Identifying habitat correlates of latent occupancy when apparent annual occupancy is confounded with availability for detection

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ABSTRACT

Estimating relationships between landscape variables and the presence of a species via occupancy modeling is a common practice for many animal species. However, estimating these relationships can be difficult for species where availability for detection is driven by factors that match the traditional primary sampling period. We present a new hierarchical formulation of the occupancy model to estimate these relationships in the presence of among-year variation in availability for detection for the threatened Mojave desert tortoise (*Gopherus agassizii*). There were large swings in apparent annual proportion of area occupied ranging from 0.19 to 0.66, with year-to-year changes in the apparent annual proportion ranging from −25.7% to 230.2%. The model estimated the true latent proportion of area occupied was 0.57 (95% Cr.I. 0.51–0.631). The predictive raster surface developed from the novel model formulation validated well using an independent data set (Pearson's $r = 0.948$), with radio-telemetered desert tortoises spending disproportionately more time in higher predicted probability of occurrence portions of the study area. The coefficients from the model, and more specifically the occupancy probability predictive raster surface developed from them, can be used by land managers to guide future survey efforts and to spatially prioritize restoration actions across a 35,000 ha conservation reserve. In general, acknowledging the challenge of confounding availability for detection with apparent annual occupancy and using the modeling framework presented here can be used to determine fundamental relationships between landscape configuration and latent occupancy for a variety of heretofore unaddressed species.

1. Introduction

A fundamental interest to applied ecology is identifying the range of environmental factors underlying the occurrence of a species on the landscape (MacKenzie and Nichols, 2004; Fuller et al., 2016). Occupancy modeling (sensu MacKenzie et al., 2002) accomplishes this by explicitly addressing the biological reality that at some rate, when a species is surveyed for at a site, it remains undetected even though it is truly present. To address imperfect detection, occupancy modeling requires multiple surveys during a period of assumed geographic and demographic closure to estimate the rate of detection given true presence, and conversely, the probability of repeated non-detections given true presence. While conceptually straightforward, this solution often becomes difficult to implement given ecological realities. Target species may be extremely cryptic, creating statistical estimation challenges (Welsh et al., 2013; Guillera-Arroita et al., 2014). Target species may temporarily emigrate out of the survey area, conflating probability of detection with availability for detection and biasing occupancy

estimates (Rota et al., 2009; Valente et al., 2017). Surveys for target species may also falsely record 'presences' via aural or visual misidentification, leading to false-positives in the dataset (Bailey et al., 2014). These myriad ecological traits have created a need for new statistical models to expand the application of occupancy modeling to these more challenging situations.

Variations of occupancy modeling usually focus on two temporal frameworks. The first is single-year static occupancy models, whereby multiple surveys (secondary periods) are conducted within a single primary period (e.g., year) within which occupancy is assumed constant (MacKenzie et al., 2002). For applied ecologists a primary motivation for single-year occupancy models is the estimation of the relationships between occupancy and landscape features to facilitate surveys, designate land management status, or spatially prioritize habitat restoration actions. The second temporal framework is multi-year dynamic models, where the occupancy state of a site is allowed to change between primary periods (i.e., years; MacKenzie et al., 2003). Applied ecologists are often interested in monitoring site occupancy rates over

time and space as a surrogate for more intensive demographic monitoring (MacKenzie and Nichols, 2004). Long-lived species with low turnover in occupancy rates (e.g., long-lived reptiles) initially seem well-suited to occupancy modeling. However, unaddressed in either temporal framework by existing occupancy models is the situation where a species may have varying probabilities of availability for detection that are confounded with primary sampling seasons. For example, O'Donnell and Semlitsch (2015) discuss the wide-ranging impact of the sporadic below-ground state of terrestrial salamanders (Plethodontidae) on negatively biasing apparent occupancy and Couturier et al. (2013) discuss how unavailability for detection can severely bias detection-corrected abundance estimates of tortoises. Several similar situations have been reported in both terrestrial and aquatic plant species, where lack of above-ground parts in a given season erroneously resulted in apparent non-occupancy for that season (Alexander et al., 1997; Chen et al., 2013; Gray et al., 2013). In this case of true presence but physical non-availability for detection, existing models using either temporal framework will generate biased occupancy estimates, inaccurate and imprecise estimates of relationships to environmental covariates, and exaggerated swings in apparent annual occupancy.

This is the case for our study species, the Mojave desert tortoise (*Gopherus agassizii*), a state- and federally-protected tortoise in the Mojave desert, southwestern USA. Desert tortoises occur at low population densities and can be both cryptic (when aboveground, necessitating multiple methods of detection) or unavailable for detection (when belowground or temporarily outside of a survey plot). Availability for detection can vary dramatically in response to weather and vegetation conditions and is generally determined for each primary period (e.g., year, generally March–June) by the availability and quality of ephemeral forbs that are driven by precipitation amounts over the previous winter (Duda et al., 1999). Winter precipitation and thus forb communities across the range of desert tortoise are strongly linked to annual El Niño Southern Oscillation conditions (Brown and Comrie, 2004), and over longer time scales to the Pacific Decadal Oscillation (Mantua et al., 2007). This means that as a long-lived species, individual tortoises may "wait out" poor forb years resulting in them being present, but unavailable for detection, at a site. This confounding of availability for detection and apparent annual occupancy presents a particular challenge for habitat restoration actions that require accurate estimates of the relationship between environmental variables and latent occupancy based on sampling in any one year.

