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Systematics and Biodiversity (2014), **12(2)**: 149–162

Taylor & Francis
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Research Article

Identifying priority conservation areas for the American burying beetle, *Nicrophorus americanus* (Coleoptera: Silphidae), a habitat generalist

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(Received 5 August 2013; revised 19 January 2014; accepted 4 February 2014)

Conservation efforts leading to the recovery of the federally endangered American burying beetle (ABB), *Nicrophorus americanus* Olivier, have been challenging because of the unknown causes of its decline, difficulty in establishing habitat requirements, and unclear population distribution across the species' range. Extant populations of this widespread generalist species occur in broadly separated regions of North America with varying habitat characteristics. A habitat suitability model for ABB in the Nebraska Sandhills was developed over the course of 3 years resulting in a final cross-validated spatial model. The succession of models from 2009 to 2011 indicated that most of the predictive variables stayed constant, but biased sampling and extrapolation areas affected classifier values differently. Variables associated with ABB occurrence were loamy sand, wetland and precipitation. Five variables, loam soil, agriculture, woodland, the average maximum temperature, and urban development, were associated with ABB absence. The 2011 cross-validated model produced an AUC value of 0.82 and provided areas designated as highly likely to support ABBs. By limiting the model extent to the Sandhills ecoregion and using threshold-dependent classifiers, the final habitat suitability model could be an important resource for wildlife managers engaged in the recovery of this habitat generalist.

Key words: Area under the curve (AUC), endangered species, habitat suitability model, Nebraska Sandhills, threshold-dependent

Introduction

The American burying beetle (ABB), *Nicrophorus americanus*, was listed as federally endangered in 1989 (*Federal Register* 54 [133]: 29652-55) after the species disappearance from over 90% of its historical range became apparent. Since that time, researchers have proposed reasons for its decline, including pesticide use, artificial lighting, pathogen infection, competition and habitat alteration (Sikes & Raithel, 2002). Although the exact causes are undetermined, certain regions throughout North America continue to support large populations, such as in the US Midwest (Jurzenski *et al.*, 2011). A recovery plan, prepared for the ABB in 1991 (USFWS, 1991), stated that of the previously known distribution covering most of the USA east of the Rocky Mountains, the species was only found on Block Island, off the Rhode Island coast and Oklahoma. The plan went on to recommend the establishment of three populations of the ABB within four broad geographical areas in its historical range: the Northeast, Southeast, Midwest and Great Lakes States as criteria for reclassifying the species from endangered to threatened. Shortly after publication of the recovery plan, isolated populations of ABB were found in Nebraska, South Dakota, Kansas and Texas. In recognition of this and other new species information, the 5-year review completed for the ABB recommended a revision of the species recovery plan, which has yet to be published (USFWS, 2008*a*). Revision of the recovery plan will involve setting new recovery goals and objectives heavily reliant on knowledge of the ABB distribution and the resources needed to sustain populations.

To better understand the decline of ABB and its importance in North America, an introduction of burying beetle

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ISSN 1477-2000 print / 1478-0933 online

http://dx.doi.org/10.1080/14772000.2014.892542

natural history and biology is needed. Carrion beetles (family Silphidae), including burying beetles, compete for vertebrate carrion needed for sustenance and developing offspring. Carrion beetles are able to locate dead vertebrates by using sensitive chemoreceptors in their capitate antennae that detect molecules released by dead and decaying organisms (Dethier, 1947; Scott, 1998). Some carrion beetles, like the ABB, are nocturnal (Ratcliffe, 1996). Competition for decaying carcasses varies depending on location, time of day, carcass age and carcass size (Scott, 1998). The competition for resources, such as carrion, can be intense because it is scarce and unpredictable in space and time. For ABB, their large size enables them to utilize larger carcasses (e.g. 80–374 g) excluding many other burying beetles (e.g. 20–100 g) from competition (Kozol *et al.*, 1988; Trumbo, 1992; Lomolino & Creighton, 1996); however, it may increase competition with larger, more dangerous vertebrate scavengers (Jurzenski & Hoback, 2011). Research has shown that ABBs are attracted to and able to reproduce on various types of carrion, including various mammals, reptiles and birds (Kozol *et al.*, 1988; Bedick *et al.*, 1999).

The *Nicrophorus* genus is characterized by a burying behaviour displayed when preparing a carcass for reproduction; in addition, they have been well-studied because of their extended biparental care of offspring (Trumbo, 1994, 1996; Eggert *et al.*, 1998; Scott, 1998). Initially, a carcass is assessed by *Nicrophorus* spp. for suitability and viability for reproduction (Scott & Traniello, 1987: Trumbo *et al.*, 1995). The surrounding habitat also plays a role in the ultimate decision to secure the carcass and create a brood chamber. Soil composition can be a limiting factor for burying beetles and if a suitable area is nearby, then the beetles will work together (or alone) to move the carcass (Muths, 1991). Smith *et al.* (2000) found that abandoned burrows, holes or cracks in the ground within 20 cm of the carcass were more likely to be used than a direct burial, and that the proportion of successful broods was higher for carcasses dragged to the holes. The parent beetles stay with developing larvae to feed them and protect them from intruders (Scott, 1990; Trumbo, 1990, 2009; Müller *et al.*, 2003). The male often leaves shortly after egg hatch (3–7 days) and the female often leaves shortly before the resource is depleted (∼14 days) (Scott & Traniello, 1990). After the female leaves, the larvae disperse in the soil and pupate. Teneral adults emerge approximately 30–60 days after carcass burial; therefore, the stability (e.g. soil structure) and suitability (e.g. moisture and temperature) of a brood chamber location is important for brood survival. Teneral ABB adults overwinter in the soil and leaf litter (Schnell et al. 2008).

The ABB occurs in a variety of habitats, including wet meadows, partially forested loess canyons, oak-hickory forests, shrub land and grasslands (Kozol *et al.*, 1988; Creighton *et al.*, 1993; Lomolino *et al.*, 1995; Lomolino & Creighton, 1996; Jurzenski *et al.*, 2011). Creighton & Schnell (1998) recorded movement of individual ABBs from open grassland to woodland, which suggests they are not restricted by the overall habitat structure. Given the known distributions and different habitat types in Nebraska, Oklahoma and Rhode Island, ABB are successful across several landscape types and can have a larger niche breadth than many other *Nicrophorus* species (Lomolino & Creighton, 1996).

