

Landscape- and Micro-scale Habitat Selection by Greater Short-horned Lizards

by

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ABSTRACT

Identification of critical habitat for species at risk is an essential component of the protection of rare species under Canada's Species at Risk Act. In this study, I identified important microsite and landscape-level habitat characteristics for endangered greater short-horned lizards (*Phrynosoma hernandesi*) at their northern range limit in Grasslands National Park, Saskatchewan, Canada. A total of 650 km of transect surveys were used to analyze habitat selection based on locations where lizards were detected relative to available random locations. At the microsite level, I compared occupied locations (n = 118) to random landscape (n = 234) and random home range locations (n = 117) in 0.3 m² ground cover plots and 0.12 m² thermal plots using a classification and regression tree. Comparisons of occupied and random landscape microsites suggested that lizards selected microsites with higher diversity of ground cover types, especially in areas with high cover of exposed soil. At the home-range scale, lizards selected habitats with complex combinations of ground cover types and thermal characteristics. Selection was greatest for microsites with low vegetation height, low cover of lichens and mosses, and minimum temperatures that were >26.2°C, although other combinations of microsite characteristics were also supported at the home-range scale. A model of landscape-scale habitat selection (resource selection function) was also estimated for the Park using 101 lizard locations and 5000 random available locations sampled along 650 km of meander transects. Habitat selection in summer was predicted best by juniper-dune vegetation community,

vegetation patchiness, and perhaps paradoxically areas of lower solar radiation. This model was used to define critical habitat for conservation management and to estimate an index of population size for the Park using the number of lizards detected, strip width of transects and classified habitat resulting in ~13,000 adult lizards. This population index provides a baseline for monitoring the success of conservation actions. As new information becomes available for this understudied species, improvements in the definition of critical habitat should be considered.

PREFACE

This thesis is an original work by Krista Allison Fink. The research project, of which this thesis is a part, received research ethics approval from the University of Alberta, Research Ethics Board, “Greater Short-Horned Lizard Research: Population Surveys, Habitat Relationships, and Critical Habitat Designation”, Protocol Number 687905, May 5, 2009 and Protocol Number 687905 Mod 2, May 1, 2010.

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CHAPTER 1. GENERAL INTRODUCTION

1. INTRODUCTION

Habitat protection is a tool used to facilitate the long-term persistence or recovery of an endangered species (Heinricks et al. 2010). Habitats that contribute to long-term conservation combine all the necessary components and interactions critical for survival and reproduction. In the case of reptiles, this includes suitable thermal conditions, available hibernation and nesting sites, shelter from predators, and available prey species (Valentine et al. 2007; Andersson et al. 2010; Santos et al. 2011; Dubey et al. 2012). Identifying suitable habitats is thus a critical first step in conserving reptile populations.

Thermal limitations generally restrict the distribution of reptiles (Thomas et al. 1999). Northern peripheral populations often have unique physiological and behavioral traits that allow persistence in a near-hostile climate (Besson and Cree 2010; Doody and Moore 2010). Despite these adaptive traits however, individuals in such populations are often thermally limited (Thomas et al. 1999), and exploit large-scale and micro-scale habitat features that create suitable small-scale thermal conditions in order to survive and reproduce in a marginal landscape (Suggitt et al. 2012).

In an effort to improve our understanding of the interactions between thermal conditions and habitat selection, I evaluated daytime active season habitat selection for the Greater Short-horned Lizard (*Phrynosoma hernandesi*), at the northern extent of its range during the active season. Two scales of analysis were explored. First, I used landscape-scale habitat characteristics to predict relative

probability of occurrence for Greater Short-horned Lizards in Grasslands National Park. On a smaller scale, I tested whether Greater Short-horned Lizards select warm microhabitats at their northern range edge or whether vegetation and substrate are more important to local habitat selection.

2. STUDY SPECIES AND AREA

Greater Short-horned Lizards are cryptic insectivorous lizards found in southwest Saskatchewan, southeast Alberta, and throughout the Great Plains as far south as central Mexico (COSEWIC 2007). The species is listed as endangered in Canada due to its limited distribution, severe habitat fragmentation, and because habitat quality and extent are thought to be declining (COSEWIC 2007).

Characteristics of Greater Short-horned Lizard habitat were assessed in the West Block of Grasslands National Park in southwest Saskatchewan (49°06'13"N, 107°25'14"W). This area represents 28,400 hectares of mixed grass prairie dominated by *Stipa* spp., riparian areas of shrub with *Shepherdia argentea*, *Symphoricarpos occidentalis*, and *Salix* sp., having an understory dominated by *Bromus inermis*, and deeply dissected shale dune badlands characterized by exposed shale substrate stabilized by *Juniperus horizontalis*. Climate is continental, with mean January and July temperatures of -12.4°C and 18.3°C respectively. Temperatures in January can be as cold as -49°C, whereas summer maximum temperatures in July can be as high as 41°C. Mean annual precipitation is 348 mm, most of which falls in June and July (Environment Canada,

unpublished data). Greater Short-horned Lizards do not occur further north than Grasslands National Park in Saskatchewan and this represents the northern extent of their range.

3. SPATIAL PREDICTION OF HABITAT

Critical habitat is defined by Canada's Species at Risk Act as "...the habitat that is necessary for the survival or recovery of a listed wildlife species..." (Species at Risk Act 2003, subsection 2(1)). This definition often encompasses qualitative, quantitative, and spatial characteristics. While a definition of critical habitat is not necessarily exclusively spatial, a physical delineation greatly clarifies how physical protection on the ground can be achieved for listed species.

A model-based approach is frequently used to predict where a species' existing distribution, and may also be used to predict a species' potential distribution (Williams et al. 2009; Cianfrani et al. 2010). Critical habitat is defined as the habitat necessary for survival or recovery; thus, when the entire distribution is unknown or unconfirmed, it may be necessary to model a species' potential distribution in addition to delineating the current distribution for the purposes of defining critical habitat.

Habitats occupied by Greater Short-horned Lizards vary widely throughout their range. In the core of their range, they occupy habitats as diverse as forested mountain ranges (Nevada) and alkaline flats (Utah). In the portion of their range in southeast Alberta, Greater Short-horned Lizards occupy the ecotone between upland prairie and coulee bottoms, coulee rims with southern exposures, and shale

dunes stabilized by *Juniperus horizontalis* (Powell and Russell unpubl. report 1996; James 2002). Habitat in southwest Saskatchewan mostly consists of stabilized shale dunes (Powell et al. 1998). While this description is useful in identifying general areas that may be suitable, it is not specific enough to delineate boundaries of critical habitat. A spatially explicit habitat model specific to the northern marginal range would be useful for predicting areas of critical habitat for Greater Short-horned Lizards in Canada.

4. SMALL-SCALE HABITAT SELECTION

Small-scale habitat for reptiles is usually described by a combination of habitat structural components and thermal attributes (Webb and Shine 1998; Mathies and Martin 2008; Pike et al. 2010). Structural habitat features largely determine local variations in thermal conditions that drive habitat selection (Suggitt et al. 2012). For example, Huey et al. (1989) found that gravid Garter Snakes (*Thamnophis sirtalis*) selected retreats sites under rocks of medium thickness (as compared to thin or thick rocks), where the variation in temperatures occurring throughout day was within the range preferred by the snakes. In the case of the endangered Broad-headed Snake (*Hoplocephalus bungaroides*) in southeastern Australia, rock crevices where preferred body temperature could be achieved (approximately 30°C) were strongly selected (Webb and Shine 1998). In both these examples, a specific cover type characteristic is indicative of important thermal characteristics. The strong interrelationships between structural components and thermal

conditions suggest that both should be investigated when attempting to describe microhabitat selection for reptiles.

Past research indicates that Greater Short-horned Lizards utilize thermal refuges (structural habitat features that moderate microclimates, such as beneath rocks, vegetation, or buried in soft substrate) during periods of thermal extremes (Powell and Russell unpubl. report 1996). During active periods, Greater Short-horned Lizards shuttle between sun and shade in an effort to thermoregulate (Powell and Russell 1985). Thermal factors likely limit the range of Greater Short-horned Lizards in Saskatchewan (Powell et al. 1998). If thermal factors are limiting the range of the species, lizards in Grasslands National Park may be exploiting warmer microclimates to persist at the northern edge of the range. A description of small-scale structural and thermal microhabitat should be included as a component of Greater Short-horned Lizard critical habitat.

5. THESIS OVERVIEW

The primary objective of this research was to identify habitat required for the survival and reproduction of Greater Short-horned Lizards in Grasslands National Park. This provides a basis for a formal critical habitat designation for Greater Short-horned Lizards in Saskatchewan. I achieved this objective using two complementary approaches: a landscape-scale spatially-explicit habitat model and a micro-scale study of the structural and thermal habitat features selected by Greater Short-horned Lizards. Two data chapters are followed by a short chapter focused on synthesis and management implications.

In Chapter 2: “Defining critical habitat for Greater Short-horned Lizards”, I used a resource selection function to predict relative probability of occurrence of the species in Grasslands National Park. The model was subsequently used to estimate an index of population size, an important indicator of successful conservation and species status.

In Chapter 3: “Do Greater Short-horned Lizards select hot spots or are other microsite characteristics more important?” I examined small-scale habitat selection. This chapter measures microhabitat characteristics selected by Greater Short-horned Lizards at their northern range extent. This chapter contributes an important component to Greater Short-horned Lizard critical habitat designation by identifying important small-scale habitat attributes within the coarse-scale modeled habitat defined in the previous chapter.

Finally, in chapter 4 I present a brief discussion of general conclusions of the thesis relating my work to conservation, identify limitations of my research and recommended future research required to enhance the conservation of Greater Short-horned Lizards.

Format of all chapters follows that of Herpetological Conservation and Biology.

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CHAPTER 2. DEFINING CRITICAL HABITAT FOR GREATER SHORT-HORNED LIZARDS

1. INTRODUCTION

For many species, habitat loss or degradation is the most common cause of population decline (Fischer and Lindenmayer 2007). Protected spaces, whether to protect an entire ecosystem or multiple wildlife species (e.g. National Wildlife Areas, Migratory Bird Sanctuaries), is one common approach used for conserving rare animals (Geldmann et al. 2013). Care must be taken, however, to ensure individual species' habitat needs are actually accommodated by such protection.

A complementary approach to wildlife conservation is based around the single-species legal protection afforded to many threatened and endangered species (e.g. USA, Endangered Species Act 1988; Canada, Species at Risk Act 2003). Canada's Species at Risk Act (2003) protects both threatened and endangered species and their critical habitat. Critical habitat is defined as "...the habitat that is necessary for the survival or recovery of a listed wildlife species..." (Species at Risk Act 2003, subsection 2(1)). When the habitat of rare species is preserved, we assume the web of biotic and abiotic factors necessary for long-term survival is preserved. A significant challenge associated with the single-species habitat-centric approach to conservation is the need to adequately identify the habitat of the species that includes the components and interactions critical for the persistence of the species.

Identifying critical habitat for small reptiles is particularly challenging. Reptiles are difficult to locate using standard survey techniques, making it difficult to

identify their habitat associations, extent of their occupied habitat, or population size (Harvey 2005; Santos et al. 2006). One such reptile, the Greater Short-horned Lizard (*Phrynosoma hernandesi*), is listed as an endangered species under Canada's Species at Risk Act (2003). Greater Short-horned Lizards are designated as endangered in Canada due to their limited distribution, severe habitat fragmentation, and because habitat quality and extent are thought to be declining (COSEWIC 2007). Some portions of existing habitat are threatened by agricultural activities, oil and gas development, urbanization, and proliferation of roadways (ASRD 2004). Habitat protection is an important tool that could be used to ensure the long-term persistence of Greater Short-horned Lizards in the Canadian portion of their range.

Most Greater Short-horned Lizard habitat identified thus far in Canada is within southwestern Alberta (Powell and Russell 1994; James 2002, 2003). Studies there suggested that lizards typically inhabit one of three distinct types of habitat: (1) ecotone between upland prairie and coulee bottoms; (2) rims of canyons and coulees with southern exposures; and (3) friable shale dunes stabilized by mats of *Juniperus horizontalis*, which is most similar to habitat in occupied areas of Saskatchewan (Powell et al. 1998; James 2002). The majority of known occupied habitat in Saskatchewan falls within the current and proposed boundaries of or is adjacent to Grasslands National Park and is likewise composed of extensive friable shale dunes stabilized by *Juniperus horizontalis* (Powell et al. 1998). In addition to descriptive studies on habitat characteristics, a population estimate based on surveys of southeast Alberta has been conducted (ASRD 2004) and is

listed as tentative evidence for an endangered status for the species (COSEWIC 2007). No population-level information is currently available for Greater Short-horned Lizards in southwest Saskatchewan. However, population density is perceived to be lower in occupied habitat in Saskatchewan than in Alberta (Powell et al. 1998).

