Trends in Entomology
Vol. 8, 2012

Original Communication

Model of habitat suitability for American burying beetles in Nebraska's Loess Canyons ecosystem

Michelle M. McPherron[1,*], Jessica Jurzenski[2], Marc C. Albrecht[1], Kerri M. Farnsworth-Hoback[1], Thomas L. Walker[3] and W. Wyatt Hoback[1]

[1]Biology Department, University of Nebraska at Kearney, Kearney, NE 68849, [2]University of Nebraska - Lincoln, Lincoln, NE 68583, [3]Nebraska Game and Parks Commission, North Platte, NE 69101, USA

ABSTRACT

The conservation of an endangered species is important to maintaining species diversity and preserving ecosystem function. Habitat suitability models are useful tools that characterize species distribution and occurrence. The endangered American burying beetle, *Nicrophorus americanus* Olivier, was once widespread across the eastern two thirds of North America. Extensive surveys since the listing of the American burying beetle have contributed to the knowledge of this species. However, much remains to be discovered about its habitat affinities. With the American burying beetle eliminated from a large portion of its historic range, an understanding of its remaining habitat associations will assist in management efforts. We developed a model using American burying beetle survey data collected from 337 sample locations between 2001 and 2011 in eight south-central Nebraska counties. We compared presence and absence of American burying beetles with land-cover information to develop and validate a predictive habitat model for the Loess Canyons region of Nebraska. Using 2011 survey data to test the model, we found significant accuracy in predicted occurrence of the American burying beetle in the Loess Canyons. In addition, we found a significant decline ($p < 0.0001$) in American burying beetle occurrence with the presence of agriculture. These results demonstrate the successful use of habitat modeling to predict American burying beetle occurrence in the Loess Canyons of Nebraska.

KEYWORDS: rare insect, GIS, habitat suitability model, silphidae

INTRODUCTION

The conservation of biodiversity and threatened species is an important part of protecting and maintaining productive ecosystems. Habitat loss, fragmentation, and the introduction of exotic species are the most significant causes of species loss [1]. Management of threatened species depends on protecting the habitat, populations, and ecological communities of those species. However, management efforts are often limited by lack of knowledge of a species' life history and the threats that have led to its decline. Conservation efforts become even more difficult when critical habitat and habitat affinities have not been designated for the threatened species [2]. Habitat suitability models can provide a tool for conservation managers to predict areas of species occurrence and develop management plans to further protect habitats for these species.

Nicrophorus americanus Olivier, the American burying beetle, once occurred throughout the eastern half of North America and three Canadian provinces [3]. The American burying beetle is the largest silphid in North America and exhibits one of the highest levels of parental care among

*Corresponding author
shellymc5@yahoo.com

insects [4]. In 1989, the American burying beetle was listed as Federally Endangered with its known historical range reduced by approximately 90% [4-6]. Reasons for the decline have not been fully determined but are likely tied to habitat fragmentation, changing carrion base, and competition from other carrion beetles and scavengers [7]. Extensive surveys within the historical range of the American burying beetle have contributed to the knowledge of the species remaining populations, which are limited to six states [2, 8]. However, among extant populations, habitats are highly varied ranging from old growth forest to open wet meadows. In part because of its historical distribution across habitat types, the American burying beetle is designated as a habitat generalist and is one of the few endangered species that does not have critical habitat designated [5]. With a better understanding of its habitat affinities in a small area and successful predictions of its occurrence, management efforts can aid in reducing the threat of extinction and work towards meeting the goals of recovery.

Nebraska currently supports two populations of the American burying beetle, one in the Loess Canyons of south-central Nebraska and one in the Sandhills in northern Nebraska [9]. The population of American burying beetles in some areas of the Sandhills was estimated to be as high as 5.94 beetles per km^2 in 2009 and 0.67 beetles per km^2 in the Loess Canyons in 1998 [9, 10]. These two Nebraska regions are areas where human impact has been minimal because of topography, wetlands, and low population densities. The Loess Canyons and the Sandhills were designated as biologically unique landscapes in 2005 through the Nebraska Natural Legacy Project [11]. Because the Loess Canyons is one of the few areas in Nebraska that has not been manipulated by agriculture, many small mammals, birds, and insects rely on the remaining environment. Within the state of Nebraska, 14 of the 28 threatened and endangered species including the American burying beetle are found in the remnant prairie regions of the Sandhills and Loess Canyons.

Conservation of the American burying beetle would benefit from a reliable habitat suitability model that accurately portrays habitat requirements and distribution. A habitat model will also help define population ranges and allow managers to consult agencies during project reviews [2, 12-13]. Past attempts at developing a model for the American burying beetle in the Loess Canyons have been unsuccessful because of inadequate sampling and the ecological characteristics of American burying beetles. American burying beetles are nocturnal, remaining underground during the day, and are only active when climatic conditions are favorable, which exist in the months of June and August in Nebraska, which limits sampling opportunities that are needed to verify presence and absence [6].

