Received: 4 September 2020 | Revised: 15 September 2021 | Accepted: 16 September 2021

DOI: 10.1002/jwmg.22178

RESEARCH ARTICLE

THE JOURNAL OF WILDLIFE MANAGEMENT

THE WILDLIFE SOCIETY

# Use of predictive distribution models to describe habitat selection by bats in Colorado, USA

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**Funding information**

U.S. Bureau of Land Management, Grant/Award Number: L17AC00155-03

## Abstract

Numerous processes operating at landscape scales threaten bats (e.g., habitat loss, disease). Temperate bat species are rarely examined at commensurate scales because of logistical and modeling constraints. Recent modeling approaches now allow for presence-only datasets, like those often available for bats, to assist with the development of predictive distribution models. We describe the use of presence-only data and rigorous predictive distribution models to examine habitat selection by bats across Colorado, USA. We applied hierarchical Bayesian models to bat locations from 1906–2018 to examine relationships of 13 species with landscape covariates. We considered differences in type of activity (foraging, roosting, hibernation), seasonality (summer vs. winter), and scale (1, 5, 10, and 15-km buffers). These findings generated statewide probability of use models to guide management of bat species in response to threats (e.g., white-nose syndrome [WNS]). Analysis of buffers suggest selection of land cover and environmental covariates occurs at different scales depending on the species and activity. Pinyon (*Pinus* spp.)-juniper (*Juniperus* spp.) appeared as a positive association in the highest number of models, followed by montane woodland, supporting the importance of these forest types to bats in Colorado. Other covariates commonly associated with bats in Colorado include westerly longitudes, and negative associations with montane shrubland. Mechanical treatments within pinyon-juniper and montane woodlands should be conducted with caution to avoid harming bat communities. We developed hibernation models for only 2 species, making apparent the lack of winter

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records for bat species in the state. We also provide a composite predictive surface of small-bodied bats in Colorado that delineates where these species, vulnerable to WNS, converge. This tool provides managers with focal points to apply surveillance and response strategies for the impending arrival of the disease.

**KEYWORDS**

bats, Bayesian regression analysis, Colorado, habitat selection modeling, pinyon-juniper, presence-only data, probability of use

Examinations of habitat selection by bat species have historically tended to occur at small scales with presence-only records (Neubaum et al. 2007, Schorr and Siemers 2013). Often, the focus on small scales is due to the logistical constraints of monitoring these species, which are nocturnal, highly mobile, and may roost in cryptic locations (O'Shea and Bogan 2003). Despite such limitations, resource managers are regularly required to make habitat prescriptions at larger scales (e.g., state level) based on limited data (Neubaum et al. 2017). Bat species face a number of stressors linked to changes in biotic and abiotic factors that have led to population declines worldwide (O'Shea et al. 2016, Hammerson et al. 2017, Frick et al. 2019). After investigating the relationships between landscape structure, community composition, and species distribution, Jaberg and Guisan (2001) present declines in bat populations tied to landscape-level changes. Bat species in Colorado, USA, may experience population-level impacts from numerous issues including forestry practices tied to beetle kill and catastrophic fire events, urbanization, energy development, and disease (Navo et al. 2018). Multiple bat species whose range includes Colorado have been proposed for listing under the United States Endangered Species Act (U.S. Fish and Wildlife Service [USFWS] 1994) because of population declines and are now considered species of concern (O'Shea et al. 2018). In the face of these broadly dispersed threats, models may assist with prediction of bat resource selection over time at larger scales than those considered by past efforts, thereby providing for more effective management of these species.

Development of such models for bats can draw upon 2 possible sources of data, those documenting presence-only (i.e., capture records from mist nets, observation in roosts, collected for museum specimens) or those with presence-absence records (e.g., acoustic records collected with high frequency detectors). Presence-only capture data often lack information regarding sampling design, particularly how sample locations were selected for these efforts. Because of possible biases tied to presence-only capture records (Yackulic et al. 2013) and the rigorous analysis needed to properly assess them, these data have sometimes been passed over in lieu of acoustic data, with the later coming into use in the last decade with rigorous field sampling designs implemented from their inception (Reichert et al. 2018, Rodhouse et al. 2019). Acoustic records for bats, however, tend to be limited to foraging and commuting activity as bats move about on the landscape (Parsons and Szewczak 2009). Conversely, capture records offer the ability to incorporate data from roost sites and include data for seasons of the year when acoustic calls are limited or impossible to collect (e.g., winter hibernation). Consequently, capture datasets can lend themselves well to analysis of resource selection by bats if analyzed with diligence and may address issues such as roosting and hibernation that acoustic data currently cannot. In addition, many management agencies in North America, such as states and provinces, are likely to already have capture datasets that could be used for such analysis in the short-term while acoustic datasets such as those from the North American Bat Monitoring Program are being developed at the continent scale (Reichert et al. 2018).

In Colorado, the association of bat species with biotic and abiotic landscape features using capture data have been used to examine local populations (Neubaum et al. 2007, O'Shea et al. 2011*a*), but this work is infrequently undertaken at the state level. Ellinwood (1978) performed the first large-scale examination of bats in Colorado when he reviewed the known ranges of these species across the southeastern portion of the state. Adams (1990) followed this effort with an analysis of habitat use as it relates to bats in Colorado, though location accuracy was limited to within 4 km of records. Both studies occurred prior to the development of analysis techniques that account for assumptions of presence-only data. Hayes and Adams (2014) used capture data to examine the spatial distribution of the fringed myotis (*Myotis thysanodes*) across Colorado and suggest that elevation may explain their bifurcated distribution in that region. Covariates such as elevation and topographic ruggedness affect abiotic resources available for roosting, influencing resource selection by bats in those areas (Rodhouse et al. 2015, Rojas et al. 2019). For example, areas with higher topographic ruggedness are likely to have more cliff and rock resources that are commonly selected by bats for roosts in Colorado (Schorr and Siemers 2013, Snider et al. 2013, Hayes and Adams 2015, Neubaum 2017). Confounding our understanding of the relationship between bats and the landscape is their documented use of urbanized areas, illustrating the degree to which these animals are adapting to rapidly modified land cover (Everette et al. 2001, Neubaum et al. 2007). These interactions are nuanced even further within these modified settings as bats are using urban areas to varying degrees based on sex (Neubaum et al. 2006), and at multiple scales for different activities such as roosting and foraging (Neubaum et al. 2007, Johnson et al. 2008). Understanding which landscape covariates are associated with a given bat species and at what scale, provides a surrogate for resource managers to determine which species are likely to use a given area of interest when records of bats are absent (Duff and Morrell 2007). Consequently, data associated with landscape covariates and scale can guide management decisions affecting those species in the absence of rigorous population data (Neubaum et al. 2017).