Unfortunately, the limited understanding of the distribution of ABBs makes it difficult to designate priority conservation sites or select reintroduction areas. Moreover, for United States Fish and Wildlife Service (USFWS) personnel involved in making decisions about proposed habitat alterations, the identification of basic habitat affinities of ABBs, even within localized regions, would be very useful. Bishop *et al.* (2002) found that some carrion beetles in Nebraska showed preference for soil textures and land use, but did not include the ABB in the study. In Oklahoma, Crawford & Hoagland (2010) identified elevation, slope, soil association, surface geology, land cover, forest cover, annual temperature, days below freezing, last growing season day and May precipitation as predictor variables of ABB occurrence using a Maxent model. As a habitat generalist, it is possible that ABBs may not be associated with these same variables in different ecoregions. The lack of agricultural conversion and sparse human population in Nebraska's Sandhills region is thought to contribute to the continued presence of ABBs in this region, which is also consistent with the Loess Canyons area in south-central Nebraska; however, distribution information alone cannot confirm these characteristics as explanatory variables. In Nebraska, the ABB has been found in four different ecoregions, each of which have quite different soils, topography, land use and climatic conditions.

Although ABBs occur in many different habitat types, there could be other basic components within an ecoregion that have positive and negative influences on its occurrence. Habitat suitability models (HSMs) can identify important habitat characteristics and provide probabilities of occurrence, which may be useful in conservation efforts leading to recovery, including locating new populations, conserving known populations, and making science-based recommendations (Mladenoff *et al.*, 1999; Yáñez & Floater, 2000; Manel *et al.*, 2001; Franklin, 2009; Raedig & Kreft, 2011; Bystriakova *et al.*, 2012). HSMs assume that the presence of a species at a sample location indicates a favourable set of ecological variables. Following this principle, the absence of the same species indicates an unfavourable set of ecological variables. Thus, presence and absence data can be used to construct a habitat suitability model using generalized linear modelling methods (Venables & Ripley, 1994; Pearce & Ferrier, 2000; Guisan *et al.*, 2002).

A HSM using logistic regression was successful in identifying habitat requirements of a rare, mound-building ant species in the UK (Littlewood & Young, 2008). These authors found that although the model validated well with independent data, the performance declined with increased extrapolation (i.e. increased distance from the calibration data). Recommendations for habitat management and possible reserve selection were made possible for an endangered, saproxylic longhorn beetle in central Europe after developing a HSM using categorical and continuous predictor variables (Buse *et al.*, 2007). For many endangered species, understanding the species' habitat affinities is needed to develop appropriate conservation measures. Matern *et al.* (2007) found several new structural habitat requirements for an endangered carabid beetle in Germany after conducting HSMs using presence and absence pitfall data. The researchers were then better able to make restoration decisions to benefit the beetle populations. These examples of other endangered insect HSMs support the feasibility of conducting a HSM analysis to enhance our understanding of ABBs occurrence and habitat affinities.

We developed a HSM of the ABB in the Nebraska Sandhills ecoregion to provide predictive occurrence values that would contribute to the recovery of this species including designating priority conservation areas, setting recovery goals, monitoring population distributions over time, and assessing the effects of development projects to make informed conservation decisions. This evaluation specifically assessed the viability of producing a HSM for a habitat generalist in a specific ecoregion.

Materials and methods

Study area

Nebraska is part of the Great Plains region of the continental USA. Annual precipitation declines from east to west (PRISM Climate Group, 2000), with periodic and seasonal rains (i.e. 75% of precipitation occurs between April and September) (Harvey & Welker, 2000). Over a 30-year average in the Nebraska Sandhills, the upper range of precipitation is 610–711 mm and the lower range of precipitation is 406–508 mm (PRISM Climate Group, 2000). On average, summer temperatures exceed 20 °C and winter temperatures are below 0 °C (Harvey & Welker, 2000). The Sandhills ecoregion (Level III) is the largest grass-stabilized sand dune region in the western hemisphere (Bleed & Flowerday, 1989), which has retained as much as 80% of its natural vegetation in some areas and is found in both Nebraska and South Dakota (Omernik, 1987; Sieg *et al.*, 1999; Chapman *et al.*, 2001; US EPA, 2003). The Nebraska Sandhills covers over one quarter of the state with an approximate area of 57 424 km^2 (Chapman *et al.*, 2001), consisting of undulating dry sandy uplands and lowland wet meadows (Bleed & Flowerday, 1989). The region's soil is mostly composed of sand, sandy loam, loam and loamy sand (SSURGO Database, 2011).

Predominant vegetation in the Sandhills includes big bluestem (*Andropogon gerardii* Vitman), sand bluestem (*Andropogon hallii* Hack.), little bluestem (*Schizachyrium scoparium* (Michx.) Nash), sandreed (*Calamovilfa longifolia* (Hook.) Scribn.) and needle-and-thread grass (*Hesperostipa comata* (Trin. & Rupr.) Barkworth), which are medium to tall grasses (Küchler, 1964). The primary land use in the Sandhills is cattle grazing (Bleed & Flowerday, 1989). Fire control by landowners and federal and state agencies has reduced wind and water erosion, but has also resulted in the encroachment of ponderosa pine (*Pinus ponderosa* Laws.) and eastern red cedar (*Juniperus virginiana* L.) in Sandhill prairies (Steinaur & Bragg, 1987).

Model dataset selection and collection

In 2009, a database of carrion beetle trapping records from Nebraska was compiled using sampling data collected by various researchers and agencies, including USFWS, Nebraska Game and Parks Commission (NGPC), Nebraska Public Power District, US Forest Service and Nebraska Department of Roads (NDOR). Some records dated back to 1994, but the majority was from 2001 through the autumn of 2009. Trap data points were selected from the database to use in the initial modelling process for the probability of occurrence of ABB in the Sandhills ecoregion.

We selected trap data points from the database based on the following criteria: traps had corresponding GPS coordinates and a known number of survey nights; sampling was recent (since 2001) and conducted using USFWS approved trapping protocol (USFWS, 2008*b*) or very similar methods prior to the establishment of approved protocols (see ABB Surveys section); and were at least 700 m apart. These criteria were used to create a dataset that distinguishes ABB presence and absence under the same conditions as newly collected survey data described in the ABB Surveys section below. One survey night was defined as a single bucket trap set before evening, open throughout the night, and checked the following morning. The estimated attractive radius of carrion beetle bucket traps following USFWS protocols is 800 m (USFWS, 2011); therefore, 700 m was used as a boundary for trap independence to account for GPS errors. A 700 m buffer radius was created for each trap using ArcMap (ESRI, 2011) to assess overlapping trap radii, which allowed us to retain the most recent and greatest number of traps in the dataset and remove older or repetitive traps. Overlapping trap data points with both absence and presence results caused by repetitive sampling across seasons or years, or by traps being positioned too closely, were removed if the sampling occurred during different trapping periods. If the conflict occurred in the same trapping period, then the trap with ABB presence was kept in the dataset. This buffer radius was also used to reduce spatial autocorrelation by only using independent traps. Traps meeting these criteria were then further evaluated using the following conditions to eliminate false positives and false negatives.