Our goal was to develop and validate a raster surface predicting the probability of desert tortoise occupancy across a large study area as a function of landscape environmental variables and to do so in the presence of high variability in availability for detection and thus apparent annual occupancy. We present a novel statistical occupancy model that allows for multiple methods of detection, is robust to year-to-year changes in apparent occupancy driven by variation in availability for detection, and yields singular estimates of the relationship between latent occupancy and a suite of landscape predictor variables. The resultant predictive raster surface is useful for spatial prioritization of habitat restoration activities for Mojave desert tortoise and the general concept and model can be useful for a variety of species where apparent occupancy is confounded with availability for detection among primary sampling periods.

2. Materials and methods

2.1. Field sampling

The field and remote-sensed environmental data were collected within the boundaries of the 35,000 ha Boulder City Conservation Easement, an easement managed for conservation of desert tortoise and other species south of the metropolitan area of Las Vegas, Nevada, USA (Fig. 1). Surveys were conducted when the ambient air temperature at the sampling site was between 18 °C and 35 °C. Initial start times began

at 7:30 am but were shifted earlier as the season went on due to increasing temperatures. No tortoises were handled after the ambient air temperature reached 35 °C on any given day and all tortoises were handled in accordance with the Desert Tortoise Field Manual (USFWS, 2009). One field crew, consisting of two or three surveyors, walked 10-meter belt transects, back and forth across the site, beginning at the northwest corner of the sample unit. All sites were 4 ha in area. While walking transects, the first surveyor was responsible for tracking their movements within the site to ensure they remained within the boundaries of the given transect. During the survey, surveyors were expected to deviate from the belt transect to more effectively inspect all bushes, shrubs, suspected burrows, etc., to achieve 100% coverage of the site. Belt transects in each round followed the same cardinal direction. Subsequent site survey rounds were oriented in a different cardinal direction from the previous round of surveys. Sites were not sampled in any particular order but each site was sampled first in a day at least once in 2013 and 2014 and at least twice in 2015, 2016, and 2017.

We used the robust sampling design of Pollock (1982) with multiple secondary visits within each primary sampling period (i.e., March–June). We initially conducted 3 secondary sampling visits at each of 80 sites in 2013 and 2014. Because of low detections of desert tortoise we decreased our number of sites to 60 and increased our number of secondary visits to 7 (D. McKenzie, pers. comm.). Five of the dropped sites were dropped based on dominant soil type and were excluded from all analyses. The remaining 15 of the dropped sites were dropped at random and were retained in all analyses. Thus the analysis data set consisted of 75 sites, each with three independent desert tortoise presence surveys in 2013 and 2014, and a subset of 60 sites that each had seven independent desert tortoise presence surveys in 2015, 2016, and 2017. Occupancy surveys were conducted from early March to mid-June. All surveys were conducted at least one week apart at each plot. The order of plots surveyed was randomized each survey. In total there were 1710 plot surveys conducted that were used in this analysis.

Field technicians recorded two different types of indicators of the 'presence' of desert tortoise at a site: live tortoises and active burrows. Live tortoises are cryptic but mobile, whereas active burrows are static but uncommon. There were two parallel records in the detection data, one for live tortoises with a '1' if a desert tortoise was observed during the survey and a '0' if unobserved, and another for active burrows, with a '1' recorded if an active desert tortoise burrow was observed and a '0' if unobserved. Active tortoise burrows were defined as burrows occupied by a tortoise or with fresh tortoise scat or tracks. The scat needed to be fresh, mostly green and brown in color, and within 12 in. of the burrow opening. Desert tortoise tracks located at a burrow entrance classified the burrow as active. Potential burrows and caliche dens were inspected using a hand mirror (or high-powered flashlight on overcast days) to assess presence of tortoises. In the absence of a live tortoise or fresh tracks or scat visible from outside the burrow, the burrow was classified as inactive during the survey. Presence of a tortoise in a burrow was considered separately as occupancy by a live tortoise and an active tortoise burrow. We also recorded air temperature (°C) for inclusion as a predictor on daily detection probabilities. Tortoises are more active above ground at intermediate temperatures, but given our seasonal timing of sampling, we only sampled during moderate to high temperatures and thus treated temperature as a linear predictor on detection of live tortoises (Couturier et al., 2013). We hypothesized that detection probability would decrease as air temperature increased due to desert tortoises spending less time aboveground and in the open at warmer temperatures. We designed our seasonal timing to align with maximum aboveground movement of tortoises, and being temperature-dependent, this relationship may not apply in other seasons.