As valuable as these studies are, identifying critical habitat based on descriptive habitat associations and historical observations is insufficient. Habitats suitable for use by the species would not necessarily be identified as important for conservation if critical habitats are based solely on known occupied locations of the species, especially if suitable habitats have not been surveyed, or these habitats are unoccupied (Cianfrani et al. 2010). Rather, habitat associations need to be quantified and tested in a way that is conducive to mapping habitat for conservation management. As a consequence, a model-based approach that predicts potential habitat contiguously across an area of interest is needed (Williams et al. 2009). Spatially explicit habitat models are a useful tool for the conservation of rare wildlife (e.g. Bond et al. 2009; Hough and Dieter 2009; Singh et al. 2009). Models are therefore increasingly used as a way to delineate critical habitat for at-risk wildlife in Canada (e.g. Greater Sage-grouse (*Centrocercus urophasianus*), Aldridge 2005; Lungle and Pruss 2008; and Sprague's Pipit (*Anthus spragueii*), Environment Canada 2012).

Spatially explicit habitat models can be developed using sample locations of animals and spatially-distributed environmental predictors such as vegetation and topographic associations (Buskirk and Millsbaugh 2006; McLoughlin et al. 2010).

Model predictions would define the extent of habitat including, but not limited to, areas of known occurrences. Here I present a model-based approach to identifying habitat for Greater Short-horned Lizards in Grasslands National Park. General descriptions of lizard habitat in Saskatchewan identify juniper-dune habitat as the primary habitat type used (Powell et al. 1998). At a landscape-scale, this descriptive identification of habitat can be dissected into vegetation associations (juniper), substrate associations (shale substrate), and topographic associations (rugged dunes, coulee edges, steep slopes) and subsequently modeled to predict relative probability of occurrence. The literature on reptiles, especially for northern peripheral populations, also suggests that thermal conditions are important predictors of occurrence (Powell and Russell 1985). Here, I use environmental predictors based on habitat associations described in the literature to predict relative occurrence for Greater Short-horned Lizards in Grasslands National Park in southwest Saskatchewan. I predict that variables describing vegetation associations of badland habitats best predict occurrence. Vegetation is likely important because it integrates numerous characteristics of the landscape (substrate, topography, and thermal conditions) identified as important in prior research. Secondly, I apply the predictive model to estimate an index of population size for Greater Short-horned Lizards for Grasslands National Park using survey encounter rates in different habitat types. I expect local abundance to be similar to occupied habitats in other parts of the northern range.

2. METHODS

2.1 Study area.—Greater Short-horned Lizard habitat was assessed in the west block of Grasslands National Park in southwest Saskatchewan (49°06'13"N, 107°25'14"W) (Fig. 2-1). This area represents 28,400 hectares of mixed grass prairie dominated by *Stipa* sp., riparian areas of shrub with *Shepherdia argentia*, *Symphoricarpos occidentalis*, and *Salix* sp. having an understory of *Bromus inermis*, and deeply dissected open shale dune badlands stabilized in areas by *Juniperus horizontalis* and other small shrubs. The study area is bisected by the Frenchman River. Climate is continental, with mean January and July temperatures at the Val Marie, Saskatchewan weather station of -12.4°C and 18.3°C respectively. Temperature extremes in January can be as cold as -49°C, while summer maximum temperatures achieved in July can be as hot as 41°C. Mean annual precipitation is 348 mm, most of which falls in June and July (Environment Canada, unpublished data). Greater Short-horned Lizards have not been detected north of Grasslands National Park in Saskatchewan and this represents the northern extent of their range in Canada.

2.2 Study design.—Greater Short-horned Lizard locations were identified along 650 km of 2 m wide random survey strip transects walked at 2-3 km/h between 21 May 2010 and 12 August 2010 (Fig. 2.2). Transects were searched by two observers experienced in detecting Greater Short-horned Lizards. A new transect starting location was selected by the observers each day with the intention of covering as much of the study area as possible. The precise transect route was not

predetermined after the starting location. To define search effort, observers maintained a GPS tracklog while traversing transects. Environmental predictors of habitat conditions along transects and at locations where lizards were detected along transects were sampled from a geographic information system (GIS). An observer searched for lizards in a 2 m wide belt along transects by disturbing the vegetation and rocks with a walking stick and looking for the movement of fleeing lizards. All lizards detected in the survey were captured and marked on their ventral surface with a black permanent marker in order to avoid sampling the same animal twice. Neonate lizards were not included in analysis because they frequently occurred in clusters near the location where they were born and only were present during the last week of sampling. This decreased the potential for temporal biases that would lead to changes in population size among transects (time of sampling). Care was taken to search all available habitat types (upland grassland, valley bottoms, sagebrush flats), although more effort was focused on areas where Greater Short-horned Lizards were thought to occur, including coulee edges and bottoms, areas with badland topography, and exposed shale substrates (Table 2-1). Although Greater Short-horned Lizards are cryptic, detection differences between observers and across habitat types was not estimated. I therefore assumed that non-detection (detectability) occurred randomly across habitat types and did not bias estimates of lizard occurrence (Manly et al. 2002; Gu and Swihart 2003). Habitat-based estimates of population density do, however, reflect only detected lizards and thus represent a conservative estimate of local population size.

2.3. Resource selection functions.—A resource selection function (RSF) was used to model lizard habitat in Grasslands National Park based on used (lizard occurrences) and available descriptions of study locations. A Type I study design was used, which compares the habitats where individual animals occur at the population level to habitats available to the population on the landscape (Thomas and Taylor 1990; Manly et al. 2002). Available (pseudo-absence) locations were constrained to a random sample of 5,000 locations along survey transects at least 30 m apart, whereas lizard occurrences were used to define used locations. Preliminary analyses suggested that using fewer random (available) locations did not accurately characterize the distribution of the environmental variables in the areas searched. Initial analyses also indicated that the full range of environmental values were covered by random walk transects, and thus any RSF models applied to the study area are considered within the range of environments sampled.

2.4 Environmental predictors.—Greater Short-horned Lizards utilize a wide variety of habitats throughout their range (Montanucci 1981; Sherbrooke 2003). Lizards at the northern extent of their range in Canada are closely associated with juniper-stabilized badlands and south-facing coulee slopes (Powell et al. 1998; COSEWIC 2007). This habitat is characterized by steep, rugged, sparsely vegetated slopes and sandy dunes composed of Bearpaw shale, an exposed sedimentary rock that forms the primary component of the substrate in parts of northern Montana, southern Alberta and southern Saskatchewan (James et al.

1997; Powell 2010). In addition to the topography, soil type, and vegetation community, slope and aspect may play a role in defining habitat needs for Greater Short-horned Lizards. At the northern range extent of its range in Alberta, lizards have been typically associated with south-facing slopes, which I hypothesized were selected because of thermal characteristics (Powell and Russell 1991; James et al. 1997).

Landscape variables used to predict lizard habitat were divided into four categories or themes representing broad habitat characteristics. These themes include vegetation, topographic, thermal, and substrate factors (Table 2-2). Vegetation characteristics of lizard habitat were modeled using measures of vegetation cover, vegetation patchiness, and probability of an erosional vegetation community. Normalized Difference Vegetation Index (NDVI) was used as a surrogate measure of vegetation cover. NDVI is a measure of chlorophyll abundance and photosynthetic energy absorption and is calculated from the infrared and near-infrared light spectra (Myneni et al. 1995). Areas with high cover of live green plants absorb high amounts of photosynthetically-active radiation. NDVI was derived from a SPOT 5 multispectral satellite image (10 m resolution) acquired mostly in June 2008 (Environment Canada 2009) and was calculated from the near infrared and visible red spectrum bands as given by the following equation:

Equation 1)

$$NDVI = (\alpha_{nir} - \alpha_{vis}) / (\alpha_{nir} + \alpha_{vis})$$

where a_{nir} and a_{vis} represent the reflectance from the near infrared and visible red spectrum (Carlson and Ripley 1997). Given that the plant community where Greater Short-horned Lizards have been observed previously is described as ‘patchy’ (COSEWIC 2007), a measure of vegetation patchiness was calculated as the standard deviation of NDVI within a 200 m radius neighbourhood. The 200 m radius scale was selected because it is similar in size to an approximate home range for a female lizard (K. Fink, unpublished data).

A unique plant community of *Rosa* sp., *Eurotia lanata*, *Thermopsis rhombifolia*, and *Phlox hoodii* occurs in combination with juniper on eroded soils. The distribution of this erosional plant community in Grasslands National Park was modeled with predictive vegetation mapping by the Saskatchewan Research Council (unpubl. report 2009) following methodology similar to Franklin (1995). A variable describing the probability of the erosional plant community was calculated by averaging the probability of an erosional plant community over a 200 m radius.

Topographic predictors were included to represent the steep, rugged badland features selected by Greater Short-horned Lizards (Powell et al. 1998; James 2002). Predictors used to model badland topography included a measure of ruggedness, slope, landform shape, and topographic position. Elevation data used to calculate the topographic-based predictors was obtained from a 20 m digital elevation model (DEM) from Environment Canada (2003).

Ruggedness was estimated from a topographic ruggedness index, calculated using the “TRI.aml” algorithm (Evans 2004a). This index quantifies topographic

heterogeneity (Riley et al. 1999). Percent slope was derived from a DEM using ArcMap 9.3 (ESRI, Redlands, California USA). Landform shape was derived from the "landform.aml" algorithm using Bolstad's method (Evans 2004b). This algorithm identifies topographic features (ridge, slope, toe slope). Topographic position was derived using Zimmermann's (2001) algorithm "topo.aml". This algorithm estimates each position relative to all other cells in an expanding neighborhood. Small values indicate valley bottoms and large values indicate cliffs or ridge tops.

A solar radiation variable was included to test if Greater Short-horned Lizards select south-facing slopes at their northern periphery (Powell and Russell 1991, James et al. 1997). Rather than rely on aspect as a surrogate for the amount of solar radiation received, global solar radiation was calculated for a given location using the sum of Zimmermann's (2001) algorithms "shortwarc.aml" (shortwave radiation) and "diffuse.aml" (diffuse radiation) models. These algorithms estimate the amount of radiation received by a location over a specified time period ($\text{KJ/m}^2/\text{day}$). Inputs to the algorithm (latitude (49°), time period (one day), and Julian day (172)) were chosen to represent radiation typical of the active season. All "aml" algorithms were run in ArcInfo Workstation (ArcInfo 9.3, ESRI, Redlands, California, USA).

To assess the importance of substrate in predicting Greater Short-horned Lizard habitat, I included soil texture and an index of stoniness as predictors of selected habitat. Soil texture was included because lizards are associated with the Bearpaw shale soil formation in Saskatchewan, which has a coarse soil texture (Powell et

al. 1998; Powell 2010). Presence of surface rocks and stones can be a good predictor of lizard habitat because the crevices near stones provide shade opportunities and the stone surfaces provide basking locations (Beauchamp et al. 1998; Wone and Beauchamp 2003). Soil texture and stoniness data were obtained from Parks Canada, and are based on soil surveys conducted by the Saskatchewan Institute of Pedology (1992). Data were stored as discrete polygons encompassing individual soil associations. Preliminary analysis indicated that soil texture predicted lizard occurrence best when categories were combined to a simplified binary variable (coarse soil texture and fine soil texture). See Table 2-3 for a summary description and data source for each environmental predictor.

2.5 Framework for modeling lizard habitat.

2.5.1 Statistical models of relative occurrence.—Univariate analysis was conducted for each of the candidate variables (Table 2-3). Local polynomial smoothing was used to identify basic non-linear relationships (quadratics) between lizard use and each of the continuous environmental predictors. If non-linear relationships were identified in univariate analyses, quadratic terms were included in subsequent multivariate models. Following Hosmer and Lemeshow (2000), univariate analyses for all hypothesized environmental predictors were used to rank significance between factors based on the Wald test from logistic regression and p-value cut-off point of 0.25 (Hosmer and Lemeshow 2000; Bursac et al. 2008). If two variables were correlated ($|r| > 0.7$), only the variable

that explained the greatest deviance and was most biologically meaningful was retained in subsequent analysis.