The objective of our study was to develop and validate a habitat suitability model using presence and absence data for the Loess Canyons of south-central Nebraska. Survey data were also used to compare the presence of American burying beetles with the presence of agriculture.

MATERIALS AND METHODS

Study area

The Loess Canyons of south-central Nebraska are composed of dissected hills that run primarily north-south with loess soil, mixed grass prairies, and dense growths of Eastern red cedar (*Juniperus virginiana* L.) [6, 14]. The area (4,500 km^2) is sparsely populated and mostly used for grazing cattle in the canyons where row crop agriculture is not possible [10]. The native vegetation is a mixed-grass prairie dominated by grass species, such as little bluestem (*Schizachyrium scoparius* (Michx.) Nash). Grazing and suppression of wildfires has led to increases in invasive plant species presence, including Eastern red cedar and weedy brome grass species (*Bromus* spp.). What was once primarily mixed-grass prairie is becoming woodland dominated by Eastern red cedar. Surrounding the Loess Canyons is cropland mostly consisting of corn and alfalfa. The average annual high temperature for the region is 18.3°C and average annual low temperature of 1.4°C. Average annual precipitation within the region is approximately 49.9 cm [15].

Species and species data

The American burying beetle has an annual life cycle. It ranges from 25 to 45 mm in length and can be identified by having a distinct orange pronotum [16]. Most reproductive activity takes place in June and July when a male and female pair will bury a carcass, form a brood ball, lay eggs, and remain in the chamber for up to two weeks to care for the larvae. Adults typically emerge from the soil after pupation between 45 and 60 days after a brood ball is buried [17-19].

American burying beetle survey data were collected between 2001 and 2011. Trapping in 2001 followed the U.S. Fish & Wildlife Service 1991 protocol as modified by Bedick *et al*. [6], and sampling between 2002 and 2011 followed the American burying beetle Nebraska protocol from the U.S. Fish and Wildlife Service [20]. Baited pitfall traps were constructed using 18.9 L plastic buckets with a diameter of 28.5 cm. Buckets were placed at selected sample sites with a majority located along roadsides. GPS coordinates (UTM) were recorded at each site. Carrion bait consisted of a 300 $\pm$ 50 g laboratory rat (RodentPro.com), which was allowed to decompose for four days prior to trapping. Traps were open three to five nights and checked every 24 hours. The number of American burying beetles and other silphids were recorded at each trap.

Multiple surveys were conducted throughout the Loess Canyons. Any sample locations recording a presence of American burying beetles during 2001 to 2011 were considered as a positive in the model. Sites that did not capture American burying beetles during any survey were recorded as a negative. When traps were sampled for more than three days, only the results from the first three nights were used. Traps were placed a minimum of 2.2 km apart in areas of both high and low predicted probabilities of the American burying beetle.

Model development

Because habitat requirements have not been defined for the American burying beetle and it is reported to be a habitat generalist [5-6, 21] a variety of environmental variables were tested for the model. Land cover used by the model was a combination of raster layers with a 30 m grid cell resolution. The predictor variables were chosen based on known American burying beetle biology and what we believed would most likely affect carrion beetles, which consisted of grassland, woodland, cropland, developed areas, wetland, and wet meadow (Table 1). The Loess Canyons region was defined by a 10 km buffer of the canyons Biologically Unique Landscape (BUL) based on soil types and land use (Roger Grosse, personal communication 2010) (Figure 1).

Initially, all predictor variables were tested in the model (Table 1). To determine which variables best correlated with the species data set; logistic regression was used on each variable independently using Number Cruncher Statistical System (NCSS 2007, ver 07.1.20). Model fit was then compared using the variables that produced the highest Area Under the Curve (AUC) value of a Receiver Operator Characteristics (ROC) plot. Chosen variables were combined in various sets to evaluate which combinations produced the lowest

Table 1. Predictor variables used in models to determine potential suitable habitat for *Nicrophorus americanus* in the Loess Canyons region of Nebraska.

Landscape variable	Range & unit	Description
Grassland	7 categories	Predominant mix of native grasses and forbs on non-fragmented prairie. Area is typically grazed.
Woodland[1]	11 categories	Predominant mix of upland and riparian trees including shrubs.
Agriculture[1]	8 categories	Tilled and planted with row crops including corn, alfalfa, soybeans and other grains.
Developed	4 categories	Areas of urban and rural development.
Wetland	8 categories	Areas saturated with water throughout the year. Standing water present year around.
Wet meadow[1]	1 category	Areas that are saturated with water throughout part of the year. Standing water only present for brief periods during the growing season.

