

EVALUATION AND APPLICATION OF PREDICTIVE HABITAT MODELING IN
ECOLOGY

By

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PREVIEW

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EVALUATION AND APPLICATION OF PREDICTIVE HABITAT MODELING IN ECOLOGY

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University of Nebraska, 2008

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My dissertation research is an important contribution to the growing field of predictive habitat modeling in ecology. I investigate innovative approaches for evaluating the performance of different predictive habitat models and applying these methods to large scale ecological phenomena. Several predictive habitat models currently exist. It has been the focus of much research to determine which is the best model(s). However, much of this research is undermined by biased data sets. To resolve this issue, I tested model performance with simulated data that is not prone to the usual biases of real data sets. In general, my results support the findings of previous studies in that models that accurately predicted species distributions with real occurrence data also showed superior performance using simulated occurrence data. Using the conclusions from the model evaluation analysis as a basis, I applied these methods to two independent research questions. I first identified certain variables that best predicted the occurrence of chronic wasting disease (CWD) in Nebraska. Chronic wasting disease is a newly emerging infectious disease found only in members of the deer family (Family Cervidae).

Analysis of several different combinations of spatial, temporal, and environmental variables showed that the chance of recording a positive CWD case was greater the more time spent sampling and when that sampling was conducted in western Nebraska. For the second question, I predicted range expansion among six North American mammals and ascertaining what role environmental variables have in predicting those expansions. I used two predictive habitat models combined with climate, land cover, and elevation variables to predict distributions. I predicted range expansions accurately for two of the six species, suggesting that other factors influenced the distributions of the remaining species. My results demonstrate the applicability of predictive habitat modeling in ecology and provide insights into novel methods of evaluating model performance.

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INTRODUCTION

Recently, there has been increased emphasis for large scale studies in ecology. However, studying biological phenomenon at large scales has proven difficult, primarily because of limitations of time and resources as well as difficulty in experimentally manipulating systems at large scales. New and powerful computing technologies have increased our ability and efficiency in working at large scales. In addition to Geographic Information Systems, predictive habitat modeling has seen increased growth as a research tool in recent years. These modeling tools are widely applicable in the fields of ecology and biogeography. They have been used to address such issues as invasive species biology, species responses to climate change, conservation planning, and spread of diseases. Despite its clear promise, predictive habitat modeling is still in its infancy. Novel methods are needed to evaluate model performance, along with continued investigation of their applicability. These two objectives represent my overall goal for this research. In the following chapters, I present innovative means for testing the performance of predictive habitat models and use them to address specific ecological questions.

In chapter 1, I evaluate the use of four predictive habitat models. Two models commonly have been used in similar studies, whereas the other two are relatively novel methods that have been subjected to minimal testing. Many studies have conducted evaluations of predictive habitat models; however, they all suffer from one common flaw. The data used to test the models typically are data on actual occurrences of species. With this type of data, it is difficult to determine the actual occurrence of species. Therefore, using biased data sets to evaluate model performance ultimately will lead to biased

results. To address this, I used a population habitat model to simulate occurrence data of a species to use for testing. The occurrence data generated by the simulation model is completely accurate and allows me to propose unbiased conclusions.

In chapter 2, I used a predictive habitat model to determine which variables best predict the occurrence of chronic wasting disease (CWD) in Nebraska. CWD is a disease found in both wild and captive populations of deer and their relatives. I used a generalized linear model (GLM) and ten spatial, temporal, and environmental variables to ascertain which variable(s) best predicted the presence of CWD in Nebraskan deer populations. My analyses indicated that the longitudinal coordinate and year collected best explained the presence of CWD. Therefore, CWD is more likely found in parts of western Nebraska, and the more time spent sampling increases the chances of detecting infected individuals.

In chapter 3, I used predictive habitat modeling to analyze range expansions of six species of North American mammals. Range expansions have been documented in several faunal groups around the world. These events often are related to changes in climate. I used two predictive habitat models to test their abilities in accurately predicting geographic range expansion of each species given a set of environmental variables. These models successfully predicted the range expansion for only two of six species. My results suggested that additional variables, other than environmental ones, may be important for predicting changes in the distributions of species.

Finally, I have included manuscripts describing research that I have conducted during my tenure at the University of Nebraska-Lincoln in addition to my dissertation (Appendix I-IV). These include summaries of recent occurrence of formerly extirpated

carnivores in Nebraska, recent records of moose in the central United States, a morphological and colorimetric analysis of the big brown bat in Nebraska, and the prediction of occurrence and potential spread of invasive plants species along the North Platte River in Nebraska.

