RANGE AND MODELED DISTRIBUTION OF WYOMING'S SPECIES OF GREATEST CONSERVATION NEED

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TABLE OF CONTENTS

INTRODUCTION

In their Comprehensive Wildlife Conservation Strategy, the Wyoming Game and Fish Department (WGFD) identified 152 terrestrial vertebrate Species of Greatest Conservation Need (SGCN), many of which were included on the list in a precautionary sense due to a lack of information regarding their distribution and conservation status (WGFD 2005). The CWCS (now called the State Wildlife Action Plan, or SWAP), is being revised in 2010. A major goal of the revision is to compile updated information on the range and distribution of SGCN within Wyoming. To this end, the Wyoming Natural Diversity Database (WYNDD) established a collaborative project with the WGFD to refine estimates of range and distribution for these species.

This range and distribution mapping effort is part of the larger Assessment of Wildlife Vulnerability to Energy Development (AWVED) being conducted by WYNDD and the Wyoming Cooperative Fish and Wildlife Research Unit of the University of Wyoming. The AWVED project will use the refined ranges and distributions to assess the exposure and sensitivity of SGCN to energy extraction and generation activities in Wyoming. AWVED is jointly funded through the U.S. Geological Survey's Wyoming Landscape Conservation Initiative (USGS WLCI) and the State Wildlife Grants program (SWG) of WGFD.

This report represents the completion of the AWVED range mapping and distribution modeling process. It presents detailed methods and results of the distribution models, including full evaluation statistics. The range mapping effort was completed in late 2009. Range maps were delivered to WGFD as a geodatabase on January 19, 2010 and were accompanied by an explanatory report (Keinath et al. 2010). Distribution models were finalized in the spring of 2010 and were delivered to WGFD on April 28, 2010 as a geodatabase along with a summary of model output (Keinath 2010).

METHODS

Methods for range maps are presented in a previous document (Keinath et al. 2010), so the remainder of this section will focus on methods used in constructing distribution models for Wyoming's terrestrial vertebrate SGCN.

The procedure used in this effort is one commonly used in wildlife modeling studies. The environmental characteristics of locations where species have been documented to occur were statistically extrapolated to identify other areas potentially suitable for occupation (e.g., Elith et al. 2006, Greaves et al. 2006, Phillips et al. 2006, Guisan and Thuiller 2007). The basic components of creating environmental niche models are:

1) occurrence data collection and processing
2) environmental data collection and processing, and
3) model generation, validation and display.

The following sections describe methods relative to each of these components.

OCCURRENCE DATA COLLECTION AND PROCESSING

DATA COLLECTION

We compiled occurrence records for all Wyoming's terrestrial vertebrate SGCN (WGFD 2005) and several additional species currently under consideration as additions to the SGCN list, resulting in a dataset of approximately 260,000 individual records for 159 species. Records were compiled between 2007 and 2009 from a variety of sources. Major sources included the Biotics database of the Wyoming Natural Diversity Database (http://uwadmnweb.uwyo.edu/wyndd/), the Wildlife Observation System (WOS) of the WGFD (see WGFD 2005), data from annual bird monitoring efforts (notably the North American Breeding Bird Survey and surveys for the Monitoring Wyoming's Birds project), specimens from museums across the country (notably the National Museum of Natural History, University of Kansas Natural History Museum, and the University of Michigan Museum of Zoology), and unpublished data sets from local biologists.

At a minimum, records were attributed with their source, collection date, and species identification. Where additional information was available (e.g., observer notes), this information was also retained. Positional accuracy (i.e., how closely the observation site could be relocated from information in the record) was estimated based on the record's mapping protocol using standards established by the Natural Heritage Network (http:// www.natureserve.org/ prodServices/ standardsMethods.jsp). All records were stored in a geodatabase that was queried as needed for analysis and modeling.

DATA QUALITY ASSESSMENT

Sources varied in terms of data structure, positional accuracy, dates of collection, veracity of species identification, and the detail of supporting biological data provided, necessitating efforts to reconcile differences to form a single, logically-consistent dataset. Moreover, individual observations varied greatly in their quality, and were not of equal value for constructing niche models. Therefore, we scored each record for three key criteria: date of occurrence; accuracy of location; and veracity of identification (Table 1), and added these scores to compute a point quality index (PQI) for each record. Thus, high-quality points (i.e., those that were recent, accurately located, and positively identified) could achieve a maximum score of 12, while poor-quality points received a minimum score of 0. These scores were used to filter data prior to niche modeling (see below) and to assess the overall quality of the available data for each model.

TABLE 1. Scoring system used to evaluate the quality of occurrence records based on spatial precision (A), age of record (B), and taxonomic certainty of identification (C).

A. Spatial Precision of Occurrence Record

Score	***Definition***	***Example***
4	Location uncertainty ≤ 30 meters	Location via GPS
3	Location uncertainty > 30 meters and ≤ 100 m	Location via 7.5' quad map
2	Location uncertainty > 100 meters and ≤ 300 ms	Location via 100k quad map
1	Location uncertainty > 300 meters and ≤ 600 m	Location via large-scale map or detailed written directions
0	Location uncertainty > 600 meters and < ~3,000 m	Location via landscape description (e.g., 5 miles south of Laramie Peak)
U	Record is unusable; uncertainty > ~3,000 m	Museum specimen located by reference to a county

B. Age of Occurrence Record

Score	***Calendar Year of Observation***	***Definition***
4	≥ 2000	Observation made within roughly 10 years of model creation
3	1990 - 1999	Observation made within roughly 20 years of model creation
2	1980 - 1989	Observation made within roughly 30 years of model creation
1	1960 - 1979	Observation made within roughly 50 years of model creation
0	≤ 1959	Observation made within roughly 100 years of model creation
U	Historic	Record is unusable, because the record is over 100 years old, the species is known to be extirpated from the area in question, or the habitat has changed drastically since its collection.

C. Taxonomic Certainty of Occurrence Record

Score	***Category***	***Definition***
4	Confirmed Identification	Adequate supporting information exists within the occurrence record to consider it a valid observation of the species in question
2	Questionable Identification	Supporting information within the occurrence record is insufficient to *confirm* correct identification of the species (e.g., no supporting documentation or observer credentials), but neither is there any reason to assume that the record is in error
0	Possible Miss-identification	There is reason to believe that the observation could be erroneous. (e.g., extra-limital observation by amateur biologists of species that are easily misidentified)
U	Misidentification	Record is unusable. Information in the occurrence record suggests it is misidentified

DATA FILTERING

For migratory species, all occurrences outside the designated modeling season were removed from the dataset. In most cases the primary season of interest in Wyoming was the breeding season, in which case all non-breeding season occurrences were eliminated. Well-documented occurrences often specifically noted evidence of breeding, but where this was not the case estimates of breeding/migratory phenology from published species accounts (notably Birds of North America accounts; http://bna.birds.cornell.edu/bna/) were used in combination with local knowledge to estimate the timing and duration of the breeding season.