[1]Denotes variables used in the final habitat suitability model

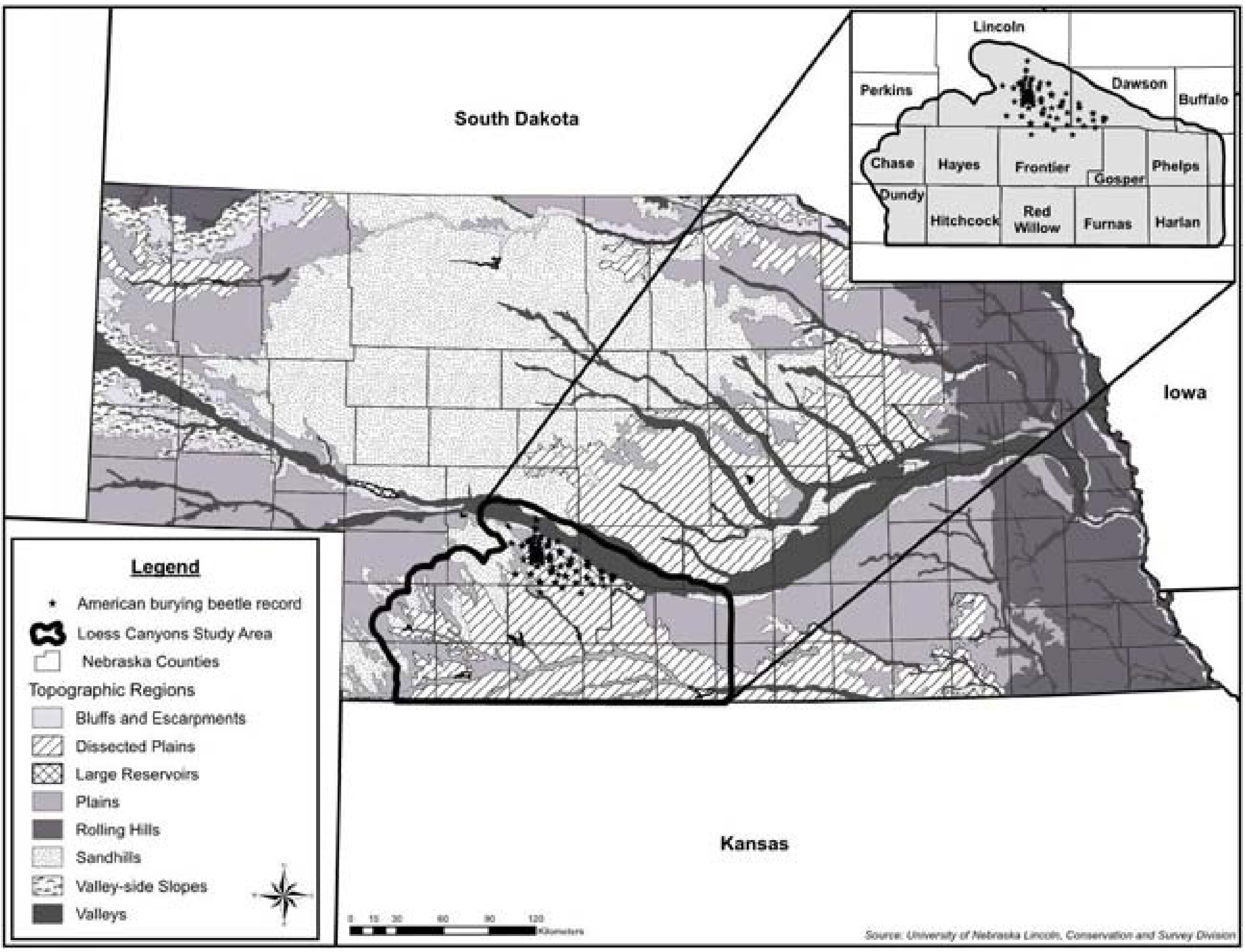

Figure 1. Study site: Loess Canyons region of south-central Nebraska.

Akaike's Information Criterion (AIC). AIC is a measure of the goodness of fit of a model and a way to statistically compare models [22]. The combination that produced the lowest AIC was considered the best for use in a predictive model. Parameter estimates for the final set of habitat variables were calculated using NCSS.

Threshold-dependent measures were calculated using values produced by the NCSS logistic regression report. These values were used to optimize the model's accuracy and practicality of the map [23]. Sensitivity, specificity and percent of data points correctly classified were recorded. The required specificity threshold was set to less than 5% of the traps where the species was observed to be absent. The required specificity was identified as High Probability. The Low Probability threshold value was defined using the cross-over of sensitivity and specificity. Maximum percent correctly classified value was designated as Moderate Probability. Areas with probability of occurrence values below the Low Probability threshold were defined as American burying beetle absence. A habitat suitability map was then created for the model that predicted areas of presence or absence.

