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Validating the performance of occupancy models for estimating habitat use and predicting the distribution of highly-mobile species: A case study using the American black bear



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ABSTRACT

Occupancy models have become a valuable tool for estimating wildlife-habitat relationships and for predicting species distributions. Highly-mobile species often violate the assumption that sampling units are geographically closed shifting the probability of occupancy to be interpreted as the probability of use. We used occupancy models, in conjunction with noninvasive sampling, to estimate habitat use and predict the distribution of a highly-mobile carnivore, the American black bear (*Ursus americanus*) in New Mexico, USA. The top model indicated that black bears use areas with higher primary productivity and fewer roads. The predictive performance of such models is rarely validated with independent data, so we validated our model predictions with 2-independent datasets. We first assessed the correlation between predicted and observed habitat use for 28 telemetry-collared bears in the Jemez Mountains. Predicted habitat use was positively correlated with observed use for all 3 years (2012: $\rho = 0.81$; 2013: $\rho = 0.87$; 2014: $\rho = 0.90$). We then predicted the probability of use within a cell where a bear mortality was documented using 2043 mortality locations from sport harvest, depredation, and vehicle collisions. The probability of habitat use at a mortality location was also positively correlated with observed use by the species (2012: $\rho = 0.74$; 2013: $\rho = 0.89$; 2014: $\rho = 0.93$). Our validation procedure supports the notion that occupancy models can be an effective tool for estimating habitat use and predicting the distribution of highly-mobile species when the assumption of geographic closure has been violated. Our findings may be of interest to studies that are estimating habitat use for highly-mobile species that are secretive or rare, difficult to capture, or expensive to monitor with other more intensive methods.

1. Introduction

Since their inception, occupancy models have been an essential tool for the conservation and management of wildlife. In its original construction, the occupancy-modeling framework enabled estimation of the static occurrence and distribution of a single species while accounting for imperfect detection (MacKenzie et al., 2002). Recent extensions of the paradigm provide the ability to investigate the dynamic nature of various ecological processes that occur over time (MacKenzie et al., 2003) or among multiple species (MacKenzie et al., 2004) and include multiple occupancy states (Nichols et al., 2007). Generalizations of the model accommodate forms of heterogeneity and bias related to variation in abundance (Royle and Nichols, 2003), non-

independence among repeated surveys at sampling units (Nichols et al., 2008), and false-positives or misidentification of species (Miller et al., 2011) while investigating hierarchical scales of occurrence (Hines et al., 2010; Nichols et al., 2008). As a testament to their flexibility, occupancy models have helped explain the mechanisms driving the breeding dynamics of amphibians (Gould et al., 2019), have been used to monitor global-terrestrial biodiversity (Steenweg et al., 2017), have predicted future impacts of population growth and development on wildlife (Brown et al., 2014), and have been used to monitor the spread and dynamics of wildlife pathogens (Russell et al., 2017).

Occupancy models in their simplest form estimate the probability of occupancy (Ψ) in relation to habitat characteristics while accounting for imperfect detection by simultaneously estimating detection

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probability (p) from repeated site visits (MacKenzie et al., 2002). When wildlife species violate the assumption that sampling units (e.g., a pond or a spatial sampling unit on the landscape) are closed to changes in occupancy state estimates of Ψ will be biased. However, if movements by a species in and out of sampling units are random, then Ψ can be interpreted as the probability a sampling unit is “used” rather than occupied and inferences about habitat use can be drawn (MacKenzie, 2006). Therefore, depending on whether closure can be assumed, occupancy modeling can be used to estimate the probability a species occurs at a site or the probability a species uses a site.

Highly-mobile species often violate the geographic closure assumption. Common sampling techniques used to collect presence-absence data for such species are often expensive and logistically challenging (e.g. telemetry collars and aerial surveys). Consequently, non-invasive sampling techniques for highly mobile species, such as camera and hair traps, have become more widely used. When noninvasive sampling techniques are coupled with occupancy modeling, a cost-effective approach arises for modeling habitat use and predicting a species' distribution that also embodies a sound statistical framework (MacKenzie et al., 2002).

For example, occupancy models have provided stakeholders with information on the predicted range of clouded leopards (*Neofelis nebulosa*) to help assess the efficacy of a conservation-corridor initiative on Peninsular Malaysia (Tan et al., 2017). They have also been used to model the effects of livestock grazing on large mammals determining that current laws are insufficient in safeguarding large mammal communities in protected reserves of the Hyrcanian forest of Iran (Soofi et al., 2018). Additionally, inferences from occupancy models have been used to develop maps of high-priority conservation areas helping inform local conservation organizations in their assessment and prioritization of land management and acquisition scenarios for forest-breeding birds in the United States (De Wan et al., 2009). Occupancy models have even been used to fight illegal activity detrimental to wildlife by providing a cost-effective method to predict and direct resources to combat poaching hotspots in Brazil (Ferreguetti et al., 2018).

Despite the common use of occupancy models, empirical studies have often failed to assess model fit and the predictive performance of the models. While some studies have examined violations in model assumptions, most studies did not identify the root cause of the violation (MacKenzie and Bailey, 2004; Royle et al., 2007; Warton et al., 2017). Furthermore, few empirical studies have used spatially-independent data to validate habitat use relationships (Babu et al., 2015; Drouilly et al., 2018; Zeller et al., 2011; but see Walpole et al., 2012). Failing to assess the fit and predictive performance of a habitat use model is particularly concerning given their importance in guiding conservation actions and wildlife policy decisions (Araújo et al., 2019; Guisan et al., 2013). Thus, the assumption that occupancy can be re-interpreted as habitat use when the assumption of geographic closure is not met for highly-mobile species has not been properly addressed.

The objective of our study was to use occupancy modeling coupled with noninvasive sampling to estimate habitat use for a highly-mobile species. We conducted a goodness-of-fit test to detect if violations of model assumptions had occurred and to evaluate the fit of the most supported model to the data. We then assessed the predictive performance of the most supported model at 2-different scales with 2-independent datasets. We show the efficacy of this approach using a case study on the American black bear (*Ursus americanus*) in New Mexico, USA.

2. Methods

2.1. Study area

We conducted our study in the Sangre de Cristo (9925 km²), Sacramento (3700 km²), and Jemez (~850 km²) Mountains, New Mexico, USA (Fig. 1). Elevation ranges from ~1500 m to 4011 m across

the 3 mountain ranges. Dominant vegetation types included subalpine coniferous forest (Engelmann spruce [*Picea engelmannii*], limber pine [*Pinus flexilis*] and subalpine fir [*Abies lasiocarpa*]), montane coniferous forest (Southwestern white pine [*P. strobiformes*], ponderosa pine [*P. ponderosa*], Douglas-fir [*Pseudotsuga menziesii*], white fir [*A. concolor*], blue spruce [*P. pungens*], and aspen [*Populus tremuloides*]), and coniferous and mixed woodland (piñon pine [*P. edulis*] and juniper [*Juniperus* spp.]; Dick-Pedie, 1993). Oak species (*Quercus* spp.) are scattered throughout mid- and low-elevation forests and are most abundant at lower elevations (Dick-Pedie, 1993). The average monthly temperature was highest in July and lowest in January ranging among the mountain ranges from 22 °C to 30 °C and –15 °C to –5 °C, respectively (Western Regional Climate Center, 2018). Average monthly precipitation varied among the mountain ranges from 7.10 cm to 12.70 cm and was highest during the monsoon season (Jul–Oct), with rainfall typically peaking in August (Western Regional Climate Center, 2018). In sum, the three mountain ranges were similar in orography, land cover, and climate.

2.2. Field sampling and genetic analysis

We used hair traps to sample black bears in the Sangre de Cristo and Sacramento mountains. Sampling within each study area was limited to primary habitat defined as all closed-canopy forest and woodland vegetation types (Costello et al., 2001). We distributed a grid of 5-km × 5-km cells with a randomly determined origin across the landscape. In each cell, we set a hair trap in a place most likely to encounter bears such as suspected travel routes, the occurrence of seasonal forage (e.g., green grass and ripe soft and hard mast), and the presence of bear sign (Kendall et al., 2009). Due to logistical constraints, a survey in the Sangre de Cristo Mountains lasted 4 weeks whereas a survey for the Sacramento Mountains was 2 weeks. We set hair traps across 4 surveys in the northern (22 Apr–5 Sep 2012) and southern Sangre de Cristo Mountains (29 Apr–9 Sep 2013) and across 6 surveys in the Sacramento Mountains (5 May–6 Aug 2014).