A trap with ABB absence was defined as zero ABB captured in a trap with at least five survey nights in either June or August, which are the peak active seasons for ABB in Nebraska (Bedick *et al.*, 1999). A trap with ABB presence was defined as the capture of at least one ABB in a trap within the first five survey nights at any time of the year. Because of limited reproductive opportunities in the non-peak active season, beetles may be more likely to explore unsuitable habitat; therefore, traps with ABB presence during these periods may be a misrepresentation of the species range. We were willing to accept this possibility to be able to make more inclusive conservation conclusions; whereas, failing to detect the species in the non-peak active seasons has an increased probability and is less desirable in developing priority conservation areas. Lastly, each trap data point was designated as either a '1' for ABB presence or '0' for ABB absence.

ABB surveys

Surveys in 2010 and 2011 used a single bucket method (18.9 L bucket) with all traps at least 1.6 km apart following the most current USFWS protocol (USFWS, 2008*b*, 2011). Each trap was sampled for five or more survey nights in June or August. GPS coordinates were recorded at each trap location. The bait consisted of a decayed rat (previously frozen 275–374 g laboratory rat, *Rattus norvegicus* (Berkenhout), RodentPro.com), which was replaced every third survey night. All silphid beetles, including ABBs, were identified and recorded for each trap in the morning after each survey night. In 2010, there were 390 traps surveyed. A large number of field technicians were used in 2011 to collect data from 775 traps. Similar to the dataset created from the 2009 database, each trap data point was designated as either a '1' for ABB presence or '0' for ABB absence.

Most traps for both the database dataset and the newly collected dataset (i.e. 2010 and 2011) were placed along roadways due to restricted access to private lands, which could create an inherent bias to roads. Roadside sampling can be problematic when the vegetation and land cover within the vicinity of the road is not representative of the general habitat being modelled (Niemuth *et al.*, 2007; McCarthy *et al.*, 2012). Within our model's 800 m trap radius, the area of roads only accounts for a maximum of 17% of any of the data points. A majority of the rural roads sampled occurred within landscapes that have not been recently modified by anthropogenic disturbances and are surrounded by natural Sandhills habitat. Also, for all three datasets, it was not necessary to exclude trap data points with more than five survey nights, because we could determine the presence or absence designations using the first five survey nights and ignore the additional survey night data. Traps that had less than five survey nights were not included in any dataset used for our models.

Model variables

The statistical model was fitted using spatially explicit independent variables derived from soil survey geographic (SSURGO) database surface textures (SSURGO Database, 2011), land cover (Bishop *et al.*, 2011), and climate data (PRISM Climate Group, 2012). The SSURGO datasets are the results of NRCS digitizing soil maps, which were at map scales ranging from 1 : 12 000 to 1 : 63 360 (SSURGO database, 2011). The land cover dataset used had a 30 m resolution (Bishop *et al.*, 2011). Thirty-year averaged (1981–2010) spatially explicit climate variables at an 800 m resolution, including minimum temperature, maximum temperature and total precipitation, were obtained from the Parameter-elevation Regression on Independent Slopes Model (PRISM) Climate Group (DiLuzio *et al.*, 2008; PRISM Climate Group, 2012). Using a Geographic Information System (GIS), we grouped and reclassified land cover and soil classifications into generalized categories that better represented the biology of the ABB, which resulted in 19 candidate variables (described in Table 1).

The soil and land cover GIS files were originally binary raster grids, where each raster cell containing the associated land cover or soils variable was set equal to '1' and everything else was set equal to '0'. We ran a moving window analysis for each binary raster grid using an 800 m circular focal window in ArcGIS (ESRI, 2011). The resulting GIS layers represented the percentage of the available land cover or soil type within 800 metres surrounding each trap, which is the distance that coincides with the estimated attractive radius of the carrion trap. In order to help maximum likelihood algorithms converge during statistical analyses and allow for direct comparison between parameter estimates, we standardized all variables by subtracting the mean $\overline{X}$ from the ith value of variable X (X_i) and divided by the standard deviation σ (Bring, 1994; Eq. 1).

Eq. 1

$$X_i' = \frac{X_i - \overline{X}}{\sigma} \tag{1}$$

Table 1. List of candidate variables used in habitat suitability modeling for the American burying beetle in the Sandhills ecoregion of Nebraska.

Habitat variables	Sandhills range (%)	Description
Loam (%)	0–84	clay loam, silt loam, silty clay, silty clay loam
Loamy sand (%)	0–100	loamy coarse sand, loamy fine sand, loamy sand, loamy very fine sand
Sand (%)	0–100	coarse sand, fine sand, sand
Sandy loam (%)	0–96	fine sandy loam, sandy loam, very fine sandy loam
Precipitation	397–699[a]	Thirty-year average of total precipitation
Minimum temperature	15.5–17.5[b]	Thirty-year average of the minimum temperatures
Maximum temperature	0.8–2.7[b]	Thirty-year average of the maximum temperatures
Agriculture (%)	0–77	Alfalfa, corn, fallow, sorghum, soybeans, sunflowers, wheat and other row crop agriculture
Developed (%)	0–38	Areas of urban and rural development, including roads
Roads (%)	0–17	Paved roads
Grass (%)	0–100	CRP grass, mixed grass, sandhills grasslands, shortgrass, tallgrass
Grass minus CRP (%)	0–100	Mixed grass, sandhills grasslands, shortgrass, tallgrass
Riparian (%)	0–15	Trees, shrubs, grasses, and CRP land adjacent to large and small waterways
Riverine (%)	0–95	River channel, river channel, sand bars, slough, wet meadow, flood plain marsh, vegetation adjacent to rivers
Wetland (%)	0–98	Playas, Sandhills wetlands, Sandhills lakes, pits, stock ponds, CRP wetlands, emergent marsh, saline marsh, rainwater basins, wet meadow, floodplain marsh, open water, river channel
Wetland minus riverine (%)	0–98	Playas, Sandhills wetlands, Sandhills lakes, pits, stock ponds, CRP wetlands, emergent marsh, saline marsh, rainwater basins, wet meadow, floodplain marsh, open water
Wetland minus wet meadow (%)	0–44	Playas, Sandhills wetlands, Sandhills lakes, pits, stock ponds, CRP wetlands, emergent marsh, saline marsh, rainwater basins, floodplain marsh, open water, river channel
Wet meadow (%)	0–95	A complex of grassland and wetland areas
Woodland (%)	0–86	CRP upland trees, CRP riparian trees, Eastern red cedar, ponderosa pine, upland woodland, juniper, riparian canopy, exotic riparian shrubland, native riparian shrubland

[a]This range is displayed in mm of precipitation, not a per cent range.
[b]This range is displayed in degrees Celsius, not a per cent range.