In addition to landscape features, bats may exhibit differential habitat selection across seasons depending on their life-history strategies. Hoffmeister (1970) presented evidence for variation in distributions of bats in Arizona, USA, between summer and winter. In Colorado, little brown myotis (*Myotis lucifugus*) and big brown bats (*Eptesicus fuscus*) were documented making seasonal migrations in elevation, rather than latitude, that ranged in distance from 4 km to nearly 100 km (Neubaum et al. 2006, Neubaum 2018). Other bat species make longer migrations in latitude that take them out of Colorado during portions of the year. Cryan (2003) refined distributions of North American tree bats (e.g., hoary bats [*Lasiurus cinereus*]) at a continental scale using museum records to reconstruct seasonal migrations and showed that these species move into the state in early summer and back out in late summer. Thus, consideration of seasonality can be important for habitat selection by bats.

With the spread of the white-nose syndrome (WNS) disease of bats into western North America, knowledge about distributions of bat species and habitat selection across those areas has become increasingly important, influencing where baseline data and surveillance efforts are focused (Brooks 2011, USFWS 2014, Lorch et al. 2016). Documenting habitat selection at the landscape scale prior to the arrival of a disease, which can cause notable declines of species, is important (Ingersoll et al. 2013, Reynolds et al. 2016). As the disease reaches the state and spreads through it, these data will be important in elucidating changes in species associations with specific biotic and abiotic features (Lilley et al. 2018), relationships that have been reported to influence bat survival and potential transmission of diseases such as coronaviruses (Davy et al. 2018, Subudhi et al. 2019). Our habitat selection models can allow for accurate representations of the changes to habitat selection patterns by bats and provide a plan for where to implement management actions such as vaccinations and probiotics (Hoyt et al. 2019, Rocke et al. 2019), should they prove viable. Consequently, good habitat selection models need to reflect a range of considerations when being developed (scale, timing, management).

The objectives of our study were to use Colorado as a large-scale study area to examine the relationships of bat species with landscape covariates; evaluate the variation in probability of habitat selection by bats that stems from different activities and behaviors (e.g., foraging, roosting), seasons (summer vs. winter), and scales (1, 5, 10, and 15-km buffers); and develop statewide probability of use models for bat species in Colorado based on these covariates. We also provide a pre-WNS probability of use model for small-bodied bats such as myotids, the bat species documented to be highly vulnerable to the disease and whose habitat selection patterns may undergo the greatest changes upon arrival of WNS (Brooks 2011), as an example tool for monitoring and future reference.

# STUDY AREA

Bat records examined in this study were collected from across Colorado, a state covering 269,601 $km^2$ with notable diversity in land cover and topography, from 1906–2018. The state is bounded by the latitudes 37°N to 41°N and longitudes 102°02′48″ to 109°02′48″. Elevations range from 1,010 m on the eastern prairie to 4,400 m in the central alpine. Short-grass prairie covers the eastern third of the state, with some canyonlands in the far southern portions, before grading into foothills forested by pinyon (*Pinus* spp.)-juniper (*Juniperus* spp.) and pine forest to the west. High mountains encompass the central third of the state, covered by montane and subalpine forest, montane shrubland, and alpine. The western portion of the state is typified by more high mountains that abruptly grade westward down into rugged canyonlands and mesas, vegetated by pinyon-juniper forest and semi-desert shrubland communities. The climate at lower elevations has been characterized by hot, dry summers (Jun–Aug) with localized monsoons and moderate winters (Nov–Mar) with occasional snowfall. Higher elevations exhibited cool, wet summers and cold winters with potential for heavy snowpack (Doesken et al. 2003, Neubaum 2018). Fauna is typical of the Rocky Mountain Region and described for Colorado by Armstrong et al. (2011).

# METHODS

## Database

We used spatial data to assess habitat selection for 13 of 19 bat species that occur in Colorado (Table 1). We compiled these data from several sources including a Colorado Parks and Wildlife (CPW) Spatial Database Engine Non-species Area Mapping bat database (CPW bat database), CPW scientific collection permit reports, and historical records (Armstrong et al. 1994). The CPW bat database was developed in 1991 to house records collected during surveys of abandoned mines by the Bats and Inactive Mines Project (Navo 2001). This database grew to include all bat records collected by CPW personnel and includes opportunistic capture sampling, abandoned mine surveys, and efforts related to WNS baseline surveys through 2018. The CPW scientific collection permits database includes location records for all bats captured under a permit authorized by the agency in Colorado from 1994–2018 for research and rehabilitation. We also digitized records from Armstrong et al. (1994) in a geographic information system (GIS; ArcMap 10.3, Esri, Redlands, CA, USA). This compilation of bat records was extracted from all published literature and cataloged museum specimens known from Colorado up to 1994. All capture records (i.e., bats in hand), regardless of the database, were collected through conventional techniques for bats (e.g., shotgun or mist netting; Kunz et al. 2009) used over the last century or were made as visual observations on site and do not include acoustic sampling. While capture data can be collected in a manner that ensures presence and absence, the sampling design for the merged capture records we assembled did not include a single standardized protocol, with many collected opportunistically or for targeted efforts. Therefore, we treat these data as presence-only because in many cases we lack sufficient information for areas where bats did not occur.

There are 24,703 locations in the combined dataset we considered, ranging in date from 1906 to 2018. Of these, 23,782 records correspond to locations with accuracy at the coordinate or section level. We removed an additional 522 records from the Colorado Department of Public Health and Environment because of their bias towards non-typical bat behavior (e.g., bats tested for rabies after coming into contact with people), leaving 23,260 records. We evaluated the probability of habitat selection during 3 activities: roosting, foraging, and hibernating (Table 1). We defined roosting and foraging activities using the capture method field in the database when provided or based on site descriptions for older records. Roosting locations were collected by vetted observers or via radio-telemetry studies and are considered day roosts. Foraging records represent those where bats were moving across the landscape foraging, drinking, or commuting, of which we could not distinguish. We defined any location collected from November through March as hibernation activity, which corresponds with other surveys of winter

**TABLE 1** Common and scientific names of bats in Colorado, USA, considered for modeling and associated activity of locations collected between 1906–2018 (Armstrong et al. 2011). We included only species-activity combinations with sufficient sample sizes (≥25 records) in final analysis. Species with inadequate sample sizes to perform analysis for any activity type are denoted with an asterisk (*) after the common name

| Common name | Scientific name | Foraging | Hibernation | Roosting | Total |
|---|---|---|---|---|---|
| Pallid bat | *Antrozous pallidus* | 49 | 0 | 18 | 67 |
| Townsend's big-eared bat | *Corynorhinus townsendii* | 49 | 105 | 275 | 429 |
| Big brown bat | *Eptesicus fuscus* | 199 | 24 | 158 | 381 |
| Spotted bat* | *Euderma maculatum* | 11 | 0 | 9 | 20 |
| Allen's big-eared bat* | *Idionycteris phyllotis* | 0 | 0 | 1 | 1 |
| Eastern red bat* | *Lasiurus borealis* | 17 | 0 | 1 | 18 |
| Hoary bat | *Lasiurus cinereus* | 173 | 0 | 4 | 177 |
| Silver-haired bat | *Lasionycteris noctivagans* | 172 | 6 | 13 | 191 |
| California myotis | *Myotis californicus* | 44 | 7 | 68 | 119 |
| Western small-footed myotis | *Myotis ciliolabrum* | 132 | 37 | 227 | 396 |
| Long-eared myotis | *Myotis evotis* | 154 | 2 | 163 | 319 |
| Little brown myotis | *Myotis lucifugus* | 144 | 2 | 79 | 225 |
| Fringed myotis | *Myotis thysanodes* | 83 | 0 | 88 | 171 |
| Long-legged myotis | *Myotis volans* | 168 | 1 | 250 | 419 |
| Yuma myotis | *Myotis yumanensis* | 85 | 0 | 31 | 116 |
| Big free-tailed bat* | *Nyctinomops macrotis* | 9 | 1 | 8 | 18 |
| Canyon bat | *Parastrellus hesperus* | 52 | 1 | 9 | 62 |
| Tri-colored bat* | *Perimyotis subflavus* | 3 | 1 | 3 | 7 |
| Brazilian free-tailed bat* | *Tadarida brasiliensis* | 22 | 2 | 13 | 37 |