A global model was fitted using sample-weighted logistic regression fitted in STATA 12 (StataCorp, College Station, Texas, USA) by specifying a binomial distribution and a logit link function. Samples were weighted such that available locations ($n = 5,000$) and used locations (much fewer than 5,000) had the same cumulative weight in the data set to reduce Type I error rates of inflated significance (used locations, weight = 1; available locations, weight = (number of used)/5000). Model variables were added individually in the order indicated by univariate ranking following Hosmer and Lemeshow's (2000) model building approach. Terms were removed from the model if their p-value was greater than 0.10 (Hosmer and Lemeshow 2000). Once all terms had been tested in the model, dropped terms were added back one at a time to identify potentially confounding variables where $P < 0.1$ and a 15% change in the parameter estimate in one of the variables in the model was observed (Bursac et al. 2008). Interaction terms hypothesized to be biologically relevant were then added to the model. Lastly, individual variables that had been dropped from the model were added back one at a time to check that none were confounding once an interaction term was retained (Hosmer and Lemeshow 2000).

A receiver operating characteristic (ROC) curve was used to estimate relative predictive accuracy of the final model. Area Under the Curve (AUC) ROC values above 0.9 were considered to represent high model accuracy, 0.7-0.9 good model accuracy and < 0.7 low model accuracy (Manel et al. 2001). In the case of

sample-weighted logistic regression and use-available designs, ROC curves give a biased estimate of predictive accuracy (Boyce et al. 2002). Despite this bias, the ROC curve provides an indication of the relative predictive accuracy among models tested.

2.5.2 Spatial predictions of lizard habitat.—Model predictions from the final selected model were at a 20-m resolution (raster size) and estimated by the equation:

Equation 2)

$$w(x) = \exp(\beta_1 x_1 + \beta_2 x_2 + \dots + \beta_k x_k),$$

where $w(x)$ is the raw RSF value for each pixel in the landscape; x_1, x_2, \dots, x_k represent the values for the predictors for each pixel; and β_1, \dots, β_k are model parameters estimated from logistic regression (Boyce et al. 1999; Manly et al. 2002; Johnson et al. 2006). The raw RSF was re-scaled between zero and one using the equation:

Equation 3)

$$\text{rescaled RSF} = \frac{(\text{raw RSF} - \text{minimum RSF value})}{(\text{maximum RSF value} - \text{minimum RSF value})}$$

2.6 Model validation.—An independent data set consisting of 68 lizard observations collected between 1994 and 2009 were used for evaluating model performance. Both neonates and adults were included in the validation data set. Surveys in 1994 and 2009 were conducted using meander transects. Additional search effort was often made in an area if an initial lizard was detected. Only

observations located a minimum of 30 m apart were retained in the validation data set to avoid sampling a single raster cell multiple times.

RSF scores were binned into 10 quantiles of equal area. Bins were collapsed such that adjacent bins with similar selection were combined until the final bins represented progressively selected habitat for the validation data set (Johnson et al. 2006). The Wilcoxon signed-rank test was used to test if selection in each bin for validation data was similar to selection in each bin for training data. Similar selection would indicate that the model was robust across different methodologies and time periods. A Spearman's rank correlation test was used to test if the selection for the training data set and validation data set increased with progressively higher selection. If the model performed well, selection would increase in each subsequent bin (Boyce et al. 2002). Model validation was completed both for the 10 initial RSF bins and collapsed bins.

2.7 Habitat-based index of population size.—To estimate an index of minimum population size for lizards in the West Block of Grasslands National Park, I assumed a 2 m wide search strip along all random survey transects (1 m on either side of the surveyor, similar to James 2002, 2003). Each transect was intersected with the RSF bin to calculate total search effort (area searched) per bin and the density of lizards in each bin calculated by dividing the number of lizards observed in that bin by the area searched. Given that detectability is likely < 1, this index of population size is considered a conservative estimate and assumes detectability is constant among habitats. A spatial mask was used to exclude non-

habitat (roads, Frenchman River and cultivated fields) from the map of classified RSF bins. The habitat-based index of population size was estimated as the sum of the product between total area of each RSF bin (minus the area of the spatial mask) and bin-specific lizard density.

3. Results

3.1 Survey results.—In total, 118 adult and juvenile lizards were observed. All 118 locations were used to fit habitat models. One hundred and one lizard locations fell within 1 m of the 650 km of random-walk transects (Fig. 2-2). These 101 locations were used to make a habitat-based population index of lizards in Grasslands National Park.

3.2 Lizard relative occurrence model.—Based on univariate analyses, I considered nine uncorrelated variables for inclusion in the global multivariate model of lizard relative occurrence. Slope and ruggedness were highly correlated ($r = 0.945$) with ruggedness chosen to be used in further analyses. Non-linear quadratic responses were included for the probability of an erosional vegetation community, for vegetation patchiness, and for topographic ruggedness. In the initial round of model variable selection, five variables were retained in the model (probability of an erosional vegetation community, vegetation cover, vegetation patchiness, and global solar radiation). Six variables (soil texture, ruggedness, stoniness, topographic position and landform shape) were not found to significantly differ in performance ($P < 0.1$) when added to the model in the order

of their univariate ranking. After adding these variables back into the model individually, it was determined that none of these variables were confounding. No first-order interactions were significant. The final model is given in Table 2-3. A map of model predictions is given in Fig. 2-3.

Greater Short-horned Lizard habitat was best predicted by probability of an erosional plant community, vegetation cover, vegetation patchiness and solar radiation (Table 2-3). Lizards generally occurred in areas with a high probability of an erosional plant community. A significant quadratic term in the model indicated that this relationship decreased in areas having a very high probability of an erosional plant community. Lizard occurrence was also associated with habitats with low vegetation cover as indicated by low NDVI values. Lizard occurrence was non-linearly related to vegetation patchiness, where there was a quadratic (hump-shaped) response. Lizards generally occurred where vegetation patchiness was high, although at very high levels of patchiness, this relationship diminished. Lastly, lizards were associated with areas of low solar radiation. Area under curve of the receiver operator characteristic (ROC) was 0.736, indicating that the model has good accuracy.

3.3 Model predictions and validation.—Reclassifying the continuous RSF into bins representing progressively selected habitat resulted five final habitat selection bins (Fig. 2-4a, b). Model validation was completed using the collapsed (five) bins.

Selection ratios in each of the five bins did not significantly differ between training and testing (validation) data sets ($W = 13.75$, $P = 0.586$, Fig. 2-4b). Habitat selection for training data increased in an ordinal manner ($r_{\text{training}} = 0.975$, $P = 0.005$). Selection ratios also increased significantly in an ordinal manner for the validation data set ($r_{\text{testing}} = 1.0$, $P < 0.001$, indicating that five bins adequately divide the continuous model into habitats experiencing progressively increased selection. A five-bin map of lizard habitat is shown in Fig. 2-5.

3.4 Habitat-based index of population size.—A habitat-based index of population size was estimated using location data from 101 adult lizards observed within the modeled area in 2010 and the reclassified relative occurrence model. Seventeen locations used in the training data set were excluded from the analysis because locations did not fall within 1 m of a random-walk transect. No lizards were observed in the “non-habitat” and “very rare” bins representing 17,091 ha of habitat and 199 km of search effort. In the “rare” bin representing 5,450 ha of habitat, 19 lizards were observed over 153 km of search effort, yielding an estimated minimum population density of 0.62 lizards/ha or 1.24 lizards per 10 km search effort. In the “moderate” bin representing 2,647 ha of habitat, 30 lizards were observed within 116 km of search effort, yielding an estimated minimum density of 1.30 lizards/ha or 2.59 lizards per 10 km search effort. And finally, in the “high” bin representing 2,513 ha, 52 lizards were encountered in 176 km of search effort, yielding an estimated minimum density of 1.48 lizards/ha or 2.96 lizards per 10 km search effort. The habitat-based index of population size

of adult lizards in Grasslands National Park based on amount of habitat was estimated at 13,632 individuals (Table 2-5).

4. DISCUSSION

Characteristics typical to the juniper-stabilized badlands described by Powell and Russell (1991), James et al. (1997), and Powell et al. (1998) were good predictors of Greater Short-horned Lizard occurrence, although additional predictors not previously described included vegetation patchiness and solar radiation. Surprisingly, relatively low solar radiation was a good predictor of lizard occurrence, contrary to what was predicted. The model developed here can be used to predict critical habitat and a habitat-based minimum population size for Greater Short-horned Lizards at the northern periphery of its Canadian range which has not been previously done. Using this model to map minimum local population density provides the means necessary to guide designation of critical habitat and thus ensure that the majority of habitats lizards occupy in Saskatchewan are protected.

4.1 Model habitats and Greater Short-horned Lizard biology.—Relationships between relative probability of occurrence of Greater Short-horned Lizards and predictor variables reveal possible biological links between Greater Short-horned Lizards and selected habitat. Lizards selected habitat that had 1) low amounts of vegetation cover, 2) moderate vegetation patchiness, 3) a moderate probability of being within an erosional vegetation community, and 4) low global solar

radiation. Probability of an erosional vegetation community and vegetation patchiness were related in a non-linear way (quadratic peak) with lizard occurrence, indicating that occurrence decreased at higher levels of vegetation patchiness or greater probability of erosional vegetation community (Figs. 2-6, 2-7, 2-8, and 2-9).

Lizards selected habitats with low amounts of vegetation cover compared to what is generally available in the study area. Lizard surveys in Alberta also found that lizards occurred in areas with low vegetation cover (approximately 50% exposed soil, James 2002). Areas with less vegetation (and conversely more bare ground) may be selected for ease of mobility. Field observations suggested that Greater Short-horned Lizards do not move well through dense vegetation (James et al. 1997). Indeed, Newbold (2005) and Rieder et al. (2010) found that the sprint speed of *Phrynosoma platyrhinos*, a closely related species with similar morphology as Greater Short-horned Lizards, was significantly decreased by increased grass cover, indicating that open ground may be important for movement.

While lizards in the study area generally selected areas with low vegetation cover, they selected areas that have some patches of scattered vegetation, similar to occupied habitat in southeast Alberta (Powell and Russell 1991). The dominant shrub *Juniperus horizontalis* stabilizes areas that are prone to erosion in the study area, creating a patchwork of exposed substrate and vegetated areas. A previous survey of Grasslands National Park determined that lizards were generally found on bare substrate between patches of vegetation (Powell et al. 1998). Patches of

vegetation may be beneficial for thermoregulation by providing ample open areas to bask in near areas of vegetated shelter (Powell and Russell 1985; James et al. 1997). Fine scale patches of vegetation are likely important for the thermal regulation of Greater Short-horned Lizards, who rely on shuttling short distances to control their body temperature (Powell and Russell 1985). Alternatively, the patchy arrangement of vegetation stabilizing the shale dunes may play an important role in providing habitat for prey species (Powell and Russell 1984). Greater Short-horned Lizards consume a wide range of insect prey types, including ants, nonsilphid Coleoptera (beetles) and Orthoptera (grasshoppers and crickets) (Powell and Russell 1984). Patches of vegetation are likely necessary to maintain the large diversity of insects that make up the diet of Greater Short-horned Lizards (Powell and Russell 1984).

Greater Short-horned Lizards in Grasslands National Park were associated with areas of erosional plant community, which is typically dominated by shrubs. Lizards in Alberta were observed in habitats with approximately 25% shrub cover, including the species *Juniperus horizontalis*, *Artemisia cana*, *Rhus trilobata*, *Sarcobatus vermiculatus*, and *Ericameria nauseosa*, although lizards were more influenced by habitat structure than by vegetative species composition (James 2002). *Ericameria nauseosa* may be of particular importance to Greater Short-horned Lizards due to the structural component it contributes to lizard habitat. *E. nauseosa* is a perennial with numerous branches extending from a crown and a thick woody taproot. On eroded slopes, the taproot is progressively exposed below the crown, leaving a sheltered hollow below the branching stems

and litter. This hollow is frequently used as shelter for lizards on hot days and overnight (K. Fink, unpublished data). Lizards were observed using similar shelters created by shrubs in Alberta (James 2002). This specific morphology in combination with the eroded conditions creates unique habitat features exploited by Greater Short-horned Lizards.