Model validation

In June 2011, 40 prospective sample locations were selected from 93 locations sampled using a random point generator in ERDAS to use for model validation. Of the 40 samples, 20 were located in above 50% occurrence probability and 20 were located in below 50% occurrence probability for the American burying beetle. The AUC of a ROC plot has been extensively used to evaluate the performance of a predictive habitat model [2, 24], and we conducted a similar test. We calculated the AUC for validation of the original data set excluding the 40 validation points and compared it to the dataset after adding the 40 validation points. An AUC index developed by Swets [25] indicates the performance of the model dataset as follows (1998): 0.5-0.69 = low accuracy; 0.7-0.89 = potentially useful; and > 0.9 = high accuracy [2].

A Mann-Whitney U test was performed on the means of the occurrence probability values comparing presence or absence results of the 40 validation data points that were randomly selected from prospective sampling in 2011 (NCSS).

Statistical analysis of species data

Habitat affinities were tested using data collected between 2007 and 2010. Geographic Information Systems (GIS) was used to assign percent agriculture to each sample site with a distance of a 2.0 km^2 area. These values ranged from 0% to 100% agriculture. Agriculture was defined as areas tilled and planted with row crops, including corn, alfalfa, soy beans, and other grains. The association between the presence of the American burying beetle and percent agriculture was analyzed using a Mann-Whitney U test to identify differences between the number of American burying beetles found in 20% or less agriculture versus the number found in areas with greater than 20% agriculture (alpha = 0.05). In a 2.00 km^2 area, agriculture is classified as covering greater than 25% of that area. Because roads are included in those percentages in the 2.00 km^2 area, we chose to use a percentage (i.e., 20%) less than 25% to analyze the association between the presence of the American burying beetle and percent agriculture.

RESULTS

The final dataset for the model contained a total of 337 sample locations across eight counties in south-central Nebraska with 95 present (28%) and 242 absent locations for the American burying beetle. All silphids captured were recorded for 299 sample locations. Of these locations, 78 (26%) contained *Nicrophorus carolinus* Linnaeus, 237 (79%) contained *Nicrophorus orbicollis* Say, and 292 (98%) captured *Nicrophorus marginatus* Fabricius. Three habitat variables with the highest correlation were chosen to model the predicted occurrence of the American burying beetle in the Loess Canyons (Table 1). The combination of woodland, agriculture, and wet meadow had the highest AUC value (0.765) and lowest AIC value. Woodland provided the strongest positive correlation in variable importance, while agriculture and wet meadow were negatively correlated (Table 2).

The percent probability of occurrence thresholds was based on threshold-dependent evaluation criteria (Table 3). The largest percent probability of occurrence values of High Probability (61-100%) represents areas with the highest predicted occurrence of the American burying beetle and reduces the number of false positives within the classified area (Figure 2). The Moderate Probability (≥ 41%) was based on the maximum percent correctly classified. The Low Probability (≥ 31%) represents areas that could possibly support a population of the American burying beetle, but the model's predictive capability is less confident within the 31 to 40% range. The resulting map indicates that suitable habitat for the American burying beetle is more likely to occur in the north-central region of the Loess Canyons (Figure 3).

Model validation

Our comparison of 40 validation traps results indicated a significant difference ($z = -4.721$, $p < 0.0001$) between the predicted probabilities of the presence (58.8% ± 0.03 se) and absence (23.9% ± 0.03 se) of the American burying beetle in the model. Performance of the model without the 40 validation pointes resulted in the category of "potentially useful" based on the AUC index value of 0.765, which increased to 0.790 with all 377 data points used.

Table 2. Parameter estimates produced by the logistic regression report using Number Cruncher Statistical System (NCSS 2007, 07.1.20).

Variable	Regression coefficient	SE	*p*
Agriculture	-0.049	0.012	< 0.0001
Woodland	0.036	0.010	0.0002
Wet meadow	-0.015	0.017	0.3922
Intercept	-0.735	0.230	0.0014

Table 3. Threshold-dependent values at three occurrence thresholds for the Nebraska Loess Canyons predicted habitat suitability model for *Nicrophorus americanus.*

Probability of occurrence threshold (%)	Model classification	True presence (no. of traps)	False presence (no. of traps)	False absence (no. of traps)	True absence (no. of traps)	Sensitivity	Specificity	Correctly classified (%)
60	High Probability	17	11	78	231	0.179	0.955	0.736
40	Moderate Probability	50	23	45	219	0.526	0.905	0.798
30	Low Probability	68	72	27	170	0.716	0.702	0.706