A hair trap consisted of a strand of barbed wire stretched 45 cm above ground and wrapped around ≥3 trees with a collection of organic material at the center (i.e., a lure pile). During each survey in the Sangre de Cristo Mountains, we randomly selected 1 of 4 non-consumable lures (cow blood/fish emulsion mixture [blood], skunk tincture/lanolin mixture [skunk], fatty acid scent tablet [FAS], or anise oil) and applied it to the lure pile. Based on this sampling, FAS and anise oil scent duration and dispersal distance appeared inferior to blood and skunk. A chi-square test of independence confirmed that the 4 lures were not collecting an equal number of samples ($\chi_3^2 = 616.29$, $P \leq 0.001$). In the Sacramento Mountains, we randomly selected and applied either blood or skunk lures to maximize detection of black bears. A sample consisted of all hair caught in one barb, and we used our best judgment to identify hair samples collected from when bears rolled around in the lure pile. We deposited each hair sample in a separate paper-coin envelope. Afterwards, we cleaned the barb wire with a propane torch to prevent false detections during subsequent surveys. We moved hair traps (100 m to 2.5 km) between surveys to help increase detection rates (Boulanger et al., 2006).

The only qualifier for an occupancy analysis is detection of the focal species (MacKenzie et al., 2002). We considered hair samples to be from a black bear if 2 odd numbered alleles were amplified for the G10J marker and if ≥4 loci were amplified across 8 additional genetic markers (G1D, G10B, G10L, G10M, G10H, G10J, G10U, MU59; Paetkau et al., 1998, 1995; Taberlet et al., 1997). The G10J marker is an indicator for black bears among North American ursids but has shown some cross-species amplification (L. Harris, Wildlife Genetics International, personal communication). All samples were exported to Wildlife Genetics International (WGI), Nelson, British Columbia, Canada under permits required by the Convention on International Trade in Endangered Species (Export Permits 12US86417A/9, 13US19950B/9, and 14US43944B/9).

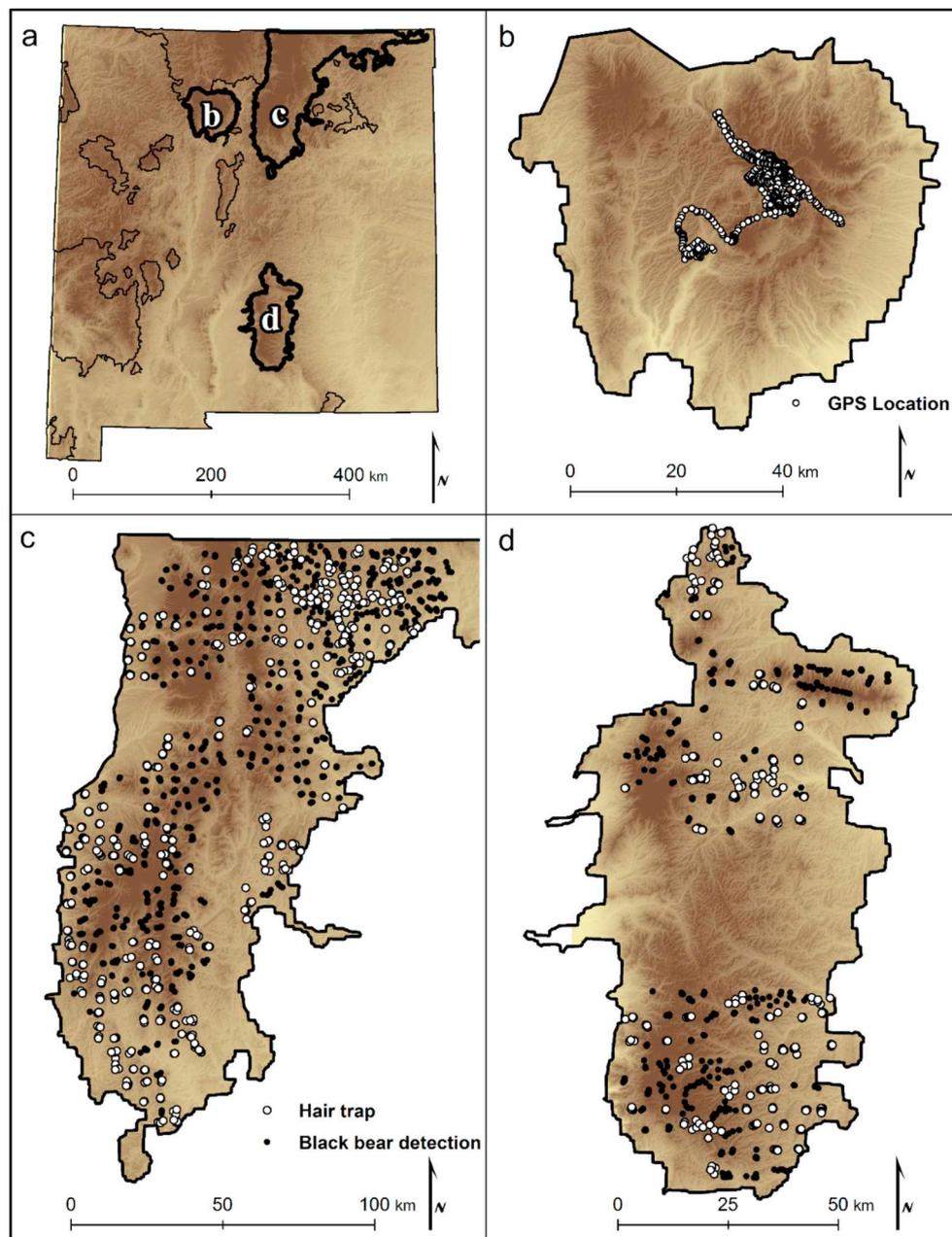


Fig. 1. (a) Location of our 3 study areas within New Mexico, USA overlaid on to a digital elevation map with hillshade where the color gradient from light to dark brown represents lower to higher elevations. (b) Telemetry locations of 1 American black bear (*Ursus americanus*) from 22 May 2013 to 31 August 2013 in the Jemez Mountains. Distribution of hair traps in the (c) Sangre de Cristo, 2012–2013 and (d) Sacramento Mountains, 2014. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Kindschuh et al. (2016) captured adult-black bears in the Jemez Mountains from June 2012–July 2014 using culvert traps and foot snares. They fitted individuals with a global positioning system (GPS) telemetry collar programmed with a 3 h fix interval (Advanced Telemetry Systems model G2110E, Isanti, Minnesota, USA or Northstar model NSG-LD2, King George, Virginia, USA). Our sampling procedures were approved by the New Mexico State University Institutional Animal Care and Use Committee (Protocols #2011-027) and New Mexico Department of Game and Fish (Scientific Collection Permit 3504). The New Mexico Department of Game and Fish (NMDGF) provided locations on statewide sport-hunted, depredation, and vehicle collision mortalities collected in 2012–2014.

2.3. Modeling habitat use

We used single-species, single-season occupancy models to investigate habitat use by black bears (MacKenzie et al., 2002). We used the results from our genetic analysis to create a detection history for each 5-km × 5-km cell. While habitat use was the primary objective of our occupancy modeling analysis, providing an accurate depiction of the detection process to eliminate negative bias is essential to the overall model fit and an accurate depiction of habitat use (MacKenzie et al., 2002). We hypothesized that detection may be influenced by the distance of a hair trap to a road (dist), lure scent (lure), and mountain range (mtn) with mtn depicting the natural variation in the movement

behavior of bears from different mountain ranges or due to differences in survey length between the Sangre de Cristo and Sacramento mountains. We predicted a lower detection probability when we set hair traps closer to roads as bears have been shown to avoid roads (Simek et al., 2015; Stillfried et al., 2015). We predicted a higher detection probability when we used blood as a lure based on the results of our chi-square test of independence. We also predicted a higher detection probability in the Sangre de Cristo Mountains because the length of the surveys was longer. We pooled the detection data by survey across the 2 mountain ranges. This resulted in the detection history having 6 total surveys with sites in the Sangre de Cristo Mountains censored in surveys 5 and 6. Due to their ineffectiveness in the Sangre de Cristo Mountains, we pooled the anise oil and FAS lures into 1 lure category.