While the relationship between lizard occurrence and vegetation-related predictor variables were consistent with prior published research, an inverse relationship observed between lizard occurrence and global solar radiation was unexpected. Lizards were associated with areas receiving relatively low amounts of solar radiation compared to what is generally available on the landscape. This is in sharp contrast with habitat associations described in Alberta, where as many as 70% of lizard observations were made on south-facing slopes (James 2002), which were hypothesized to have been selected for its adventitious warm thermal characteristics (Powell and Russell 1991, 1992; James et al. 1997). However, their search effort was not quantified by aspect and it may be that these surveys preferentially searched south-facing slopes. Cooler slopes may be selected by Greater Short-horned Lizards during the hottest part of the active season. In the eroded areas with low vegetation cover selected by lizards, south-facing slopes may be too hot for lizards during summer as surface temperatures in the study area observed with an infrared camera were as high as $>70^{\circ}\text{C}$ (K. Fink, unpublished data). Such high temperatures greatly exceed the preferred body temperature of Greater Short-horned Lizards, which is approximately 35°C (Prieto and Whitford 1971) and may explain why lizards did not select warm

slopes in the study area during the active season. Areas with high solar radiation may, however, be important during cooler times of year. Powell and Russell (unpubl. report 1996) found evidence of seasonal shifts (migration) from summer home range areas to areas of hibernation. A seasonal shift in home ranges has also been observed for other horned lizards that undergo winter dormancy (e.g. *Phrynosoma mcallii*, Wone and Beauchamp 2003). Such a shift may occur so that Greater Short-horned Lizards may utilize habitat with lower solar radiation during the hottest months of the year and then subsequently move into areas with high solar radiation to overwinter (typically September-April in the northern parts of the range), although one study in Colorado found that hibernation sites on south-facing slopes did not differ from what would be expected by a random distribution (Mathies and Martin 2008). Other factors, such as snow accumulation or soil penetrability, may be more important for lizard survival in overwintering habitat.

4.2 Habitat-based index of population size.—While habitat is important for identifying areas to be protected as critical habitat, monitoring population numbers (growth) within the protected area is important to determine successful maintenance or recovery of populations (Heinrichs et al. 2010). A habitat-based population index using a reclassified relative probability of occurrence model provides a baseline minimum population size and given similar future surveys may be useful for monitoring changes in population size. Using the reclassified model based on five habitat bins, I estimated a minimum population size of

13,632 adult lizards in Grasslands National Park. This estimate may be best interpreted as an index of minimum population size since the effects of detectability were not considered. However, habitat predicted to be suitable, but without confirmed occupancy, was included and may potentially inflate the index of population size if these areas are unoccupied. In the most recent COSEWIC assessment and update status report on the Greater Short horned Lizard, a population estimate based on surveys in southeast Alberta is listed as tentative evidence for an endangered status for the species (COSEWIC 2007). At the time of the assessment, no population-level information was available for Greater Short-horned Lizards in Saskatchewan. Surveys conducted in Alberta in 2002 determined that there were between 2,677 and 16,379 mature individual lizards in Alberta, with the population likely declining since the previous round of surveys in the early 1990s (James 2002, 2003; COSEWIC 2007). Lizard density in occupied habitat was determined to be approximately two lizards per hectare (James 2002, 2003; COSEWIC 2007). Powell et al. (1998) suggested that lizard densities in Grasslands National Park appear lower than lizard densities in occupied habitat in Alberta. In the 2009 surveys of Grasslands National Park, lizard densities ranged between 0-1.48 lizards per hectare, with the highest densities slightly lower than those observed in Alberta. Estimates of population size between Saskatchewan and Alberta cannot be easily compared due to differences in methodology (the Alberta survey did not differentiate between low- and high-density habitat; James 2002, 2003). While neither the Alberta population estimate nor this Saskatchewan population estimate are true measures of

population size, they do provide a repeatable method for monitoring populations, an important measure of the success in the conservation of an endangered species.

4.3 Identifying critical habitat in Grasslands National Park.—While the model is intended to rank areas in order of increasing conservation value, it does not identify a clear division between habitat and non-habitat. Rather, lizards appear to occur in Grasslands National Park along a continuum of low- to high-density conditions where lizards occupy a wide array of habitat characteristics. All lizard observations from the 2010 survey occurred in bins three, four, and five (out of five bins), encompassing 38% of the study area. Lizard presence in such a large proportion of the study area indicates that habitat does not occur in discrete patches, but rather on a continuum between low and high density. Greater Short-horned Lizards in southeast Alberta are considered habitat generalists, where they occupy a broad range of habitats as long as there is adequate environmental heat and there is enough prey to fuel survival and reproduction (James 2002). In other parts of their range, Greater Short-horned Lizards occupy habitat as varied as forested mountain ranges (Nevada) and alkaline flats (Utah) (Montanucci 1981). Their generalist nature may explain why lizards are found over a broad range of environmental conditions in Grasslands National Park.

The dispersed nature of occupied habitat for generalists, such as Greater Short-horned Lizards, makes the establishment of critical habitat for the species challenging. This model successfully identifies habitats that are most likely to represent increasing lizard density. In the absence of evidence of maladaptive

habitat selection (Schlaepfer et al. 2002), habitat where there is a high density of animals likely represents high-quality habitat and should be of high conservation priority for the species.

4.4 Future research needs

4.4.1 Dispersal.—Dispersal corridors may exist outside areas predicted as suitable habitat in the model. Not all historic (1994-2009) lizard observations fall within bins three, four, and five (historical observations: 7/68 were in bin two). Occurrences outside the areas predicted as suitable habitat may be the result of dispersal events, where lizards are moving permanently to a new habitat patches. Protection of dispersal corridors could be afforded by buffering locations for inclusion in critical habitat. Alternatively, these occurrences may indicate that the model does not accurately predict all combinations of suitable habitat for lizards.

In addition to the presence of lizard observations outside habitats predicted to be suitable, there are some instances of habitat patches that were predicted by the model to be suitable habitat, but do not encompass lizard observations. In some instances, these patches represent areas that have never been searched, and therefore no observations have been made. In other instances an apparently suitable patch may be isolated from colonization from occupied habitat (Taylor et al. 1993). Dispersal between patches of habitat was not modeled in this study. Dispersal is poorly understood for Greater Short-horned Lizards in all parts of their range.

Previous studies of Greater Short-horned Lizard movement have been restricted to estimates of home range size due to restrictions on the size of lizards that can carry a radio transmitter (typically only adult female *Phrynosoma* are large enough, Warner et al. 2006). Adult female Greater Short-horned Lizards spend a large portion of the summer in a restricted part of their home range (Powell and Russell unpubl. report 1996). Field observations indicate that it is likely the juvenile and adult male lizards who are the most likely dispersers across the inhospitable matrix of unsuitable habitats (Henke and Montemayor 1998). However, no sex-specific trend was evident in the observations that fell within the lowest density bin. More research is required to quantify dispersal and how it affects use of available habitat at the northern range extent.

4.4.2 Seasonal habitat.—While Greater Short-horned Lizards were observed in most areas predicted to be habitat, a portion of the study area was predicted as suitable habitat, but no lizards have been observed, both historically and in the surveys conducted for this study (compare Fig. 2-2 and Fig. 2-5). Some areas predicted to be suitable habitat may be unsuitable habitat because the area has the characteristics of good summer foraging habitat but may not have good winter hibernation habitat nearby. Hibernation habitat may in fact be the limiting factor for the species in the colder parts of its range (Mathies and Martin 2008). Past studies at the northern range extent in southeastern Alberta suggest that overwintering is a source of high mortality (Powell and Russell unpubl. report

1996). Therefore future research is needed to identify habitat attributes associated with overwinter survival at the northern range extent.

4.5 Conclusion.—A relative occurrence model and minimum population index is presented here as initial information for protecting habitat of Greater Short-horned Lizards in Saskatchewan. Future research is needed to increase our knowledge on the ecology of this elusive lizard and to better shape habitat protection based on habitat requirements of the species. The process of establishing critical habitat should be considered as a dynamic process – one that will require reiterative evaluation as new information regarding animal locations and the ecology the species becomes available.

TABLE 2-1. Search effort by vegetation type in Grasslands National Park, Saskatchewan, Canada where vegetation mapping occurred (1994 vegetation). The largest transect distance occurred in the erosional vegetation community, which is the vegetation type most often associated with Greater Short-horned Lizards. Search effort was high for the treed vegetation community, but actual distance searched in this rare vegetation type was small (396 m) since it is very rare in the study area.

General vegetation type	Area (ha)	Distance searched (m)	Search effort (m/ha)
Erosional community	5087	264267	51.9
Sloped grassland	5366	128436	23.9
Valley grassland	3919	95779	24.4
Shrub community	2237	44096	19.7
Treed community	3	396	129.7
Prairie dog colony	665	6949	10.5
Upland grassland	7843	80073	10.2
Disturbed community	1851	7106	3.8
Outside data layer	21	1904	92.0

TABLE 2-2. Independent environmental variables used to derive RSF models for Greater Short-horned Lizards in Grasslands National Park, Saskatchewan, Canada.

Variable category	Variable abbreviation	Description	Pixel Size	Variable type	Data source
Vegetation	NDVI	NDVI calculated from a multispectral image	20 m	Continuous	Environment Canada SPOT 5 10m multispectral digital ortho imagery (2008)
	NDVI_SD	The standard deviation of NDVI in a 200 m radius	20 m	Continuous	Environment Canada SPOT 5 10m multispectral digital ortho imagery (2008)
	ERODE	Averaged probability of erosional vegetation community over a 200 m radius	30 m	Continuous	Grasslands National Park (GNP) Predictive Vegetation Mapping (2009)
Topographic	TRI	Topographic ruggedness index	20 m	Continuous	tri.aml (Evans 2004, Riley et al. 1999), DEM
	SLOPE	Percent slope	20 m	Continuous	DEM
	LANDF	Landform shape index, using Bolstad's method	20 m	Continuous	Landform.aml (Evans 2004, Bolstad 1992), DEM
	TOPO	Topographic features	20 m	Continuous	toposcale.aml (Zimmermann 2001), DEM
Thermal	SOLAR	Global (diffuse and direct) solar radiation based on Julian day (172), a digital elevation model (DEM), and the latitude	20 m	Continuous	shortwavg.aml, diffuse.aml (Zimmermann 2001), DEM
Substrate	STONE	Index of the amount of stones in the surface substrate	Polygon	Categorical	GNP soil mapping (1992)
	TEX	Soil texture	Polygon	Categorical	GNP soil mapping (1992)

TABLE 2-3. Estimated coefficients (β_i), standard errors (SE), Z-scores and p-values (Wald Z statistic), standardized coefficients ($\beta_i\text{Std}$), and standardized odds ratios ($\exp(\beta_i\text{Std})$) of the final logistic regression model (RSF) predicting Greater Short-horned Lizard relative occurrence using detections (1) and search effort (0) in Grasslands National Park, Saskatchewan, Canada. Model variables were selected from an initial global set of variables using the Hosmer-Lemeshow (2000) approach to model building. The final model was used to spatially predict lizard habitat selection. Independent model validation indicated good model accuracy (AUC = 0.736). See Table 2-2 for variable definitions.

Variable	β	SE	Z	$P > Z $	βStd	SE	$\exp(\beta\text{Std})$	SE
ERODE	0.144	0.045	3.10	0.002	2.876	0.928	17.759	16.471
ERODE ² *	-1.516	0.609	-2.49	0.013	-1.978	0.796	0.138	0.110
NDVI	-18.369	6.701	-2.74	0.006	-0.567	0.207	0.567	0.117
NDVI_SD	319.478	120.965	2.64	0.008	2.496	0.945	12.131	11.464
NDVI_SD ²	-7158.4	2869.7	-2.49	0.013	-2.549	1.022	0.078	0.080
SOLAR*	-0.547	0.311	-1.76	0.079	-0.260	0.148	0.771	0.114

* SOLAR and ERODE² β and β SE values are 1000 times their actual value

TABLE 2-4. Thresholds used to define 10 approximately equal-area RSF bins predicting Greater Short-horned Lizard habitat in Grasslands National Park, Saskatchewan, Canada. The RSF was square root transformed. Number of lizard locations in each bin for both the training and validation data sets are also provided.

Bin	SQRT RSF breakpoints		Lizards observed		Area (ha)
	Min	Max	Training	Validation	
1	0	0.023	0	0	2339
2	0.023	0.035	0	0	3091
3	0.035	0.047	0	0	3161
4	0.047	0.066	0	2	3458
5	0.066	0.094	0	2	2966
6	0.094	0.125	0	3	2670
7	0.125	0.164	9	6	2693
8	0.164	0.215	13	7	2797
9	0.215	0.281	35	16	2655
10	0.281	1	61	32	2518

TABLE 2-5. Greater Short-horned Lizard habitat-based index of population size for Grasslands National Park, Saskatchewan, Canada based on estimated lizard density in each habitat bin. Bins were collapsed such that adjacent bins with similar habitat selection were combined until the final bins represented progressively selected habitat. Greater numbers of lizards were encountered per unit search effort in highly selected habitats.