2.2. Environmental variables

We used remote-sensing analysis in a Geographic Information System (GIS) to develop predictor variables that we expected to be
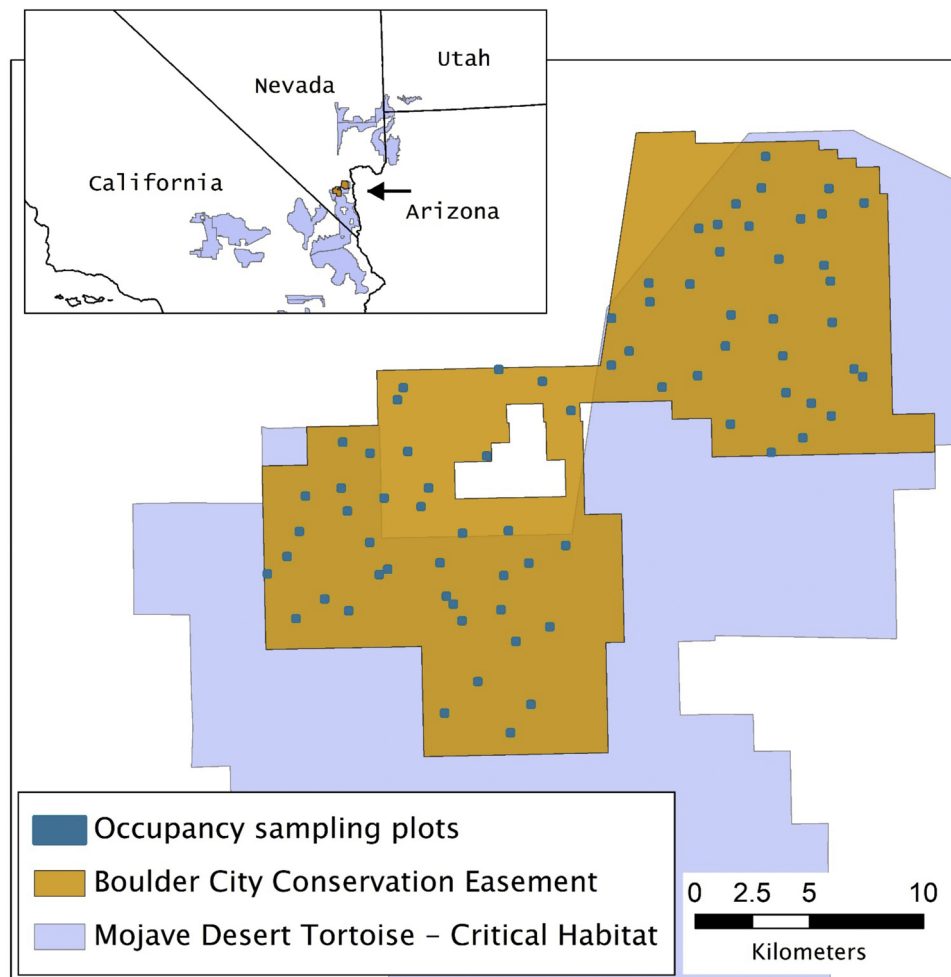
Fig. 1. Study area location in southern Nevada for modeling Mojave desert tortoise occupancy in relation to landscape predictors from 2013 through 2017. Inset figure shows location of study area (to the left of the arrow) within designated critical habitat for Mojave desert tortoises (USFWS 1994).

associated with desert tortoise occupancy (Table 1). Predictor variables were classified into three types: topographic, edaphic, and vegetative. Topographic features relate to desert tortoise ability to move around on the landscape, the potential for stable burrow construction, and to some extent exposure to predators (e.g., slightly rough landscapes may provide improved hiding cover for desert tortoises). The edaphic predictor variable was included it was potentially associated with occupancy via facilitating stable burrow construction. The vegetative variables reflected biotic habitat influences, including being a general measure of food availability and shade/cover availability (e.g., creosote bush, *Larrea tridentata*, and white bursage, *Ambrosia dumosa*). We examined conditional density plots of observed tortoise or burrow detections against all variables to evaluate potential quadratic relationships. We included quadratic terms for the predictor variables distance to road, roughness, slope, and wash density.

All remote-sensed predictor variables were initially generated on a 5 m × 5 m raster grid (see Young et al., 2017 for detailed discussion of variable creation). We resampled variables as the average of all grid cells within the 4 ha occupancy sampling plots. Some variables were adjusted (e.g., divide all values by 100) from Young et al. (2017) to improve statistical model convergence and to facilitate a natural interpretation of the intercept values in the model (Table 1). All variables were centered (i.e., mean subtracted from observed) to facilitate analysis.

Table 1

Types and units of remote-sensed predictor variables assessed in the statistical model for Mojave desert tortoise latent occupancy on the Boulder City Conservation Easement, Clark County, Nevada, USA.

Type of predictor	Predictor variable	Units; notes
Topographic	Distance to road	Euclidean distance (100 m) to nearest paved/unpaved road
	Roughness[a]	Root mean square diff in raster cell elevation from neighbor (×10); lower values = smoother area.
	Slope[a]	Percent slope, in tenths of a percent; 100% = 45°.
	Wetness[a]	Unipath wetness index (×10); low values = drier area.
	Washes[a]	Average density of washes (10 m/ha) w/in 25 m of cell.
Edaphic	Dominant soil[a]	Soil Great-Group type
Vegetative	Creosote cover[a]	Areal coverage of creosote (sq. decimeters/25 m^2)
	Bursage cover[a]	Areal coverage of bursage (sq. decimeters/25 m^2)

[a] These variables calculated by Young et al. (2017). Most variables were transformed to facilitate model convergence and interpretation of the intercept.
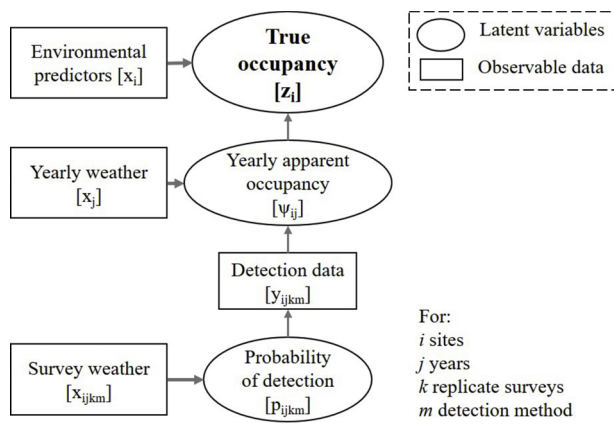
Fig. 2. Conceptual model for estimating latent true occupancy given inter-annual variation in apparent annual occupancy and standard within-year detection probabilities. Left column represents possible predictor variables for unobservable levels of the hierarchy.