We modeled habitat use by developing a suite of a priori models. We hypothesized that habitat use would be influenced by: 1) spatio-temporal variation in primary productivity because food availability influences reproduction and survival (Costello et al., 2003), 2) terrain complexity because it reflects hydrological profiles that may influence security cover, forage diversity, and primary productivity (Berryman et al., 2015), and 3) road density because of increased human disturbance and perceived risk and reduced survival (Hostetler et al., 2009). We selected the enhanced vegetation index (EVI), its coefficient of variation (EVICV), and dominant land cover type (cover) as covariates correlated with food availability (Merkle et al., 2013; Nijland et al., 2016). We predicted higher use in cells with a higher mean EVI (a measure of productivity) and mean EVICV (a measure of seasonality; Requena-Mullor et al., 2014). We predicted a positive relationship with seasonality because pulses of productivity that occurred predominantly during the summer would be more advantageous for bears as they prepare for hibernation (Wiegand et al., 2008). The EVI has been shown to be sensitive to spatial and temporal variation in photosynthetic activity and has improved corrections for aerosols and cloud cover compared to NDVI (Huete et al., 2002). We predicted higher use of mixed conifer and spruce-fir land cover, which tend to occur at mid- to high-elevations, because these classifications likely represent early-seasonal grasses and soft-mast plant communities that contain important black bear food during the period that our study was conducted (Guntly, 2016). We predicted a positive association with the terrain ruggedness index (TRI) because greater terrain complexity would result in more diverse hydrological profiles that should yield higher forage diversity and primary productivity (Berryman et al., 2015; Nellemann et al., 2007). We predicted that a higher density of roads open to mechanized travel would be used less due to increased anthropogenic disturbance (Gaines et al., 2005; Hostetler et al., 2009). Last, we assigned mtn as a group variable to evaluate if habitat use was specific to or similar across mountain ranges.

We calculated EVI using 16-day, 250 m Moderate Resolution Imaging Spectrometer (MODIS) datasets (Huete et al., 2002). We generated a single EVI and EVICV value for each cell by averaging all 250 m pixels within a 5-km \times 5-km cell for each MODIS image and then averaging all MODIS images across all surveys. We reclassified the 30 m LANDFIRE land cover data into 5 classes that represented black bear habitat: mixed conifer (combination of aspen, Douglas fir, white pine), piñon pine-juniper, ponderosa pine, spruce-fir, and all remaining classes (www.landfire.gov; Rollins, 2009). We assigned a sixth classification of “heterogeneous” when no classification represented $\geq 50\%$ of the area within the cell. We calculated TRI using a National Elevation Dataset 30 m digital elevation model (www.nationalmap.gov) and the Benthic Terrain Modeler in ArcMap. We generated a single, averaged TRI value for each cell. We measured road density and distance to roads using the U.S. Census Bureau's 2010 TIGER/Line county-road dataset (www.rgis.unm.edu). We extracted all model covariates using ArcMap 10.2.1 (Environmental Systems Research Institute, Inc., Redlands, California, USA).

We used a multi-step modeling process to determine the final model structure for p and Ψ (Doherty et al., 2012). First, we standardized all

continuous covariates by subtracting the mean and dividing by 2 standard deviations (Gelman, 2008). We assessed multicollinearity between continuous covariates by calculating Pearson's sample correlation (r) between all covariate combinations, with $r \geq 0.60$ disqualifying use of a covariate combination in a model. We used box plots to visually evaluate trends between the categorical land cover variable and each continuous covariate. Land cover and EVI were correlated, so we did not include them in the same model. We first modeled p by dist, lure, mtn, all additive combinations of the 3 covariates, or constant while using the global model for Ψ . We then incorporated the model structure from the top model for p into our subsequent modeling of Ψ using all additive combinations of the uncorrelated covariates except for EVICV, which was only included in models with EVI. We also included an interaction between TRI and EVI as we hypothesized cells with high EVI and low TRI may be used less by bears because the cell may be more accessible to human activity or contains more open fields than forest cover.

We used Akaike's Information Criterion corrected for small sample size (AICc; Hurvich and Tsai, 1989) to rank and determine relative support among models. We used the AICc weights (w_i) to assess proportional support for each model (Burnham and Anderson, 2002). We assessed the goodness-of-fit for the top-ranked model using visual diagnostic plots based on simulated Dunn-Smyth residuals for occupancy following methods in Warton et al. (2017). If the 95% confidence interval (CI) of the simulation overlapped 0, then we assumed the model fit the data and that there were no violations of model assumptions. We performed our occupancy analysis and model ranking using program MARK (White and Burnham, 1999). All other analyses were performed in program R (v. 3.4.4 and v. 3.5.1; R Core Team, 2017, 2018).

2.4. Validating the habitat use model

We used the parameter structure for Ψ from the top model to predict the distribution of black bears at 2-spatial scales, the Jemez Mountains and New Mexico state. We limited predicted habitat use in the Jemez Mountains to primary habitat to evaluate how well the top model predicted habitat use in a mountain range that is similar in habitat but independent of the Sangre de Cristo and Sacramento mountains (Costello et al., 2001). We did not limit predicted habitat use for New Mexico to primary habitat to evaluate how well the model performed outside of the conditions used to construct it. We validated these maps by comparing predicted to observed habitat use based on GPS and mortality locations for each respective scale. We selected GPS locations that were collected during the same time that hair samples were collected in the Sangre de Cristo and Sacramento mountains, whereas, we used all mortality locations collected in 2012–2014.

First, from a random starting location, we overlaid a grid of 5-km \times 5-km cells over primary bear habitat within the Jemez Mountains and across all of New Mexico. We then predicted the probability of use for each cell. We scaled the predicted probabilities of the cells to sum to 1, grouped them into 20-equally sized bins, and then summed within each bin:

$$P(\text{use}) = \sum_j^{N_i} \hat{\psi}_{ij}$$

where i is the bin identifier, j is the grid cell, and $\hat{\psi}$ is the probability of habitat use for 1 to N grid cells (Boyce et al., 2002; Howlin et al., 2004). Next, we summed the proportion of observed habitat use for each grid cell by bin:

$$O(\text{use}) = \sum_j^{N_i} \frac{r_{ij}}{r}$$

where i is the bin identifier, j is the grid cell, and r is the observed collar and mortality locations in the study area (Boyce et al., 2002; Howlin et al., 2004). We then conducted a Spearman's rank correlation test to

assess the correlation between predicted and observed habitat use and assumed predicted and observed use would be positively correlated ($\rho \geq 0.60$; Boyce et al., 2002). We also generated a histogram that described the distribution of mortality locations across the distribution of predicted use probabilities for New Mexico. We assumed that each source of mortality was proportional to use, and locations would be found in cells with a higher probability of use. If not, the habitat use model was not a good predictor of habitat use across New Mexico, or the source of mortality may have biased locations towards low-quality habitat due to higher road densities resulting in greater hunter access (sport-harvest), greater anthropogenic attractants (depredation), or higher road densities in areas outside of non-primary habitat (vehicle collision).

3. Results

3.1. Field sampling and genetic analysis

We set 397 and 148 hair traps that were open for 43,951 and 12,080 trap days in the Sangre de Cristo and Sacramento mountains, respectively. These traps collected 2485 and 1198 hair samples with 60% and 53% of hair traps collecting ≥ 1 black bear hair sample. We obtained DNA suitable for amplification from 1813 and 851 hair samples, and we identified 1046 and 546 samples as black bear in the Sangre de Cristo and Sacramento mountains, respectively. In the Jemez Mountains, Kindschuh et al. (2016) live-captured 28 individual bears (19 male; 9 female) from which the telemetry collars obtained 30,660 (22,429 male; 8231 female) GPS locations that coincided with sampling periods in the Sangre de Cristo and Sacramento mountains. New Mexico Department of Game and Fish collected 711, 776, and 556 mortality locations during a 3-yr period (2012–2014), respectively.

3.2. Modeling habitat use

The top-ranked detection model included lure and mtn as covariates and was supported almost twice as much ($w_i = 0.61$) as the second ranked model ($w_i = 0.32$; Appendix Table A.1). The second ranked model differed from the top model by only 1 parameter and both had nearly identical deviances. The additional covariate in the second-ranked model (dist) was uninformative and the competitiveness of the two models was a consequence of a model structure that was similar to the top-ranked model (Arnold, 2010). Therefore, we used the model structure from the top-ranked model for our subsequent modeling of Ψ . As we predicted, detection probability was highest for the blood lure and in the Sangre de Cristo Mountains (Fig. 2). The 95% CIs for the beta coefficients did not overlap 0 for all detection probability covariates (blood: $\beta = 1.28$, 95% CI = 0.99–1.58; skunk: $\beta = 0.73$, 95% CI = 0.43–1.02; mtn: $\beta = 0.39$, 95% CI = 0.11–0.66). The ratio between standardized beta coefficients showed blood had the largest effect relative to skunk (1.76) and mtn (3.33) and skunk had a larger effect than mtn (1.89).