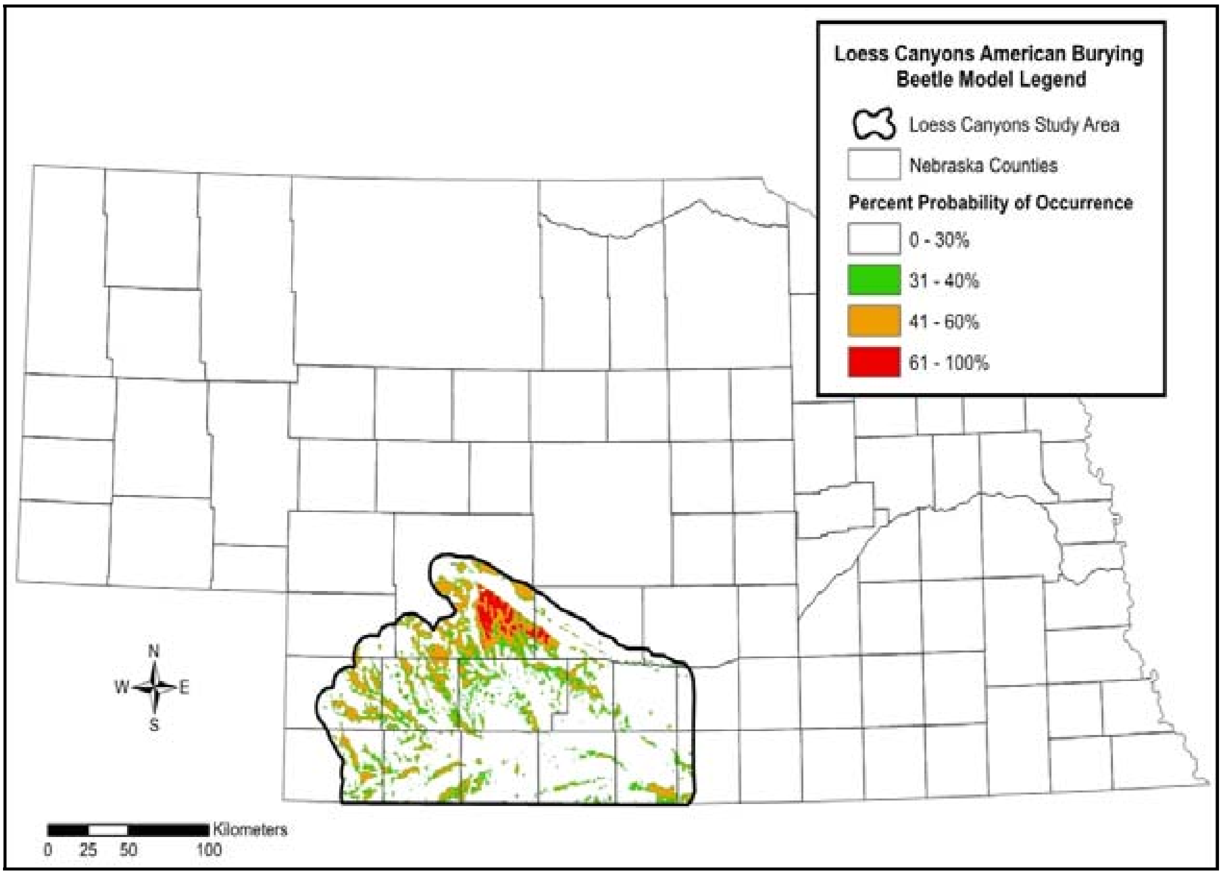

Figure 2. Predicted habitat suitability model for *Nicrophorus americanus* in the Loess Canyons region, Nebraska based on logistic regression model using three landscape variables: agriculture, woodland, and wet meadow.

Agriculture comparison

The number of American burying beetles captured at each sample site with < 20% agriculture was significantly less than the amount found in > 20% agriculture ($p < 0.0001$) (Table 4). The total number of American burying beetles trapped from 2007 to 2010 in < 20% agriculture was 395, while 9 were caught in areas with > 20%. The number of *N. orbicollis* captured at each sample site with < 20% agriculture was also significantly more than