Opportunistically-collected datasets can suffer from autocorrelation artifacts arising from non-uniform sampling across the area of interest, which can sometimes bias environmental niche models (Jimenez-Valverde and Lobo 2006, Johnson and Gillingham 2008). To mitigate such impacts, we used target-group background data for model building (Phillips et al. 2009), and used a multi-pass filtering technique to construct a minimally-biased modeling dataset for each species that was drawn from the entire collection of occurrence records, as follows:

Step 1: We removed all unusable points from the dataset (i.e., points that have a score of 'U' for any quality measure; Table 1).

Sept 2: We thinned dense clusters of occurrences resulting from oversampling by removing those occurrences with lower PQI scores that were within 1,600 meters (roughly one mile) of other, higher-quality occurrences. Where equal quality occurrences occurred within 1,600 meters, we randomly selected which occurrence to remove.

Step 3: We constructed a final model set by drawing occurrences from the remaining occurrences with geographic stratification based on 12-digit hydrologic units. This was accomplished by first selecting the best quality (i.e., highest PQI) point from each occupied hydrologic unit. We then added the next-highest quality occurrence from each hydrologic unit to our selection and repeated this until additional occurrences were selected from less than 20% of the previously selected hydrologic units. This cutoff guarded against model bias by preventing occurrences from clustering in a small subset of the species' range. In other words, it helped assure an even distribution of occurrences across the modeled area, even when sampling was not evenly distributed. The 20% cutoff was modified for some species based on expert review of draft models, as noted in the species-specific reports of Appendix 3.

ENVIRONMENTAL DATA COLLECTION AND PROCESSING

All environmental predictor layers must be raster datasets with matching projection, extent, and cell size and alignment to be used in building a Maxent model. All predictor layers were re-projected to WYLAM projection and resampled to a 30 m cell size, such that their projection, extent, cell size, and alignment were consistent. These processes were performed in ArcGIS 9.3, unless otherwise noted, and all environmental layers were then converted to Maxent raster format (.mxe) for more efficient modeling.

Environmental data layers used in modeling generally fell within six major categories: climate, hydrology, land cover, landscape structure, substrate, and terrain (See Appendix 2 for a more detailed explanation each variable used). Climate variables were generated by applying the BIOCLIM algorithms (Nix 1986) to DAYMET data (Thornton et al. 1997, Thornton and Running 1999, Thornton et al. 2000), resulting in 35 bioclimatic parameters useful in predicting species' distributions. These variables described means, extremes, ranges, and timing of temperature, precipitation, radiation, and humidity. Hydrology variables described the distance to or prevalence of various water features on the landscape, and were generated by running Euclidean distance or neighborhood functions on subsets of the National Hydrography Dataset (Simley and Carswell 2009). Land cover variables primarily were derived from LANDFIRE (Comer et al. 2003), GAP Land Cover (Gap Analysis Program 2010), or the USGS Sagebrush dataset (Homer et al. 2009), and represent the vegetative components of habitat, including bare ground, herbaceous, shrub, and forest cover, and estimated percent cover of overstory species of particular importance, such as ponderosa pine, sagebrush, and cottonwood. Landscape structure variables included indices of landscape fragmentation and patchiness. Substrate (Soil Survey Staff n.d., Love and Christiansen 1985) data were used to generate indices related to soil depth and texture, and to identify specific habitat features such as caves and cliffs. Finally, terrain variables, derived from the National Elevation Dataset (Gesch et al. 2009), provided data on important topographic attributes, including elevation, slope, aspect, ruggedness, and site moisture.

MODEL GENERATION, VALIDATION AND DISPLAY:

MODEL GENERATION

Maximum Entropy methods were used to identify pertinent predictor variables for each species and to generate distribution models (Phillips et al. 2006, Phillips and Dudik 2008), as it has been consistently shown to be among the most accurate and robust algorithms for constructing niche models from opportunistically collected data, particularly with small sample sizes (Graham and Elith 2005, Hijmans and Graham 2006, Graham et al. 2008, Wisz et al. 2008). We used Maxent® version 3.3.1 (http:// www.cs.princeton.edu/ ~schapire/ maxent/) to implement this algorithm. To minimize the impact of sampling bias we used target-group background data for model-building, wherein background points (i.e., points to which the occurrences are compared) are drawn from a non-target species locations from the occurrence database (Phillips et al. 2009). To be effective, this procedure requires that species within target groups be roughly similar in terms of the approach with which they are surveyed, and that the total number of occurrences in each target group be on the order of 10,000. We grouped species into 5 target groups (Table 2).

TABLE 2. Target modeling groups.

Group	*Number of SGCN in Group*	*Number of Occurrences (unfiltered)*	*Description*
Bird Surveys	62	*12,253*	Birds that are surveyed with standard, short-range acoustic or visual surveys (i,e., all birds except raptors and game species).
Game Survey	5	*8,392*	Species that are subject to permitted hunting, and are therefore tracked relative to hunter activities (i.e., grouse and ungulates).
Localized Survey	91	*8,140*	Relatively narrowly-ranging species that are typically surveyed using a relatively small sampling unit and/or specialized survey techniques. Surveys in this group can take many forms, from visual encounter surveys (e.g., reptiles, amphibians), trapping (e.g., small mammals), acoustic surveys (e.g., bats, owls), visual/tracking surveys (e.g., ground squirrels) or a combination thereof (e.g., weasels, ringtails).
Special Survey - Large Area	19	*15,770*	Species that require specialized, targeted surveys that generally occur using a large sampling area because the species are wide-ranging (i.e., large and mid-sized carnivores and diurnal raptors). These surveys generally take the form of long-range visual surveys (e.g., golden eagle, wolves) or specialized trapping or tracking over fairly large areas (e.g., lynx, swift fox, wolverine).

Maxent allows for model tuning through a limited number of parameters, controlled by adjusting settings in the software. Generally, we used the default settings for each parameter, as these settings have been optimized through empirical testing (Phillips and Dudík 2008). Where necessary, we adjusted feature types and/or the regularization multiplier to improve model performance (see notes in the model reports for each species, Appendix 3). The parameter we adjusted most frequently was the list of feature types used to create models. Feature types refer to the data models used to represent the relationship between a particular environmental layer and the probability of occurrence for the species. They include Linear, Quadratic, Product (i.e., "interaction"), Threshold, Hinge, and Categorical (Phillips et al. 2006). The default setting for this parameter is "Auto Features," which constrains the possible features to be used based on the number of sample points (Phillips and Dudík 2008). In some cases, we found it necessary to constrain the feature types further to prevent overfitting that was apparent after expert review of either the partial plots or the output surface for a species. The second parameter we adjusted in some cases was the "Regularization Multiplier" (Phillips et al. 2006; Phillips and Dudík 2008). Again, this adjustment was made to prevent overfitting of the input data.