bat records collected across western North America (Perkins et al. 1990, Priday and Luce 1997, Hendricks 2012). To ensure that the locations used for modeling correspond to the period for which the mapped landscape covariates are relevant, we restricted the dataset to the most recent 30 years, yielding 21,422 locations. We further restricted consideration of the dataset by aggregating locations that were within the same general area, defined by the resolution of the spatial data (25 m), to avoid spatial bias in opportunistic sampling (largely attributable to repeat sampling of the same locations in urban areas). This produced a final dataset of 2,985 records.

## Covariate layers and scale

To address biases associated with modeling presence-only records, we took steps to prepare the dataset (Yackulic et al. 2013). Following the framework of Johnson's (1980) proposed levels of selection, we operated at the third order, which is the use of various habitat components within the range of a population (e.g., seasonal or activity-based distributions). By discretizing the landscape as a raster of grid cells, we produced defined resource units. The product of our models guides the relative probability of use of each of these resource units (grid cell) by the target bat populations (Lele et al. 2013). We are not implying frequencies of bat presence across the landscape (i.e., the probability that a specific unit will be used *k* number of times during a specified interval; Lele et al. 2013), only how likely that cell is to be selected by a bat at some point. Similar to Lele et al. (2013), we applied an exponential probability of selection model and identified the resource selection probability function (RSPF) for each resource unit (Manly et al. 2002, Johnson et al. 2006). Thus, we modeled the selection of available resource units to be used by bats for various activities and behaviors (i.e., foraging, hibernating, roosting).

We used landscape layers relating to land cover classes (agriculture, alpine tundra, grassland, montane shrubland, montane woodland, pinyon-juniper woodland, riparian-wetland-water, rock-disturbed soil, semi-desert shrubland, subalpine forest meadow, urban areas) based on those described by Armstrong et al. (2011) and topography (elevation, longitude, and topographic ruggedness index [TRI; Riley et al. 1999]). We selected these land cover predictor variables based on the roosting and foraging resources they may provide that are well documented within the broader bat literature. For example, woodlands, rock, and areas with higher TRI provide important roost resources (Arnett and Hayes 2009, Snider et al. 2013, Neubaum 2018), while areas with water (e.g., riparian-wetland-water) and open meadows offer productive foraging opportunities (O'Shea et al. 2011*b*). We considered some topographic variables because of their ability to influence climate and productivity, and their ability to present geographic barriers at the larger scales we targeted. In Colorado, temperature and precipitation are generally correlated with elevation and the land cover classes representing distinct vegetation communities we considered, as has been seen in other western states (Rodhouse et al. 2015). The state also contains geographic barriers such as high-elevation mountains and low-elevation dry deserts that preclude use by some bat species (Hayes and Adams 2014). We used the Colorado Vegetation Classification Project (CVCP; Colorado Division of Wildlife and Bureau of Land Management 2003) product with Landsat Thematic Mapper imagery data collected from 1993 to 1995 for our categorical vegetation type layer. We reclassified the 103 cover types from the CVCP to fit the 11 ecoclasses described in Armstrong et al. (2011). We generated percent-cover land cover class layers from this CVCP product by calculating the percent of each cell that was classified as each vegetation type. We applied all covariates to all species given the lack of specific information regarding habitat associations for most bats in Colorado as they relate to ≥1 components of their seasonal, scale, and activity type. We transformed location and covariate data to the Albers equal-area conic projection.

We allowed for the possibility that bat movement may be influenced differentially for each covariate based on the spatial distribution of the specific covariate. For example, a bat may move according to the percent cover of rock or disturbed soil land cover at 1 scale (e.g., 5 km) while accounting for presence of a certain TRI at another scale (e.g., 10 km). We use spatial buffers of 5 km, 10 km, and 15 km around locations (radii) to accommodate this scale-dependency. These scales reflect the range of typical movements noted for bat species in Colorado (Neubaum et al. 2007, O'Shea et al. 2011*a*, Neubaum 2017).

## Available locations selection

To select samples of available locations for each species with a sufficient sample size (>25 records; van Proosdij et al. 2016), we followed the methods proposed by Northrup et al. (2013). Briefly, this entailed performing a linear regression with a subset of candidate covariates and an increasing number of available locations. We selected 2 variables of high resolution (TRI, elevation) and 1 land cover layer that we expected to have biased locations for many species (urban) to ensure a conservative estimate for number of available locations (Northrup et al. 2013). We started by regressing all used locations against 10 random locations each (i.e., locations at which no bat records had been recorded). We monitored the posterior mean value of the 3 target coefficients for the first iteration, and then continued the process with successively larger numbers of available locations in each subsequent iteration. We used a sequence of available locations up to 20 times the number of used locations, with each iterative increase equal to the number of used locations divided by 20. We took the point at which the value for the coefficients for the target covariates stabilized as the sample of available locations and considered this number of available locations as adequately representing the landscape available to the species.

We selected available locations according to a random background sampling frame (Northrup et al. 2013). An alternative sampling frame from which to draw available locations was proposed by Phillips et al. (2009), and involves randomly sampling locations from observed locations of a target group, with the goal of accounting for bias in the observation process. We chose not to use this technique because of the lack of a target group population dataset from which to draw available locations. We excluded 6 species of bats that occur in Colorado because we lacked sufficient sample size to apply the model. Therefore, we did not have a reference target group with a sufficient sample size from which to draw the available locations. Finally, we determined it was of greater value to randomly sample available locations from across the entire background (i.e., all of CO) as a way to capture at least some locations that were likely representations of areas in which these species would be absent, than to sample within a set distance of the observed locations (e.g., 5–20 km, the approximate daily movement distance of these bat species; Northrup et al. 2013). While the latter approach would also account for sampling bias, it would limit inference of our models to those areas that our focal bat species occupied and inhibit extrapolation to the state level. Developing state-level models was the primary goal of our effort to guide monitoring practices and management decisions for these species, so we opted for a random sampling of the background habitat to generate the set of available locations to include in our models.