Bin	Lizards	Survey length (m)	Area (ha)	Encounter rate (lizards/10 km searched)	Density (lizards/ha)	Estimated individuals
1: Non-habitat	0	57893	8279	0	0	0
2: Very rare	0	141124	8812	0	0	0
3: Rare	19	153083	5450	1.24	0.62	3382
4: Moderate	30	115635	2647	2.59	1.30	3434
5: High	52	175900	2513	2.96	1.48	6816

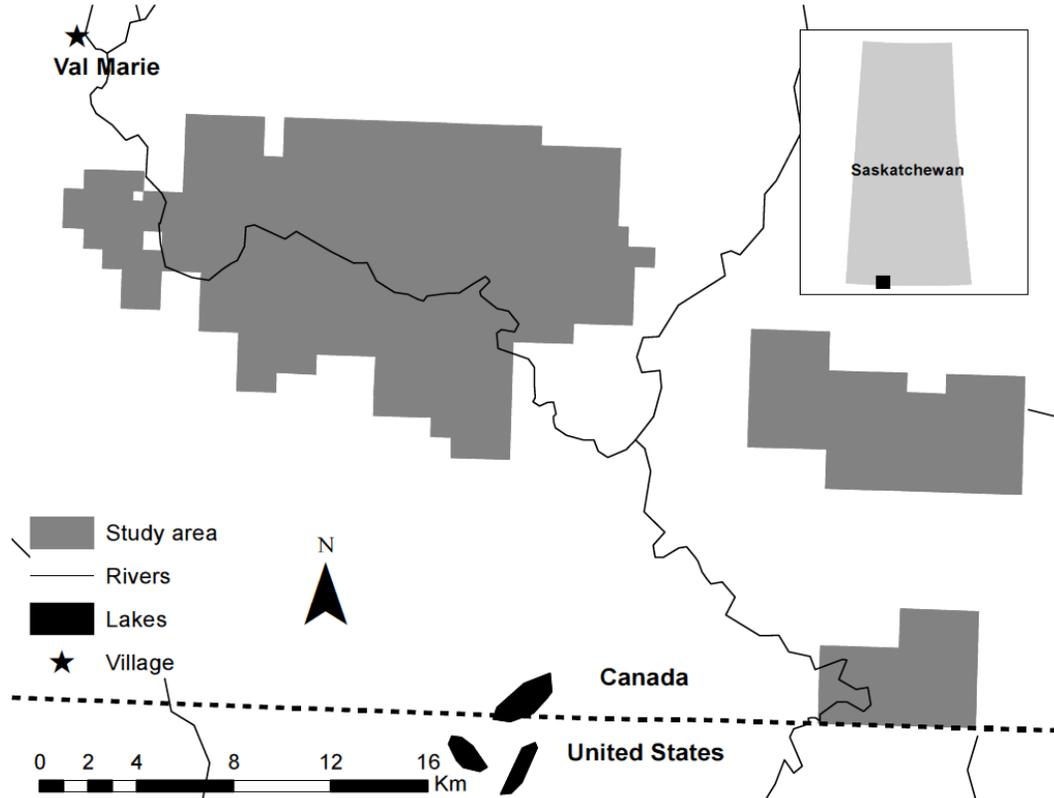


FIGURE 2-1. The study area was within the 2007 boundary of the West Block of Grasslands National Park in southwest Saskatchewan, Canada. The vegetation community is dominated by mixed grass prairie dissected by deep bearpaw shale coulees and dunes stabilized by creeping juniper (*Juniperus horizontalis*) associated with the Frenchman River drainage.

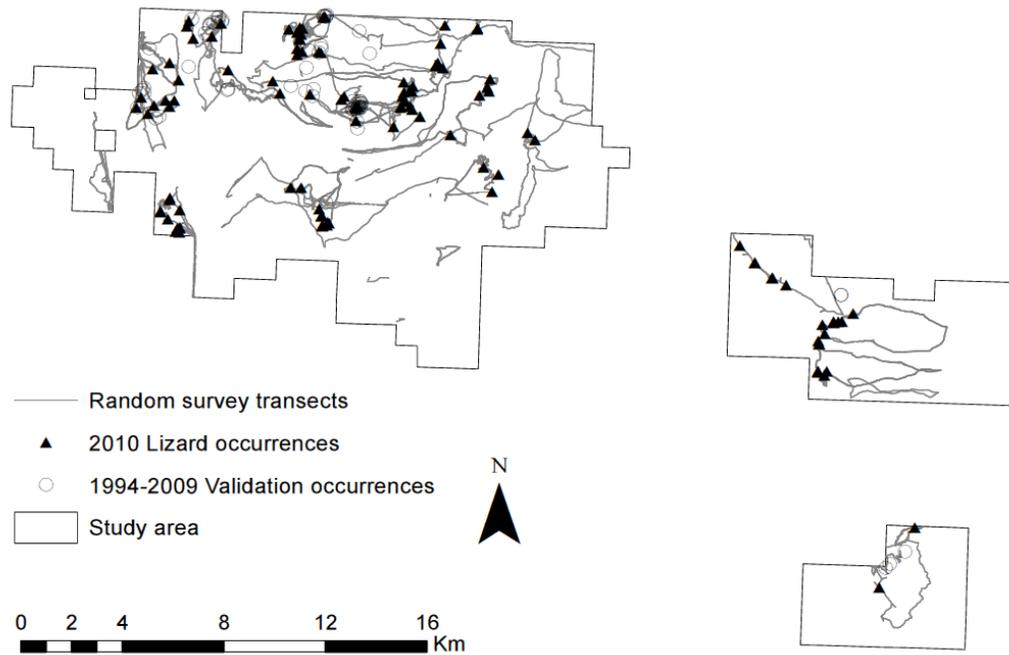


FIGURE 2-2. Location of random survey transects searched between 21 May 2010 and 12 August 2010 in Grasslands National Park, Saskatchewan, Canada. Triangles indicate where Greater Short-horned Lizards were observed while walking transects (n = 118). Open circles indicate observations of Greater Short-horned Lizards from 1994-2009 that were used for model validation (n = 68).

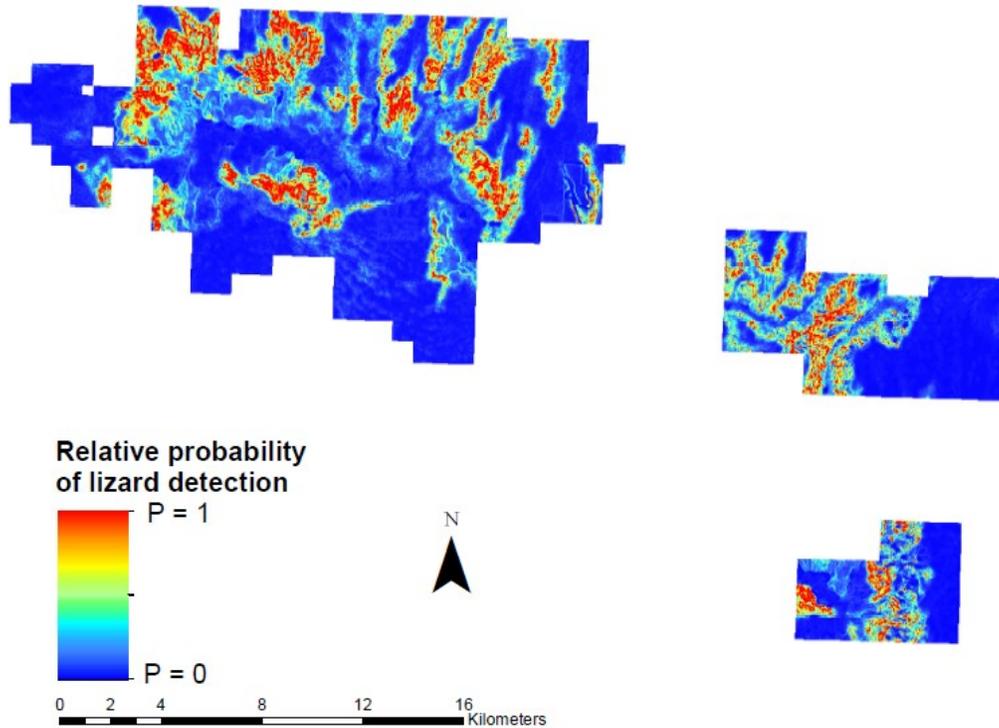
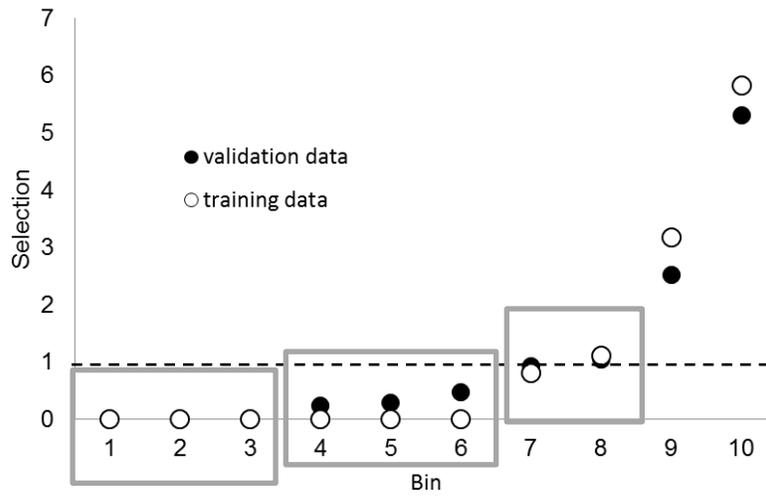


FIGURE 2-3. Predicted relative probability of Greater Short-horned Lizard detection in Grasslands National Park, Saskatchewan, Canada. Covariates from the RSF were used to predict areas of high detection. Since detection is assumed to be constant across habitat types, areas with a high probability of detection are assumed to be areas with high probability of lizard occurrence.

a)



b)

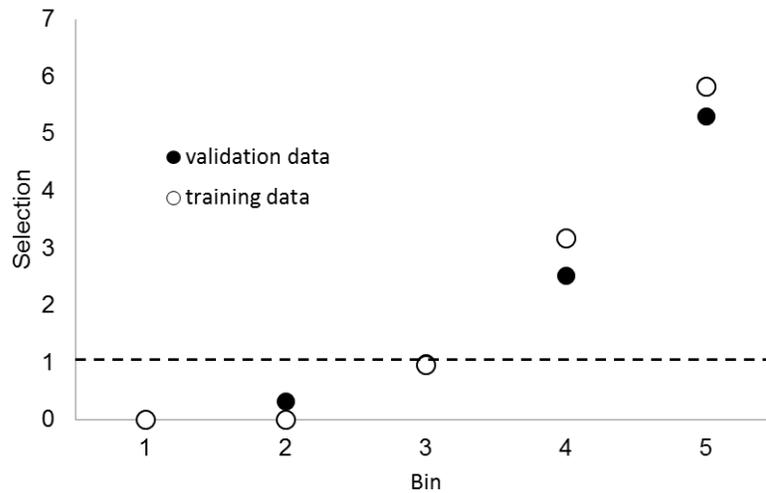


FIGURE 2-4. Selection in each of the ten original RSF bins for both the training data set ($n = 118$) and the independent validation data set ($n = 68$) (a). Selection is equal to the proportion of use locations divided by the proportion of area in a bin (values <1 would be considered ‘avoided’ [use $<$ available]). Bins with similar selection ratios for the training dataset were combined such that selection increases in each subsequent bin (b). The gray rectangle indicates combined bins (a).