The hypotheses that primary productivity and road density affect black bear habitat use were supported. The top-ranked model for Ψ included EVI, EVICV, and road density, however, this model received just over a third of the total model weight ($w_i = 0.36$). The second and third ranked models differed from the top model by only 1 parameter and had nearly identical deviances as the top model. Like the results for modeling p , the competitiveness of the 2 models was a consequence of a model structure that was similar to the top-ranked model. Thus, we eliminated the 2 models with the uninformative covariates (TRI and mtn) from our model set and the w_i for the top-ranked model increased to 0.52 (Appendix Table A.2). The next 11 models contained a cumulative weight of 0.45 and all but 2 had EVI as a covariate. Consistent with our predictions, habitat use increased with increasing EVI and EVICV and decreased with increasing road density (Fig. 2). The 95% CIs for the beta coefficients did not overlap 0 for all probability of use

covariates (EVI: $\beta = 2.66$, 95% CI = 1.90–3.42; EVICV: $\beta = 0.84$, 95% CI = 0.20–1.47; road: $\beta = -0.53$, 95% CI = -1.02 to -0.05). The ratio between standardized beta coefficients showed that EVI had the largest effect on probability of use relative to EVICV (3.18) and road density (4.97) and EVICV had a larger effect than road density (1.56). The visual diagnostic plots did not show a lack-of-fit for the top model as the 95% CIs for all simulations overlapped 0 (Appendix Figs. B.1 and B.2). The observed proportion of cells used across both mountain ranges was 0.58 and when corrected for imperfect detection, the estimated probability of cell use was $\hat{\Psi} = 0.74$ (SE = 0.03).

3.3. Validating the habitat use model

We used the model structure for Ψ from the top-ranked occupancy model to predict habitat use for bears in the Jemez Mountains and New Mexico because it received $5\times$ more support than the second-ranked model and because nearly all of the remaining models contained EVI (Appendix Table A.2). Predicted habitat use was positively correlated with observed use for all 3 years in the Jemez Mountains (2012: $\rho = 0.81$; 2013: $\rho = 0.87$; 2014: $\rho = 0.90$) and across New Mexico (2012: $\rho = 0.74$; 2013: $\rho = 0.89$; 2014: $\rho = 0.93$). Eighty-two percent, 72%, and 77% of all mortality locations in 2012–2014, respectively, fell within cells that had a predicted probability of habitat use of ≥ 0.90 even though these cells represented only 18–19% of the total cells in New Mexico during the 3 years (Fig. 3; Appendix Fig. C.1). When separated by cause-specific mortality cells that had a predicted probability of habitat use of ≥ 0.90 contained the highest number of mortalities (sport-hunted: 82–87%; depredation: 50–67%; vehicle collision: 37–50%; Appendix Fig. C.1).

4. Discussion

4.1. Benefits of occupancy modeling

Occupancy modeling is a flexible and reliable statistical method that separates the observation process from the ecological process (i.e., p and Ψ) and yields a more accurate representation of where a species has been detected and how it uses the landscape (Kéry et al., 2013; Lahoz-Monfort et al., 2014). This level of inference is valuable because environmental characteristics can affect the detection of a species and bias descriptions of habitat use leading to ill-informed conservation and management plans (MacKenzie, 2006). Our research highlights the utility of occupancy modeling, coupled with noninvasive sampling, to estimate habitat use for highly-mobile species. A unique aspect of our study was the opportunity to use independent data to assess the predictive performance of our model. Our empirical validation procedure reinforces the view that occupancy modeling can be used to estimate habitat use when the assumption that geographic closure of sampling units is violated by a highly-mobile species.

Additionally, when paired with thoughtful and flexible study designs occupancy models can help achieve multiple research objectives. For example, Gould et al. (2018) used noninvasive genetic sampling to estimate the density of black bears, and then we used these data to explore habitat use over large-spatial scale that would have been too financially exorbitant with telemetry collars. In studies that use camera traps, researchers could use occupancy modeling to simultaneously analyze range and community dynamics, investigate species interactions, and monitor biodiversity (Kéry et al., 2013; Rich et al., 2017; Robinson et al., 2014). Occupancy modeling, however, may not always be the most appropriate method for a study. For instance, research on cause-specific mortality, foraging behavior, and 2nd–4th order resource selection requires detailed spatiotemporal location data necessitating the use of telemetry collars (Manly et al., 2002). Despite its strengths, the decision to use occupancy modeling will depend on the ecological questions of interest and monetary constraints of a project.

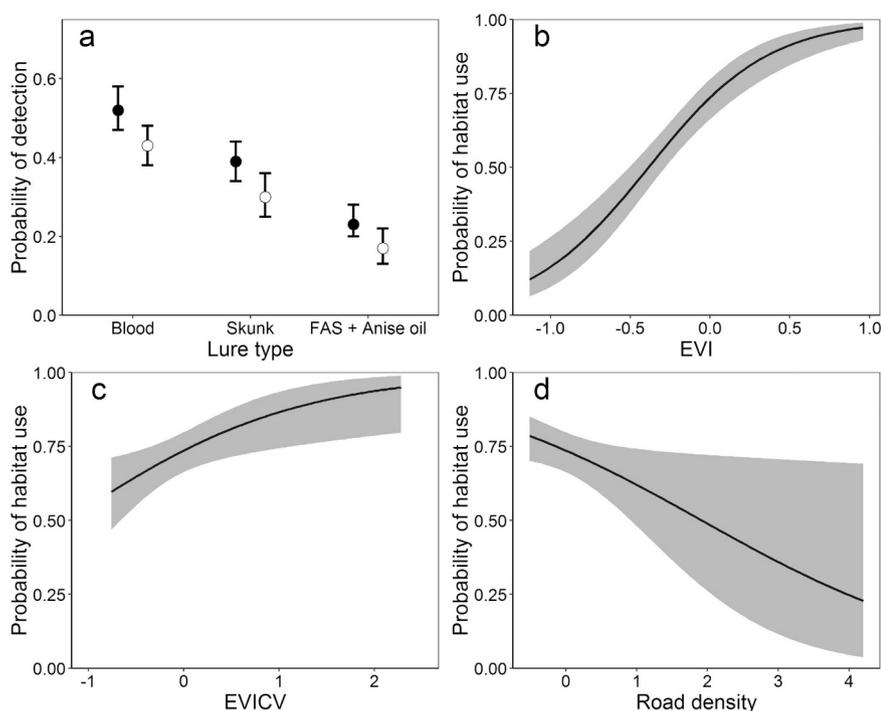


Fig. 2. (a) The probability of detection as a function of lure type (blood, skunk, fatty acid scent tablet [FAS] and anise oil) and mountain range (Sangre de Cristo Mountains = filled circles, Sacramento Mountains = unfilled circles) and (b) the probability of habitat use (Ψ) with respect to the enhanced vegetation index (EVI), (c) its coefficient of variation (EVICV), and (d) road density. Gray shade represents the 95% confidence intervals of the probability of habitat use.

4.2. Validating the habitat use model

Our predicted species distribution maps for black bears exhibited high spatiotemporal concordance with observed habitat use at both spatial scales. Model predictions are often not validated or are validated without using independent data because these data are often difficult and costly to obtain. Instead, researchers typically split the occurrence data into training and testing datasets. They then use the training dataset to generate a single habitat use model, or iteratively generate multiple habitat use models, and validate the model(s) using the testing dataset (e.g., k-fold cross-validation; Boyce et al., 2002). A more informative approach would be to estimate habitat use using the full dataset ensuring a larger sample and greater statistical power to describe patterns of habitat use. Then validate the predictive performance of the model using independent data. Yet, researchers rarely have access to additional independent data, whereas, we were fortunate to have 2-independent datasets available to evaluate our habitat use model.