2.3. Model development

We modified the approaches of Royle and Kéry (2007), Nichols et al. (2008), and Mordecai et al. (2011) to treat apparent annual occupancy of site i as arising from a constant latent true occupancy state for that site and to do so in a Bayesian state-space hierarchical model with two methods of detection, which can greatly improve precision of estimating occupancy parameters (Fig. 2; Graves et al., 2012). In the model presented in Fig. 2, example foci of statistical inference could include simple estimation of the true latent occupancy for site i, the relationships between landscape predictors and latent true occupancy (as we did here), the relationships between predictor variables and changes in yearly apparent occupancy (e.g., factors driving availability for detection), or using survey-level predictor variables to minimize heterogeneity in detection probabilities (Miller et al., 2015). We can also reformulate the conceptual model of Fig. 2 as a table of possible detection histories, contingent on true occupancy, apparent annual occupancy, and detection probability for multiple survey methods (Table 2).

We compared the proportion of area occupied under our latent constant occupancy model with what we would have estimated as the year-specific proportion of area occupied under independent single-year models. We did this to contrast how a naïve approach would imply inter-annual swings in estimated occupancy that we explicitly incorporated in our latent occupancy model.

For our purposes with desert tortoise, we were primarily interested in how landscape predictor variables were associated with latent true occupancy (z_i). We modeled these relationships as $z_i = \text{logit}(\beta_0 + \beta_n x_n)$ for β coefficients and x predictor variables of number n. We modeled apparent occupancy ψ_{ij} for site i in year j as $\psi_{ij} \sim \text{Bernoulli}(z_i * \phi_j)$ where ϕ_j is the across-site apparent occupancy rate in year j. This provided a link between the observed data, the across-site variation in apparent occupancy among years, and doing so conditional on latent true occupancy. We also included a survey-level detection probability covariate for live tortoise detections to account for temperature-

Table 2
Probability of observed survey outcome y given true latent occupancy z, at site i, using survey method m, in year j, on survey k, as a function of apparent site occupancy ψ. Although omitted here for simplicity, we modeled method-specific detection probabilities independent among years (e.g., p_{mj}). This formulation assumes no false positives.

True occupancy	$P(y_{mjk} = 0 \mid z_i)$	$P(y_{mjk} = 1 \mid z_i)$
$z_i = 0$	1	0
$z_i = 1$	$(1 - p_{mj}) * \psi_{ij}$	$p_{mj} * \psi_{ij}$

induced changes in availability for detection (e.g., above ground) and detection probability (e.g., active or in the open) $\text{logit}(p_j) = p.\text{year}_j + \beta_{temp} * \text{Temp}_{ijk}$ where p_j was the detection probability for live tortoises in year j conditional on an intercept for detection probability in year j ($p.\text{year}_j$) and the air temperature during the survey at site i in year j on survey k. All priors were uninformative.

We considered probabilities of latent true occupancy of site i to reflect relative variation in the frequency of desert tortoise encounters because of the potential for temporary emigration within primary periods and the inability to separate yearly apparent occupancy from availability for detection. Nonetheless, throughout this manuscript we refer to predicted desert tortoise encounter frequencies as relative probabilities of occupancy for consistency with the general occupancy literature.

2.4. Predictive surface development

We used the estimated relationships between latent true occupancy and landscape predictor variables to develop a continuous predictive raster surface in a GIS that represented the spatial variation in the relative probability of occupancy of desert tortoises across the study area. We developed this surface as an applied tool for land managers to spatially prioritize habitat restoration actions within the study area. This allows actions to be designed that either 'shore up' habitat in areas with relatively high tortoise occupancy or 'lift up' habitat in areas with low tortoise occupancy.

2.5. Model and predictive surface validation

We verified the performance of the occupancy model using three increasingly robust techniques. First, model performance was assessed internally through inspection of Markov Chain Monte Carlo (MCMC) plots and R-hat diagnostics, seeking convergence of the independent MCMC chains for all parameters and R-hat diagnostics < 1.05 (Gelman et al., 2004). Second, we used logistic regression to test whether the mean value of the predictive surface raster within the plot was positively related to whether an occupancy sampling plot ever had a live tortoise or active burrow detection. Third, we used independent desert tortoise radio-telemetry locations to determine if resident tortoises used the study area proportional to what was predicted by the occupancy predictive surface. To do this we used correlation analysis to test whether the number of telemetry locations increased in each successive bin rank of the five-binned predictive raster surface.

We also conducted a post-hoc test of the assumption within the model that latent true occupancy was constant across our study period. We generated independent across-site apparent occupancy rates for each year, then performed a simple linear regression on apparent occupancy rates over time. We hypothesized that if the regression line showed a clear positive or negative trend (with full or near statistical significance, $\alpha < \approx 0.2$) that would be evidence for rejecting the assumption of constant occupancy. Conversely, we hypothesized that if the linear trend point estimate was near zero with $\alpha > \approx 0.2$ there was no evidence to reject our working hypothesis. We used a fuzzy threshold ($\alpha < \approx 0.2$) for assumption rejection because of the arbitrary nature of using p-values as thresholds and to be conservative in failing to reject the assumption. In the linear regression we included the offset 'effort' to account for unequal number of site visits between the first two years (three visits per year) and the latter three years of the study (seven site visits per year).