When dealing with a large number of species and limited computational capacity, variable selection for each model can be problematic. Deciding which variables to include in a model is ultimately a judgment that seeks to include enough variables to achieve adequate model validation without exceeding computational limits or unduly increasing model complexity and overfitting. To achieve this balance we first constructed "full models" for all species using the complete set of predictor variables. The complete set of predictor variables consisted of a "base" set of predictor variables that was the same across all species and additional variables deemed important for a particular species or group of species (see Appendix 3 for a detailed list). For example, while annual temperature was a base variable used for all species, distance to cave-forming substrate was included as an additional predictor for cave-roosting bats, but was not used for other species. From these models, the variable contribution scores and jackknife estimates of regularized training gain with and without each variable were used to rank variable importance, and area under the curve statistics (AUC) of receiver operating characteristic curves were used to estimate model performance. We built final models to achieve 90% of full model performance (i.e., 90% of the AUC for the full model) using as few variables as possible, which was generally achieved by using the 5 – 7 highest-ranked variables.

MODEL VALIDATION

To avoid biases associated with any one validation technique, we evaluated models quantitatively and qualitatively using multiple methods, including prediction accuracy based on ten-fold cross-validation, statistics derived from receiver operating characteristic analyses, evaluations of input data quality, and the expert opinion of biologists regarding how well final models reflected their understanding of species' distributions (e.g., Fielding and Bell 1997, Freeman and Moisen 2008). Evaluation metrics are explained in Appendix 1 and provided for each species in Appendix 3.

MODEL DISPLAY

Several adjustments were made to model output, largely for display purposes. First, the models were clipped to species' known and suspected ranges within the state, thus limiting predictions to areas of the state that are believed to be part of the species' ranges. Second, although Maxent® creates a continuous model estimating (for each 30-meter raster cell within Wyoming) the probability of that cell being of suitable habitat for the species in question, WGFD was interested in a binary prediction. To create maps for the SWAP, a binary threshold was specified that divided the continuous output into two categories: predicted presence and predicted absence. For most SGCN, this threshold was selected to maximize the sum of training sensitivity (i.e., true positive rate) and estimated training specificity (true negative rate), which theoretically maximizes the discriminant ability of the binary output (see Appendix 3 for exceptions).

Third, end-users requesting models from WYNDD are often interested in output that goes beyond binary prediction, but is not as detailed as the full continuous output. We therefore created a four-category version where the two highest categories fall within binary predicted presence (i.e., "predicted present – high probability" and "predicted present – medium probability") and the two lowest categories fall within binary predicted absence (i.e., "predicted absent – low probability" and "predicted absent – very low probability"). The threshold separating the two upper categories was generally selected so the "high-probability" category captured the most-similar 50 percent of input occurrences (i.e., 50-percentile training threshold). The threshold separating the two lower categories was generally selected so the "very low probability" category included the 5 percent of occurrences that were most different from the rest (i.e., 5-percentile training threshold). In practice, particularly when there are very few occurrences, there can be very little separation between categories, so some models are only presented using 2 or 3 categories (see Appendix 3 for exceptions).

RESULTS AND DISCUSSION

Results are fully enumerated in Appendix 3, which contains a full list of species with selected summary statistics as well as detailed results for each SGCN. The primary results presented in Appendix 3 are range maps and distribution models for all terrestrial vertebrate SGCN.

Range maps define the best estimate of the total geographic space thought to be occupied by each SGCN in Wyoming, as determined by panels of state and regional experts (see Keinath et al. 2010 for full explanation). Range considers species presence based solely on geographic space and doesn't explicitly consider habitat features. Thus, range maps tend to over-estimate where a species occurs, because they generally include much unsuitable habitat that is never used by the species in question. Therefore, they are of limited utility for conservation planning, where more explicit information on habitat suitability is valuable. Despite this shortcoming, the proportion of range deemed known based on documented occurrences, as opposed to suspected based on hypothesized habitat availability, is a useful metric summarizing how much is known about populations of SGCN (see Appendix 3 for this information).

Distribution models are intended to address the shortcomings of range maps and maps of species observations. While range maps tend to over-estimate where a species occurs, locations of documented occurrence usually underestimate where a species occurs, particularly when systematic survey efforts are lacking, as is the case for most of Wyoming's SGCN. Distribution models bridge this gap by using the occurrence data to quantify environments where a species is known to occur and spatially mapping similar areas throughout that species' range. For example, some small-mammal and reptile SGCN have ranges encompassing more than half of Wyoming, while there are only a handful of documented occurrences in the state. Using the environmental attributes of these few documented locations, we created distribution models that provide spatially explicitly estimates of where else the species are likely to be found.

Distribution models identify areas where species are most likely to occur based on currently available observations and environmental data layers, and they *should not be interpreted as depicting known occurrence*. Models are only as good as the data use to create them, so models with few known occurrences and/or poor validation statistics should be used with caution. Further, SGCN distribution models were created at the scale of Wyoming and are only suitable for analyses conducted at a similar scale, such as identifying coarsely-defined areas of conservation concern or quantifying state-wide patterns of potential distribution. They should not be used alone to make conclusive decisions regarding specific conservation sites.

On the whole, distribution models performed well. Species-specific evaluation of distribution model quality suggested that 35 species had high-quality models, 75 had medium-quality models, and 49 had low-quality models. This assessment is based on both quantitative evaluation statistics and qualitative expert opinion (see explanation under Distribution Modeling Methods and in Appendix 1). In general, we feel that models classified as high-quality or medium-quality are apt to be reliable depictions of true distribution. In many cases, low-quality models can also be reasonable depictions of distribution, but they often have notable shortcomings (e.g., very low sample size or low validation statistics) and should therefore be used with some caution. For example, low-quality models may provide an accurate depiction of a species' distribution in areas that have been sampled adequately, but they may provide less accurate depictions of distribution in areas that are poorly sampled. Models of all quality levels can offer useful insights into the distribution of otherwise poorly-understood species.