In the United States, state wildlife management agencies commonly collect mortality information on multiple species so such data are often available to serve as independent data sets. Mortality locations, however, can be biased depending on the cause of mortality. For example, sport harvest locations may be biased due to hunter selectivity and the accessibility of an area to motorized vehicles. Depredation mortalities may be biased if artificial attractants occur outside of high-use habitat. While vehicle collisions may be biased dependent on road type (e.g., interstate vs. dirt). All mortality sources will likely be affected by differential movements of the species due to sex and age (e.g., dispersing juveniles) and increased and uncommon movement patterns due to drought-induced failure of food crops (Costello, 2010; Jones et al., 2015; Kerley et al., 2002). The mortality data we used was male-biased as more males were either killed by sport harvest (1.5–1.6 males:1.0 female), removed because of depredation events (2.0–4.0 males:1.0 female), or killed by vehicle collisions (1.1–2.0 males:1.0 female) across the 3 years. The larger proportion of males is likely a combination of male biased harvest limits, larger movement rates relative to females, and female-biased philopatry, which could increase a male's risk of mortality due to increased interaction with roads and humans (Lee and Vaughan, 2003; Costello, 2010; Gould et al., 2018). Despite these

concerns, it seems logical that bears would use areas that are either easier to travel through, to conserve energy, or contain the resources they need to meet their energy requirements. Our assumption seems reasonable, given most of the cause-specific mortality locations were found in areas with a predicted probability of use ≥ 0.90 (Appendix Fig. C.1).

4.3. Modeling habitat use

The simulated Dunn-Smyth residuals for occupancy did not show any pattern and the 95% CIs for all simulations overlapped 0 suggesting that the model fit the data well and that the assumptions of the model were not violated (Appendix Figs. B.1 and B.2). The model assumption of geographic closure, however, was indeed violated due to the extended sampling period (Gould et al., 2018). Instead, these results likely indicate that movement in and out of the sampling units by the species was random and the probability of occupancy could be interpreted as use.

Habitat use by black bears in New Mexico had a positive relationship with primary productivity and its variation, which likely describes the spatiotemporal distribution of food resources. This relationship can be explained by their omnivorous diet, which is comprised predominantly of vegetative matter (Costello et al., 2001; McLellan, 2011). The positive relationships between primary productivity and habitat use is consistent with various ursid studies that have shown a correlation between primary productivity and population-level habitat selection, habitat quality, and patterns in density (Duquette et al., 2017; Stetz et al., 2018; Wiegand et al., 2008).

Incorporating variables on ecosystem functions (i.e., covariates representing multiple rather than a single ecosystem process) into modeling habitat use has become increasingly popular because they more realistically track ecological patterns (Cabello et al., 2012). Ecosystem functioning variables have improved predictions by species distribution models (Requena-Mullor et al., 2014) and have helped explain diet patterns, population cycles, and habitat use in several mammalian species (Schmidt et al., 2018; Squires et al., 2013; Tsuji et al., 2015). We used EVI and EVICV to represent primary productivity and seasonality, respectively. Land cover combined with road density, however, had a similar performance as the top model as the 2 had nearly identical

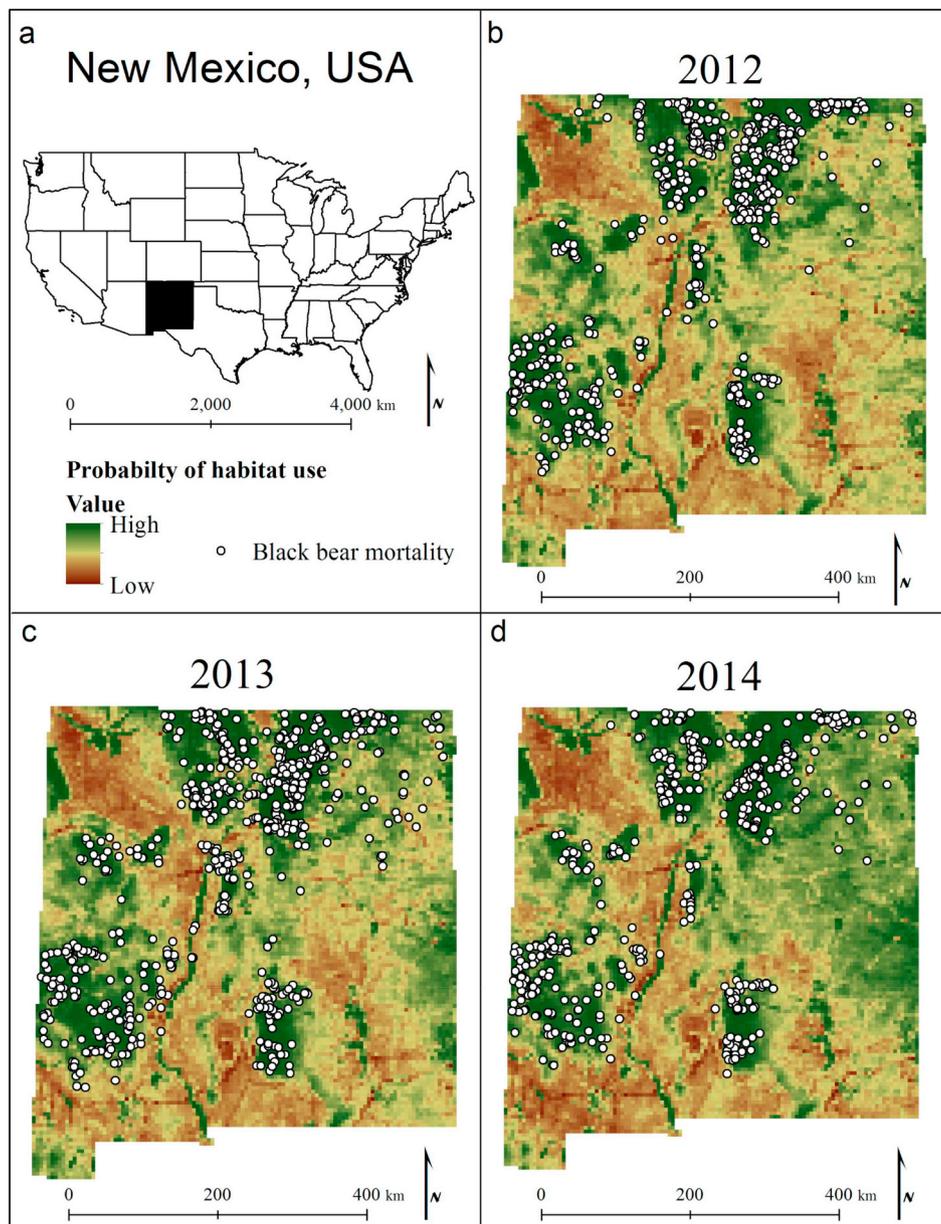


Fig. 3. The predicted probability of habitat use for American black bears (*Ursus americanus*) across (a) New Mexico, USA overlaid with black bear mortality locations in (b) 2012, (c) 2013, and (d) 2014.

deviance values. The similarity in performance most likely arose because EVI and land cover were correlated, but land cover was not ranked highly due to parsimony (Burnham and Anderson, 2002). Thus, land cover may be a good predictor of bear habitat use, but ecosystem functioning variables are more advantageous because they can often be assessed with a single, continuous variable resulting in 2 parameters (intercept and slope) and can characterize the dynamic, spatiotemporal heterogeneity in ecosystem processes more efficiently than a categorical land cover variable. The occupancy model, however, over-predicted habitat use in east-central New Mexico along the Texas border. The EVI and EVICV were likely sensitive to agriculture-based irrigation and the presence of shinnery oak (*Quercus havardii*), a deciduous and low-growing shrub. Therefore, some subjectivity based on biological expertise may be necessary when constructing and interpreting habitat use models that are extrapolated outside the area they were generated.

Our results also suggest that habitat use is influenced by road density, but to a much lesser degree than primary productivity. The

negative relationship between road density and habitat use is consistent with a large body of research that has highlighted the negative impact of roads on ursids, including increasing habitat loss, reducing habitat quality, heightening genetic isolation, and increasing mortality rates (Dixon et al., 2007; Little et al., 2017). Roads are also negatively correlated with habitat use of other mammals, from marsupials to small rodents and large-obligate carnivores with greater impacts on species exhibiting low reproduction and high vagility (i.e., highly-mobile species; Kerley et al., 2002; McAlpine et al., 2006; Kelly et al., 2013; Rytwinski and Fahrig, 2011).

We found no support that habitat use was related to terrain complexity or differences between mountain ranges (Appendix Table A.2). Terrain complexity may not have been supported because the scale of our study and the sample of available units was limited to mountain ranges. If we had broadened the geographic scale of sampling for the development of our occupancy model, a greater proportion of less rugged areas would have been included and terrain complexity likely would have been an important predictor of broad-scale habitat use for black bears.