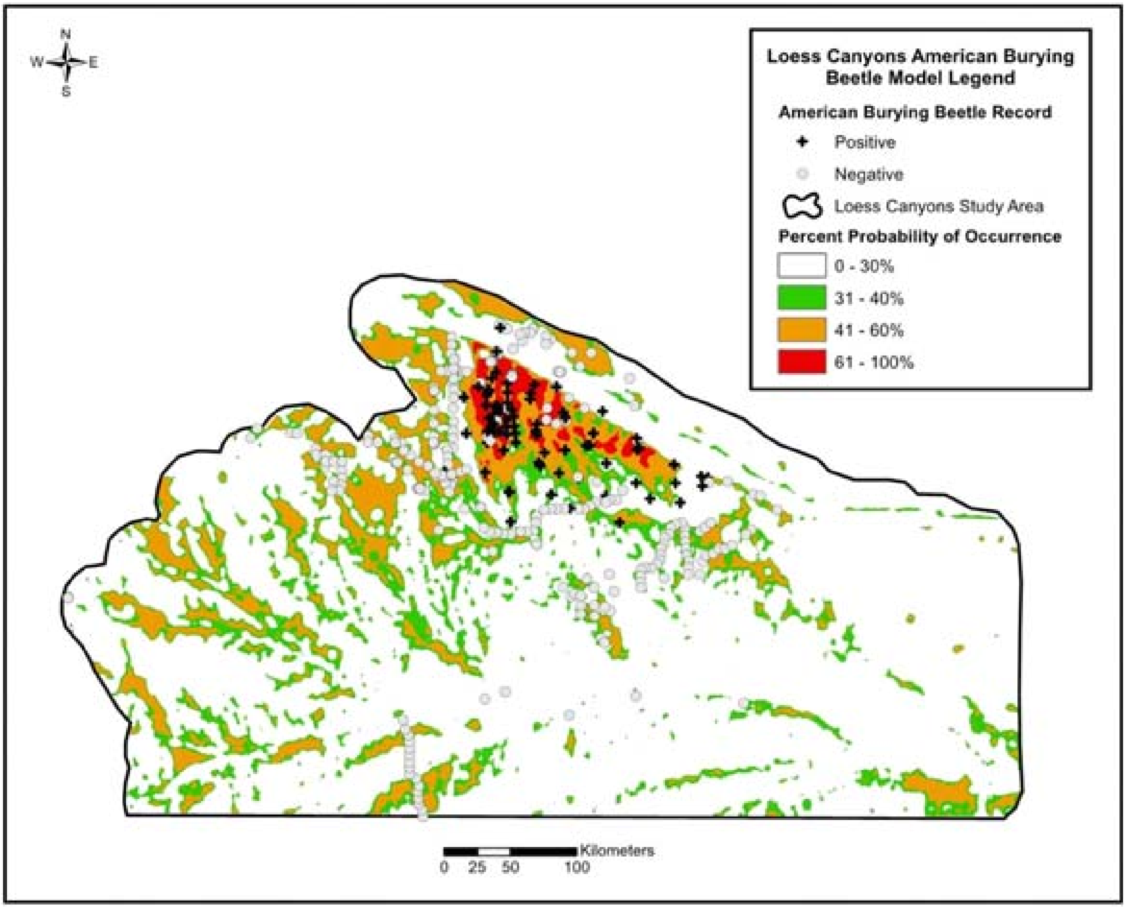

Figure 3. Predicted habitat suitability model for *Nicrophorus americanus* in the Loess Canyons region, Nebraska and sample locations. For geographical locations see Figure 2.

Table 4. Total number of beetles captured and p-values for the Mann-Whitney U Test for differences between numbers of selected *Nicrophorus* species found in areas with < 20% or > 20% agriculture within 2.0 km^2. Significance defined as $p < 0.05$ marked by star (*), n=26.

Species	Total number captured < 20% agriculture	Total number captured > 20% agriculture	p-value
N. americanus	395	9	<0.0001*
N. orbicollis	4,172	795	<0.0080*
N. carolinus	55	251	<0.0262*
N. marginatus	27,347	11,008	0.4704

in > 20% agriculture ($p < 0.008$) (Table 4). Significantly more *N. carolinus* ($p = 0.0262$) were found associated with agriculture (Table 4). No significant differences were found for *N. marginatus*.

DISCUSSION

The model presented in this paper is the first habitat suitability model to be developed for the American burying beetle in the Loess Canyons region of Nebraska. The predictions of suitable habitat for presence of the American burying beetle corresponded strongly with results from 2011 sampling. Although the Loess Canyons region of Nebraska is large (450,000 hectares), the model predicts only a small portion (32,219 hectares) supports American burying beetles based on the High Probability threshold.

Woodland was positively correlated with the presence of the American burying beetle, while agriculture and wet meadow were negatively correlated. Woodland provided the most gain in variable importance because areas in the Loess Canyons region with American burying beetle occurrence have higher percentages of tree cover. Walker and Hoback [14] recorded more captures of American burying beetles in open grasslands than in Eastern red cedar dominated areas in the Loess Canyons; however, current cedar coverage in the Loess Canyons is 20% to 40% with a rate of increase of 2% per year [14]. Previous studies suggest that the American burying beetle occurred primarily in forests with deep, loose soils [4]. Yet, Lomolino *et al*. [5] concluded that American burying beetles are habitat generalists. Several studies have found American burying beetles in unfragmented habitats with a grassland and woodland mixture [6, 10, 14]. These habitats tend to provide abundant suitable reproductive resources needed by American burying beetles.

Although fragmentation and habitat alteration for agriculture have often been suggested as causes of American burying beetle decline, our data and model are the first to demonstrate the negative effects. There was a significant difference between the numbers of American burying beetles present in < 20% agriculture areas compared to areas with > 20% agriculture (Table 4). This suggests that areas with greater than 20% agriculture greatly reduce the numbers of American burying beetles. This was also true with *N. orbicollis*. Habitat fragmentation reduces areas required to maintain a viable population, reduces the amount of carrion, and establishes barriers to dispersal [26-28]. An increase in fragmentation by agriculture into suitable habitats has likely affected American burying beetle populations in the Loess Canyons region [6]. Because sample sites were placed along edges of suitable habitat and agriculture, some traps with a presence of the American burying beetle may have attracted beetles to the trap from a distance of 1.6 km. One trap can attract an American burying beetle from a distance of up to 10.0 km in one night [15]. Placing sample sites in different percentages of agriculture in the future will allow for a better understanding of the correlation between agriculture and the presence of the American burying beetle. The reasons that agriculture reduce occurrence of American burying beetles are unknown but could include use of pesticides, irrigation, lack of habitat heterogeneity, or soil disturbance.