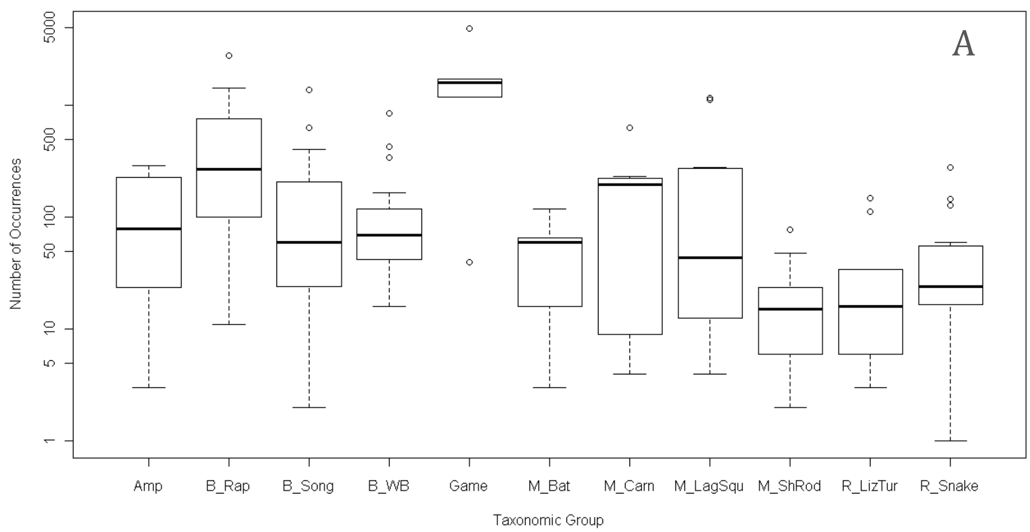
Lack of adequate occurrence data impacted model quality for numerous species. In general, small mammals and reptiles (particularly lizards) were poorly sampled (Figure 1). Game species and species receiving attention under the U.S. Endangered Species Act (ESA) had more documented occurrences than other non-game species (Figure 2a), though this was not also true for occurrence quality (Figure 2b). Lack of suitable occurrence data seemed to translate into poor model quality, as small mammals and reptiles with poor datasets (Figure 2) also demonstrated a disproportionate number of species with low-quality models (Figure 3a). In contrast, species that experienced ESA attention had generally better datasets (Figure 2) and had a relatively large proportion of high-quality models (Figure 3b).

A primary way to improve distribution models and inform range maps is to increase the number and quality of known species locations. This is particularly true for groups of species with few occurrences, including small mammals and reptiles (Figure 1). To achieve better distribution models, attention must be given to recording high-quality occurrence data throughout species' suspected ranges (i.e., occurrences where the species is accurately identified, locations are precisely recorded, and supporting documentation is provided).

A second, but equally important, way to improve distribution models is to improve state-wide maps of environmental characteristics. For example, lack of adequate wetlands information hindered distribution modeling for a variety of wetland-associated species, including waterfowl, shorebirds, and amphibians. Similarly, lack of detailed soil maps hindered modeling the distribution of partly fossorial mammals, such as pocket gophers, ground squirrels, prairie dogs and pygmy rabbits, while lack of complete and accurate maps depicting vegetation structure hindered modeling of species selecting particular vegetation characteristics, such as juniper obligates.

The range and distribution data presented herein will be used to update Wyoming's SWAP and will inform a spatially explicit assessment of the potential vulnerability of these species to development activities across the state. These products will be maintained and updated by WYNDD as new information becomes available and as funding allows. Range maps and models are available for anyone to use by contacting WYNDD (http://uwadmnweb.uwyo.edu/wyndd/). When viewing and using models, it is important to pay attention to model quality (as summarized in the species-specific reports of Appendix 3), and to conduct analyses at the appropriate scale (i.e., models were created at the scale of Wyoming and are suitable for analyses conducted at a similar scale).

FIGURE 1. Number of occurrences (A) and mean occurrence quality (B) plotted as a function of taxonomic groupings. Game species were addressed separately as they were generally outliers within their taxonomic groups. Game species had many more occurrences than other groups, but not higher point quality. Amphibians have the highest mean point quality of any group. *Taxonomic groups* are as follows: Amp = amphibians, B_Rap = raptors, B_Song = songbirds, B_WB = waterbirds, Game = game species, M_Bat = bats, M_Carn = carnivores, M_LagSqu = diurnal small mammals (lagomorphs and squirrels), M_ShRod = cryptic small mammals (shrews and rodents), R_LizTur = lizards and turtles, R_Snake = snakes. *Point quality index* (described in methods) ranges from 0 to 12, with higher values representing higher-quality occurrences.



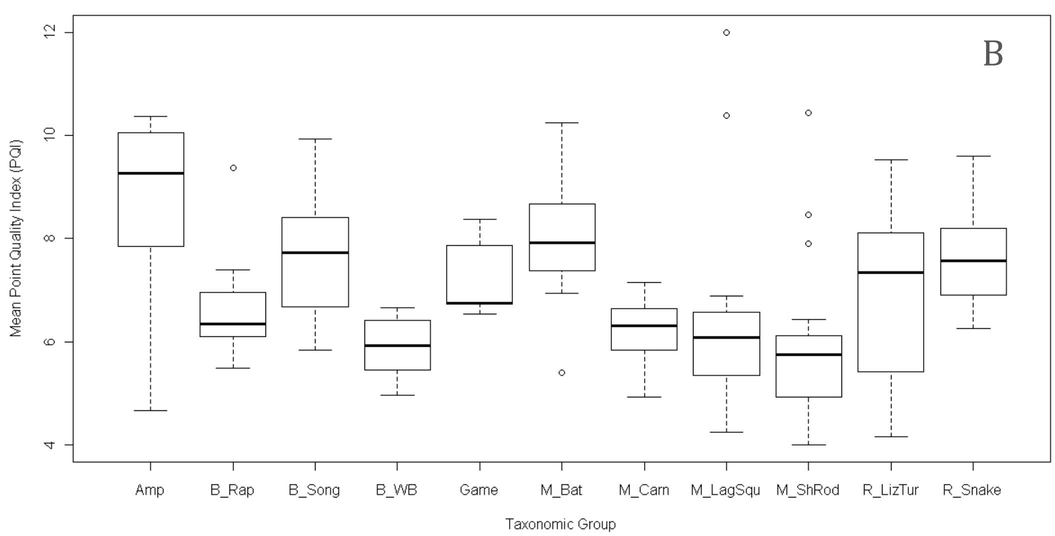


FIGURE 2. Number of occurrences (A) and quality of occurrences (B) plotted as a function of management groups. *Management groups* are as follows: ESA = species petitioned and/or listed under the U.S. Endangered Species Act, Game = species managed by WGFD as permitted game species, General Non-Game = species listed by WGFD as non-game and not subject to special federal regulation. *Point quality index* (described in methods) ranges from 0 to 12, with higher values representing higher-quality occurrences.