Model analysis and selection

All statistical analyses were performed using the statistical software package 'R' (R Core Team, 2013). To avoid multicollinearity, we examined the pairwise correlations among the remaining explanatory variables using Spearman's ranked correlation coefficient, which is well suited for the analysis since it makes no assumptions about linearity (Zar, 1996; Rhodes *et al.*, 2009). Values above 0.6 indicated that over 60% of the variation in the response variable was similar to its paired explanatory variable, in which case these paired variables were assessed using biological relevance and ROC values to eliminate one of the variables from further testing. The remaining variables were kept for statistical analyses in order to help determine the driving factors predicting ABB occurrence.

We used binomial generalized linear models (logistic regression) to model ABB occurrence (Zuur *et al.*, 2007). We developed a candidate set of models, where each model contained a set of explanatory variables that we predicted, based on the biology of the species, would influence ABB occurrence. We used the log likelihood to calculate Akaike's Information Criterion corrected for small sample size (AICc) to assess model fit of the data (Akaike, 1974; Burnham & Anderson, 2002). The model with the lowest AICc values (smaller AICc values indicate goodness-of-fit and complexity; Franklin, 2009) was selected to represent the best combination of variables predicting ABB presence and was best supported by the data (Burnham & Anderson, 2002). To create a predictive spatial model for ABB occurrence, we combined the linear predictor, parameter estimates and the spatially explicit predictor variables identified in the top-ranked model using the inverse logit function and entered it into the Raster Calculator in ArcGIS 10.0 (ESRI, 2011). The resulting HSM raster had a resolution of a 30 × 30 m grid. We evaluated the predictive performance of our top-ranked model by calculating sensitivity, specificity, receiver-operator characteristic (ROC), area under the ROC curve (AUC) and Kappa using the 'PresenceAbsence' package in 'R' (Freeman & Moisen, 2008*b*). These measurements were used to establish per cent probability of occurrence (PPO) thresholds.

The sensitivity, AUC, Kappa, correctly classified percentages and specificity were used to select map thresholds to maximize the usefulness of the ABB spatial model and assess predictive performance (Freeman & Moisen, 2008*a*). Sensitivity measures the proportion of ABB traps truly present that are correctly identified, which makes it the most restrictive threshold and identifies the areas with the most accurate probability of ABB occurrence. The required sensitivity, a threshold-dependent measure (Fielding & Bell, 1997), was used to designate the PPO threshold for Presence 1. AUC, which is a threshold-independent measure, indicates the proportion of time a randomly selected ABB presence trap data point scored a higher probability than a randomly selected ABB absence data point (Fielding & Bell, 1997; Franklin, 2009). The AUC value was used to designate the PPO threshold for Presence 2. The AUC value indicates the performance of the model in discriminating between presence and absence; hence, probability values above the Presence 2 threshold are more likely to indicate ABB presence than ABB absence. The PPO threshold value for Presence 3 corresponded to both the maximum Kappa and highest per cent correctly classified values, where traps containing probability values greater than this threshold were more likely to truly have that probability of ABB capture than they were by chance. Specificity measures the proportion of traps with ABB absences that are correctly identified, which identifies the threshold where lower probability values have the most accurate probability of ABB absence. We set the required sensitivity to less than 5% of the trap locations where the species was present and required specificity to less than 1% of the trap locations where the species was absent. Relatively low per cent cut-offs were set for the sensitivity and specificity because we are modelling an endangered species and want to identify upper and lower thresholds with more confidence. The ability to define areas with ABB absence will be an important aspect of this model, which is why the required specificity was set to a very low value. The Presence 4 PPO threshold was set by the specificity. Probability values above the specificity measure (i.e. Presence 4 threshold), but below the maximum Kappa (i.e. Presence 3 threshold), are the most unreliable occurrence probabilities and should not be interpreted as areas with either ABB presence or absence. Areas with PPO threshold values below the required specificity threshold or Presence 4 were designated as habitat without ABBs (i.e. absence).

The modelling process described above was initially conducted using data points from the 2009 database. This provided a baseline model to identify areas to improve and select prospective sampling areas. The process was then repeated with the addition of survey data in 2010 and then again separately in 2011. Many survey locations were selected by identifying extrapolation areas on the 2009 and 2010 model maps (Hirzel & Le Lay, 2008). Descriptive statistics were also calculated for each candidate variable in 2009 and 2010 to evaluate sampling bias and identify corresponding sample areas to reduce the biases. In 2011, sample locations were placed in areas predicted in the 2010 model to have either greater than or less than 50% probability of ABB occurrence or areas with little information concerning ABB presence or absence.

We validated the top-ranked 2011 model using a 10-fold cross-validation approach (Verbyla & Litvaitis, 1989; Geisser, 1993; Kohavi, 1995). We assessed prediction error by producing a training-testing dataset using a 10-fold cross-validation algorithm in 'R', which calculated the predicted probability of occurrence values by refitting the top-ranked 2011 statistical model using 90% of the data and making predictions on the remaining 10%. This process was repeated 10 times. During each of the 10 iterations, the training-testing data points from the 2011 dataset were selected at random with replacement. The predicted probability of occurrence values and the observed presence-absence values in the validation dataset were also used to calculate AUC. Spatial models having an AUC value over 0.7 are generally deemed useful at predicting species occurrence (Swets, 1988; Manel *et al.*, 2001). Also, a Mann–Whitney U-test was conducted using the validation data to compare the predicted probability of occurrence values produced using parameter estimates from the 2011 statistical model when separated into the observed presence and absence.