During this study, several factors may have contributed to the performance of the model. Habitat suitability models are often hampered by a lack of data, biased sampling, and a deficit with the model specifications [2, 29]. Errors in specifications of presence and absence models usually appear in two forms: false negatives and false positives [30]. False negatives often occur when using absence data points from surveys [30]. Using absence data points may not truly denote unsuitable habitat for the American burying beetle. The use of presence-only models reduces the error of false negatives especially when encountered frequently [2, 31-32]; however, presence-only habitat suitability models require many years of data incorporated with annual variation [33].

Because the majority of survey locations were placed along roadsides and in a transect-like pattern, a geographic bias may exist in our data. Surveys were primarily conducted along roadsides because of surveys required for construction projects or because of the lack of access to private lands. The assumed trapping radius of 0.8 km per trap should allow sufficient coverage of areas in suitable habitat [15]. Moreover, the American burying beetle can be attracted to carrion from distances of 0.25 - 10.0 km with an average of 1.6 km/night [9, 15, 34].

Habitat models, such as the one presented in this paper, are based on land cover data and often lack detailed land characteristics such as type of vegetation and its structure, climatic variables, and prey availability. These characteristics likely affect habitat selection by a species [33, 35]. Because the American burying beetle appears to be a habitat generalist across its range, difficulty arises in modeling because the species is not specifically correlated to certain predictor variables [2, 5-6, 21]. Schnell *et al*. [36] indicated the presence of carrion having a direct impact on the overwinter survival of the American burying beetle. Decreasing abundance of optimal sized carrion due to habitat fragmentation is likely one of the main reasons for the decline of the American burying beetle across its historic range [3, 7, 21]. Climatic variables, such as precipitation and soil moisture, may also influence habitat selection by the American burying beetle. Because of their small size and body structure, burying beetles are particularly susceptible to water loss [37]. Bedick *et al*. [37] found that when exposed to desiccating environments, *N. marginatus* will die after losing 30% of their body mass. Although challenging, incorporating these variables in the American burying beetle habitat suitability model would likely improve the performance of the model and should be taken in consideration during conservation planning.

Species occurrence and distribution may also be influenced by ongoing changes to the landscape including fires, land use, and vegetative succession [2]. The American burying beetle may be affected by changes to the landscape, such as fragmentation and woody plant encroachment. Although the occurrence of the American burying beetle was positively associated with woodland variables in our model, woody plant encroachment is affecting the population in the Loess Canyons [14]. Walker and Hoback [14] found more American burying beetles were collected in open habitat. Fragmentation of the canyons has also taken place in the past 30 years by loss of connectivity of the canyons because of cropland expansion [14]. Areas that have not been affected by fragmentation caused by agriculture currently show a presence of American burying beetles (Figure 3).

CONCLUSION

Models that lack sufficient amounts of data can still prove to be useful in conservation planning. Ideally, habitat models used for management of a species should include data collected over many years along with demographic parameters [33]. Our results suggest a valid habitat suitability model for the American burying beetle in the Loess Canyons of Nebraska can provide direction for future sampling and can be used in plans for integrated landscape-level conservation planning. The High Probability threshold (i.e., > 60%) area corresponds well with the actual occurrence of American burying beetles (Figure 3) and will likely be a useful target for conservation efforts. The identification of row crop agriculture as a negative predictor of American burying beetle occurrence indicates its importance and should be carefully evaluated in the future.

ACKNOWLEDGEMENTS

This study was funded by the Nebraska Department of Roads, U.S. Fish & Wildlife Service, Nebraska Game and Parks Commission, and the University of Nebraska at Kearney. We thank the Rainwater Basin Joint Venture including Andy Bishop, Roger Grosse, and John Reins for assistance in the development of the models and with data input. Statistical advice was received from Neal Niemuth. We also thank Lara Fondow, Jess Lammers, and Lindsay Vivian for their assistance in collection of survey data.