## Habitat selection model

We used 2 steps to select which covariates from our global set to apply to each species. First, we removed variables from the model if their generalized variance-inflation factors (VIF; Fox and Monette 1992, Fox and Weisberg 2018) exceeded 2.5, indicating collinearity with other variables. When VIFs for multiple variables exceeded 2.5, we retained the variable with a greater $R^2$ and reran the model. A VIF threshold of 2.5 is conservative relative to typical recommendations of 5 (Kline 1998) or 10 (Hair et al. 2009), though empirically supported (Fox 2016). This was desirable in our case because we sought to minimize the number of parameters in the models, thereby achieving parsimony and not unduly burdening wildlife officials tasked with monitoring and managing focal landscape features. Second, we used the dredge function from MuMIn (Barton 2018) in R for model selection (according to Bayesian Information Criterion [BIC]). In cases in which multiple models had adequate support ($\Delta$BIC ≤ 2), we relied on model averaging across all models on coefficients using standardized estimates.

We used the layers precipitating from the covariate selection process as covariates in a generalized linear model (GLM) to evaluate the differential selection of habitats across the landscape. This process creates a model by species for each activity type where sample sizes permit. While there are other presence-only modeling methods that are available and well-vetted in the literature (MaxEnt; Phillips et al. 2006), we chose this approach for its accessibility in terms of covariate responses and effects, and model selection process. By constructing the hierarchical models in a Bayesian framework, we were able to more explicitly and accurately address the uncertainty surrounding the posterior estimates for the covariate coefficients and the resource unit predictions (i.e., the probability of use estimates per cell). Also, the features of our dataset (i.e., the species considered here have ranges extending beyond the extent of the state bounds) mitigate concerns of bias introduced via the imprecise definition of the range in which available locations are selected (Rodhouse et al. 2015).

We applied the GLM via JAGS in R using the R2jags package (Su and Yajima 2015). We iterated the models 50,000 times across 4 chains with a burn-in of 25,000 iterations. We achieved convergence for all variables (assessed by evaluating $\hat{R}$, when $\hat{R} < 1.1$, convergence is achieved; Gelman and Rubin 1992). The model had the following form:

$$\begin{aligned} &Y \sim \text{dbern}(P(Y)) \\ &\text{logit}(P(Y)) = \beta_0 + \beta_1 \times X_1 + \cdots + \beta_n \times X_n, \end{aligned} \tag{1}$$

where $Y$ is the response variable (predicted probability of use) and $X$ represents the $n$ predictor covariates. We used non-informative priors for the variance (inverse of the precision), taking uniform distributions from 1 to 100 and non-informative hyperpriors for model hyperparameters, taking normal (or Gaussian) distributions with means of zero and variance of $1 \times 10^6$.

We extrapolated predicted probability of use maps across Colorado. In a few cases such as the canyon bat (*Parastrellus hesperus*) and foraging and roosting activities for the California myotis (*Myotis californicus*), this meant extrapolating beyond the predicted range of the species. We derived the probability of use for each cell across Colorado by substituting the posterior mean estimates for covariate coefficients ($\beta$s) in Equation 1.

To evaluate model performance, we performed a repeated $k$-fold cross validation with training (80%) and testing (20%) datasets (Johnson et al. 2006). We set $k = 10$ and repeated the cross-validation 5 times. As is recommended for use-availability designs, we relied on the Spearman-rank correlation ($r_s$) to evaluate model prediction accuracy (Boyce et al. 2002). Values closer to 1 indicate a stronger relationship and, in this case, better performance of the model (Boyce et al. 2002). We regressed $r_s$ with the sample size per species to identify potential effects of the number of locations on model prediction accuracy.

Additionally, we calculated the probability of use surfaces for each species-activity combination using the values for the posterior coefficient credible interval widths (difference between the 97.5% and 2.5%). These surfaces represent our level of certainty (or lack thereof) in our prediction at each cell across the state to reflect the confidence of the models. The R coding used for model analysis is presented in Supporting Information (S1).

### White-nose syndrome comparative tool

As an example of how to apply these models to address a specific threat, we examined probability of use for small-bodied bats in Colorado because they are the most susceptible cohort likely to experience declines from WNS once it becomes established in the state. We developed a single map, showing the probability of use for these species combined. We took the mean value per cell across species to compile this map. We applied no weighting scheme and did not attempt to quantify priority of some species over others. Species we considered vulnerable to WNS that we used for this analysis included California myotis, western small-footed myotis (*Myotis ciliolabrum*), long-eared myotis (*Myotis evotis*), little brown myotis, fringed myotis, long-legged myotis (*Myotis volans*), Yuma myotis (*Myotis yumanensis*), and canyon bat. This map is intended to provide an approximate year-round baseline habitat selection expectation, for use in comparison with future wildlife disease or climate change modeling efforts. Areas with higher probability of use by these species are reflected by higher values.

## RESULTS

### Available locations

We modeled the probability of use for 24 combinations of species-activity pairs (Figure 1). Sample sizes were sufficient for us to apply models to 13 species and multiple activity types for most species (Table 1). We modeled pallid bat (*Antrozous pallidus*), hoary bat, silver-haired bat (*Lasionycteris noctivagans*), and canyon bat use in only a single activity type (foraging in all 4 cases) because the number of roosting and hibernation locations were insufficient to meet the ≥25 record minimum. We did not examine 6 species in our analysis because of an inadequate number of locations in any of the activity types (Table 1).

For 17 species-activity pair combinations, simulations estimated that 5 times the number of used locations served as a suitable sample size of available locations to adequately represent the landscape. For 5 species-activity combinations (Townsend's big-eared bat [*Corynorhinus townsendii*] roosting, silver-haired bat foraging, little brown myotis roosting,

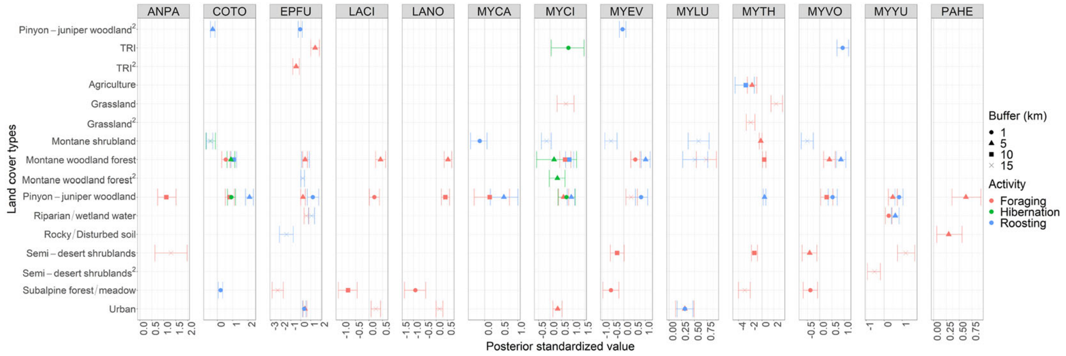

**FIGURE 1** Posterior estimates for covariates included in each model (i.e., combination of bat species and activity data) of bat habitat use in Colorado, USA, 1906–2018. Species abbreviations are referenced as follows: pallid bat (ANPA), Townsend's big-eared bat (COTO), big brown bat (EPFU), hoary bat (LACI), silver-haired bat (LANO), California myotis (MYCA), western small-footed myotis (MYCI), long-eared myotis (MYEV), little brown myotis (MYLU), fringed myotis (MYTH), long-legged myotis (MYVO), Yuma myotis (MYYU), and canyon bat (PAHE). Landscape layer covariates are listed along the *y*-axis (topographic ruggedness index = TRI), with their corresponding posterior mean (standardized) estimate along the *x*-axis. Whiskers correspond to the 95% credible interval about the mean estimate. The shape of the posterior mean estimate point indicates the scale of the buffer (km) applied to the covariate (1 = circle, 5 = triangle, 10 = square, and 15 = x), and colors indicate type of activity the model was applied to (red = foraging, green = hibernation, and blue = roosting) to summarize each pixel in the landscape

fringed myotis foraging, canyon bat foraging), simulations estimated that 20 times the number of used locations represented a sufficient sample size for coefficient convergence. For the Yuma myotis, simulations demonstrated coefficient convergence only after 100 (foraging) and 300 (roosting) times the number of used locations were sampled.