We ran the final model for 100,000 MCMC iterations on three separate chains. The first 10,000 iterations were discarded for burn-in and the remaining iterations were thinned to every 30th draw to reduce autocorrelation in the posterior draws, resulting in 9000 iterations saved for inference. We present 95% Bayesian credible intervals (Cr.I.) along with all parameter estimates. Statistical analyses were completed using 'r2jags' in R 3.4.0, and, for the single-season occupancy contrast
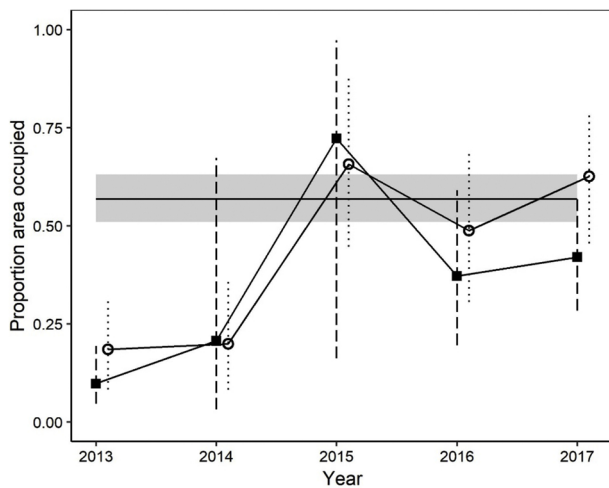
Fig. 3. Estimated proportion area occupied derived under the latent constant occupancy model, yearly apparent occupancy, and single-year naïve estimates of proportion area occupied. Latent proportion of area occupied with 95% credible interval bounds are horizontal black line and surrounding gray band, respectively. Annual apparent occupancy estimates under latent model are open circles; dotted vertical lines are 95% credible intervals. Single-year naïve estimates are black squares; dashed vertical lines are 95% confidence intervals. Single-year naïve estimates represent 'typical' approach to modeling multiple years of site occupancy and imply large inter-annual swings in the proportion of sample sites that were occupied. Survey effort was considerably lower in 2013 and 2014 compared to subsequent years.

Fig. 4. Year-specific detection probabilities for live desert tortoises and active burrows at occupied sites in the Boulder City Conservation Easement, Clark County, Nevada, USA, 2013–2017. Light gray bars are active burrows, dark gray bars are live encounters. Error bars are 95% credible intervals.

models, using Program PRESENCE (Hines, 2006). All spatial calculations, including building the predictive surface using the Raster Calculator tool, were done in ArcGIS 10.4.1. See online Appendix for all statistical code for data processing and analysis.

3. Results

We recorded 96 live tortoise detections across all sites and years, with 10, 6, 22, 22, and 36 observations in years 2013 through 2017, respectively. There were 63 active burrow detections, with 12, 5, 8, 9, and 29 in years 2013 through 2017, respectively.

There were large swings in yearly apparent occupancy rates across our sample sites, ranging from 0.10 to 0.72 for naïve proportion of area occupied and 0.19 to 0.66 for latent occupancy model estimates (Fig. 3). Calculated as proportional year-on-year changes in model-estimated proportion of area occupied, changes in apparent occupancy from 2013 to 2014 was 7.6%, and for subsequent year-on-years was 230.2%, −25.7%, and 28.3%, respectively (Fig. 3). Both naïve and latent model-based estimates were similar within years, and both highlighted large apparent swings in occupancy. In contrast, the across-year latent true proportion of area occupied was estimated as 0.57 (95% Cr.I. 0.51–0.63; Fig. 3). Linear regression on latent model-based yearly apparent occupancy, after accounting for the different survey effort in 2013–2014 versus 2015–2017, found that there was no trend in yearly apparent occupancy ($\beta = -0.42$, 95% C.I. -5.44–4.60, $p = 0.885$), thus failing to find evidence to support rejecting our working assumption of constant latent occupancy within our time frame.

There was considerable variation among years in detection probabilities for both methods (Fig. 4). The probability of detecting a live tortoise decreased as air temperature increased ($\beta_{temp} = -0.074$, 95% Cr.I. $= -0.087, -0.060$). The temperature coefficient indicated that for every 10 °C increase in air temperature there was a 52.3% decrease in the odds of detecting a live tortoise.

After inspection of the posterior densities from a saturated model, we removed the variables quadratic slope, wetness, and wash density
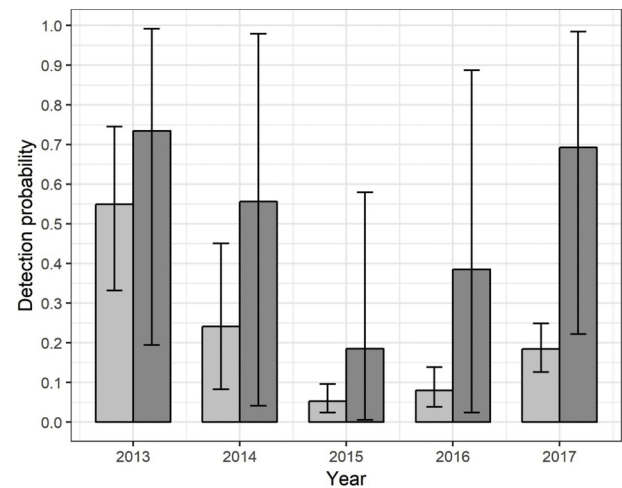
from further consideration because the posterior densities broadly overlapped zero. We also removed dominant soil type from the final model because it resulted in extreme logit values that distorted the coefficient estimates of the other variables. The final statistical model for latent true occupancy was $logit(z_i) = z0_i + \beta_{distrd} * Distrd_i + \beta_{distrd2} * Distrd_i^2 + \beta_{rough} * Rough_i + \beta_{rough2} * Rough_i^2 + \beta_{slope} * Slope_i + \beta_{creosote} * creosote_i + \beta_{bursage} * bursage_i$ where z_i was the latent true occupancy of site i, $z0_i$ was an intercept occupancy value in the absence of covariates, and β_x were the coefficient estimates for predictor variables x.