Post-processing of model information included the calculation of sampling density and area of model interpolation/extrapolation. Sampling density was calculated by dividing the total area of all traps using an 800 m radius (performed in ArcGIS) by the total area of the Sandhill ecoregion. A polygon was drawn including all trap points to define the area of interpolation. The area of interpolation was then subtracted from the total area of the Sandhill ecoregion to calculate the amount of area (sq. km) in the model that was extrapolated. An additional map was then created illustrating the presence 1 area as priority conservation areas and all ABB survey traps in the updated database from 1980 to 2012 with three survey nights or greater. Previous sampling protocols required only three survey nights, which were not included in the model datasets, but we wanted to be able to show as much of the known ABB distribution data as possible.

Results

Out of 2315 survey traps previously sampled in Nebraska, we identified 234 that met the criteria to be included in the 2009 Sandhills model analysis. Sampling in 2010 and 2011 increased the total number of traps meeting the model criteria to 775 with more than 400 different

Table 2. Descriptive statistics for the Nebraska Sandhills American burying beetle (ABB) habitat suitability models.

Model dataset characteristics	2009	2010	2011
No. of ABB presence traps	150	224	433
No. of ABB absence traps	84	166	342
Prevalence of ABB (% presence traps)	64.1	57.4	57.9
% of trap data from before 2008	51.7	25.9	15.3
Area of extrapolation (sq. km)	36 567	n/a	24 516
Sampling density	0.01	0.01	0.02

locations with ABB presence (Table 2). By utilizing the 2009 and 2010 models, two new county records were identified through prospective sampling and extended the spatial extent of the ABB sampling effort (Jurzenski *et al.*, 2011). Variables positively associated with ABB presence in our 2011 model included loamy sand soil, wetlands land cover and precipitation (Table 3). Loam soil, crop land cover, woodland land cover, developed land cover and maximum temperature were found to have a negative relationship with ABB presence (Table 3). In 2009 and 2010, the wetland land cover variable that excluded wet meadows was used in the best fit model; whereas, in 2011, the best fit model was found using a wetland land cover variable with wet meadows included.

All of the models produced AUC values above 0.8 and the cross-validation model scored 0.82 (Fig. 1). The prevalence of ABBs in each model dataset was greater than 50% (Table 2). Sampling in 2010 and 2011 increased the interpolation area by 21%, which reduced the extrapolation area within the Sandhills region (Table 2). The sampling density increased from 0.01 to 0.02 from 2009 to 2011.

A Mann–Whitney U-test showed that the mean probability of occurrence values for ABB presence traps (69.1% ± 3.20 S.E.) were significantly greater than the ABB absence traps (39.1% ± 4.07 S.E.) ($U = 2\,611\,600$, $P < 0.001$) (Fig. 2). The interquartile range is slightly larger for the presence values than the absence with over half of the presence traps occurring at a per cent probability of occurrence value above 52% (Fig. 2). This validation test of the 2011 model agrees with the 45% or greater probability of occurrence threshold calculated for Presence 3 (Fig. 3). The final 2011 model with all eligible traps shows a large portion of the Sandhills was sampled to create the final model (Fig. 3).

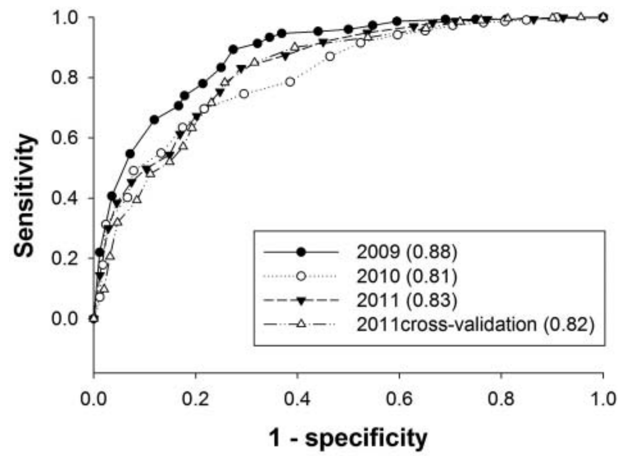

Fig. 1. A receiver operator characteristic (ROC) plot for three American burying beetle habitat suitability models and a validation dataset of 200 traps. Area under the curve (AUC) values are indicated in parentheses in the legend key.

The 85% PPO for Presence 1 reduces the number of false positives within that classification area providing a classification group that is the most indicative of ABB presence (Table 4, Fig. 4). A 45% PPO, identified by the maximum Kappa value, provides a classification group that is just below random chance for ABB presence; whereas, the 82% PPO classification group provides a more reliable indicator of ABB presence. The low PPO values of Presence 4 indicate that there were false absences that occur at PPO values between 20 and 45%.

Table 3. American burying beetle habitat suitability model's best fit variables for all three models and logistic regression equation values for the final 2011 model.

Influence on ABB presence					Regression coefficient (±S.E.)	
Predictor variables		2009	2010	2011	2011	*P*
Soil textures	loamy sand		+	+	0.2847 (± 0.13)	0.030
	loam		–	–	−0.5125 (± 0.13)	<0.001
Land cover	wetland[a]			+	0.5551 (± 0.14)	<0.001
	wetland (minus wet meadow)[b]	+	+			
	agriculture	–	–	–	−0.2832 (± 0.11)	0.013
	developed	–	–	–	−0.2819 (± 0.10)	0.006
	woodland	–	–	–	−0.2819 (± 0.11)	0.044
Climate averages	precipitation	+		+	0.6458 (± 0.10)	<0.001
	maximum temperature	–	–	–	−0.3358 (± 0.12)	0.005
				Intercept	0.3444 (± 0.09)	<0.001

[a] This variable was part of the best fit model in 2011 and includes wet meadow land cover.
[b] This variable was part of the best fit model in 2009 and 2010 and does not includes wet meadow land cover.

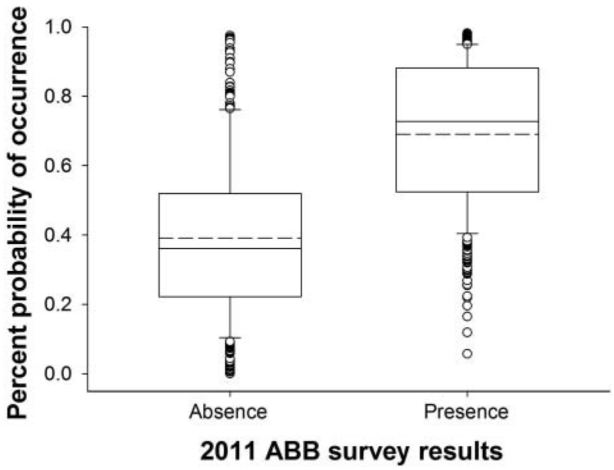

Fig. 2. A box and whisker plot produced using the 2011 prospective sampling data collected for 2011 model validation comparing American burying beetle (ABB) presence and absence. Presence and absence (x-axis) indicates the actual outcome of traps and the y-axis indicates the corresponding per cent probability of occurrence for each trap when input into the 2011 cross-validation model. The mean per cent probability of occurrence is marked by a dashed line, the box encompasses the interquartile range, and the whiskers mark the last data point within 1.5 times the interquartile range. Outliers are marked by a hollow circle.