PREVIEW

CHAPTER 1

Evaluation and Application of Predictive Habitat Models with Simulated and Real Species Occurrence Data

INTRODUCTION

Predictive habitat modeling has become an important tool in ecology because of its ability to investigate relationships between a species' occurrence and the environment (Segurado and Araújo 2004, Austin 2007). Results from these analyses can be used to produce habitat-suitability maps, which can infer the potential distribution of a species. Such predictions are useful for ecosystem studies (Ferrier et al. 2002, MacNally and Fleishman 2004), conservation planning (Polasky and Solow 2001, Gibson et al. 2004, Johnson et al. 2004), and studying large-scale biogeographical issues, such as contraction of geographic ranges (Gates and Donald 2000, Donald and Greenwood 2001) and management of invasive species (Peterson 2003, Herborg et al. 2007, Loo et al. 2007).

Although these methods are commonplace in the scientific literature, much debate centers on which model is most suitable for predicting distributions of species. Studies address this issue by evaluating performance of different models with a variety of data sets and model-fitting methods (Guisan and Zimmermann 2000, Segurado and Araújo 2004, Elith et al. 2006). Most studies use real empirical data that are inherently biased, and therefore, it is impossible to identify which model is most "correct." One solution is to use simulated data on species occurrences to evaluate model performance (e.g. Tyre et

al. 2001). The benefit of using simulated data to test model performance is that the true ecological relationships are known.

Predictive models of distributions can be placed generally into one of two categories based on the type of data they require (Guisan and Zimmermann 2000). The first category requires data on both the presence and absence of a species (presence-absence models), while the second requires only presence data (presence-only models). Most comparative studies agree that good quality presence-absence data sets provide more robust and accurate predictions of a species' distribution (Guisan and Zimmermann 2000, Zaniewski et al. 2002, Brotons et al. 2004, Segurado and Araújo 2004); however, there are problems associated with these data sets, primarily because of the difficulty in accurately and consistently verifying absences (Tyre et al. 2003, Mackenzie 2005, Wintle et al. 2004). Dispersal tendencies of most organisms make it problematic to assume a species truly is absent from a given area (Rushton et al. 2004). Other issues, such as fragmentation, population demographics, and competition (Araújo and Williams 2000, Loehle and LeBlanc 1996, Hanski 1994, Tyre et al. 2001, Anderson et al. 2002) also may exclude species from otherwise suitable habitat. Therefore, assuming that absence of species is the result of unfavorable environmental conditions may not always be valid. Additionally, presence-absence data sets are time consuming and expensive to collect (Austin et al. 1994, Franklin 1998).

Several issues also have been identified for presence-only data sets. These data sets reside primarily in herbaria and museum collections, commonly are biased towards certain locations, and generally are not collected in a systematic fashion. Also, there is a general bias between common and rare species (Zaniewski et al. 2002), and most of the

data lack precision and accuracy (Engler et al. 2004). These sources of error and uncertainty make it more difficult to distinguish between sampling and process variance. Given these caveats, evaluations of predictive modeling with simulated data sets are warranted.

Use of simulated data to test the performance of predictive habitat models has been minimal (e.g. Hirzel et al. 2001). In general, simulated methods are statistical or highly phenomenological models, rather than ecological models with realistic population processes. I suggest using a model with an underlying ecological platform that generates presence-absence points which can be systematically sampled to determine occupancy to evaluate model performance. Use of this methodology reduces the amount of bias because data would be generated from a model not used to make the predictions and the collection of data will closely resemble an ecological survey of a region.

The primary aim of this research was to evaluate the ability of presence-absence and presence-only models in predicting distributions of species when provided with high-quality, simulated presence-absence data. I compared the performances of two well known presence-absence models with two relatively novel presence-only models. To illustrate the application of these techniques, I applied my approach to a case study, one with real occurrence data, on the habitat requirements of the black-tailed prairie dog (*Cynomys ludovicianus*) in Nebraska.

MATERIALS AND METHODS

I compared 4 methods of modeling habitat parameters and evaluated their ability to predict distributions of species. Generalized linear (GLM) and generalized additive

(GAM) models are generalized regression techniques popular in modeling distributions of species because they are robust, easily applicable to many situations, and have a strong statistical background (Austin 2002). These methods relate a response variable, the presence-absence of a species, to one or more predictor variables, which in most cases is a set of environmental predictors (Guisan and Zimmermann 2000). The GLMs are a flexible family of regression models that can readily support several statistical distributions of the response variable. These models combine the predictor variables to form a linear predictor that is related to the response variable through a link function (Agresti 1996, Guisan et al. 2002). The GAMs are a non-parametric generalization of GLMs that incorporate a smoothing spline to fit non-linear functions, making them better suited for modeling complex ecological situations (Yee and Mitchell 1991, Austin et al. 1994., Zaniewski et al. 2002).

The two remaining modeling approaches are the maximum entropy model (MAXENT 2.3) -< <http://www.cs.princeton.edu/~schapire/maxent/>>- and the discrete choice model (DCM). MAXENT is a “general-purpose” presence-only modeling method that estimates the probability distribution by predicting the maximum entropy based on a set of constraints (Phillips et al. 2006). MAXENT characterizes the background environment with a sample of background points or pseudo-absences from the study region, but unlike the presence-absence models, species occurrences at these background points are unknown. One criticism of presence-only models is that they over-fit the data. To address this issue, MAXENT employs a regularization function to prevent over-fitting (Phillips et al. 2006). MAXENT is a relatively new method and has been subjected to minimal evaluation (Phillips et al. 2005, Hernandez et al. 2006, Elith et al. 2006);

however, in these tests, MAXENT performed well compared to other presence-only and presence-absence models.