We found that a site was more likely to be occupied the further it was from a road ($\beta_{road} = 5.73$, 95% Cr.I. $= -1.16, 12.52$; $\beta_{road2} = 0.96$, 95% Cr.I. $= 0.18, 1.56$). Sites were more likely to be occupied at low levels of topographic roughness, and likelihood of non-occupancy increased rapidly as roughness increased ($\beta_{rough} = -3.84$, 95% Cr.I. $= -37.24, 28.98$; $\beta_{rough2} = -3.71$, 95% Cr.I. $= -8.17$, -0.21). As creosote coverage increased, a site was non-significantly less likely to be occupied ($\beta_{creosote} = -0.92$, 95% Cr.I. $= -3.00$, 1.02). Sites were more likely to be occupied with higher coverage of bursage ($\beta_{bursage} = 0.89$, 95% Cr.I. $= 0.15, 1.66$). The odds ratio for bursage indicated that a site was 2.44 (95% Cr.I. $= 1.15, 5.23$) times more likely to be occupied with every 1 decimeter^2/25m^2 increase in bursage cover. Although the variable 'slope' was retained in the final model, the 95% Credible Interval of the coefficient estimate broadly overlapped zero and was therefore not significant or meaningful ($\beta_{slope} = 5.617$, 95% Cr.I. $= -5.03, 16.91$).

Mean distance to road across the plots was 1020.1 m (SD 878.0), mean roughness index was 0.73 (SD 0.36), mean slope was 2.74% (SD 1.1), mean areal coverage of creosote was 0.56 m^2 per 25 m^2 (SD 0.31), mean coverage of bursage was 2.47 m^2 per 25 m^2 (SD 0.66), mean wetness index was -5.37 (SD 0.79), and mean wash density was 0.011 m/ha (SD 0.008). There were four dominant soil types: Haplargids, Haplocalcids, Torriorthents, and Torripsamments. The proportion of sites that ever had a detection of a live tortoise or active burrow was higher for sites in Haplocalcid soils (56.0% had detections) and Torriorthent soils (54.3%) than at sites in Haplargid soils (21.4%) and Torripsamment soils (0.00%; only a single site in this soil type).

We used the coefficient estimates in the final statistical model for latent true occupancy above and the landscape variable input rasters to generate a predictive raster surface of the relative variation in probability of desert tortoise occupancy across the study area. Then, we reclassified the raster surface into five equal area bins, such that 20% of the study area was classified as lowest occupancy probability, 20% was
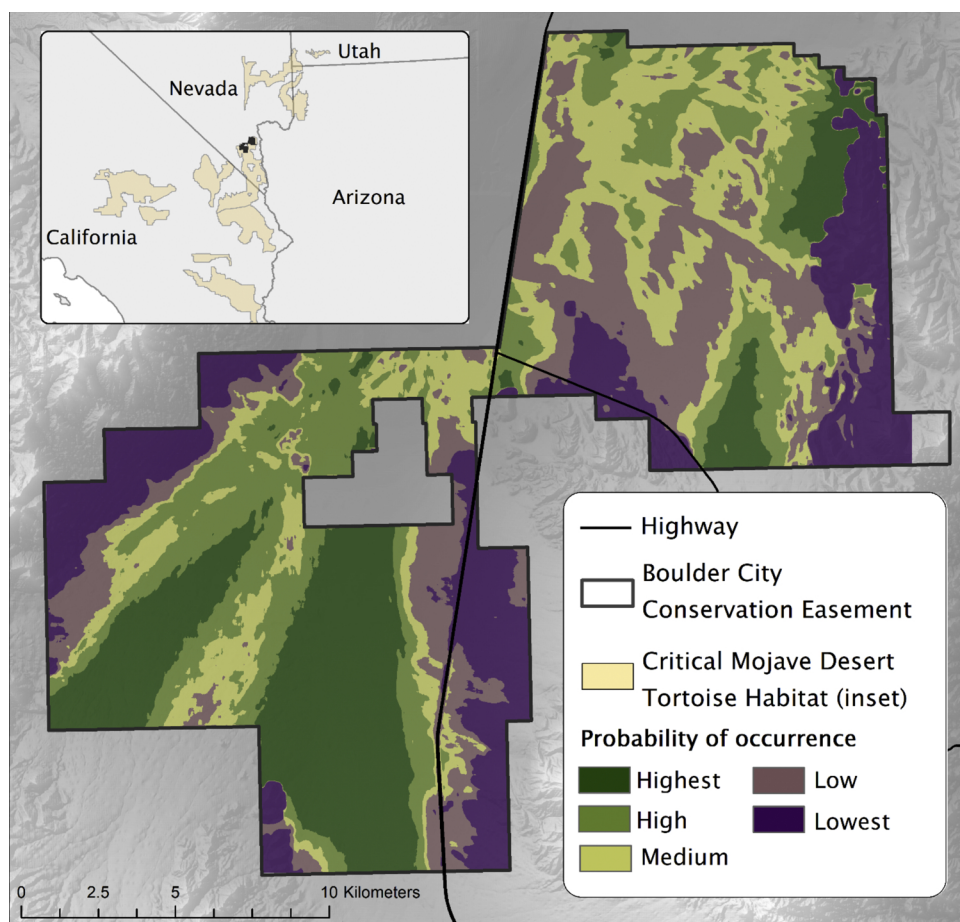
Fig. 5. Predicted relative probability of occupancy of Mojave desert tortoises across the Boulder City Conservation Easement, Clark County, Nevada, USA, 2013–2017. Raw values for relative predicted occupancy was reclassified into five equal-area bins ranging from '1' (lowest probability) to '5' (highest probability). Inset map shows location of study area (dark polygons in center) within regional distribution of critical Mojave desert tortoise habitat (U.S. Fish and Wildlife Service USFWS, 1994).