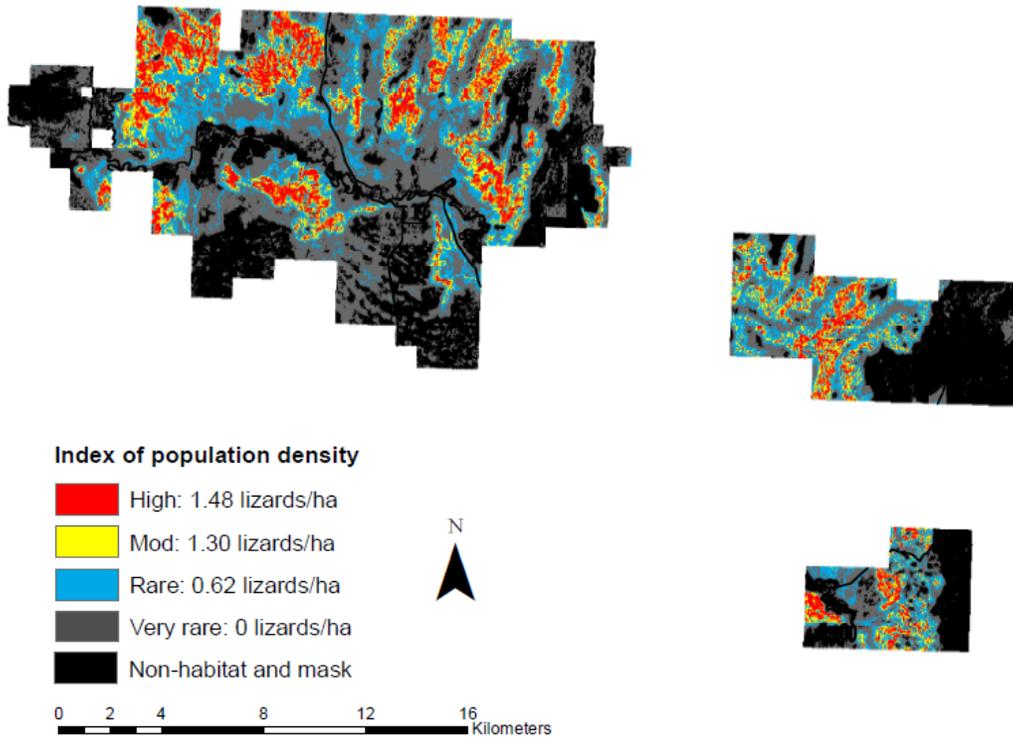


FIGURE 2-5. Binned and reclassified habitat model based on the continuous model predicting relative probability of detection. Bins represent increasing levels of selection calculated from both the training data set and an independent validation data set. The index of population density within each bin was calculated from encounter rates in the 2010 survey. No lizards were encountered in the 2010 survey in area categorized as very low population density, but some historical observations did occur in the area. The Frenchman River, cultivated land, and roads were not considered in calculations of population size (mask).

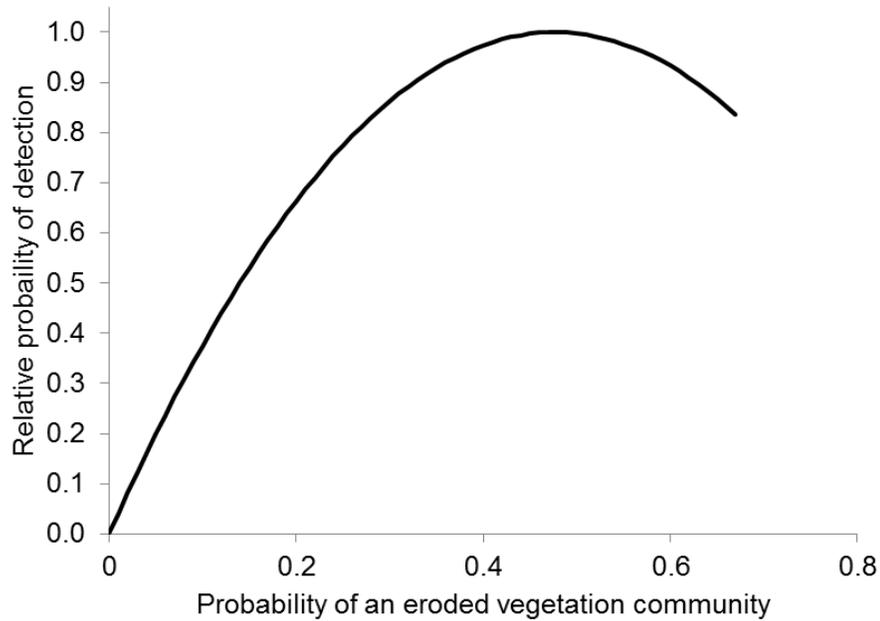


FIGURE 2-6. Relationship between relative probability of detection of Greater Short-horned Lizards and probability of an erosional vegetation community. Coefficients were taken from the RSF model (Table 2-3). The alternate variables were held constant at their means.

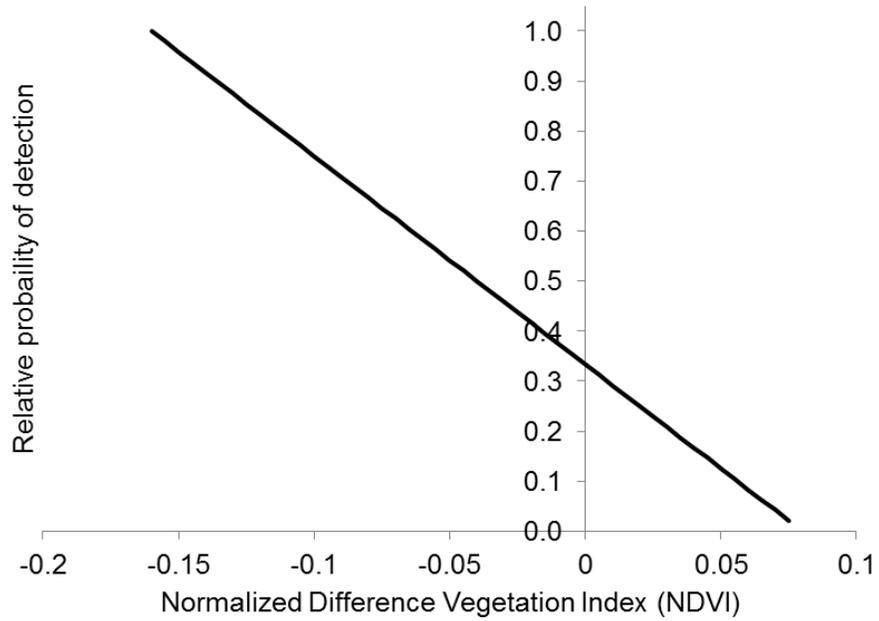


FIGURE 2-7. Relationship between relative probability of detection of Greater Short-horned Lizards and Normalized Difference Vegetation Index (NDVI). Coefficients were taken from the RSF model (Table 2-3). The alternate variables were held constant at their means.

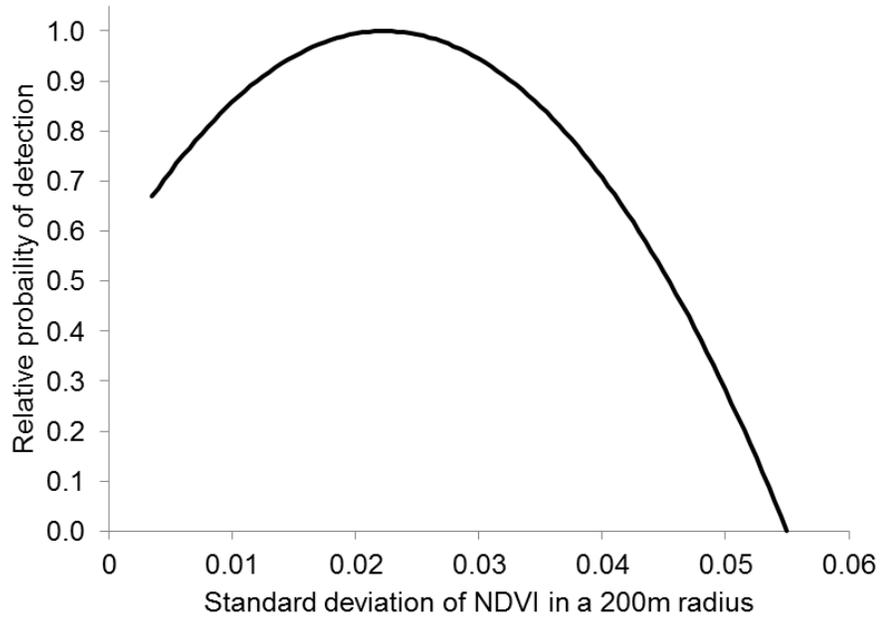


FIGURE 2-8. Relationship between relative probability of detection of Greater Short-horned Lizards and standard deviation of the normalized difference vegetation index (NDVI) in a 200m radius. Coefficients were taken from the RSF model (Table 2-3). The alternate variables were held constant at their means.

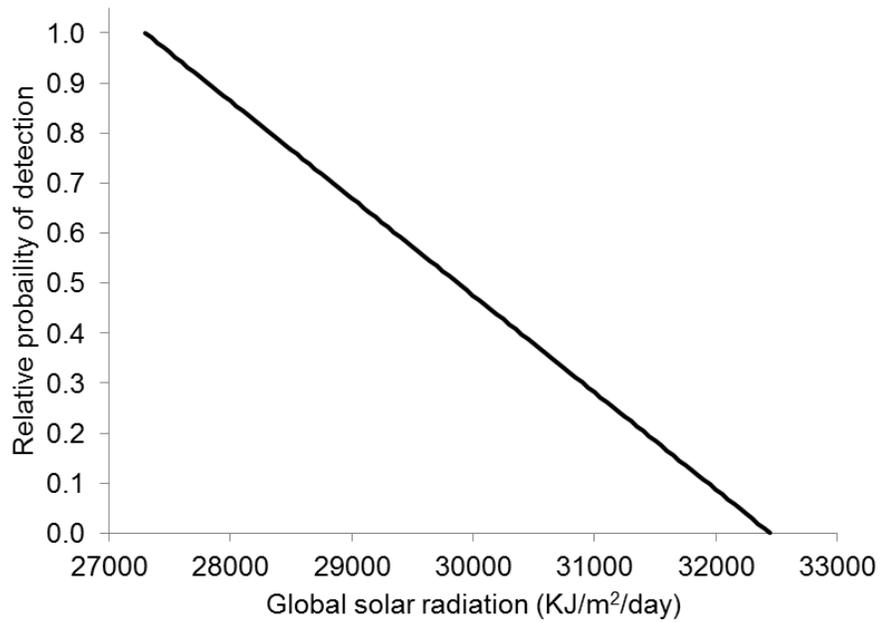


FIGURE 2-9. Relationship between relative probability of detection of Greater Short-horned Lizards and global solar radiation. Coefficients were taken from the RSF model (Table 2-3). The alternate variables were held constant at their means.

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CHAPTER 3. DO GREATER SHORT-HORNED LIZARDS SELECT HOT SPOTS OR ARE OTHER MICROSITE CHARACTERISTICS MORE IMPORTANT?

1. INTRODUCTION

In numerous reptile species, patterns of small-scale habitat selection are largely determined by thermoregulatory needs (Huey 1991; Pringle et al. 2003; Díaz and Cabezas-Días 2004). This may be especially true for reptiles at the edge of their range, where thermal limitations may restrict distribution (Thomas et al. 1999). Warmer microsites may be exploited in colder edge-of-range environments thus allowing local persistence of the species (Bryant et al. 2002; Suggitt et al. 2011). Structural habitat features largely determine local variations in thermal conditions (Huey et al. 1989; Suggitt et al. 2012). For example, a seemingly small habitat alteration, such as repositioning a rock, can change structural conditions that in turn impact thermal conditions, rendering a refuge site too hot or too cool to be used by an animal (Pike et al. 2010). This illustrates the complex relationship between small-scale cover features, thermal conditions, and habitat suitability for reptiles.

Such complexity is evident in the habitat selection of Greater Short-horned Lizards (*Phrynosoma hernandesi*). The species occupies the northern edge of its range in southwest Saskatchewan and southeast Alberta, Canada where it occurs in a patchy distribution (Powell and Russell 1998; Powell et al. 1998). Greater Short-horned Lizards residing at the northern edge of its range are hypothesized to be thermally limited (Powell and Russell 1985), but this hypothesis has not been tested.

If the distribution of Greater Short-horned Lizards at their northern range-edge is limited by cold temperatures, than individuals occupying the edge of range should select warm microhabitat features compared to features generally available on the landscape (Pringle et al. 2003; Suggitt et al. 2011). While this type of thermal habitat selection would occur at a population-level, previous studies of thermal habitat selection have focused on within-population comparisons. Individual Greater Short-horned Lizards in Alberta were found to vary their selection of thermal patches as a function of body size, where small lizards used warmer substrates and maintained a higher body temperature than larger lizards (Powell and Russell 1985). However, no comparisons have been made between the microsites selected by lizards and what is generally available on the landscape at a population-level.

Alternatively, if Greater Short-horned Lizard populations are not thermally limited, microhabitat selection may be for specific structural, substrate, or vegetation characteristics, rather than for warm microsites in a cool landscape (Martine and Salvador 1995; Valentine et al. 2007). Previous investigations describing Greater Short-horned Lizard habitat at their northern range edge have focused on the substrate and vegetation characteristics of occupied microsites indicating that lizard habitat is associated with juniper dune terrain with exposed Bearpaw shale substrates (James 2002, 2003; Powell et al. 1998). In Alberta, Greater Short-horned Lizards are associated with south-facing slopes, which may be a coarse-scale topographic feature selected for its warm thermal characteristics (Powell and Russell 1998).