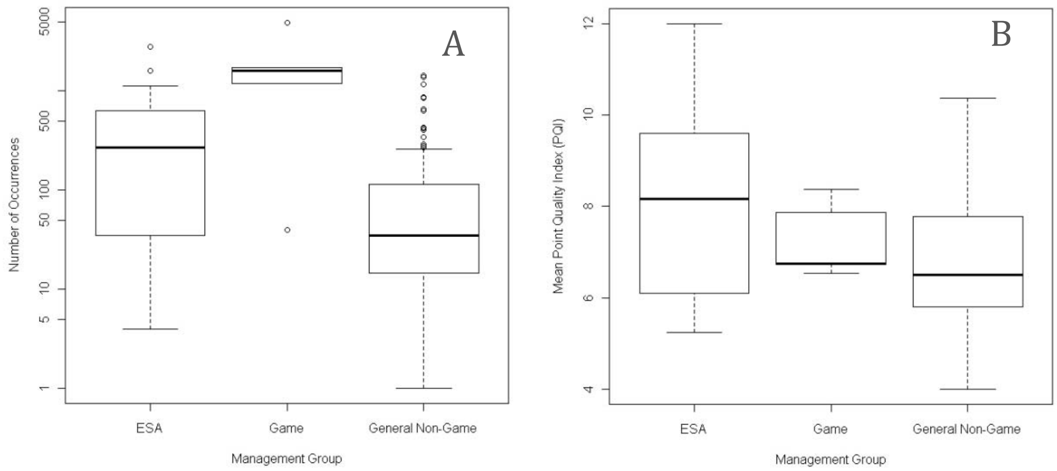
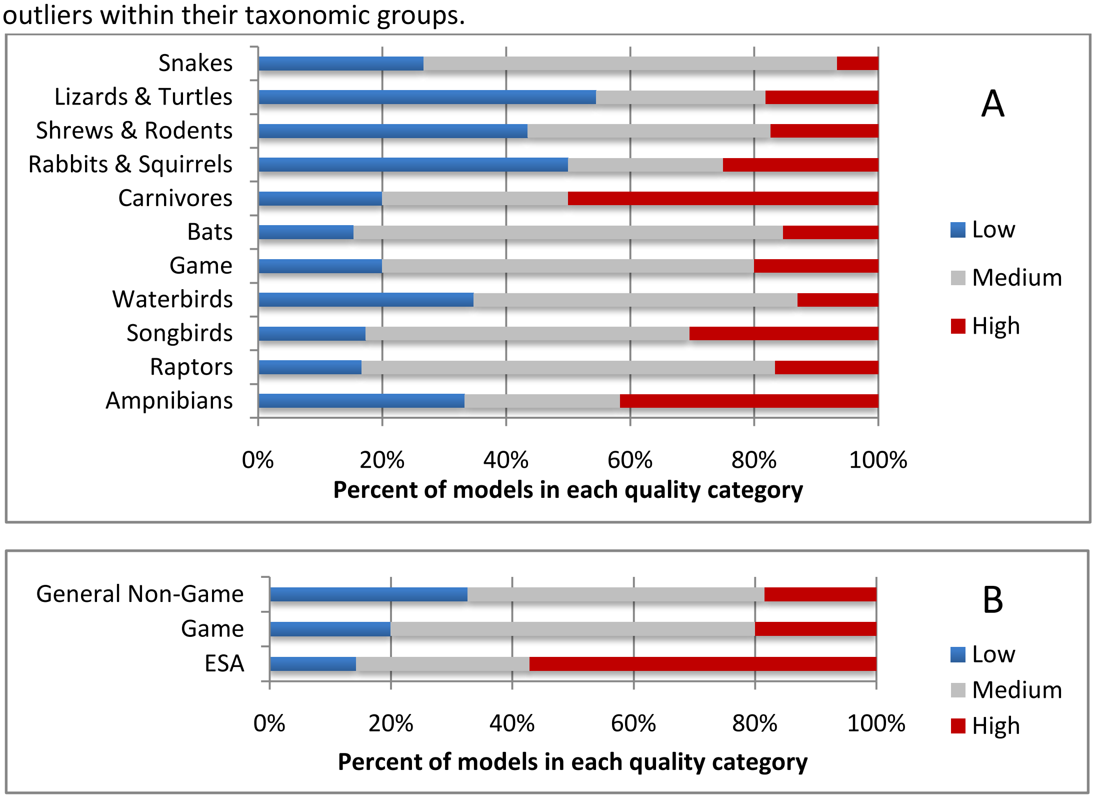


FIGURE 3. Proportion of models in each quality category (low, medium, or high) plotted as a function of taxonomic grouping (A) and management grouping (B). Game species were addressed separately to agree with presentation in Figure 2, where they were generally outliers within their taxonomic groups.



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APPENDIX 1 – EXPLANATION OF SPECIES REPORTS

This is Appendix 1 of the following report: *Keinath, D.A., M.D. Andersen and G.P. Beauvais. 2010. Range and modeled distribution of Wyoming's species of greatest conservation need. Report prepared by the Wyoming Natural Diversity Database, Laramie Wyoming for the Wyoming Game and Fish Department, Cheyenne, Wyoming and the U.S. Geological Survey, Fort Collins, Colorado. August 20, 2010.* All information in this document and the related reports was compiled by the Wyoming Natural Diversity Database (WYNDD; http://uwadmnweb.uwyo.edu/ wyndd/) to support the 2010 revision of Wyoming's State Wildlife Action Plan.

This is intended to be stand-alone document explaining information provided in species-specific reports (e.g., "Range Map and Distribution Model Summary for Boreal Toad (*Anaxyrus boreas boreas*)"), each of which presents statistics regarding the final range map and potential distribution for one of Wyoming's SGCN. Each of the following sections refers directly to an item presented in these reports.

RANGE MAP – OCCUPANCY

Range occupancy was mapped via 10-digit hydrologic unit (HUC). Each HUC was classified as follows (Keinath et al. 2010):

1. Known Recent Resident ("Known") -- This attribute indicates that the range mapping team was aware of a recently documented observation of the species in that particular watershed, and that the species was believed to occupy that watershed at the time of mapping. Experts collectively agreed that 1985 would be used as a cutoff for recent occurrence for this map set. Thus, for a HUC to be labeled as "Known," there must have been a documented occurrence of the species in that HUC in or since 1985.

2. Suspected Recent Resident ("Suspected") -- This value indicates that the range mapping team was not aware of a recently documented observation of the species in that particular watershed, but they still believed the species likely occupied that watershed at the time of mapping. Again, the cutoff for recent residency was 1985. Therefore, a "Suspected" HUC can fit one of two descriptions (not mutually exclusive):

3. Accidental Occupant ("Accidental") -- This indicates that the range mapping team was aware of a recently documented observation of the species in that particular watershed, but the species is not believed to be a regular occupant or "resident," in the common understanding of that term. This designation was most common for migratory birds, wide-ranging mammals (e.g., wolverine, lynx) and species that are incidentally transported by humans (e.g., turtles, snakes collected as 'pets').

4. Historical Resident ("Historical") -- This indicates that the range mapping team believed a watershed was historically part of a species' range, but did not believe it was part of the current range. This category was used only when recent evidence clearly suggested local extirpation.

5. Never a Resident (“Never”) -- This indicates that the range mapping team believed that these watersheds were not, and never have been, part of a species’ range. This designation means that the HUC must also have a Seasonality value of “Never” for the target species.