Discussion

The models in this study generalize spatial characteristics to predict the probability of ABB occurrence in the Nebraska Sandhills region. Eight variables best fit the presence and absence of ABB in each model, which were very similar across models (Table 3). AUC measured each model's ability to discriminate between presence and absence that was not dependent on the prevalence of ABB (Freeman & Moisen, 2008*a*). Because this calculation is a threshold-independent measure, it was used for the Presence 2 PPO classification, which was a very similar threshold as the Presence 1 PPO (Hirzel *et al*., 2006). The 2011 model (Fig. 3) produced an AUC of 0.82 (Fig. 1), which is considered a moderately performing model (Franklin, 2009).

ABB occurrence was modelled using similar methods for the Loess Canyons region of Nebraska (McPherron *et al*., 2012). The models from these two different ecoregions identified different variables and different positive or negative associations to predict ABB occurrence. For example, the 2011 Loess Canyons model found woodland to have a positive influence on ABB occurrence and wetland to have a negative influence.

It is likely that in the Sandhills model an abundance of traps with ABB absence in the human-planted Nebraska National Forest near Halsey, Nebraska created a negative bias towards woodlands. There were few traps sampled in

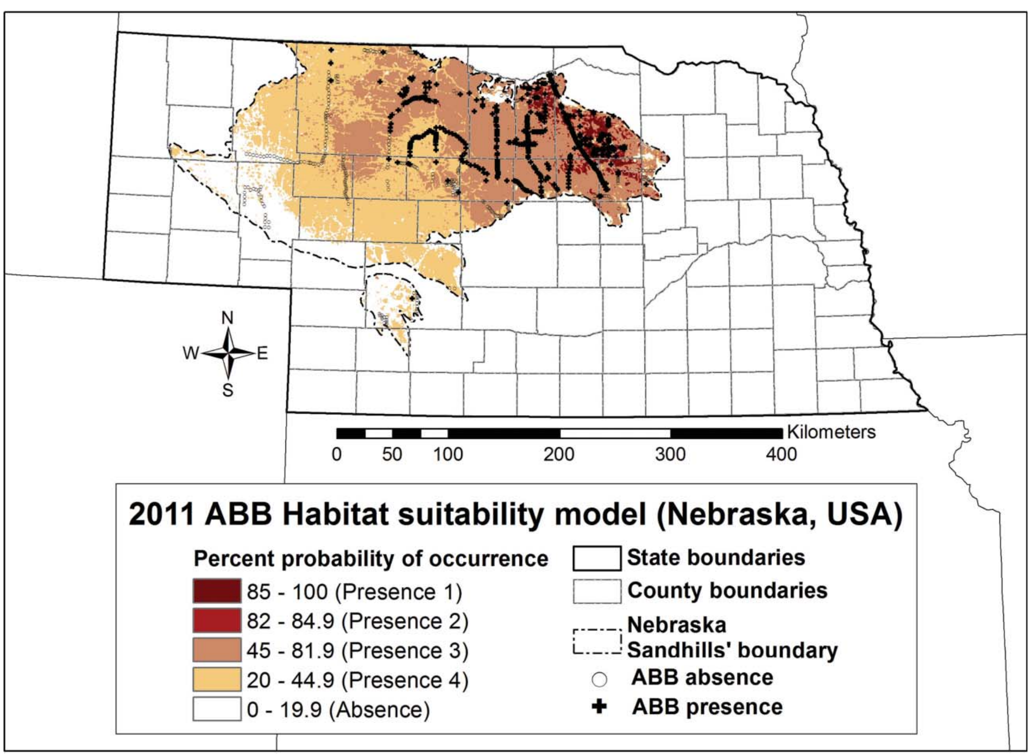

Fig. 3. The 2011 predictive model map for the American burying beetle (ABB) in the Sandhills ecoregion with sampling data points used in model selection.

Table 4. Threshold-dependent values at four occurrence thresholds for the Nebraska Sandhills American burying beetle habitat suitability models.

Model classification	Per cent probability of occurrence (PPO) threshold	Kappa	Sensitivity	Specificity	Correctly classified (%)
2009					
Presence 1	90	0.303	0.407	0.964	60.7
Presence 2	88	0.409	0.547	0.929	68.3
Presence 3	55	0.631	0.893	0.726	83.3
Presence 4	35	0.557	0.953	0.560	81.2
2010					
Presence 1	85	0.258	0.313	0.976	59.5
Presence 2	81	0.306	0.402	0.933	62.8
Presence 3	60	0.468	0.696	0.783	73.3
Presence 4	30	0.330	0.955	0.349	69.7
2011					
Presence 1	85	0.305	0.384	0.954	62.4
Presence 2	83	0.347	0.453	0.926	65.2
Presence 3	50	0.547	0.831	0.711	78.1
Presence 4	30	0.372	0.970	0.372	71.8
2011 validation					
Presence 1	85	0.250	0.319	0.953	59.9
Presence 2	82	0.287	0.393	0.915	62.3
Presence 3	45	0.541	0.850	0.684	77.7
Presence 4	20	0.250	0.991	0.240	65.9

other woodland areas of the Sandhills to offset this bias; therefore, it is possible that woodland does not really have a negative or positive relationship with ABB presence in the Sandhills. The general lack of trees in the Sandhills supports that although a bias may be present, it would not affect many areas of the model.