Here I test whether Greater Short-horned Lizards select warm microhabitats at their northern range edge in southern Saskatchewan or if vegetation and substrate are more important to local habitat selection. I predict that warm microsites measured at local scales ($< 1 \text{ m}^2$) will be selected by lizards in Saskatchewan. Habitat characteristics that can be exploited for raising body temperatures, such as rocks and exposed substrates, are expected to be present in greater amounts at locations occupied by lizards than generally occurs the landscape.

2. METHODS

2.1 Study area.—Microsite characteristics of Greater Short-horned Lizard habitat were assessed in the West Block of Grasslands National Park in southwest Saskatchewan ($49^{\circ}06'13''\text{N}$, $107^{\circ}25'14''\text{W}$). This area represents 28,400 hectares of mixed-grass prairie dominated by *Stipa* sp., riparian areas of shrub with *Shepherdia argentea*, *Symphoricarpos occidentalis*, and *Salix* sp. having an understory of *Bromus inermis*, and deeply dissected shale dune badlands that are characterized by exposed shale stabilized by *Juniperus horizontalis* and other small shrubs. The study area is bisected by the Frenchman River. Climate is continental, with mean January and July temperatures at the Val Marie, Saskatchewan weather station of -12.4°C and 18.3°C respectively. Temperature extremes in January can be as low as -49°C , whereas summer maximum temperatures, achieved in July, can be as high as 41°C . Mean annual precipitation is 348 mm, most of which falls in June and July (Environment Canada, unpublished data). Greater Short-horned Lizards do not occur further north than

Grasslands National Park in Saskatchewan and the park represents the northern extent of their range.

2.2 Study design and microsite habitat measurements.—Greater Short-horned Lizard locations were identified along 650 km of 2-m wide meander survey strip transects searched between 21 May 2010 and 12 August 2010 between 800 h – 1700 h. Transects were searched by two observers experienced in detecting Greater Short-horned Lizards. A new transect starting location was selected by the observers each day with the intention of covering as much of the study area as possible. The precise transect route was not predetermined after the starting location. Care was taken to search all available habitat types (upland grassland, valley bottoms, sagebrush flats), although more effort was focused on areas where lizards were thought to occur, including coulee edges and bottoms, areas with badland topography, and exposed shale substrates (Table 2-1). Observers searched for lizards by disturbing the vegetation and rocks with a walking stick and looking for the movement of fleeing lizards.

Once a lizard was detected, the point where the lizard originally occurred was marked and the location was sampled as an occupied microsite. A microsite presumed to be within the lizards home range was chosen using a random compass bearing (0° to 359°) and distance ranging between 5 and 70 m, which represented the largest daily movement rates of female lizards measured with radiotelemetry in the summer of 2009 (K. Fink, unpublished data). Random landscape microsites were chosen along the transect at hourly intervals (an alarm

would signal the hourly interval and thus location, see Fig. 3-1 for a sampling schematic).

At each microsite location (occupied, paired home range, and random landscape), I simultaneously measured the infrared spectrum and the visible light spectrum of the soil surface (Fig. 3-2) using a handheld thermal imager (Fluke, model Ti32). Images were taken from 1 m above the ground at an angle perpendicular to the general slope of the microsite. Thermal images captured approximately 0.12 m² of ground surface (38.1 cm x 31.75 cm), while the visible image was slightly larger, capturing 0.30 m² of ground surface (60 cm x 50 cm).

In addition to the infrared and visible imagery, I measured air temperature and wind speed at 1 m above the ground, slope, aspect, vegetation canopy structure, and soil penetrability at the center of the images. I also recorded the date and time of the observation as air and ground surface temperatures were related to seasonal and diurnal patterns.

Soil penetrability was measured at the center of each microsite with a pocket penetrometer (Durnham geoslope indicator, kg/cm²). Indices of vegetation density and height were measured using Robel's visual obstruction method. A Robel pole (150 cm tall, 3 cm diameter, divided into 10 cm segments) was secured vertically at a sample location and was viewed 4 m away 1 m above the ground. The highest segment that was 50% obscured and the highest segment that was at all obscured by vegetation was recorded in each of the cardinal directions and averaged for each microsite (Robel et al. 1970). See Table 3-2 for descriptions of all variables used to describe microsites.

2.3 Thermal image processing and groundcover estimation.—I measured microthermal habitat characteristics using thermal imaging in order to record the surface temperature characteristics of lizard microhabitat. Past applications of thermal imaging (thermography) have been primarily industrial, such as using thermal images to identify areas of high friction in machinery. Thermal imaging has also been used monitor physiological heat on the surface of animals (Lancaster et al. 1996; Weissenbock et al. 2010). Thermal imaging, as applied in this study, was used to collect data on the spatial arrangement of heat in habitat occupied by lizards compared to locations nearby (paired home range locations) or at random locations along transects.

Temperature data from infrared thermal images were recorded as spatial matrices. Data from each pixel of the infrared thermal images were extracted and converted to vector format (76,800 pixels per image). Mean, median, standard deviation, maximum, minimum and range of temperature values within each thermal image were determined. Predicted potential annual direct radiation (hereafter “solar potential”) was estimated for each microsite based on the slope, aspect, and latitude of sample sites in a laboratory setting using the equation from McCune and Keon (2002). Solar potential was calculated from slope and aspect data as:

Equation 1)

$$\text{Solar potential} = \text{EXP}(-1.467 + 1.582 * \cos(\text{latitude}) * \cos(\text{slope}) - 1.5 * \cos(\text{aspect}) * \sin(\text{slope}) * \sin(\text{latitude}) - 0.262 * \sin(\text{latitude}) * \sin(\text{slope}) + 0.607 * \sin(\text{aspect}) * \sin(\text{slope})),$$

where latitude, slope, and aspect are in radians. Output is in MJ/cm²/year.

Cover of juniper, woody litter, fine litter, forbs and shrubs, graminoids (grasses and sedges), soil, rock, and cryptograms (bryophytes and lichens) was estimated from the visible spectrum images in a laboratory setting. Cover classes (ordinal ranks) used to rank abundance of individual items included zero (absent), one (< 1%), two (1%-5%), three (5%-25%), four (25%-50%), five (50%-75%), six (75%-95%) and seven (>95%). Initial analyses revealed that a diversity of cover types was an important predictor of lizard occurrences; therefore, a modified Shannon's diversity index was calculated from cover type data as:

Equation 2)

$$H' = \sum_{i=1}^T (p_i \ln p_i)$$

where the proportion p for cover type i (midpoint cover class) was estimated for each of the T cover classes.

2.4 Statistical analyses.—Microhabitat analyses were completed using a classification and regression trees (CART) in R 2.11.1 (R Development Core Team 2010). CARTs are well suited to complex ecological data, where categorical and continuous variables, non-linear relationships, and complex interactions can be analyzed (De'ath and Fabricius 2000; Kintsch and Urban 2002; Bourg et al. 2005). A CART analysis is a series of binary splits such that after each split, new subsets are composed of a larger proportion of, in this case, animal occurrences (“success”) or absences (“failures”) than the parent set (Clark et al. 1999). CARTs have been used to predict species occurrence (Howes and

Lougheed 2004, MacLeod et al. 2007) and for designing habitat restoration (Maslo et al. 2011). CART yielded combinations of microsite characteristics selected by lizards (used more frequently than available), or combinations that were avoided (used less frequently than available). Selection (proportion of lizard occurrences divided by the proportion of paired home range or random microsities) for each branch of the tree was calculated. Selection values > 1 indicate that a combination of microsite characteristics were selected, whereas selection values < 1 indicates that a combination of characteristics was avoided.

CART analysis was conducted with the *mypart* package and variable importance values estimated using the *randomForest* package (bootstrapped CART). Variable importance was based on the percent increase in mean square error and node purity, which measured the homogeneity for each node within the tree (Breiman et al. 1984).

Three different CARTs were constructed. The first CART compared occupied locations to random landscape locations. The second compared occupied locations to paired home range locations. The third compared paired home range locations to random landscape locations (Fig. 3-3). Initial analysis included all three response variables (occupied, paired home range and random landscape) in a single CART; however, the response categories could not be differentiated indicating that at least two of categories are very similar. For subsequent analysis, I chose to compare each level of selection separately (one-to-one comparisons). Alternative variables and the percent variation explained were determined for each split in the trees.

3. RESULTS

Using two splits The model comparing occupied and random microsites explained 22.1% of the total variation in microsite selection by lizards (Fig. 3-4). The majority of lizard locations were in areas of high diversity of cover types (diversity ≥ 1.23 , lizard locations 80/118). The cover type diversity split alone accounted for 16.9% of total variation in microsite selection. Thirty-eight lizards occurred in areas with low cover type diversity (diversity < 1.23). In areas where cover type diversity was high, lizards selected locations where exposed soil was also high (soil cover class ≥ 4 , 25-100% cover, lizard locations 61/80), explaining 5.2% of the total variation in microsite selection. Cover type diversity and exposed soil may be present in the same microsite because soil cover is one type of cover in the visible spectrum images. Selection was highest for sites with high cover type diversity and high soil cover (selection = 4.83). Areas with low diversity of cover types (diversity < 1.23) were avoided by Greater Short-horned Lizards (selection = 0.43).

Diversity of cover types did not have an alternate variable that could explain similar amounts of variation in the data (16.9%). The best alternate variables were juniper and woody litter cover, which explained 8.9% and 8.5% of total variation respectively (Table 3-3.). Moreover, when cover type diversity was removed, percent increase in mean square error approached 40% (Fig. 3-5). Cover type diversity was also the most important variable contributing to node purity (Fig. 3-5).

A second model compared microsites occupied by lizards to microsites within a hypothetical home range (Fig. 3-6). This explained 13.7% of the total variation in within home range microsite selection. Four splits in the tree were supported suggesting that no single factor strongly explained lizard microhabitat selection within their home range. Selection within the home range was highest for sites with short vegetation (vegetation height index ≤ 2.75), low cover of bryophytes and lichens (cryptogram cover < 3 , 0-5%), and warm minimum surface temperatures ($\geq 26.2^{\circ}\text{C}$) (lizard locations = 21/118, selection = 21.0). Only one paired home range microsite had the same microsite characteristics (home range microsites = 1/117). Selection also occurred for locations with shorter vegetation, higher cover of bryophytes and lichens (cryptogram cover ≥ 3 , $> 5\%$), and average soil surface temperatures less than 34.6°C (lizard locations = 5/118, selection = 5.0). Despite selection for shorter vegetation, more than half of lizard locations (70/118) occurred where there was high vegetation (vegetation height index > 2.75). Selection was low (selection = 0.8) because Higher vegetation is common within the home range (91/117 paired home range microsites).

Most of the variables used for the models comparing occupied and paired home range microsites could be substituted for other variables without affecting model variance explained (Table 3-3). Soil cover (≤ 2) and minimum soil surface temperature ($< 23.6^{\circ}\text{C}$) could be substituted for vegetation height index (≤ 2.75) without greatly reducing the amount of variance explained. Alternative variables to cryptogram cover (< 3 , 0-5%) included soil cover (< 3 , 0-5%) and fine litter cover (< 4 , 0-25%). The split in the tree created by minimum soil surface

temperature ($< 26.2^{\circ}\text{C}$) could also be made using solar potential (< 0.73 MJ/cm²/yr) or median soil surface temperature ($< 36.3^{\circ}\text{C}$).

The most important variables for differentiating occupied and paired home range microsites (based on percent increase in mean square error) were cryptogram cover and vegetation height. Thermal variables, such as average temperature and minimum temperature, had very little effect on the mean square error of the tree. Minimum temperature, solar potential, and vegetation height were, however, important for increasing node purity in the tree (Fig. 3-7).

No support was found distinguishing microsites locations between paired home range and landscape sites.

4. DISCUSSION

Contrary to what was predicted and supported at meso-scales in the literature, thermal variables at the three scales tested here during daylight periods in the active summer period were not strongly related to microhabitat selection by Greater Short-horned Lizards. Lizards do not appear to be exploiting microsite thermal differences facilitating persistence within a thermally marginal landscape. Rather, vegetation characteristics were greater contributors to microhabitat selection. Clear distinctions were identified between occupied and random landscape microsites, whereas occupied and home range microsites were not as clearly distinguished from each other. No differences were found between random landscape and home-range microsites.

Cover type diversity was the most important characteristic differentiating microsites selected by Greater Short-horned Lizards from what is available on the landscape. This is consistent with habitat selection of other *Phrynosoma*, such as the Texas Horned Lizard *P. cornutum*, which selected locations with a mosaic of different cover types (bare ground, herbaceous vegetation, and woody vegetation) in close proximity (Burrow et al. 2001).