4.4. Conclusions

Predictive maps highlighting wildlife-habitat use and predicting a species' distribution can be valuable tools for developing a better understanding of a species' spatial ecology, thereby informing species management and conservation plans. Occupancy models provide practitioners with the ability to estimate and predict these relationships while accounting for imperfect detection of a species. Using 2-validation datasets, we assessed the performance of occupancy models for estimating habitat use and predicting the distribution of a highly-mobile species, the American black bear. Despite our predictions occurring in an independent mountain range and outside of the habitat conditions upon which the model was constructed, predicted and observed habitat use were positively correlated. Our validation procedure supports the notion that occupancy models can be an effective tool for estimating habitat use and predicting the distribution of highly-mobile species when the assumption of geographic closure has been violated. Our findings may be particularly useful when conservation and management agencies are charged with estimating habitat use for highly-mobile species that are secretive or rare, difficult to capture, or expensive to monitor with other more intensive methods.

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2019.03.010>.

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References

- Araújo, M.B., Anderson, R.P., Barbosa, A.M., Beale, C.M., Dormann, C.F., Early, R., Garcia, R.A., Guisan, A., Maiorano, L., Naimi, B., O'Hara, R.B., Zimmermann, N.E., Rahbek, C., 2019. Standards for distribution models in biodiversity assessments. *Science Advances* 5, eaat4858. <https://doi.org/10.1126/sciadv.aat4858>.
- Arnold, T.W., 2010. Uninformative parameters and model selection using Akaike's Information Criterion. *Journal of Wildlife Management* 74, 1175–1178. <https://doi.org/10.2193/2009-367>.
- Babu, S., Karthik, T., Srinivas, G., Kumara, H.N., 2015. Linking critical patches of sloth bear *Melursus ursinus* for their conservation in Meghamalai hills, Western Ghats. *India. Current Science* 109, 7. <https://doi.org/10.18520/v109/i8/1492-1498>.
- Berryman, E.M., Barnard, H.R., Adams, H.R., Burns, M.A., Gallo, E., Brooks, P.D., 2015. Complex terrain alters temperature and moisture limitations of forest soil respiration across a semiarid to subalpine gradient. *Journal of Geophysical Research: Biogeosciences* 120, 707–723. <https://doi.org/10.1002/2014JG002802>.
- Boulanger, J., Proctor, M., Himmer, S., Stenhouse, G., Paetkau, D., Cranston, J., 2006. An empirical test of DNA mark-recapture sampling strategies for grizzly bears. *Ursus* 17, 149–159. [https://doi.org/10.2192/1537-6176\(2006\)17\[149:AETODM\]2.0.CO;2](https://doi.org/10.2192/1537-6176(2006)17[149:AETODM]2.0.CO;2).
- Boyce, M.S., Vernier, P.R., Nielsen, S.E., Schmiegelow, F.K., 2002. Evaluating resource selection functions. *Ecological Modelling* 157, 281–300. [https://doi.org/10.1016/S0304-3800\(02\)00200-4](https://doi.org/10.1016/S0304-3800(02)00200-4).
- Brown, M.L., Donovan, T.M., Schwenk, W.S., Theobald, D.M., 2014. Predicting impacts of future human population growth and development on occupancy rates of forest-dependent birds. *Biological Conservation* 170, 311–320. <https://doi.org/10.1016/j.biocon.2013.07.039>.
- Burnham, K.P., Anderson, D.R., 2002. *Model Selection and Multi-model Inference: A Practical Information-Theoretic Approach*, 2nd ed. Springer-Verlag New York, New York, NY, USA.
- Cabello, J., Fernández, N., Alcaraz-Segura, D., Oyonarte, C., Piñeiro, G., Altesor, A., Delibes, M., Paruelo, J.M., 2012. The ecosystem functioning dimension in conservation: insights from remote sensing. *Biodiversity and Conservation* 21, 3287–3305. <https://doi.org/10.1007/s10531-012-0370-7>.
- Costello, C.M., 2010. Estimates of dispersal and home-range fidelity in American black bears. *J Mammal* 91, 116–121. <https://doi.org/10.1644/09-MAMM-A-015R1.1>.
- Costello, C.M., Jones, D.E., Green Hammond, K.A., Inman, R.M., Inman, K.H., Thompson, B.C., Deitner, R.A., Quigley, H.B., 2001. A Study of Black Bear Ecology in New Mexico With Models for Population Dynamics and Habitat Suitability (Final Report No. W-131-R). Federal Aid in Wildlife Restoration Project. New Mexico Department of Game and Fish, Santa Fe, New Mexico, USA.
- Costello, C.M., Jones, D.E., Inman, R.M., Inman, K.H., Thompson, B.C., Quigley, H.B., 2003. Relationship of variable mast production to American black bear reproductive parameters in New Mexico. *Ursus* 14, 1–16.
- De Wan, A.A., Sullivan, P.J., Lembo, A.J., Smith, C.R., Maerz, J.C., Lassoie, J.P., Richmond, M.E., 2009. Using occupancy models of forest breeding birds to prioritize conservation planning. *Biological Conservation* 142, 982–991. <https://doi.org/10.1016/j.biocon.2008.12.032>.
- Dick-Pedie, W.A., 1993. *New Mexico vegetation, past, present and future*. University of New Mexico Press. In: Albuquerque, New Mexico, USA.
- Dixon, J.D., Oli, M.K., Wooten, M.C., Eason, T.H., McCown, J.W., Cunningham, M.W., 2007. Genetic consequences of habitat fragmentation and loss: the case of the Florida black bear (*Ursus americanus floridanus*). *Conservation Genetics* 8, 455–464. <https://doi.org/10.1007/s10592-006-9184-z>.
- Doherty, P.F., White, G.C., Burnham, K.P., 2012. Comparison of model building and selection strategies. *J Ornithol* 152, 317–323. <https://doi.org/10.1007/s10336-010-0598-5>.
- Drouilly, M., Clark, A., O'Riain, M.J., 2018. Multi-species occupancy modelling of mammal and ground bird communities in rangeland in the Karoo: a case for dryland systems globally. *Biological Conservation* 224, 16–25. <https://doi.org/10.1016/j.biocon.2018.05.013>.
- Duquette, J.F., Belant, J.L., Wilton, C.M., Fowler, N., Waller, B.W., Beyer, D.E., Svoboda, N.J., Simek, S.L., Beringer, J., 2017. Black bear (*Ursus americanus*) functional resource selection relative to intraspecific competition and human risk. *Can. J. Zool.* 95, 203–212. <https://doi.org/10.1139/cjz-2016-0031>.
- Ferreguetti, Á.C., Pereira-Ribeiro, J., Prevedello, J.A., Tomás, W.M., Rocha, C.F.D., Bergallo, H.G., 2018. One step ahead to predict potential poaching hotspots: Modeling occupancy and detectability of poachers in a neotropical rainforest. *Biological Conservation* 227, 133–140. <https://doi.org/10.1016/j.biocon.2018.09.009>.
- Gaines, W.L., Lyons, A.L., Lehmkuhl, J.F., Raedeke, K.J., 2005. Landscape evaluation of female black bear habitat effectiveness and capability in the North Cascades, Washington. *Biological Conservation* 125, 411–425. <https://doi.org/10.1016/j.biocon.2005.03.023>.
- Gelman, A., 2008. Scaling regression inputs by dividing by two standard deviations. *Statistics in Medicine* 27, 2865–2873. <https://doi.org/10.1002/sim.3107>.
- Gould, M.J., Cain, J.W., Roemer, G.W., Gould, W.R., Liley, S.G., 2018. Density of American black bears in New Mexico: density of black bears in New Mexico. *The Journal of Wildlife Management* 82, 775–788. <https://doi.org/10.1002/jwmg.21432>.
- Gould, W.R., Ray, A.M., Bailey, L.L., Thoma, D., Daley, R., Legg, K., 2019. Multistate occupancy modeling improves understanding of amphibian breeding dynamics in the Greater Yellowstone Area. *Ecological Applications* 29, e01825. <https://doi.org/10.1002/eap.1825>.
- Guisan, A., Tingley, R., Baumgartner, J.B., Naujokaitis-Lewis, I., Sutcliffe, P.R., Tulloch, A.I.T., Regan, T.J., Brotons, L., McDonald-Madden, E., Mantyka-Pringle, C., Martin, T.G., Rhodes, J.R., Maggini, R., Setterfield, S.A., Elith, J., Schwartz, M.W., Wintle, B.A., Broennimann, O., Austin, M., Ferrier, S., Kearney, M.R., Possingham, H.P., Buckley, Y.M., 2013. Predicting species distributions for conservation decisions. *Ecology Letters* 16, 1424–1435. <https://doi.org/10.1111/ele.12189>.
- Guntly, K.M., 2016. Black Bear (*Ursus americanus*) Movements, Diet, and Impacts on Ungulate Neonate Survival on the National Rifle Association Whittington Center, New Mexico. Texas Tech University, Lubbock, TX, USA.
- Hines, J.E., Nichols, J.D., Royle, J.A., MacKenzie, D.I., Gopalaswamy, A.M., Kumar, N.S., Karanth, K.U., 2010. Tigers on trails: occupancy modeling for cluster sampling. *Ecological Applications* 20, 1456–1466. <https://doi.org/10.1890/09-0321.1>.
- Hostetler, J.A., Walter McCown, J., Garrison, E.P., Neils, A.M., Barrett, M.A., Sunquist, M.E., Simek, S.L., Oli, M.K., 2009. Demographic consequences of anthropogenic influences: Florida black bears in north-central Florida. *Biological Conservation* 142, 2456–2463. <https://doi.org/10.1016/j.biocon.2009.05.029>.
- Howlin, S., Erickson, W.P., Nielson, R.M., 2004. *A Validation Technique for Assessing Predictive Abilities of Resource Selection Functions*. pp. 1–13.
- Huete, A., Didan, K., Miura, T., Rodriguez, E.P., Gao, X., Ferreira, L.G., 2002. Overview of the radiometric and biophysical performance of the MODIS vegetation indices. *Remote Sensing of Environment* 83, 195–213. [https://doi.org/10.1016/S0034-4257\(02\)00096-2](https://doi.org/10.1016/S0034-4257(02)00096-2).
- Hurvich, C.M., Tsai, C.-L., 1989. Regression and time series model selection in small samples. *Biometrika* 76, 297. <https://doi.org/10.2307/2336663>.
- Jones, M.D., Berl, J.L., Tri, A.N., Edwards, J.W., Spiker, H., 2015. Predicting harvest vulnerability for a recovering population of American black bears in western Maryland. *Ursus* 26, 97–106. <https://doi.org/10.2192/URSUS-D-15-00019.1>.
- Kelly, C.A., Diggins, C.A., Lawrence, A.J., 2013. Crossing structures reconnect federally endangered flying squirrel populations divided for 20 years by road barrier: Road Crossing Structures for Flying Squirrels. *Wildlife Society Bulletin* 37, 375–379. <https://doi.org/10.1002/wsb.249>.
- Kendall, K.C., Stetz, J.B., Boulanger, J., Macleod, A.C., Paetkau, D., White, G.C., 2009. Demography and genetic structure of a recovering grizzly bear population. *The Journal of Wildlife Management* 73, 3–16. <https://doi.org/10.2193/2008-330>.
- Kerley, L.L., Goodrich, J.M., Miquelle, D.G., Smirnov, E.N., Quigley, H.B., Hornocker, M.G., 2002. Effects of roads and human disturbance on amur tigers. *Conservation Biology* 16, 97–108. <https://doi.org/10.1046/j.1523-1739.2002.99290.x>.
- Kéry, M., Guillera-Arroita, G., Lahoz-Monfort, J.J., 2013. Analysing and mapping species range dynamics using occupancy models. *Journal of Biogeography* 40, 1463–1474. <https://doi.org/10.1111/jbi.12087>.