REFERENCES

1. Ewers, R. M. and Didham, R. K. 2006, Biol. Rev., 81, 117.
2. Crawford, P. H. and Hoagland, B. W. 2010, J. Insect. Conserv., 14, 511.
3. U.S. Fish & Wildlife Service 1991, American burying beetle (*Nicrophorus americanus*) recovery plan, Newton Corner, MA.
4. Anderson, R. L. 1982, Coleopt. Bull., 36, 362.
5. Lomolino, M. V., Creighton, J. C., Schnell, G. D. and Certain, D. L. 1995, Conserv. Biol., 9, 605.
6. Bedick, J. C., Ratcliffe, B. C., Hoback, W. W. and Higley, L. G. 1999, J. Insect. Conserv., 3, 171.
7. Sikes, D. S. and Raithel, C. J. 2002, J. Insect. Conserv., 6, 103.
8. U.S. Fish & Wildlife Service 2008a, American burying beetle (*Nicrophorus americanus*) 5 year review: Summary and evaluation. Newton Corner, MA.
9. Jurzenski, J., Snethen, D. G., Brust, M. L. and Hoback, W. W. 2012, Great Plains Res., 21, 131.

10. Peyton, M. 2003, Great Plains Res. A J. Nat. and Soc. Sci., 13, 127.
11. Schneider, R., Stoner, K., Steinauer, G., Panella, M. and Humpert, M. (Eds.) 2011, The Nebraska Natural Legacy Project: State Wildlife Action Plan, 2nd Ed. TheNebraska Game and Parks Commission, Lincoln, NE.
12. Hirzel, A. H., Le Lay, G., Helfer, V., Randin, C. and Guisan, A. 2006, Ecol. Model., 199, 142.
13. Tole, L. 2006, Ecol. Model., 194, 344.
14. Walker, T. L. Jr. and Hoback, W. W. 2007, Environ. Entomol., 36, 297.
15. Bedick, J. C., Ratcliffe, B. C. and Higley, L. G. 2004, Coleopt. Bull., 58, 57.
16. Peck, S. B. and Anderson, R. S. 1985, Quaest. Entomol., 21, 247.
17. Pukowski, E. 1933, Tier, 27, 518.
18. Milne, L. J. and Milne, M. J. 1976, Sci. Am., 235, 84.
19. Scott, M. P. 1990, Behav. Ecol. Sociobiol., 26, 31.
20. U.S. Fish & Wildlife Service 2008b, Endangered species protocol: American burying beetle Nebraska sampling protocol. Available at www.fws.gov/mountain-prairie/endspp/protocols/protocols.html.
21. Holloway, A. K. and Schnell, G. D. 1997, Biol. Conserv., 81, 145.
22. Zeiler, M. 1999, Modeling our world: The ESRI guide to geodatabase design. Redlands, California: Environmental Systems Research Institute, Inc.
23. Freeman, E. A. and Moison, G. G. 2008, Ecol. Model., 217, 48.
24. Elith, J., Graham, C. H., Anderson, R. P., Dudik, M., Ferrier, S., Guisan, A., Hijmans, R. J., Huettmann, F., Leathwick, J. R., Lehmann, A., Li, J., Lohmann, L. G., Loiselle, B. A., Manion, G., Moritz, C., Nakamura, M., Nakazawa, Y., Overton, J. M., Peterson, A. T., Phillips, S. J., Richardson, K., Scachetti-Pereira, R., Schapire, R. E., Soberon, J., Williams, S., Wisz, M. S. and Zimmermann, N. E. 2006, Ecography, 29, 129.
25. Swets, J. A. 1988, Science, 240, 1285.
26. Klein, B. C. 1989, Ecology, 70, 1715.
27. Saunders, D. A., Hobbs, R. J. and Margules, C. R. 1991, Conserv. Biol., 5, 18.
28. Trumbo, S. T. and Bloch, P. L. 2000, J. Insect. Conserv., 4, 245.
29. Barry, S. and Elith, J. 2006, J. Appl. Ecol., 43, 413.
30. Fielding, A. H. and Bell, J. F. 1997, Environ. Conserv., 24, 38.
31. Brotons, L., Thuiller, W., Araújo, M. B. and Hirzel, A. H. 2004, Ecography, 27, 437.
32. Pearson, R. G., Thuiller, W., Araújo, M. B., Martinez-Meyer, E., Brotons, E. L., McClean, C., Miles, L., Segurado, P., Dawson, T. P. and Lees, D. C. 2006, J. Biogeogr., 33, 1704.
33. Niemuth, N. D., Estey, M. E. and Loesch, C. R. 2005, Developing spatially explicit habitat models for grassland bird conservation planning in the Prairie Pothole region of North Dakota, USDA Forest Service General Technical Report PSW-GTR-191:469.
34. Creighton, J. C. and Schnell, G. D. 1998, Biol. Conserv., 86, 281.
35. Madden, E. M., Murphy, R. K., Hansen, A. J. and Murray, L. 2000, Am. Midl. Nat., 144, 377.
36. Schnell, G. D., Hiott, A. E., Creighton, J. C., Smyth, V. L. and Komendat, A. 2008, J. Insect. Conserv., 12, 483.
37. Bedick, J. C., Hoback, W. W. and Albrecht, M. C. 2006, Physiol. Ent., 31, 23.