## Habitat selection model

Covariates were included at the pixel (1-km), 5, 10, and 15-km buffer scales in 15, 18, 12, and 16 of the 24 species-activity pair combinations, respectively (the sum of these counts exceed 24 because multiple buffer scales can occur in the same model). Scale of selection varied within and across both bat species and activity type, without consistent patterns in either category (species or activity; Figure 1). A longitudinal index (not buffered) was included in 14 species-activity pair combinations. On average, models contained 5 covariates (not including the intercept term; Figures S2.1–S2.24, available in Supporting Information), with a range of 2 for the Townsend's big-eared bat foraging, little-brown myotis foraging, and Yuma myotis roosting models up to 9 for the fringed myotis foraging model. Distributions of used and available locations varied for each Colorado bat species based on the covariates considered in the final habitat selection models (Figures S3.1–3.24, available in Supporting Information). The high number of simulations required by the Yuma myotis roosting model to converge belies a high degree of uncertainty in predictions for this species and is reflected in a highly restrictive probability of use surface (Figure S4.23, available in Supporting Information).

The term for pinyon-juniper woodland land cover was included more than any other covariate (linearly in 18 of the 24 species-activity pair combinations, and as a quadratic in 3 combinations; Figure 1; Figures S2.1–S2.24). Pinyon-juniper woodland occurred as a positive parameter in all of these linear models, as a positive quadratic parameter once, and with upper and lower bounds overlapping zero for the 2 remaining quadratic relationships (Figures S2.1–S2.24). Other commonly occurring covariates across models (Figure 1) were montane woodland-forest (15 linear, 2 quadratic), the longitudinal index (2 linear, 12 quadratic), montane shrubland (8 linear), subalpine forest-meadow (7 linear), and urban (7 linear). Models containing montane-woodland-forest were all positive relationships. All linear models that included the TRI and urban covariates had a positive relationship also. Conversely, 7 of 8 linear models with montane shrubland were negative, as were 6 of the 7 linear models that included subalpine forest-meadow. Predicted probability of use maps for the 24 species-activity pairs generated by models varied widely depending on the covariates influenced by the location distribution (Figures S4.1–S4.24).

Specific to activity type, foraging models were developed for all 13 bat species modeled in our analysis, as reflected by efforts to sample bats away from roosts (e.g., mist netting), which make up the highest proportion of records in the dataset (Table 1). The most common covariates supported in the foraging models include pinyon-juniper woodlands (11), montane woodlands (9), longitude (8), subalpine forest meadow (6), and urban areas (5; Figure 1). Roosting models were developed for 9 species including all 7 *Myotis* species. The remaining species, with inadequate records to develop a roosting model, included the pallid bat, 2 tree bat species (hoary and silver-haired bats), and the canyon bat. Common covariates for roosting models were generally similar to foraging models, including pinyon-juniper woodlands (8), montane woodlands (6), montane shrubland (6), and longitude (4), with all remaining covariates appearing in 2 or fewer models (Figure 1).

Two species, the Townsend's big-eared bat and western small-footed myotis, had sufficient sample sizes within the date range we defined for hibernation to model this activity. For both species, pinyon-juniper woodland was positively and linearly associated with the hibernation models at the pixel level (1 km; Figure 1). Montane woodland-forest was also included in these models (linearly for Townsend's big-eared bats and as a quadratic for western small-footed myotis, though the 95% credible interval overlapped zero for the later, suggesting weak relationships with this forest type during hibernation for this species). The longitudinal index (quadratic) was also included in the final models for both species, suggesting more hibernacula have been identified on the west slope of Colorado. The western small-footed myotis hibernation model also included TRI (1 km, linear).

Spearman-rank correlation estimates ranged from a low of 0.34 for the little brown myotis foraging model to a high of 0.89 for the western small-footed myotis roosting model (Table 2). Of the 24 species-activity combinations, 21 demonstrated $r_s$ values >0.5 and 10 were >0.7, indicating generally good predictive accuracy of the models. The remaining 2 models with poor fit were for hoary bat foraging and long-eared myotis roosting (Table 2). There was minimal relationship between sample size and $r_s$, with an $R^2$ of 0.13.

### White-nose syndrome comparative tool

Small-bodied bats show the highest probabilities of use among the western canyonlands near the Colorado-Utah, USA, border, and along the Front Range of Colorado where the eastern plains transition into the foothills in the north-central portion of the state (Figure 2). These areas both have high levels of topographic ruggedness and proximity to forested land cover. The highest probability of use areas are localized and scattered, with large interspersed swaths of lower (<0.25) probability of use areas throughout the west slope of Colorado. There is minimal support for use of the eastern plains by these small-bodied bats.

## DISCUSSION

Presence-only datasets resulting from capture work if used carefully to address biases (e.g., detection probability, variations in or lack of information on sampling design), can be useful in describing relationships of species with environmental covariates (Yackulic et al. 2013). O'Shea and Bogan (2003) delineate how detection probability can be inherently difficult to measure for bat populations, regardless of whether methodology uses traditional capture or acoustic techniques. Following guidelines from Yackulic et al. (2013), we have addressed such biases by resampling the data on a regular grid to reduce the effect of over- and under-sampling certain resource types

**TABLE 2** Model performance of the best performing habitat use model for each bat species in Colorado, USA, between 1906–2018, in terms of deviance (deviance information criterion [DIC]), and prediction accuracy (Spearman-rank correlation [$r_s$])

| Species name | Activity | DIC | $r_s$ |
|---|---|---|---|
| Pallid bat | Foraging | 156.39 | 0.70 |
| Townsend's big-eared bat | Foraging | 215.11 | 0.61 |
| | Hibernation | 403.59 | 0.81 |
| | Roosting | 1,653.01 | 0.88 |
| Big brown bat | Foraging | 781.78 | 0.62 |
| | Roosting | 520.54 | 0.81 |
| Hoary bat | Foraging | 871.42 | 0.41 |
| Silver-haired bat | Foraging | 1,262.89 | 0.51 |
| California myotis | Foraging | 112.56 | 0.52 |
| | Roosting | 134.86 | 0.52 |
| Western small-footed myotis | Foraging | 591.28 | 0.57 |
| | Hibernation | 138.11 | 0.65 |
| | Roosting | 893.72 | 0.89 |
| Long-eared myotis | Foraging | 654.86 | 0.75 |
| | Roosting | 590.17 | 0.40 |
| Little brown myotis | Foraging | 678.96 | 0.34 |
| | Roosting | 530.54 | 0.78 |
| Fringed myotis | Foraging | 439.28 | 0.70 |
| | Roosting | 357.74 | 0.71 |
| Long-legged myotis | Foraging | 711.49 | 0.86 |
| | Roosting | 948.83 | 0.88 |
| Yuma myotis | Foraging | 708.46 | 0.62 |
| | Roosting | 362.40 | 0.52 |
| Canyon bat | Foraging | 241.50 | 0.52 |