low-moderate occupancy probability, etc. (Fig. 5).

The MCMC sampler diagnostics showed that all three chains converged on the same distributions for parameters, including deviance, and showed a high degree of mixing. For most monitored parameters, including deviance, there was low autocorrelation in the sample draws. R-hat indices, a measure of the mixing ratios of each parameter's posterior distribution across the three chains, were below 1.05 for all but three of the 103 monitored parameters, often below 1.002, indicating reliable inference from the posterior distributions of the parameters of interest.

The detection history at sample sites was well predicted by the underlying predictive raster surface. Logistic regression found that as the mean predicted probability of occupancy within the site increased, the site was more likely to have ever had a detection of a live tortoise or active burrow (β_{mean} = 0.518, 95% C.I. = 0.127, 0.909; p = 0.009).

Locations of free-ranging independent radio-telemetered desert tortoises were well-predicted by the predictive raster surface, with fewer locations in the predicted relatively lower occupancy portions of the BCCE and increasingly more locations in the increasingly higher predicted occupancy bins (Pearson's r = 0.948, p = 0.014; Fig. 6).

4. Discussion

Occupancy modeling has dramatically improved our ability to monitor populations and assess habitat relationships by explicitly addressing imperfect detection of a species during single surveys (MacKenzie et al., 2002; Bailey et al., 2014). However, for species whose availability for detection may be driven by forces that operate at the same temporal scale as the primary sampling period, such as Mojave desert tortoise, availability for detection across the primary sample period can be inseparable from apparent annual occupancy. When the

ultimate goal of occupancy modeling is applied habitat management (e.g., identifying areas to target restoration activities based on occupancy probability of the target species), simple occupancy models could result in poor or biased estimation of the relationship between habitat features and the latent occupancy state. Based on naïve single-year
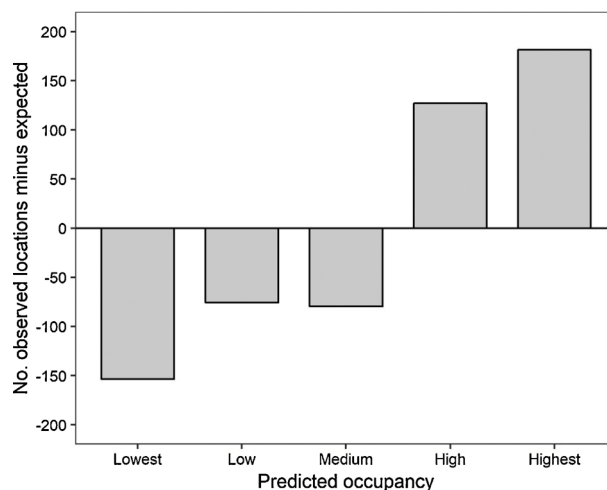

Fig. 6. Difference between the number of observed independent desert tortoise locations in each predicted relative probability of occupancy bin compared to the number expected at random in the Boulder City Conservation Easement, Clark County, Nevada, USA. For example, approx. 150 fewer locations occurred in the lowest predicted occupancy bin than expected if independent tortoises were using the study area randomly with respect to the predictive raster surface.

occupancy estimates, we would have estimated dramatically different proportions of our study area as being occupied in any single year and, depending on the year, may have had biased an imprecise parameters estimates for landscape covariates. Here, we present a simple model that explicitly subsumes variability in availability for detection among a short set of primary periods to estimate latent occupancy over this set of periods. We found no evidence for an underlying trend in occupancy over our five-year time period and our resultant predictive raster surface validated well both internally and externally using an independent data set. This model may prove useful for species that exhibit population changes over larger time periods than single years and that require multiple methods of detection to more precisely estimate how latent occupancy is related to landscape features.