The ABB needs to avoid desiccation, which is more likely to occur in dry upland areas with quick-draining sand. Wetland areas in the Sandhills generally have different soil, geological and topographical characteristics from the typical upland sandy soils allowing the wetlands to retain water and have more moisture. Thus, it makes sense

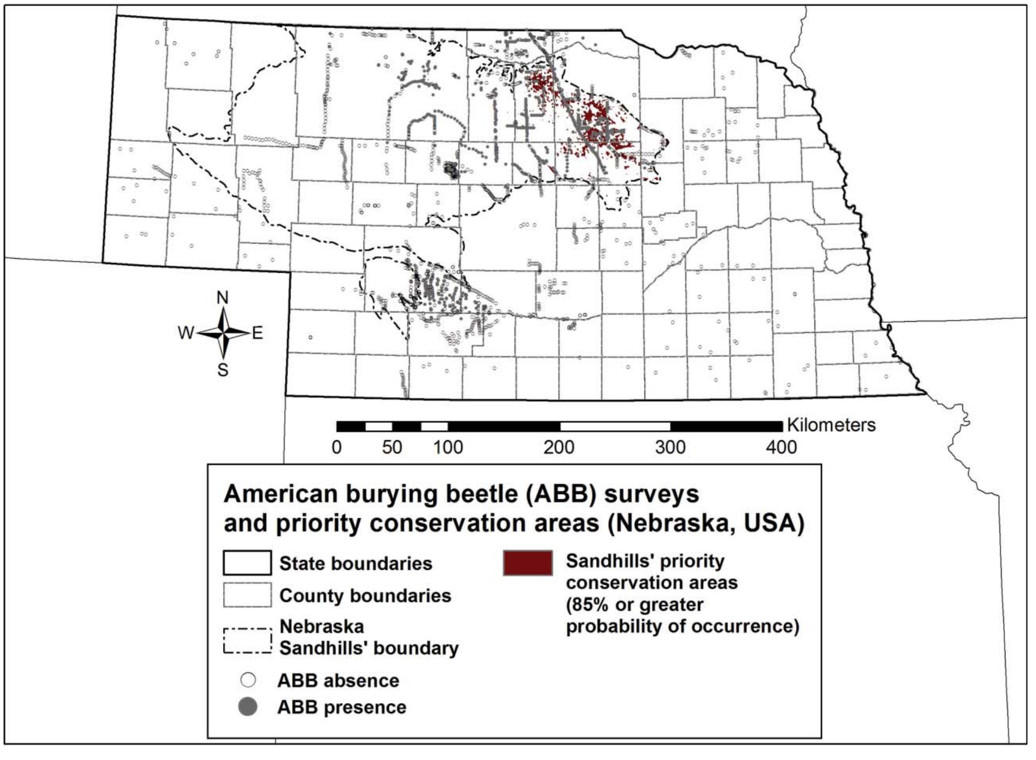

Fig. 4. ABB survey results with three trap nights or greater from 1980 to 2012 is shown with our recommended priority conservation areas, which contains model values 85% or greater probability of occurrence.

that the ABB would have an affinity for wetland areas in the Sandhills, but the affinity may not be as strong in areas without drier upland areas. Similarly, not all wetlands are suitable for the ABB because the continued inundation of some perennial wetlands during summer would exclude them as possible brood chambers sites. Within the Loess Canyons ecoregion, wetlands are not very abundant in the most connected canyons where ABBs are most often found. It is possible that this ecoregion's different soil type allows for prolonged moisture during the summer, unlike the sandy soil areas of the Sandhills. Some sources in the Loess Canyons, such as small creeks, may provide nearby soils with the needed moisture for the beetles. Also, Eastern red cedar canopy cover (Walker & Hoback, 2007) probably keeps more moisture in the soil over the summer ABB breeding months, offsetting the need for wetland habitat.

These differences in Nebraska elucidate the local differences of ABB occurrence and that extrapolation beyond specific ecoregions should be done with caution. Although Szalanski *et al*. (2000) did not find significant genetic differences between ABB populations in different States, it would be useful to re-evaluate the genetic relatedness between the beetles occurring in the Sandhills and Loess Canyons in Nebraska. The potential differences in habitat affinities could be causing some genetic drift, which would need to be considered when making conservation decisions for the different ecoregions within Nebraska.

A variable found in the Loess Canyons' model that was in agreement with the Sandhills' model was the negative influence of agriculture. The negative relationship found between agriculture development and ABB presence in both models supports the idea that within Nebraska ABBs are restricted to their current range because of habitat destruction and modification (Sikes & Raithel, 2002). The same thought applies to the Sandhills' model selection of developed areas as a negative predictor. Anthropogenic changes, such as artificial lighting, and increased abundance of vertebrate scavengers associated with human populations are also thought to have undesirable impacts on ABB movement and reproductive success (Sikes & Raithel, 2002; Jurzenski & Hoback, 2011).

The importance of soil texture variables, such as loam and loamy sand, in predicting the probability of ABB occurrence is not surprising because they may determine whether or not a carcass is successfully buried underground for brood rearing. Looney *et al.* (2006) found that two different types of parent soil material were correlated with different carrion beetle communities. Of the seven silphid beetle species identified, they found that three *Nicrophorus* species, including *N. marginatus*, were more abundant in loessal soils and two *Nicrophorus* species were more abundant in granitic soils. Similar niche partitioning associated with soil type was found for several Nebraska burying beetles in areas without ABB presence (Bishop *et al.*, 2002). Soil texture candidate variables were not part of the best subset of variables for the Loess Canyon's ABB suitability models and the region has high silt content, which is very different from the sandy soils of the Sandhills. A possible explanation is that ABB can utilize many soil types, but is more sensitive in drier environments, which is supported by the positive association with precipitation and the negative association with higher temperatures. Lomolino *et al.* (1995) found that ABB presence increased in areas with increased sand content and decreased in areas with increased silt or clay percentages; however, the sand content did not exceed 80%. An affinity for sandy soils would likely make burial of carcasses easier, but sand alone would not hold moisture or be very stable for brood chambers. The combination of loamy sands, which do exceed 80% sand content, and wetland habitats is probably an important factor for ABBs when occupying drier ecoregions, such as the Sandhills. These same variables would not be as critical or as extreme in ecoregions with different climatic conditions and habitat characteristics, such as the Loess Canyons or even the northern, adjacent ecoregion with ABB presence, Northwestern Great Plains.