Although MAXENT, GLMs, and GAMs use background points to create suitability maps, these are not chosen in the same way (see above). To assess the true performance of MAXENT, it is necessary to use a model that uses a similar analysis strategy. Discrete choice models (DCM) are a relatively new approach in ecology and primarily to examine resource selection by individuals (Cooper and Millspaugh 1999, McDonald et al. 2006, Telesco and Van Manen 2006, Thomas et al. 2006). The DCMs compare attributes of a chosen site to those of adjacent non-chosen sites selected randomly from within a “choice set.” A choice set is defined as a set of all possible resources available to the individual at a specific place and time (Cooper and Millspaugh 1999). For each presence point, a set of non-chosen or absence points are selected randomly within the choice set, similar to MAXENT. Cooper and Millspaugh (1999) suggested that DCMs could be used for predicting habitats, although most ecological applications have focused on the analysis of individual localities obtained through telemetry, rather than presence of species obtained through surveys.

To generate presence-absence datasets, I used a spatial population model based on the life history of the greater glider (*Petauroides volans*) of Australia: the “Virtual Ecologist” (see Tyre et al. 2001 for details). This approach allowed me to create a dataset from an ecological model not associated with the predictive models I was testing. This model also has been used to evaluate the power of presence-absence surveys to detect population trends (Rhodes et al. 2006). I only describe each of these components in general terms; for details see Tyre et al (2001).

To generate high quality presence-absence data, I created a reasonable underlying process simulation of the species. The simulation was individual based, tracking the locality and states of life history all females in the population at one-year intervals. I ignored males in this implementation for simplicity and because they do not contribute individually to population growth. That is, females are the limiting sex. The basic spatial unit was the home range of a female. All runs of the simulation were performed on a 128 x 128 grid of home ranges, using a six-cell hexagonal neighborhood. There were four important components of the simulation: (1) a landscape of spatially varying quality of habitat, (2) a population of individuals, (3) a connection between habitat quality and vital rates (survival and fecundity) of individuals, and (4) dispersal rules used by individuals to move around the landscape. The parameters of the model are summarized in Table 1.1.

Each home range on the landscape had an associated habitat quality. I used a midpoint displacement algorithm (Saupe 1988) to create surfaces with a specific fractal dimension, H . At higher fractal dimensions, there was more fragmentation, resulting in isolated patches of high quality habitat interspersed with patches of low quality habitat. An example of a high-dimension habitat variable is the number of hollow trees (Lindenmayer et al. 1990). Landscape processes lead to trees occurring in clusters. Slope or soil types are examples of habitat variables with a lower fractal dimension. I linearly re-scaled the output of the fractal algorithm to keep habitat quality within the range 0–100.

Each individual had an annual probability of giving birth to a single female offspring and an independent probability of dying because of predation, aging, or another catastrophe. The heterogeneous landscape influenced individuals through either their

probability of surviving from one age class to the next or their probability of giving birth to a daughter. Both of these vital rates are probabilities bounded between zero and one. I assumed that habitat quality had a linear effect on the log-odds of survival or reproduction, and that animals can detect small differences in quality of habitat.

Little is known about how individuals disperse in a heterogeneous landscape (Wolfenbarger 1946, Gustafson and Gardner 1996, Zollner and Lima 1999). I assumed that individuals moved towards territories with greater habitat quality, controlled by a single parameter α . If $\alpha = 0$, all directions were equally likely regardless of their relative qualities. If $\alpha = 1$, each direction was chosen in direct proportion to its habitat quality. If $\alpha > 1$, good quality directions were weighted even more. For high α values, this strategy leads dispersers to remain in high-quality habitat during dispersal. Field studies indicated that some species stay within favorable habitat during dispersal (e.g., Wolfenbarger 1946, Holekamp 1984, Merriam and Lanoue 1990, Kindvall and Ahlen 1992, Nelson 1993, Haas 1995). I called this rule the “biased random walker.”

The biased random walker is distinct from a “correlated random walk” (e.g., Kareiva and Shigesada 1983, Zollner and Lima 1999) or “self-avoiding random walk” (Gustafson and Gardner 1996), where the direction chosen is correlated with the previous direction, but it has nothing to do with variation in the underlying landscape. Dispersal models responsive to landscape heterogeneity have been used for brown bears (Wiegand et al. 1998) and birds (Brooker et al. 1999). Individuals stop moving when they encountered a vacant territory, regardless of the habitat quality. Each individual has a probability of dying on each dispersal step. The number of steps taken is different for every individual and also depends on the local density of individuals, because in crowded