(e.g., urban land cover) and excluded disproportionate numbers of records associated with unusual studies before analysis. We have also included estimated response curves and parameters for comparison, and restricted our inferences largely to those that are supported by existing literature, with the caveat that these previous studies were conducted at smaller scales. This approach has allowed us to use an already existing presence-only capture dataset to generate predictive distribution models and make inferences about habitat selection by bats across a large-scale study area.

Our findings suggest that the prevalence of multiple buffer scales occurring in many of the models highlights the importance of accounting for multi-scale decision making by bats while prospecting for suitable roosting and foraging resources. Although biological assumptions about nightly movements of bats published in the literature guided our decision to cap the maximum buffer scale at 15 km (Chambers et al. 2011), we anticipated computational issues would also preclude consideration of larger buffer scales given the combination of resolution

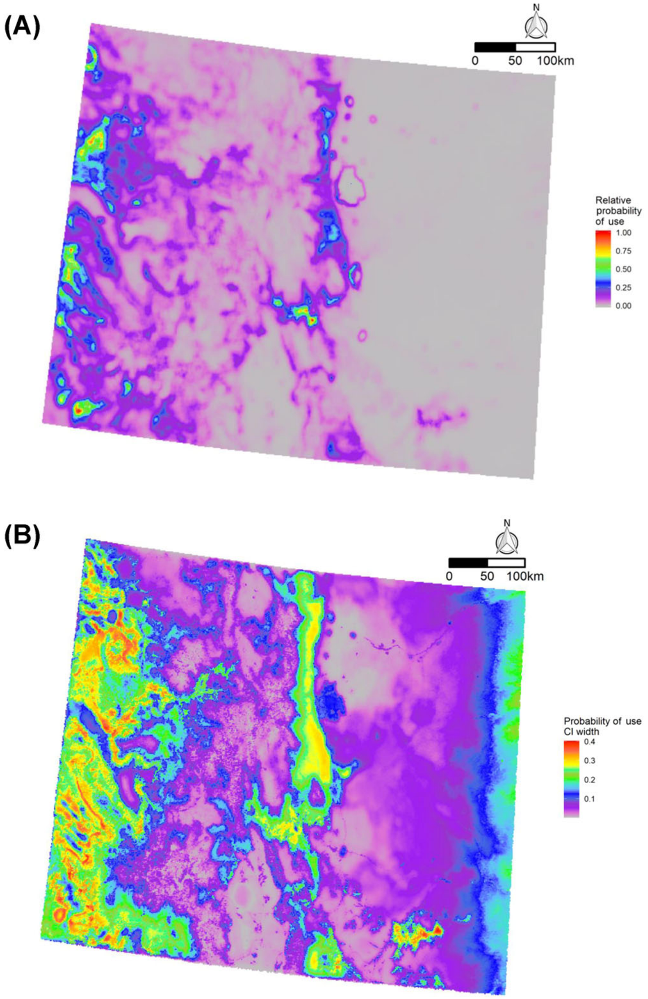

**FIGURE 2** A) Composite probability of use surface for species of small-bodied bats (California myotis, western small-footed myotis, long-eared myotis, little brown myotis, fringed myotis, long-legged myotis, Yuma myotis, canyon bat) in Colorado, USA, based on habitat use data collected in 1906–2018, where white-nose syndrome has not been detected as of 2019. This map represents the average probability of use in the state for all 8 species taken at once. Warm values (red) represent the highest probability of use and no shading (grey) the least probability of use. B) Composite credible interval width of probability of use surface from part A, showing the difference between the 97.5% and 2.5% credible intervals bounds

and area of the study site (the entire state of Colorado evaluated at the 1-km scale). The smaller buffer scales we included (5 and 10 km) are more reflective of those noted for smaller-bodied bats (Henry et al. 2002, Randall et al. 2014). Future modeling efforts to better elucidate biologically meaningful scales of habitat selection by bats (potentially varying across species or activity type) would be useful in this context.

Twelve of the 13 species we modeled were associated with pinyon-juniper for ≥1 activity and 7 for both roosting and foraging activity, suggesting that this land cover is important to multiple bat species in Colorado. All 7 myotis species modeled were associated with pinyon-juniper for at least foraging or roosting activity. Townsend's big-eared bats and western small-footed myotis show year-round and multi-purpose associations (roosting, hibernation, foraging models) with pinyon-juniper (Figure 1). Pinyon-juniper land cover has been associated with use by multiple bat species in Colorado (Adams 1990, Chung-MacCoubrey and Bogan 2003, O'Shea et al. 2011*a*) and across western North America (Chung-MacCoubrey 2005, Ives 2015, Anthony and Sanchez 2018). Notably, pinyon-juniper is one of the most abundant land cover types in Colorado, comprising approximately 50% of all forest (10–15% of the total land cover) in the state, making its management for bat conservation of high importance (Adams 1990, Armstrong et al. 2011). This forest type may show high probability of use by bats in Colorado because of its overlap with additional roosting resources, such as rock crevices and mines (Perkins and Peterson 1997, Hayes et al. 2011, O'Shea et al. 2011*a*, Neubaum 2017). Pinyon-juniper forests are often mechanically treated where they are encroaching into areas historically dominated by sagebrush in an effort to improve biotic resources for obligate species like sage-grouse (*Centrocercus* spp.; Cook et al. 2017). Bat and songbird species associated with this land cover should be considered when developing such treatment prescriptions (Lukacs et al. 2015, Anthony and Sanchez 2018, Navo et al. 2018).

Montane woodland, such as ponderosa pine (*Pinus ponderosa*) and Douglas-fir (*Pseudotsuga menziesii*), was also associated with foraging and roosting models for multiple bat species (Figure 1). The association between montane forests and bat species such as fringed and long-eared myotis has been identified elsewhere in their ranges (Rabe et al. 1998, Arnett and Hayes 2009). In Colorado, montane forest composes much of the woodlands at middle elevations along the Front Range and throughout central and western portions of the state. For the past 2 decades, mortality of evergreen species from mountain pine and spruce beetle has varied in intensity and location across Colorado (Barry et al. 2018, Negrón and Cain 2018), undoubtedly altering forested land cover for multiple bat species.