RANGE MAP – SEASONALITY

Range seasonality was mapped via 10-digit hydrologic unit (HUC). Each HUC was placed into one of the following categories (Keinath et al. 2010):

1. Summer -- Occupancy within the watershed is primarily during the summer, which is often synonymous with the breeding season. This designation refers primarily to migratory species or species that undergo annual range shifts within Wyoming. It is understood that HUCs supporting summer occupation are also largely occupied by the target species during migratory periods.

2. Winter -- Occupancy within the watershed is primarily during the winter. This designation refers primarily to migratory species or species that undergo annual range shifts within Wyoming. It is understood that HUCs supporting winter occupation are also largely occupied by the target species during migratory periods.

3. Spring/Fall Only -- Occupancy within the watershed is almost exclusively during the spring and/or fall seasons, and generally represents migratory range for the species.

4. Year-Round -- Occupancy within the watershed occurs year-round. This typically refers to ranges of non-migratory taxa, but occasionally refers to migratory taxa with “leapfrog” migrations or similar dynamics that result in different population segments occupying the same area in different seasons.

5. Unknown -- Insufficient data exist to determine seasonal usage within the watershed.

6. Never -- The range mapping team believes that these watersheds are not, and never have been, part of the species’ range, during any season. This designation means that the particular HUC must also have an Occupancy value of “Never” for the target species.

RANGE MAP NOTES

Version: This is the date that the range map was finalized.

Proportion of range deemed known based on documented occurrences: This is the proportion of HUC’s that were classified as known divided by the total number of HUC’s that were either known or suspected. It serves as an indicator of how well the species range has been documented.

DISTRIBUTION MODEL

The map presents the output of the final distribution model, with continuous output summarized in 5 categories, summarized below. In practice there can be very little separation between categories, particularly when there are very few occurrences. Therefore, not all models contain all categories.

1. ***Predicted Present – High Probability of Occurrence***: Areas falling within this category are most similar to locations of known occurrence and are thus most likely to be part of the species' actual distribution. Generally, the threshold separating this from the next category was selected such that this category captured the most-similar 50 percent of input occurrences (i.e., 50-percentile training threshold).
2. ***Predicted Present – Medium Probability of Occurrence***: Areas within this category fall within the area predicted as "present," but are less likely to fall within the species actual distribution than the high-probability areas. The threshold separating this from the absent categories is the binary threshold rule noted under Model Parameters, which varies from species to species but was typically selected to maximize the sum of training sensitivity (i.e., true positive rate) and estimated training specificity (true negative rate), which theoretically maximizes the discriminant ability of the binary output.
3. ***Predicted Absent – Low Probability of Occurrence***: These areas are predicted NOT to contain the species, but fall marginally below the binary threshold. The threshold separating this category from the very low category was generally selected so the low probability category excluded the 5 percent of occurrences that were most different from the rest (i.e., 5-percentile training threshold).
4. ***Predicted Absent – Very Low Probability of Occurrence***: These areas are predicted NOT to contain the species and fall well below the binary threshold. The threshold separating this category from the next higher one (i.e., the low category) was generally selected so this category included 5 percent of occurrences that were most different from the rest (i.e., 5-percentile training threshold).
5. ***Predicted Absent – Outside Species Known/Suspected Range***: This category is not technically a model category. Rather, it describes areas that were removed from the model because they were outside the known and suspected range of the species, as defined in preceding range maps. Expert opinion suggests that occurrences of the species in these areas are highly unlikely, accidental, and/or not within the specified modeling season.

MODEL PARAMETERS

Season Modeled: Species distributions often change throughout the year, particularly for migratory species. "Season modeled" refers to the time of year represented by the model and can be one of three categories: Breeding (or summer), Winter, and Year-round.

1. Breeding/Summer: This represents species occurring in Wyoming largely during warm months, often migrating from other areas. The date range refers to the period of the year within which records were deemed to reliably represent animals on their summer grounds. Occurrences outside this range of dates were deemed migratory and/or accidental winter records and were not used to construct the model.

2. Winter: This represents species occurring in Wyoming largely during cold months, often migrating from other areas. The date range refers to the period of the year within which records were deemed to reliably represent animals on their winter grounds. Occurrences outside this range of dates were deemed migratory and/or summer records and were not used to construct the model.

3. Year-round: At the scale of Wyoming, year-round species occupy largely similar habitats throughout the year, so occurrences used to build the model were not filtered by time of year.

Algorithm: This is the version of the Maxent® program used to construct the model. More information on this program, as well as access to the most recent versions can be found online: http://www.cs.princeton.edu/~schapire/maxent/.

Feature Types: This lists the Maxent® feature types used to build the environmental relationships in the final model. Available feature types include Linear, Quadratic, Product (i.e. "interaction"), Threshold, Hinge, and Categorical (see Phillips et al. 2006 for further explanation).

Binary Threshold Rule: This is the rule used to convert the continuous model to binary output of predicted present versus predicted absent. In most cases, the threshold rule used was "maximum training sensitivity plus specificity," which theoretically maximizes the discriminant ability of the binary output. Other rules were used when validation statistics and/or expert evaluation suggested that this rule resulted in a low-quality model (see the following for explanations of other rules: Phillips et al. 2006, Phillips and Dudik 2008).

Threshold Values: These numbers represent the cutoffs used to classify the final model into the categories shown on the distribution model map (see above). Users with the full continuous output can re-create the categorical map by classifying cells according to these values. All cells greater than or equal to the binary threshold value are classified as predicted present, while lower values are classified as predicted absent. Cells greater than or equal to the high-probability threshold are classified as predicted present – high probability. Cells less than the low-probability threshold are classified as predicted absent – very low probability.

MODEL EVALUATION – ROC PLOT

This is a variation of receiver operating characteristic (ROC) curve generated by the Maxent® program. Details on using ROC curves can be found in a variety of sources (see for example Fawcett 2006). The mean ROC curve across all runs is shown in red, which approximates the performance of the final model. Better models will have a ROC curve farther above the light-blue diagonal representing random prediction. The dark blue area surrounding the red line represents variability introduced by cross-validation. A wider band of dark blue suggests that model performance is sensitive to inclusion/exclusion of occurrence data and the final model should therefore be viewed with more caution.

MODEL QUALITY SUMMARY

Overall Assessment of Model Quality: The overall assessment of model quality was scored on a 3-category scale: high-quality, medium-quality, or low-quality. This was a subjective assessment considering all of the individual assessments noted below. Generally speaking, a majority rule was followed such that if most individual assessments were high or low, the overall score was similar. Models with complex combinations of individual assessment scores (i.e., some high scores, some low scores, and/or some medium scores) were usually given an overall assessment of medium. In most cases, the expert assessment served as an upper limit for the overall assessment (e.g., if experts classified the model as low-quality, the overall assessment was also deemed low-quality, even when most other individual assessments suggested medium quality.)