- Kindschuh, S.R., Cain, J.W., Daniel, D., Peyton, M.A., 2016. Efficacy of GPS cluster analysis for predicting carnivory sites of a wide-ranging omnivore: the American black bear. *Ecosphere* 7, e01513. <https://doi.org/10.1002/ecs2.1513>.
- Lahoz-Monfort, J.J., Guillera-Arroita, G., Wintle, B.A., 2014. Imperfect detection impacts the performance of species distribution models: imperfect detection impacts species distribution models. *Global Ecology and Biogeography* 23, 504–515. <https://doi.org/10.1111/geb.12138>.
- Lee, D.J., Vaughan, M.R., 2003. Dispersal movements by subadult American black bears in Virginia. *Ursus* 14, 162–170.
- Little, A.R., Hammond, A., Martin, J.A., Johannsen, K.L., Miller, K.V., 2017. Population growth and mortality sources of the black bear population in Northern Georgia. *Journal of the Southeastern Association of Fish and Wildlife Agencies* 4, 130–138.
- MacKenzie, D.I., 2006. Modeling the probability of resource use: the effect of, and dealing with, detecting a species imperfectly. *The Journal of Wildlife Management* 70, 367–374. [https://doi.org/10.2193/0022-541X\(2006\)70\[367:MTPORUJ\]2.0.CO;2](https://doi.org/10.2193/0022-541X(2006)70[367:MTPORUJ]2.0.CO;2).
- MacKenzie, D.I., Bailey, L.L., 2004. Assessing the fit of site-occupancy models. *JABES* 9, 300–318. <https://doi.org/10.1198/108571104X3361>.
- MacKenzie, D.I., Nichols, J.D., Lachman, G.B., Droege, S., Royle, J.A., Lantim, C.A., 2002. Estimating site occupancy rates when detection probabilities are less than one. *Ecology* 83, 2245–2255. [https://doi.org/10.1890/0012-9658\(2002\)083\[2248:ESORWD\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2002)083[2248:ESORWD]2.0.CO;2).
- MacKenzie, D.I., Nichols, J.D., Hines, J.E., Knutson, M.G., Franklin, A.B., 2003. Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. *Ecology* 84, 2200–2207. <https://doi.org/10.1890/02-3090>.
- MacKenzie, D.I., Bailey, L.L., Nichols, J.D., 2004. Investigating species co-occurrence patterns when species are detected imperfectly. *Journal of Animal Ecology* 73, 546–555. <https://doi.org/10.1111/j.0021-8790.2004.00828.x>.
- Manly, B.F., McDonald, L., Thomas, D., McDonald, T.L., Erickson, W.P., 2002. *Resource Selection by Animals: Statistical Design and Analysis for Field Studies*, 2nd ed. Springer, Netherlands.
- McAlpine, C.A., Rhodes, J.R., Callaghan, J.G., Bowen, M.E., Lunney, D., Mitchell, D.L., Pullar, D.V., Posingham, H.P., 2006. The importance of forest area and fragmentation relative to local habitat factors for conserving forest mammals: a case study of koalas in Queensland, Australia. *Biological Conservation* 132, 153–165. <https://doi.org/10.1016/j.biocon.2006.03.021>.
- McLellan, B.N., 2011. Implications of a high-energy and low-protein diet on the body composition, fitness, and competitive abilities of black (*Ursus americanus*) and grizzly (*Ursus arctos*) bears. *Canadian Journal of Zoology* 89, 546–558. <https://doi.org/10.1139/z11-026>.
- Merkle, J.A., Robinson, H.S., Krausman, P.R., Alaback, P., 2013. Food availability and foraging near human developments by black bears. *Journal of Mammalogy* 94, 378–385. <https://doi.org/10.1644/12-MAMM-A-002.1>.
- Miller, D.A., Nichols, J.D., McClintock, B.T., Grant, E.H.C., Bailey, L.L., Weir, L.A., 2011. Improving occupancy estimation when two types of observational error occur: non-detection and species misidentification. *Ecology* 92, 1422–1428. <https://doi.org/10.1890/10-1396.1>.
- Nellemann, C., Stoen, O.-G., Kindberg, J., Swenson, J.E., Vistnes, I., Ericsson, G., Katajisto, J., Kaltenborn, B.P., Martin, J., Ordiz, A., 2007. Terrain use by an expanding brown bear population in relation to age, recreational resorts and human settlements. *Biological Conservation* 138, 157–165. <https://doi.org/10.1016/j.biocon.2007.04.011>.
- Nichols, J.D., Hines, J.E., Mackenzie, D.I., Seamans, M.E., Gutiérrez, R.J., 2007. Occupancy estimation and modeling with multiple states and state uncertainty. *Ecology* 88, 1395–1400. <https://doi.org/10.1890/06-1474>.
- Nichols, J.D., Bailey, L.L., O'Connell Jr., A.F., Talancy, N.W., Campbell Grant, E.H., Gilbert, A.T., Annand, E.M., Husband, T.P., Hines, J.E., 2008. Multi-scale occupancy estimation and modelling using multiple detection methods. *Journal of Applied Ecology* 45, 1321–1329. <https://doi.org/10.1111/j.1365-2664.2008.01509.x>.
- Nijland, W., Bolton, D.K., Coops, N.C., Stenhouse, G., 2016. Imaging phenology; scaling from camera plots to landscapes. *Remote Sensing of Environment* 177, 13–20. <https://doi.org/10.1016/j.rse.2016.02.018>.
- Paetkau, D., Calvert, W., Stirling, I., Strobeck, C., 1995. Microsatellite analysis of population structure in Canadian polar bears. *Molecular Ecology* 4, 347–354. <https://doi.org/10.1111/j.1365-294X.1995.tb00227.x>.
- Paetkau, D., Shields, G.F., Strobeck, C., 1998. Gene flow between insular, coastal and interior populations of brown bears in Alaska. *Molecular Ecology* 7, 1283–1292. <https://doi.org/10.1046/j.1365-294x.1998.00440.x>.
- R Core Team, 2017. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.
- R Core Team, 2018. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Requena-Mullor, J.M., López, E., Castro, A.J., Cabello, J., Virgós, E., González-Miras, E., Castro, H., 2014. Modeling spatial distribution of European badger in arid landscapes: an ecosystem functioning approach. *Landscape Ecology* 29, 843–855. <https://doi.org/10.1007/s10980-014-0020-4>.
- Rich, L.N., Miller, D.A.W., Robinson, H.S., McNutt, J.W., Kelly, M.J., 2017. Carnivore distributions in Botswana are shaped by resource availability and intraguild species. *Journal of Zoology* 303, 90–98. <https://doi.org/10.1111/jzo.12470>.
