81, 18.34]	7.84 [2.81, 14.64]	6.36 [2.37, 11.98]
(2)	*p*	0.66 [0.31, 0.95]	0.76 [0.36, 1]	0.83 [0.48, 1]	0.84 [0.43, 1]
	σ (m)	------------------	------------------	68.66 [64.83, 72.99]	185.34 [176.7, 194.18]
	Ψ	0.11 [0.05, 0.19]	0.09 [0.03, 0.16]	0.08 [0.03, 0.14]	0.06 [0.02, 0.11]
	Density	9.61 [7.69, 15.38]	9.02 [3.55, 15.53]	7.84 [3.85, 13.46]	6.36 [2.96, 10.8]
(3)	*p*	0.3 [0.01, 0.67]	0.34 [0, 0.77]	0.61 [0.17, 1]	0.48 [0, 0.89]
	σ (m)	------------------	------------------	226.92 [216.69, 236.15]	244.84 [232.04, 257.66]
	Ψ	0.1 [0.03, 0.25]	0.09 [0.02, 0.21]	0.05 [0.01, 0.11]	0.05 [0.01, 0.11]
	Density	9.61 [4.81, 23.07]	8.73 [2.07, 20.56]	4.59 [1.48, 10.36]	4.88 [1.33, 10.95]
(4)	*p*	0.45 [0.07, 0.82]	0.61 [0.19, 1]	0.73 [0.28, 1]	0.69 [0.23, 1]
	σ (m)	------------------	------------------	97.74 [82.67, 113.58]	138.54 [132.17, 145.72]
	Ψ	0.11 [0.03, 0.22]	0.08 [0.02, 0.17]	0.06 [0.02, 0.12]	0.06 [0.02, 0.11]
	Density	9.61 [5.77, 19.22]	8.14 [2.22, 16.57]	5.77 [2.07, 11.39]	5.33 [2.07, 10.36]
(5)	*p*	0.14 [0.02, 0.33]	0.11 [0.01, 0.33]	0.11 [0.01, 0.3]	0.06 [0, 0.22]
	σ (m)	------------------	------------------	24.29 [23.45, 25.09]	92.75 [89.39, 95.83]
	Ψ	0.51 [0.25, 0.87]	0.49 [0.21, 0.85]	0.46 [0.2, 0.83]	0.44 [0.18, 0.83]
	Density	50.94 [25.95, 85.54]	48.67 [21.3, 84.76]	46.15 [19.53, 82.4]	43.64 [18.49, 82.99]
(6)	*p*	0.2 [0.05, 0.41]	0.18 [0.03, 0.41]	0.2 [0.03, 0.42]	0.11 [0.01, 0.31]
	σ (m)	------------------	------------------	28.71 [27.7, 29.83]	84.44 [81.92, 86.86]
	Ψ	0.57 [0.32, 0.89]	0.54 [0.26, 0.86]	0.48 [0.25, 0.81]	0.49 [0.24, 0.83]
	Density	56.71 [30.76, 85.54]	53.99 [28.55, 87.87]	47.93 [24.85, 80.92]	48.96 [23.22, 81.95]
(7)	*p*	0.3 [0.04, 0.56]	0.35 [0.03, 0.69]	0.31 [0.04, 0.61]	0.44 [0.06, 0.81]
	σ (m)	------------------	------------------	47.95 [45.73, 50.05]	141.93 [134.56, 149.41]
	Ψ	0.33 [0.15, 0.59]	0.27 [0.12, 0.52]	0.25 [0.11, 0.46]	0.17 [0.08, 0.31]
	Density	32.68 [18.26, 57.67]	27.37 [11.54, 51.04]	25.3 [11.09, 46.01]	17.16 [8.58, 30.18]
(8)	*p*	0.59 [0.27, 0.9]	0.6 [0.22, 0.94]	0.59 [0.24, 0.91]	0.71 [0.32, 0.99]
	σ (m)	------------------	------------------	42.05 [40.71, 43.43]	164.26 [156.8, 171.83]
	Ψ	0.17 [0.08, 0.28]	0.15 [0.07, 0.27]	0.14 [0.07, 0.24]	0.1 [0.05, 0.17]
	Density	16.34 [11.53, 24.99]	15.24 [7.1, 26.63]	14.05 [7.25, 23.67]	9.91 [5.33, 16.57]

Parameter		Model 1b Non-spatial, heterogeneous *p*	Model 2b Base SCR, heterogeneous *p*	Model 3b SCR Three-day Locations, heterogeneous *p*	Model 4b SCR Complete Telemetry, heterogeneous *p*