As with most models, some of the modelled region contained extrapolated data, because of sampling limitations associated with funding, time and large tracts of private land. There was a lack of western and centrally located ABB presence traps in the 2009 model creating a large extrapolated absence area on the western half of the Sandhills ecoregion. Some of this area actually matched a true absence area that was eventually supported by the addition of over 50 absence traps in the 2011 model. As evidenced above, we were able to reduce extrapolated regions with additional sampling in 2010 and 2011, which strengthened our final model. Hirzel & Le Lay (2008) reported at least five causes for false absences (i.e. fallacious absences), of which three can be related to ABB sampling: local extirpation, alternative habitats and biotic interactions. As a habitat generalist, it is possible that ABBs use alternative habitats for breeding and overwintering, which could have contributed to the four false absences found below the Presence 4 PPO threshold of 20%. During reproduction, ABBs are underground and unavailable for sampling. This usually occurs in July, which is why absence data from that time frame was not used; however, even within June and August it is possible that absence traps were located in favourable habitat with ABB populations, but the beetles were unavailable for sampling (i.e. not seeking food). A false positive is also problematic because it is difficult to identify and the data contribute false information to the modelling process. Individuals flying into unsuitable habitat by random events, attraction to a carcass for short-term feeding, or overcrowding in suitable habitat can explain the occurrence of false positives. The presence of both false absences and false presences introduces sampling locations with almost identical ecological variables, but with conflicting classifications, which will degrade the performance of the model (Fielding & Bell, 1997). In our models, the use of threshold-dependent values as absence and presence classifiers helped reduce the effects of false absences and presences on the performance in predicting ABB occurrence.

This model provides important information concerning defined conservation areas, which will be useful in the development and justification of consultation methods for the conservation and protection of the ABB. Presence 1 represents the area with the greatest sensitivity, which will be the most useful in designating priority conservation sites (Fig. 4). Presence 2 and 3 correspond to thresholds delineating the ability to distinguish presence and absence. Presence 4 represents the largest area predicting possible ABB occurrence, which is most useful when making conservation decisions concerning habitat alteration. It is likely that ABBs are in a non-equilibrium situation because it does not seem to be occupying the entire range of available suitable habitat, which is why Presence 4 areas without current survey data need to be continually assessed (Cianfrani *et al.*, 2010).

Future research and modelling for this species should take into account the density of ABBs per trap night and incorporate known distributions of both potential animal resources and competitors. Potentially, limiting the model extent to a smaller sample area with more fine-scale variables, including consumable resources, could help distinguish between suitable feeding habitat and reproductive or overwintering habitat characteristics. An ABB breeding habitat requirement study by Lomolino & Creighton (1996) showed that more offspring were produced in an upland forest area compared with an adjacent grassland area, but the brood chambers were deeper and had less fly competition in the grassland area. These differences could be attributed to soil texture and compaction or other land cover variables. Additional information on the distribution and density of other carrion beetles found in the Sandhills ecoregion could be utilized in future modelling efforts because of the possible influence of niche partitioning (Bishop *et al*., 2002; Dobesh, 2007).

Crawford & Hoagland (2010) pointed out a number of difficulties in modelling ABB occurrence, such as problems determining grain size (i.e. effective trapping radius), the use of attractive traps to assume presence, biased sampling along roads and the ability of ABB to disperse and utilize different habitats. Our models were similarly affected by these concerns. The 800 m effective trapping radius used in the Sandhills ABB model likely minimized the effects of bias in roadside sampling because the radius still encompassed the representative habitat near the data point and did not overlap with nearby roads. McCarthy *et al.* (2012) found that roadside sampling did not significantly affect the performance of their occurrence model, which used a 100 m radius for data point variables. The authors compared the results of two model validations using on-road and off-road validation data points. They also concluded that the surrounding landscape within the vicinity of the road was sufficient to offset the potential roadside sampling bias. We tried to reduce the likelihood of spatial autocorrelation by using a sampling radius buffer to identify independent samples and restricting the moving window to the same radius, which would change if future research suggests a different effective trapping radius for these methods. Biotic interactions, such as competition, predation, mutualism and parasitism, are not easily incorporated into models. These factors are likely key components in explaining both the current distribution of ABB and the disappearance of the species from over 90% of its historical range (USFWS, 1991; Sikes & Raithel, 2002).

A limited number of references could be found identifying habitat suitability models specifically for habitat generalists. A comparison of two habitat generalist and specialist plants showed the habitat generalist species could not be successfully modelled because of inconsistent results for variables when using different model methods and overall low model performance when compared with the specialists' model performance (Evangelista *et al.*, 2008). In contrast, Mueller *et al.* (2009) found that generalist crows could be successfully modelled when different habitat designations and spatial scales were considered. Grey wolves are a wide-ranging habitat generalist with the potential to have conflicts with humans and livestock. Mladenoff *et al*. (1999) used newly collected and previously collected data to successfully validate a model used to assess the probability of recolonization areas. The resulting ABB models of this study found that the predictor variables were relatively stable across multiple years and predictive performance was likely successful due to the use of an ecoregion to define extent and prospective sampling to increase sampling density. These examples, in addition to our model, indicate that with proper methods useful and well-performing habitat suitability models are possible for habitat generalist species.

The 2011 cross-validation model performed moderately well as indicated by the threshold-independent measure, AUC (Fig. 1) and was made meaningful by selecting presence classifiers based on threshold-dependent measures (Fig. 3). The use of prospective sampling for model development in 2010 and 2011 verified that model-based sampling was more efficient than random sampling (Le Lay *et al.*, 2010). The American burying beetle likely does not have specific habitat requirements that agree across its entire known range, yet the final model presented in this paper showed that the beetles' occurrence can be adequately explained within an ecoregion. This information will be important in future conservation efforts for this federally endangered animal, especially when considering priority conservation and reintroduction sites.

Acknowledgements

We thank Neal Niemuth for his guidance in model criteria selection and providing statistical advice and software. Bob Harms and Mike Fritz provided critical assistance in the development and completion of this project. Michelle (Shelly) McPherron, Amy Smith, Andy Royle and two anonymous reviewers helped with very useful revision comments. Many thanks to the field technicians that made sampling possible, including S. Butler, L. Workman, M. McPherron, J. Carlson, A. Mijone, S. Santiago, C. Rosim, M. Parenti, S. Maestrello and J. Lammers. Rainwater Basin Joint Venture and US Fish and Wildlife Service provided funding and use of their GIS lab for the creation of these models. The findings and conclusions in this article are those of the authors and do not necessarily represent the views of the US Fish and Wildlife Service. Nebraska Game and Parks Commission and Nebraska Department of Roads helped provide vehicles and funding for field sampling. ABB trapping was conducted under US Fish & Wildlife Service Permit No. TE045150-0. This study was funded in part through grants from the Federal Highway Administration [and Federal Transit Administration], US Department of Transportation. The views and opinions of the authors expressed herein do not necessarily state or reflect those of the US Department of Transportation.

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