Both pinyon-juniper and montane woodlands have the potential to undergo large-scale changes from threats such as beetle kill and fire that may affect bat populations in Colorado and should be considered when developing forest management prescriptions (Navo et al. 2018). Although beetle kill has affected portions of these land cover types, levels have been lower than in subalpine forest in the state (Barry et al. 2018). Evidence suggests that bat communities may be more resilient to large-scale declines of forest from beetle kill than previously thought (Lawson et al. 2019). Bats also show resilience to large-scale fires in areas where alternate roosting resources such as rock crevices are available (Snider et al. 2013). Future modeling efforts should examine large landscapes affected by these threats across the state to determine if the probability of use by bats has changed from the levels noted here.

Foraging records for a number of species are tied to western longitudes of the state representing canyonlands (Figure 1, Supplemental Information S3 and S4). Not surprisingly, pallid bats, California myotis, and canyon bats showed a strong foraging association with western Colorado. The California myotis also exhibited high roosting use at western longitudes (Armstrong et al. 2011). Colorado's west slope contains the majority of lower elevation, arid canyon country generally associated with these species (Rodhouse et al. 2015). Similar canyon country can be found in extreme southeastern portions of the state, which explains the presence of pallid bat, canyon bat, and Yuma myotis by the quadratic relationship for the longitudinal index covariate in the foraging models for these species (Figure 1, Supplemental Information S3 and S4). The long-legged myotis foraging model was also associated with western longitudes but across a weaker gradient then that of other west slope species. Findings for this species include a higher probability of use in portions of the central longitudes of the state encompassed by high-elevation mountains. The long-legged myotis appears across a wide gradient of elevations as evidenced by the inclusion of the pinyon-juniper and subalpine forest covariates in its foraging and roosting models (Storz and Williams 1996, Armstrong et al. 2011). We noted a bias reflecting low sampling effort at high-elevation locations, which may account for low probability of use in subalpine for some bat species in Colorado such as the little brown myotis (Storz and Williams 1996, Neubaum 2018). Future sampling efforts should target such under-sampled areas to discern whether or not bats actually use them.

Adams (1990) suggests that sagebrush and grassland may be important land covers for bats in Colorado because a high percentage of species were confirmed using them. Selection of these cover types were represented for many species by a small number of records (sometimes as low as 1 location) known at that time. Accurate representation of habitat associations across large landscapes benefit from consideration of robust datasets. Our findings were able to consider a large dataset of used locations for each species examined in comparison to available locations to provide probabilities of occurrence and found only weak to slightly negative associations with these land cover types (semidesert shrublands and grasslands; Figure 1, Supplemental Information S2 and S3), suggesting lower levels of selection by bats in Colorado. In addition to a larger dataset of locations, the improved land cover mapping resources we used (CVCP) likely account for some of these differences. Some areas coarsely mapped as sagebrush in the Adams (1990) study may have been mapped as pinyon-juniper woodland in our study because the 2 land cover types often gradate into each other to varying degrees. Colorado's eastern plains (i.e., grasslands) have not been surveyed for bats as rigorously as other land cover types in the state because of the general lack of roosting resources, which may influence our findings. Identifying areas with sampling deficiencies within these larger landscapes through such modeling exercises can provide land managers with targeted areas of interest to direct future sampling. For example, as efforts such as North American Bat Monitoring Program gain momentum, sampling in these underrepresented areas that do not appear to offer good biotic and abiotic features for bats will need to be defensible if land managers are going to focus limited resources there over areas of known use.

Topographic ruggedness index was included in relatively few species or species-activity models in our study (Figure 1). Rodhouse et al. (2015) incorporated a measure of roughness in a large-scale acoustic analysis in the Pacific Northwest and generally did not find it to be influential with the exception of Townsend's big-eared bat. Rodhouse et al. (2015) did find the cliff land cover to be associated with several species. In our study, the land cover rock-disturbed soil (comparable to cliff) appeared in only 2 models, a weak relationship for the big-brown bat roosting model and a strong relationship for the canyon bat foraging model (Figure 1). The degree of accuracy to which the rock, cliffs, and bare soil is mapped in Colorado by the CVCP layer we used determined how this resource influenced models. Tree cover may obscure rocks that occur in forest understory, diminishing the representation of some rock resources. Cliffs, although more obvious when depicted by a TRI, can be missed from an aerial view that runs parallel to them. Consequently, thought should be given how to best represent these resources that are increasingly being supported in studies of smaller scale as providing important year-round roosting habitat to western bat species (Bogan et al. 2003, O'Shea et al. 2011*a*, Johnson et al. 2017, Neubaum 2018).

Only 2 species, Townsend's big-eared bat and western small-footed myotis, had enough winter records to develop hibernation models (Table 1; Figure 1). The apparent lack of winter records for most bats in Colorado is important when considering distributions of these species in the state. Most literature that describes the natural history of bats in Colorado (Adams 2003, Armstrong et al. 2011) suggests that they select caves and abandoned mines for hibernation, as these locations are commonly selected for by the same or similar bat species in eastern North America (Raesly and Gates 1987, Furey and Racey 2016). Across Colorado, abandoned mines account for the majority of sites surveyed during winter (Weller et al. 2018), mainly detecting small aggregations of Townsend's big-eared bats (Hayes et al. 2011) and to a lesser extent western small-footed myotis (Navo et al. 2018). Hibernation records for these species suggest a higher concentration of selection in the uranium mines located in the slickrock canyonlands of western Colorado. Surveys of caves and abandoned mines in an area of dense karst formation of central Colorado also indicate that these features are generally selected for by small aggregations of bats in winter, with the majority of records accounted for by Townsend's big-eared bats (Neubaum 2018). Notable surveys of caves and mines across much of western North America suggest low-level selection of these features with records dominated by this species (Weller et al. 2018).

Most of the target species and their associated activity areas spanned the state, but some were restricted (e.g., west slope specific, plains specific). Foraging activity for the canyon bat (mostly western range) and foraging and roosting activities for the California myotis (western range) models serve to reinforce species range maps, with little to no probability of use in the eastern plains. The canyon bat shows a patch of low probability of use in the southeast corner of the state, which is consistent with the presence of canyonlands this bat is associated with inhabiting. The results of the models for these species and activities adhere well to the known ranges of these bats, increasing our confidence in our results.

Selection of rock crevices as hibernacula by big brown bats and little brown myotis may explain the paucity of winter records from underground sites such as caves and mines in Colorado (Neubaum et al. 2006, Neubaum 2018). Study of these cryptic hibernacula in Colorado (e.g., talus, cliff bands, crevices in boulders) presents unique challenges to winter bat surveys because they are less accessible for inspection, owing to constricted access and snow cover, than caves and mines, limiting the amount of data available for modeling winter ranges. Consequently, our ability to develop probabilities of use for bat species hibernating in the state is expected to continue being a challenge into the near future. This challenge carries important implications tied to the management of WNS. Areas with higher TRI values generally have rock crevices available at the surface in the form of cliff faces and talus slopes, potentially providing a suitable surrogate covariate for predicting hibernacula of some species, but TRI is vulnerable to mapping discrepancies as previously discussed. Topographic ruggedness index was included in the best hibernacula model for the western small-footed myotis but not for the Townsend's big-eared bat (Figure 1). In addition, the site-specific microclimates of hibernacula are undoubtedly important in determining bat selection and will be harder to predict accurately from surrogate measures (Neubaum et al. 2006, Klug-Baerwald et al. 2017, Neubaum 2018).