This model rests on one explicit assumption, that latent occupancy within a site is truly constant across the full sampling period. Because the true occupancy state is latent for sites and years without a positive detection, it is ultimately unobservable whether or not a site's occupancy state remained constant. Other recent occupancy models have overcome this challenge in a variety of ways. Nichols et al. (2008) and Mordecai et al. (2011) relax the spatial closure assumption in occupancy models via modeling occupancy at multiple overlapping scales whereby sub-units need not assume constant occupancy to classify a larger unit as occupied. Separately, violation of the constant occupancy assumption within primary sampling periods (i.e., temporary emigration) has been shown to bias occupancy estimates (Rota et al., 2009; Otto et al., 2013; O'Donnell et al., 2015; Valente et al., 2017). This bias can be addressed via explicit modeling of the temporary emigration process, but to date this has only been done for temporary emigration among secondary sampling periods within a single primary period. These variations on occupancy modeling have two factors in common. First, they require additional data and sampling effort to tease apart detection probability versus availability for detection, which can be difficult to achieve with species that fundamentally have low or highly variable detectability or availability for detection. Second, they were developed for case study species that had the ecological potential to exhibit rapid off-site temporary emigration and high rates of occupancy state turnover among years. Neither modeling option deals with species where availability for detection itself is variable among and inextricably linked to primary sampling periods, a common situation for terrestrial and aquatic plants (Alexander et al., 1997; Chen et al., 2013; Gray et al., 2013) and terrestrial reptiles and salamanders (Couturier et al., 2013; O'Donnell and Semlitsch, 2015), among other species. We suggest that the latent occupancy model presented here is a useful complement to existing occupancy models in that by making the simplifying assumption of constant latent occupancy over a short number of primary periods, we can side-step teasing apart detection probability and availability for detection and thus leverage limited detection data to effectively estimate the fundamental relationships between latent occupancy and landscape features.

he assumption of constant occupancy may not always be valid, and it is critical to test it whenever possible. Here, we conducted two validation tests. The first was whether the independent yearly apparent occupancy rates showed a clear temporal trend. After adjusting for unequal survey effort in different years, we found no evidence for a temporal trend. The second test was validation of the resultant predictive surface using an independent data set. We found that the predictive occupancy raster surface effectively predicted how independent desert tortoises used our study area, suggesting that for management purposes the predictive raster was robust to any potential mild violation of the constant occupancy assumption that may have gone undetected in our analysis of trend in yearly apparent occupancy rates. One reviewer pointed out that trends in occupancy rates may only be present in areas of population expansion or contractions, and that sporadic changes in occupancy among years may occur. We concur with this statement in the general sense, but suggest that sporadic changes in annual occupancy around a latent constant average occupancy over time could be interpreted as constant occupancy. This ties into our

original goal of estimating relationships between landscape variables and latent occupancy given large swings in apparent annual occupancy, which given the natural history of our study species, are not possible in a non-trend scenario. Nonetheless, we caution that in other cases and systems this assumption must be critically evaluated prior to making inference on which to base management actions.

We also observed wide credible intervals around annual detection probabilities, especially for live tortoises. Within each year, this is likely due to the estimates being a combination of both detection probability and availability for detection (e.g., temporary emigration). Thus, though the final predictive surface validated well for management purposes, we suggest that future models may benefit from work on teasing out temporary emigration from detection probability (Valente et al., 2017).

Specific to our study species, the Mojave desert tortoise, we found negative relationships between occupancy and proximity to roads, higher topographic roughness, and higher coverage of creosote bush. We found a positive relationship between occupancy and higher coverage of bursage. Some of these results are similar to other research with Mojave desert tortoise. Relative indices of desert tortoise abundance and survival are higher when further from roads and from roads with lower traffic levels (Nafus et al., 2013). In contrast, previous research has found that when juvenile desert tortoise are near burrows, they select areas with higher creosote and lower bursage cover than is available (Todd et al., 2016). The proximity and density of washes, a variable that we found unrelated to occupancy, have been positively related to desert tortoise habitat selection and survival (Todd et al., 2016; Nafus et al. 2017). One possible reason for the discrepancy may be that we measured a different metric of desert tortoise ecology. Probability of simple occupancy may be related to different factors than those that affect survival or 3rd-order habitat selection (Johnson, 1980). Desert tortoise may be more likely to occur in landscapes with lower creosote and higher bursage cover, but within those landscapes may prefer locations with higher creosote and lower bursage cover. Similarly, conditions suitable for burrow construction and viability may be correlated with different landscape features than those selected by desert tortoise when away from burrows. Management actions based on patterns underlying occupancy probability should also consider the composition of environmental variables underlying other important drivers of population sustainability, such as survival.

Both specific to desert tortoise and generalizable to other species and systems, the latent true occupancy model we have presented here has useful implications for applied ecology. Managers can use the predictive map to spatially prioritize restoration actions to either uplift poor-quality habitat or shore up high-quality habitat. When evaluated within a GIS, the raster surface can be used to identify which landscape variables are primary drivers of high or low occupancy for any specific spot on the landscape. And in a larger context, the predictive map can be used to target future occupancy surveys, stratify surveys, or delineate areas for conservation protection status that are more likely to contain the species of concern. We suggest that this latent occupancy model can be a useful addition to the existing suite of occupancy models, especially for species where detection probability and availability for detection are low, variable, and conflated with primary sampling periods.

5. Conclusions

Previous studies on a wide variety of taxa, including terrestrial and aquatic plants, salamanders, and tortoises, has found that individuals can be present during a survey but physically unavailable for detection, resulting in potential biases in occupancy rates and detection probabilities. Here, we present a novel occupancy model to estimate true latent occupancy rates, and the relationship between latent occupancy and landscape features, in the presence of availability for detection being confounded with the primary sampling period. Our model and

predictive raster surface of Mojave desert tortoise occurrence across a large study area validated well internally and with independent desert tortoise data. This approach to occupancy modeling may be useful for improving the conservation and management of a wide variety of species and systems.

Declaration of competing interest

We, the authors, declare that we have no real or perceived conflict of interest associated with this study. We have made all appropriate acknowledgements and have disclosed all funding sources. We have no direct financial benefits that could result from publication.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2019.108246.

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