(9)	*p*	0.74 [0.42, 0.97]	0.63 [0.25, 0.95]	0.67 [0.32, 0.96]	0.67 [0.28, 0.99]
	σ (m)	------------------	------------------	62.72 [59.17, 66.16]	140.37 [131.92, 148.8]
	Ψ	0.12 [0.05, 0.19]	0.11 [0.05, 0.2]	0.1 [0.04, 0.17]	0.08 [0.04, 0.15]
	Density	10.57 [8.65, 15.38]	11.24 [5.18, 20.12]	9.76 [4.14, 16.57]	8.28 [3.85, 14.5]
(10)	*p*	0.05 [0, 0.34]	0.05 [0, 0.37]	0.03 [0, 0.32]	0.08 [0, 0.55]
	σ (m)	------------------	------------------	79.44 [64.35, 95.7]	150.04 [132.22, 168.56]
	Ψ	0.18 [0.01, 0.67]	0.15 [0.01, 0.62]	0.15 [0.01, 0.6]	0.07 [0, 0.42]
	Density	16.34 [2.88, 66.32]	14.35 [1.04, 62.28]	14.35 [1.04, 60.65]	6.8 [0.59, 42.01]
(11)	*p*	0.11 [0, 0.37]	0.1 [0, 0.42]	0.08 [0, 0.35]	0.13 [0, 0.58]
	σ (m)	------------------	------------------	45.19 [36.98, 53.97]	205.9 [194.29, 218.17]
	Ψ	0.27 [0.07, 0.67]	0.24 [0.06, 0.65]	0.22 [0.05, 0.61]	0.11 [0.02, 0.35]
	Density	26.91 [8.65, 65.36]	24.41 [5.33, 63.76]	22.34 [4.73, 60.95]	10.95 [2.66, 34.91]
(12)	*p*	0.36 [0.09, 0.64]	0.36 [0.05, 0.7]	0.47 [0.12, 0.79]	0.57 [0.18, 0.95]
	σ (m)	------------------	------------------	72.81 [70.52, 75.01]	198.27 [190.81, 205.75]
	Ψ	0.32 [0.16, 0.55]	0.29 [0.13, 0.53]	0.21 [0.1, 0.37]	0.15 [0.07, 0.25]
	Density	31.72 [18.26, 51.9]	28.7 [13.61, 52.96]	21.15 [10.5, 36.69]	14.79 [7.69, 25]
(13)	*p*	0.16 [0, 0.6]	0.31 [0, 0.81]	0.21 [0, 0.66]	0.44 [0, 0.88]
	σ (m)	------------------	------------------	26.59 [25.62, 27.66]	193.58 [177.25, 212.28]
	Ψ	0.06 [0, 0.28]	0.04 [0, 0.16]	0.05 [0, 0.19]	0.03 [0, 0.08]
	Density	5.77 [1.92, 27.87]	4.29 [0.3, 15.24]	4.88 [0.44, 18.93]	2.66 [0.3, 7.4]
(14)	*p*	0.33 [0.04, 0.62]	0.45 [0.08, 0.84]	0.6 [0.24, 0.94]	0.68 [0.27, 1]
	σ (m)	------------------	------------------	64.32 [62.18, 66.58]	176.18 [166.1, 186.32]
	Ψ	0.22 [0.1, 0.43]	0.18 [0.07, 0.33]	0.13 [0.06, 0.23]	0.1 [0.05, 0.18]
	Density	21.15 [11.53, 39.41]	17.6 [6.95, 32.4]	13.31 [6.21, 23.08]	9.91 [4.73, 17.01]
(15)	*p*	0.4 [0.03, 0.75]	0.34 [0, 0.72]	0.37 [0, 0.72]	0.5 [0.03, 0.9]
	σ (m)	------------------	------------------	60.82 [57.25, 64.54]	218.79 [202.61, 235.49]
	Ψ	0.11 [0.03, 0.22]	0.1 [0.03, 0.23]	0.09 [0.02, 0.19]	0.06 [0.02, 0.13]
	Density	9.61 [5.77, 20.18]	10.36 [2.96, 23.08]	8.8 [2.66, 19.08]	5.92 [1.78, 11.98]
(16)	*p*	0.45 [0.11, 0.8]	0.41 [0.02, 0.77]	0.49 [0.13, 0.86]	0.55 [0.13, 0.97]
	σ (m)	------------------	------------------	55.54 [50.69, 60.48]	225.58 [207.79, 244.22]
	Ψ	0.15 [0.06, 0.27]	0.14 [0.05, 0.28]	0.11 [0.04, 0.22]	0.08 [0.03, 0.15]
	Density	14.42 [8.65, 24.99]	14.05 [4.73, 27.66]	11.39 [4.59, 21.01]	7.69 [3.25, 14.94]