Expert Assessment: The expert assessment of model quality was scored on a three-category scale: high quality, medium quality, and low quality. It presents the qualitative assessment of wildlife experts at WYNDD and/or WGFD regarding how well the model represents their notion of the species distribution in Wyoming. This is primarily a visual assessment of how well the categorical output matches their knowledge of suitable habitat across the state.

Occurrence Sample Size: The assessment of sample size was scored on a 5-category scale: high, medium-high, medium, low, and very low. In general, high-quality models were based on more than 100 occurrence points, medium-high-quality models were based on between 50 and 100 occurrence points, medium-quality models were based on between 20 and 50 occurrence points, low-quality models were based on between 5 and 20 occurrence points, and very-low-quality models were based on less than 5 points. These cutoffs were loosely based on published sample-size analyses (Hernandez et al. 2006, Phillips and Dudik 2008)

Quality of Occurrences: The assessment of occurrence quality was scored on a 3-category scale: high, medium, and low. All occurrences were rated using a point quality index (PQI) ranging from a minimum of zero to a maximum of twelve (see master report for details). High-quality occurrences were accurately located, demonstrated positive identification of the species in question, and were relatively recent, while low quality occurrences lacked one or more of these attributes (i.e., they were poorly located, did not demonstrate positive identification of the species, and/or were old records). High-quality datasets had an average PQI in the 75% quantile of all species (i.e., roughly 7.9 or greater). Low-quality datasets had an average PQI in the 25% quantile of all species (i.e., roughly 5.8 or less). Medium-quality datasets had an average PQI between the 25% and 75% quantiles.

Positive Success Rate: This represents an assessment of quality based on omission rate calculations from cross-validation scored on a 4-category scale: very high, high, medium, and low. Several models were run based on subsets without replacement, or folds, of the total occurrence dataset. Each model held out a unique subset of the occurrences (usually 10%), for which we assessed the proportion that were accurately classified by the binary expression of that model. Low average omission error across all folds corresponds to high positive success and therefore suggests a higher-quality model. Very high-quality models had an omission rate less than or equal to 10%. High-quality models had an omission rate between 10% and 20%. Medium-quality models had an omission rate between 20% and 30%. Low-quality models had an omission rate of more than 30%.

Test AUC and Model Gain: Model performance was assessed using area under the curve (AUC) from ROC plots based on test data. This assessment used a 3-category scale: high quality, medium quality, and low-quality. Models with an average test AUC higher than 0.9 were deemed high quality, those with an average test AUC between 0.75 and 0.9 were deemed medium quality, and those with an average test AUC less than 0.75 were deemed low quality. This basic assessment was occasionally modified if the form of the ROC plot or the test gain suggested that AUC was misleading.

MODEL EVALUATION STATISTICS

FINAL MODEL STATISTICS

Training AUC: Training AUC is the area under the ROC curve based on data used to build the final model (i.e., training data). An AUC of 0.5 suggests that the model in question was no better than random, while an AUC of 1.0 suggests perfect classification. Within this range, models with higher AUC values are better at discriminating between occupied and unoccupied habitat (Bradley 1997, Fawcett 2006), although this should be interpreted with caution (Lobo et al. 2008). Since training AUC is based on the same points used to build the model, it is generally higher than test AUC, which is based on a separate set of occurrence locations that were not used to construct the model.

Regularized Training Gain: Gain is used by Maxent® to measure model fit (see Phillips et al. 2006, Phillips 2008). It is a likelihood statistic that maximizes the probability of the presence in relation to the background data. It effectively represents progress toward achieving an optimal model, beginning at zero during the initial iterations of the Maxent® algorithm and increasing to an undefined asymptote as the model progresses. Higher values of training gain theoretically indicate better fit to the input data.

CROSS-VALIDATION STATISTICS

During cross-validation, multiple models were constructed, each of which used a fraction of the available occurrence locations. Remaining locations were withheld from model-building and used to test the resulting models. The default was 10-fold cross-validation, in which 10 models were generated, each using 90% of occurrences to build the model and withholding 10% of the occurrences to test model performance. Occurrences used to build the model were termed "training data," while those used to test model performance were termed "test data". Fewer folds were used for species with less than 10 occurrences. Herein, we report average statistics across all folds of the cross-validation process along with their standard deviations.

Average Test AUC: This is the average area under the ROC curve based on test data across all folds of the cross-validation process. An AUC of 0.5 suggests that the model in question is no better than a random, and an AUC of 1.0 suggests perfect classification. Within this range, models with higher AUC values are better at discriminating between occupied and unoccupied habitat (Bradley 1997, Fawcett 2006), although this should be interpreted with caution (Lobo et al. 2008). Since test AUC is based on a set of occurrence locations that were not used to construct the model, it is generally lower than training AUC, but is better for estimating predictive power of the model.

Upper Bound on Test AUC: Since Maxent® is based on presence-only data, it estimates the horizontal axis of the ROC curve using fractional predicted area (see Phillips et al. 2006, Phillips 2008). This implies that the maximum achievable AUC is less than 1. This statistic estimates what the maximum possible test AUC would be if the test data were drawn from the Maxent® distribution itself.

Average Test Gain: This is the average gain based on test data across all folds of the cross-validation process. Gain is discussed above under "training gain." Since test gain is based on test data rather than training data, it is a better indicator of the predictive power of the resulting model. As with training gain, minimum test gain is zero and higher values indicate better fit, up to an unspecified maximum.

Average Omission Error: Omission error is the fraction of test occurrences that were incorrectly predicted by the binary expression of a model (i.e., if there were 10 test occurrences, and the binary model correctly classified the locations of 6 of them as present, then the omission error was 0.4). The value presented here is the average omission error across all folds of the cross-validation process. Higher errors of omission suggest lower model performance.

OCCURRENCE DATA FOR DISTRIBUTION MODEL

OCCURRENCE MAP

The occurrence map shows all occurrence locations in Wyoming used to build Maxent® models for a given species (i.e., occurrences remaining after filtering). Locations older than 1985 are distinguished, because expert review panels agreed they should not be considered recent (Keinath et al. 2010). Occurrences are displayed over the species range, which is presented in more detail earlier in the report.

OCCURRENCE SUMMARY STATISTICS

Number of occurrences in master dataset: This is the total number of documented occurrences collected by WYNDD to inform range mapping and distribution modeling within Wyoming. All occurrences were considered in evaluating range maps, but many were not used to construct distribution models (see below).

Number of occurrences used to create distribution model: This is the number of points used to construct Maxent® models of species potential distribution. Many available points were not used to create distribution models because they information that was similar to that contained by other points (i.e., they were too close to other occurrences) or they were deemed of insufficient quality (i.e., they were too coarsely located, they didn't provide sufficient information to confirm species identification, or they were too old).

Average Point Quality Index: This presents the mean and standard deviation of the Point Quality Index (PQI) for occurrences used to create the distribution model. Every occurrence in the dataset was given a PQI score range from 0 (very low quality) to 12 (very high quality), as discussed in the main report. Higher average PQI values indicate more current and well-defined datasets.