- Robinson, Q.H., Bustos, D., Roemer, G.W., 2014. The application of occupancy modeling to evaluate intraguild predation in a model carnivore system. *Ecology* 95, 3112–3123. <https://doi.org/10.1890/13-1546.1>.
- Rollins, M.G., 2009. LANDFIRE: a nationally consistent vegetation, wildland fire, and fuel assessment. *Int. J. Wildland Fire* 18, 235–249. <https://doi.org/10.1071/WF08088>.
- Royle, J.A., Nichols, J.D., 2003. Estimating abundance from repeated presence-absence data or point counts. *Ecology* 84, 777–790. [https://doi.org/10.1890/0012-9658\(2003\)084\[0777:EAFRPA\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2003)084[0777:EAFRPA]2.0.CO;2).
- Royle, J.A., Kéry, M., Gautier, R., Schmid, H., 2007. Hierarchical spatial models of abundance and occurrence from imperfect survey data. *Ecological Monographs* 77, 465–481. <https://doi.org/10.1890/06-0912.1>.
- Russell, R.E., Katz, R.A., Richgels, K.L.D., Walsh, D.P., Grant, E.H.C., 2017. A framework for modeling emerging diseases to inform management. *Emerg Infect Dis* 23, 1–6. <https://doi.org/10.3201/eid2301.161452>.
- Rytwinski, T., Fahrig, L., 2011. Reproductive rate and body size predict road impacts on mammal abundance. *Ecological Applications* 21, 589–600. <https://doi.org/10.1890/10-0968.1>.
- Schmidt, J.H., Rexstad, E.A., Roland, C.A., McIntyre, C.L., MacCluskie, M.C., Flamme, M.J., 2018. Weather-driven change in primary productivity explains variation in the amplitude of two herbivore population cycles in a boreal system. *Oecologia* 186, 435–446. <https://doi.org/10.1007/s00442-017-4004-3>.
- Simek, S.L., Belant, J.L., Fan, Z., Young, B.W., Leopold, B.D., Fleming, J., Waller, B., 2015. Source populations and roads affect American black bear recolonization. *Eur J Wildl Res* 61, 583–590. <https://doi.org/10.1007/s10344-015-0933-5>.
- Soofi, M., Ghoddousi, A., Zeppenfeld, T., Shokri, S., Soufi, M., Jafari, A., Ahmadvand, M., Qashqaei, A.T., Egli, L., Ghadirian, T., Chahartaghi, N.R., Zehzad, B., Kiabi, B.H., Khorozyan, I., Balkenhol, N., Waltert, M., 2018. Livestock grazing in protected areas and its effects on large mammals in the Hyrcanian forest, Iran. *Biological Conservation* 217, 377–382. <https://doi.org/10.1016/j.biocon.2017.11.020>.
- Squires, J.R., DeCesare, N.J., Olson, L.E., Kolbe, J.A., Hebblewhite, M., Parks, S.A., 2013. Combining resource selection and movement behavior to predict corridors for Canada lynx at their southern range periphery. *Biological Conservation* 157, 187–195. <https://doi.org/10.1016/j.biocon.2012.07.018>.
- Steenweg, R., Hebblewhite, M., Kays, R., Ahumada, J., Fisher, J.T., Burton, C., Townsend, S.E., Carbone, C., Rowcliffe, J.M., Whittington, J., Brodie, J., Royle, J.A., Switalski, A., Clevenger, A.P., Heim, N., Rich, L.N., 2017. Scaling-up camera traps: monitoring the planet's biodiversity with networks of remote sensors. *Frontiers in Ecology and the Environment* 15, 26–34. <https://doi.org/10.1002/fee.1448>.
- Stetz, J.B., Mitchell, M.S., Kendall, K.C., 2018. Using spatially-explicit capture-recapture models to explain variation in seasonal density patterns of sympatric ursids. *Ecography* 41, 1–12. <https://doi.org/10.1111/ecog.03556>.
- Stillfried, M., Belant, J.L., Svoboda, N.J., Beyer, D.E., Kramer-Schadt, S., 2015. When top predators become prey: black bears alter movement behaviour in response to hunting pressure. *Behavioural Processes* 120, 30–39. <https://doi.org/10.1016/j.beproc.2015.08.003>.
- Taberlet, P., Camarra, J.-J., Griffin, S., Uhrès, E., Hanotte, O., Waits, L.P., Dubois-Paganon, C., Burke, T., Bouvet, J., 1997. Noninvasive genetic tracking of the endangered Pyrenean brown bear population. *Molecular Ecology* 6, 869–876. <https://doi.org/10.1111/j.1365-294X.1997.tb00141.x>.
- Tan, C.K.W., Rocha, D.G., Clements, G.R., Brenes-Mora, E., Hedges, L., Kawanishi, K., Mohamad, S.W., Mark Rayan, D., Bolongon, G., Moore, J., Wadey, J., Campos-Arceiz, A., Macdonald, D.W., 2017. Habitat use and predicted range for the mainland clouded leopard *Neofelis nebulosa* in Peninsular Malaysia. *Biological Conservation* 206, 65–74. <https://doi.org/10.1016/j.biocon.2016.12.012>.
- Tsuji, Y., Ito, T.Y., Wada, K., Watanabe, K., 2015. Spatial patterns in the diet of the Japanese macaque *Macaca fuscata* and their environmental determinants: spatial patterns in the diet of Japanese macaques. *Mammal Review* 45, 227–238. <https://doi.org/10.1111/mam.12045>.
- Walpole, A.A., Bowman, J., Murray, D.L., Wilson, P.J., 2012. Functional connectivity of lynx at their southern range periphery in Ontario, Canada. *Landscape Ecology* 27, 761–773. <https://doi.org/10.1007/s10980-012-9728-1>.
- Warton, D.I., Stoklosa, J., Guillera-Arroita, G., MacKenzie, D.I., Welsh, A.H., 2017. Graphical diagnostics for occupancy models with imperfect detection. *Methods in Ecology and Evolution* 8, 408–419. <https://doi.org/10.1111/2041-210X.12761>.
- Western Regional Climate Center, 2018. *Cooperative Climatological Data Summaries: Period of Record General Climate Summaries for Capitan, Cimmaron, Cloudcroft, Jemez Springs, Los Alamos, Pecos, Red River, Ruidoso, and Wolf Canyon*. Mexico, New.
- White, G.C., Burnham, K.P., 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* 46, S120–S139. <https://doi.org/10.1080/0006359909477239>.
- Wiegand, T., Naves, J., Garbulsky, M.F., Fernández, N., 2008. Animal habitat quality and ecosystem functioning: exploring seasonal patterns using NDVI. *Ecological Monographs* 78, 87–103. <https://doi.org/10.1890/06-1870.1>.
- Zeller, K.A., Nijhawan, S., Salom-Pérez, R., Potosme, S.H., Hines, J.E., 2011. Integrating occupancy modeling and interview data for corridor identification: a case study for jaguars in Nicaragua. *Biological Conservation* 144, 892–901. <https://doi.org/10.1016/j.biocon.2010.12.003>.