With the exception of the long-eared myotis, all models that included alpine and subalpine land covers in our analysis indicate bats had negative associations with high-elevation areas (Figure 1). These findings do not reflect selection of high-elevation talus slopes by little brown myotis in autumn (Neubaum 2018); however, dates of locations associated with that study were collected for the date of first detection, which occurred just prior to the window considered in the hibernation analysis we modeled here. In general, a review of our dataset suggests a sampling bias is evident for the alpine areas, with fewer efforts to capture bats at these high-elevation locations, regardless of season. Although we excluded the elevation covariate because it was highly correlated with land cover type, it likely plays an important role and may warrant future investigation in a topography-specific modeling exercise (Hayes and Adams 2014, Rodhouse et al. 2015).

In general, most models were well fit. Given the number of covariates included in the models on average and the consistent proportion of unexplained variance in almost every modeling context, it would be highly beneficial to refine the tools available for evaluating habitat relationships for temperate bats in Colorado and elsewhere. Identifying methods to include climatic variables (e.g., temperature, precipitation, humidity) may prove fruitful, although challenging (Rodhouse et al. 2015). Because many bat species use roosting environments as microrefugia to address seasonal thermal challenges (Chruszcz and Barclay 2002, Humphries et al. 2002, Johnson et al. 2019), climatic data across the landscape would need to be examined at an exceptionally fine scale to accurately reflect the small variations in metrics that bats are using as cues for internal roost selection.

Efforts to reduce the sampling bias in the dataset (i.e., aggregating locations within pixels to eliminate non-independent, repeat locations) were effective in that they allowed additional covariates to be identified for 2 generalist species, big brown bats and little brown myotis, which were heavily represented by urban records. The urban covariate was included in the foraging and roosting activity models for these 2 species at the 5-km scale (Figure 1). The same issue is likely to occur for models of Brazilian free-tailed bats (*Tadarida brasiliensis*) if sample sizes had allowed them to be examined, as many records for this species in Colorado come from urban settings. Representation of urban settings can be inflated in models as people inherently come into contact with these bats more often than their wild counterparts because of their proximity and use of anthropogenic structures (O'Shea et al. 2011*b*), creating a biased sample. In addition, caution should be exercised if using health department records because these locations may not reflect the normal routines of healthy bats. Foraging models for several other species (hoary bat, silver-haired bat, big-brown bat) included the urban covariate but at the 5- or 15-km buffer, indicating that these species likely use the insect resources from these highly vegetated areas but may or may not roost within them at high levels. Hoary and silver-haired bats may roost in deciduous trees within urban areas but their locations are seldom detected. Big brown bats have been well-documented using urban areas for roosting purposes, which was a supported in this species-activity model, so it is not surprising that they commonly forage in urban areas (Everette et al. 2001, Neubaum et al. 2007).

Little brown myotis exhibited a relatively small extent in our study, particularly when referencing them against range maps for this species (Armstrong et al. 2011). Adams (1990) used distributions to examine generalist versus specialist tendencies, albeit with a smaller dataset and notably lower levels of location accuracy at that time, and suggested that little brown myotis are generalists, discordant with our results. The willingness of this species to use occupied anthropogenic structures was given as support for this trend along with its presence in most land cover types, even if at low levels (Johnson et al. 2019). That our findings for little brown myotis differ somewhat with those of Adams (1990) nearly 3 decades later, is highly relevant for this species prior to the arrival of WNS in the West. Such findings may suggest that some species' populations have declined or are not as widespread across western portions of their range as they historically were noted to be, particularly when compared to eastern portions of North America already affected by the disease. Caution should be used for interpretation of little brown myotis with respect to species abundance, which we did not examine, or to the foraging component because this model had a lower fit (Table 2).

## MANAGEMENT IMPLICATIONS

The utility of our models may be particularly beneficial when applied to threats operating at different scales such as beetle kill, catastrophic fire risk and associated treatments, or diseases such as WNS. For example, the 3 largest wildfires in Colorado history burned in 2020. Resource managers can use these models to target specific species most likely to be affected by these large-scale fires based on the woodland land covers they are selecting for in our models. Managers may also proactively determine future woodlands within their jurisdiction that are likely to be selected by a species of concern and target them for fuels reduction efforts.

In respect to disease, our findings provide a baseline of habitat selection by bats in Colorado prior to arrival of WNS. Consequently, we created a predictive distribution map of small-bodied bat species in Colorado to determine hot spots to focus future surveillance and treatment efforts (Figure 2). In the absence of more rigorous population-level data, these probability of use models can guide decisions for future WNS management efforts. Areas of Colorado's west slope and plains-mountain interface have the highest convergence of selection by species most susceptible to WNS and thus are good areas of foci for surveillance efforts. Targeted surveillance in areas with high probability of use by vulnerable species may lead to better detection rates of the fungus that causes WNS, *Pseudogymnoascus destructans*, and the associated disease once it arrives. These locations can then be prioritized for novel treatments such as vaccinations and probiotics if practicable. Although our models are restricted to Colorado for proof of concept in using presence-only data, and to provide state-level management guidance, we encourage future efforts to extend the scale of analysis to the full range of a species by facilitating multi-state or province efforts that allow capture datasets to be merged, similar to those underway for acoustic datasets.

### ACKNOWLEDGMENTS

We thank K. W. Navo and R. J. Sacco for having the foresight to establish and maintain the CPW bat database, and C. Strobel for managing the CPW Scientific Collections database that provided much of the GIS data used for this analysis. T. S. Jackson and B. F. Petch facilitated recent upgrades to the databases and supported work to improve their cohesiveness for which we are grateful. We also thank J. Edge for digitizing historical locations from documents and publications, and K. M. Keisling for improving the accuracy and entering numerous records. M. B. Rice and M. M. Flenner provided helpful input on the early development of the models and GIS layers for this analysis. We are grateful to N. D. Rayl, R. Y. Conrey, J. P. Runge, and T. S. Jackson for providing helpful comments on early drafts of this manuscript. Funding provided by an assistance agreement from the U.S. Bureau of Land Management (grant number L17AC00155-03) aided in database development.

### ETHICS STATEMENT

Data analyzed from the CPW scientific collection permit database included animal handling protocols approved by the State prior to capture work. Additional data we considered that pre-date the CPW scientific collection permit followed protocols and guidelines for bat species in effect at the time of data collection.

## DATA AVAILABILITY STATEMENT

All GIS layers used in our analysis are available or can be constructed using the referenced links. The dataset of bat locations we used for our analysis contains sensitive locations (e.g., vulnerable roost locations, private lands information). Colorado Parks and Wildlife can make portions of the data available upon request with the application of a non-disclosure agreement or other formal data sharing agreement.

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*Associate Editor: Andrea Litt.*

## SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

**How to cite this article:** Neubaum, D. J., and K. Aagaard. 2022. Use of predictive distribution models to describe habitat selection by bats in Colorado, USA. Journal of Wildlife Management 1–20. https://doi.org/10.1002/jwmg.22178