Most recent occurrence used: This presents the calendar year of the most recent documented occurrence used to build the distribution model.

Oldest occurrence used: This presents the calendar year of the oldest documented occurrence used to build the distribution model.

Occurrence file: This presents the name of the file containing the occurrences used to build the final distribution model. Its primary use is as a reference to WYNDD staff for tracking model construction.

COMMENTS

This section provides a variety of comments regarding the construction and/or validation of the distribution model. Most commonly, these comments present caveats associated with the model in question.

PREDICTOR VARIABLES USED IN THE DISTRIBUTION MODEL

Table A1-1 (below) lists the predictor variables used in this modeling effort, with their units and a brief explanation of scale, where appropriate.

PERCENT CONTRIBUTION (PC) TO FINAL MODEL

This table lists the variables used to create the model of potential distribution, listed in descending order of the degree to which they contributed to the final model. Descriptions of specific variables are presented in Appendix 2 of the master report. Percent contribution is calculated by Maxent® by keeping track of how much model gain is improved when small changes are made to values of each variable, then summing these small gains and presenting them as a proportion of all contributions. These values can be useful as a thumbnail sketch of which variables were important in structuring the model, although relative importance can be misrepresented if variables are highly correlated (Phillips et al. 2006, Phillips 2008).

RESPONSE CURVES

Maxent® generates a response curve for each variable used in the final model that shows how predicted likelihood of occurrence varies over the range of values for a variable when all other variables are excluded from the model. Response curves can be used to get a general sense of the dependence of species distribution on each variable (e.g., likelihood of occurrence generally increases with increasing precipitation), but should not be viewed in absolute terms, as the final model is a complex combination of all variables. Vertical axes display predicted suitability, which can be roughly interpreted as the probability of species occurrence ranging from 0 (no occurrences have the given value of the variable) to 1 (all occurrences have the given value of the variable). Horizontal axes span the range of values for the variable in question. Although low values are always on the left and higher values on the right, the units and range of values are different for each predictor. Units for each variable are provided in Table A1-1.

TABLE A1-1. Brief summary of predictor layers used in distribution models, with notes on units and scale.

Predictor Layer	Units	Notes on Units and Scale
Terrain		
Elevation	Meters	Elevation above sea level
Degree Slope	Degrees	Ranges from 0 (flat) to 90 (vertical)
8-Category Aspect	Categorical	-1 (Flat); 0 (North); 1 (Northeast); 2 (East); 3 (Southeast); 4 (South); 5 (Southwest); 6 (West); 7 (Northwest)
A^1 (Transformed Aspect)	Unitless	Ranges from 0 (southwest aspect) to 2 (northeast aspect)
Radiation Load	Unitless	Ranges from near 0 (flat southwest aspect) upward toward 180 (steepest northeast aspect)
Vector Ruggedness Measure	Unitless	Ranges from 0 (flat) to 1 (most rugged)
Compound Topographic Index	Unitless	Lower values represent drier areas, higher values represent wetter areas
Landform Classification	Categorical	1 (Canyons, incised streams); 2 (Midslope drainages, shallow valleys); 3 (Upland drainages, headwaters); 4 (U-shape valleys); 5 (Plains); 6 (Open Slopes); 7 (Upper slopes, mesas); 8 (Local ridges, hills in valleys); 9 (Midslope ridges, small hills in plains); 10 (Mountain tops, high ridges)
Potential for Rock Outcrop	Meters	Distance to potential rock outcrops
Distance to cliffs	Meters	Distance to areas of steep slope
Landscape Structure		
Contagion Index	Unitless	Low values represent areas with high patch interspersion, higher values represent landscapes with fewer, larger patches.
Distance to primary & secondary roads	Meters	
Human Footprint	Meters	Distance to developed areas
Land Cover		
Vegetation Indices (includes forest cover, ponderosa pine, pinion-juniper, herbaceous, sagebrush, shrub cover, cottonwood, conifer, and deciduous forest)	Unitless	Higher values indicate greater potential prevalence of the specified vegetation type. Ranges from 0 (specified vegetation does not occur within 800 meters) to 1 (all area within 800 meters is likely to contain the specified vegetation).
Sagebrush	Percent	Percent cover of sagebrush
Percent Forest Cover	Percent	Percent cover of trees
Distance to permanent snow	Meters	
Bare Ground index	Unitless	Higher values indicate greater potential for prevalence of bare ground. Ranges from 0 (no bare ground) to 1 (entirely bare ground).

TABLE A1-1. Continued.

Predictor Layer	Units	Notes on Units and Scale
Soil and Geology		
Depth to Shallowest Restrictive Layer	Centimeters	Distance from soil surface to bedrock.
Soil texture	Categorical	Ordinal variable ranging from 0 (finest) to 5 (coarsest).
Soil - Fraction Sand	Percent	
Soil - Fraction Clay	Percent	
Distance to cave-forming formations	Meters	
Hydrology		
Distance to Water (several layers based on different features)	Meters	
Prevalence of water features within neighborhood (several layers based on different features and neighborhood sizes)	Unitless	Corresponds to the percentage of pixels in a defined neighborhood that contain the selected water features. Range from 0 (no pixels contain water features) to 1 (100% of pixels contain water features)
Climate		
Precipitation (includes mean annual precipitation, precipitation of the wettest month, precipitation of the driest month, annual precipitation range, precipitation of the wettest quarter, precipitation of the driest quarter, precipitation of the warmest quarter, precipitation of the coldest quarter, and variation of monthly precipitation)	0.1 cm	Values are presented in tenths of centimeters, representing depth of water.
Humidity (includes annual mean relative humidity, relative humidity of the most humid month, relative humidity of the least humid month, annual relative humidity range, and variation of monthly Relative Humidity)	0.10%	Values are presented in hundredth-percentages of relative humidity.
Radiation (includes annual total radiation, radiation of the lightest month, radiation of the darkest month, annual radiation range, and variation of monthly radiation)	0.01 MJ/m²/day	Values are presented in hundredths of millijoules per meter square of surface per day.
Temperature (includes annual mean temperature, mean diurnal range, hottest month mean maximum temperature, coldest month mean minimum temperature, annual temperature range, isothermality, standard deviation of monthly temperature, wettest quarter mean temperature, driest quarter mean temperature, warmest quarter mean temperature, and coldest quarter mean temperature)	0.1 °C	Values are presented in tenths of a degree Celsius.
Annual number of Frost-free Days	0.1 Days	Values are presented in tenths of days.
Interannual variation in annual number of frost days	0.1 Days	Values are presented in tenths of days.
Miscellaneous		
Black-Tailed/White-Tailed Prairie Dog Combined Models	Unitless	Ranges from 0 (lowest probability of Prairie Dog occurrence) to 1 (highest probability of Prairie Dog occurrence)
Public land	Categorical	0 = Private; 1 = Public