Greater Short-horned Lizards did not select microsites with high solar potential, which indicates that lizards are not thermally limited at the northern edge of range in Grasslands National Park during the active season. This differs from habitat selection of Greater Short-horned Lizards in other parts of the northern range edge, such as in southeast Alberta, where lizards appear to be restricted to south-facing slopes, even during the summer active summer period (Powell and Russell 1998). Animals at the edge of their climactic range are expected to take advantage of slopes and aspects that maximize heating potential (Thomas et al. 1999; Bryant et al. 2002), but this pattern was not observed in this study.

Small-scale thermal conditions may not drive microhabitat selection because of a behavioural response by Greater Short-horned Lizards to sub-optimal thermal conditions (Díaz and Cabezas-Díaz 2004; Besson and Cree 2010). Such a behavioural response has been identified in Tuataras (*Sphenodon punctatus*), a reptile adapted to cool climates. Tuataras were shown to adjust their behaviour to thermoregulate more accurately and maintain higher body temperatures when thermal habitat quality was poorer (Besson and Cree 2010). Greater Short-horned Lizards may increase active thermoregulation in locations with low thermal

habitat quality in order to take advantage of locations with greater prey availability or greater cover from predators (Díaz 1997).

The only instance of thermal habitat selection identified in this study occurred when comparing occupied and random home-range locations. Thermal habitat selection was secondary to vegetation height and bryophyte and lichen cover for differentiating occupied and random home-range locations (Fig. 3-6). Once splits in the data were made based on the cover type variables, some thermal variables were useful in increasing node purity. However, selection did not occur for the warmest microsites as predicted. Rather, lizard selection was strongest for microsites with average temperatures less than 34.6°C or minimum temperatures greater than or equal to 26.2°C. This indicates that Greater Short-horned Lizards within their home range select moderate thermal conditions.

I expected Greater Short-horned Lizards to select microsites with cover types that contribute to warmer thermal conditions, such as microsites with high rock cover or low amounts of shading vegetation cover. Lizards did select microsites with high amounts of exposed soil (> 25%) compared to what was randomly available (selection = 4.83, compared to selection = 1.11 for exposed soil < 25%). Exposed soil likely contributes to greater warming potential, due to its ability to retain solar heat (Heusinkveld et al. 2004) and due to the lack of shade on exposed soils. Exposed soil may also be selected for reasons other than thermal potential. Greater Short-horned Lizards may select areas with patches of bare soil to facilitate easier movement. Dense vegetation decreases the sprint-speed of *Phrynosoma platyrhinos* by 50-70% compared to bare substrate speeds (Newbold

2005; Rieder et al. 2010). Greater Short-horned Lizards have a similar body shape, size, and gait as *P. platyrhinos* and are likely to have similar difficulties moving quickly through thick vegetation. Rapid movement across bare soil may also facilitate the ambush-type attack *Phrynosoma* use to catch their prey (Powell and Russell 1984).

While selection of attributes derived from the visible spectrum image (cover type variables) was identified by the models, a potential source of error may be the small size of the area sampled by the visible and thermal images (0.30 m² and 0.12 m² respectively). This small size was used due to the limitations in the equipment available and the portability of such equipment in the rugged terrain that lizards occupy. Also, the area sampled is likely similar to the scale lizards experience thermal conditions (Suggitt et al. 2011). However, such a small sampled area may be a source of error due to the fleeing behaviour of lizards (Powell and Russell 1985). If the lizard has moved more than a few centimeters before it is noticed by the searcher, the location sampled as occupied may not be representative of true microhabitat used by the lizard. Rather, the habitat sampled may be more similar to the type of habitat lizards select when fleeing a predator, where cover and crypsis are selected for (Andersson et al. 2010).

Alternatively, thermal habitat selection may not have been identified by the models because thermal limitations do not occur during the active season. Rather, thermal limitations may occur at other times of year, such as during winter hibernation, or during exceptional weather events in the fall and spring (e.g. late spring snowstorms, early fall frost) (Powell and Russell unpubl. report 1996). For

example, lizards near the northern range periphery emerge from hibernation as early as April (Laird and Leech 1980), a month where below-freezing temperatures and snowfall is common (Environment Canada, unpublished data). While northern lizards may have physiological adaptations to deal with thermal extremes, microhabitat selection may play an important role in survival under extreme conditions. The thermal characteristics of selected habitat at this sensitive time may be more important than habitat selection during the active summer season. More research is needed to identify factors limiting the distribution of Greater Short-horned Lizards at the northern extent of their range in Canada.

TABLE 3-1. Search effort by vegetation type in Grasslands National Park, Saskatchewan, Canada where vegetation mapping occurred (1994 vegetation). Largest transect distance occurred in the erosional vegetation community, which is the vegetation type most often associated with occurrence of Greater Short-horned Lizards in past research. Search effort was high for the treed vegetation community, but actual distance searched in this vegetation type was small (396 m) since it is very rare in the study area.

General vegetation type	Area (ha)	Distance searched (m)	Search effort (m/ha)
Erosional community	5087	264267	51.9
Sloped grassland	5366	128436	23.9
Valley grassland	3919	95779	24.4
Shrub community	2237	44096	19.7
Treed community	3	396	129.7
Prairie dog colony	665	6949	10.5
Upland grassland	7843	80073	10.2
Disturbed community	1851	7106	3.8
Outside data layer	21	1904	92.0

TABLE 3-2. Description of variables used to describe microhabitat for Greater Short-horned Lizards in Grasslands National Park, Saskatchewan, Canada.

Variables	Description	Units	Data range
<i>Vegetation variables</i>			
juniper	Juniper cover	Ordinal	0-10
woody litter	Woody litter cover	Ordinal	0-10
fine litter	Fine litter cover	Ordinal	0-10
forb/shrub	Forbs and/or shrub cover	Ordinal	0-10
graminoid	Grass and sedge cover	Ordinal	0-10
cryptograms	Moss and lichen cover	Ordinal	0-10
diversity	Modified Shannon diversity index of cover type diversity	Unitless	0.37-2.11
<i>Substrate variables</i>			
rock	Rocks (≥ 1 cm diameter) cover	Ordinal	0-10
soil	Bare soil and/or small shale fragment (< 1 cm diameter) cover	Ordinal	0-10
<i>Thermal variables</i>			
median	Median temperature in thermal image	$^{\circ}\text{C}$	19.98-49.80
average	Average temperature in thermal image	$^{\circ}\text{C}$	19.80-49.00
minimum	Minimum temperature in thermal image	$^{\circ}\text{C}$	12.87-33.76
maximum	Maximum temperature in thermal image	$^{\circ}\text{C}$	21.72-70.75
st. dev.	Standard deviation in temperature in thermal image	$^{\circ}\text{C}$	0.61-8.00
spread	Difference between maximum and minimum temperature in thermal image	$^{\circ}\text{C}$	5.57-43.21
<i>Other variables</i>			
veg density	Vegetation density index	Unitless	0-3.25
veg height	Vegetation height index	Unitless	0-8.25
solar	Annual direct radiation	$\text{MJ}/\text{cm}^2/\text{year}$	0.29-0.85
season	Seasonality	Categorical	cool, warm
time	Time of day	Categorical	morning, afternoon, evening

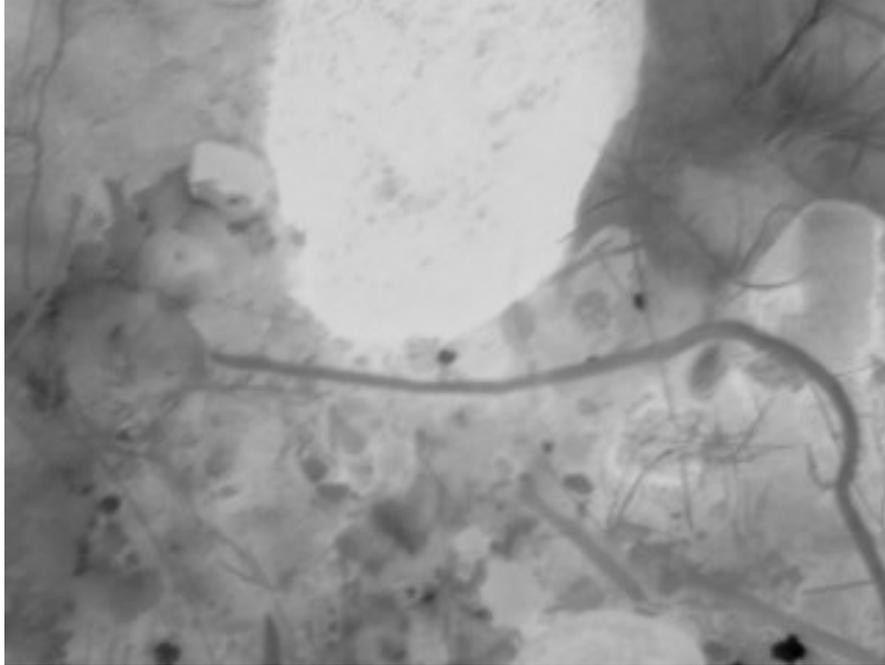
TABLE 3-3. Alternate split variables for CART model differentiating occupied and random landscape microsites for Greater Short-horned Lizards in Grasslands

National Park, Saskatchewan, Canada.

Split variable	Threshold (right side)	Variance explained (%)
diversity	≥ 1.23	16.9
juniper	≥ 1	8.9
woody litter	≥ 1	8.5
soil	> 3	5.2
juniper	≥ 1	5.0
woody litter	≥ 1	4.6

TABLE 3-4. Alternate split variables for the CART differentiating occupied and paired home range microsites for Greater Short-horned Lizards in Grasslands National Park, Saskatchewan, Canada.

Split variable	Threshold (right side)	Variance explained (%)
veg height	≤ 2.75	3.39
soil	≤ 2	3.31
minimum	$< 23.6^{\circ}\text{C}$	3.28
cryptograms	< 3	3.39
soil	< 3	3.34
fine litter	< 4	2.82
average	$< 34.6^{\circ}\text{C}$	3.39
spread	$< 22.1^{\circ}\text{C}$	3.39
median	$< 35.1^{\circ}\text{C}$	2.58
minimum	$\geq 26.2^{\circ}\text{C}$	3.39
solar	$< 0.73 \text{ MJ/cm}^2/\text{year}$	3.27
median	$< 36.3^{\circ}\text{C}$	2.58



a)



b)

FIGURE 3-2. The thermal image (a) represents the temperature of each pixel with a different grayscale value (light areas are hot, dark areas are cool). Thermal data is stored for each pixel in the image. The corresponding visible spectrum image (b) was used to estimate the area of different cover types present at the location.

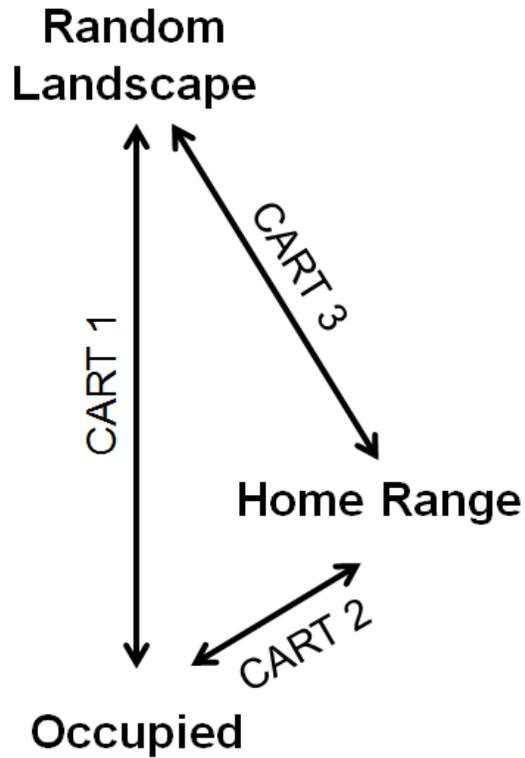


FIGURE 3-3. Schematic depicting the pair-wise comparisons in CART analyses. The first comparison is between occupied and random landscape locations. These are expected to be the most dissimilar. The second CART compares occupied and paired home range locations. If these sets of microsites are distinguishable in CART analyses, it would suggest that lizards select microsites within their home ranges that are distinct from the home range in general. A third CART model compares random landscape and home range locations. If these sets are dissimilar, it suggests that lizards select home ranges with distinct characteristics compared to what is available on the broader landscape.

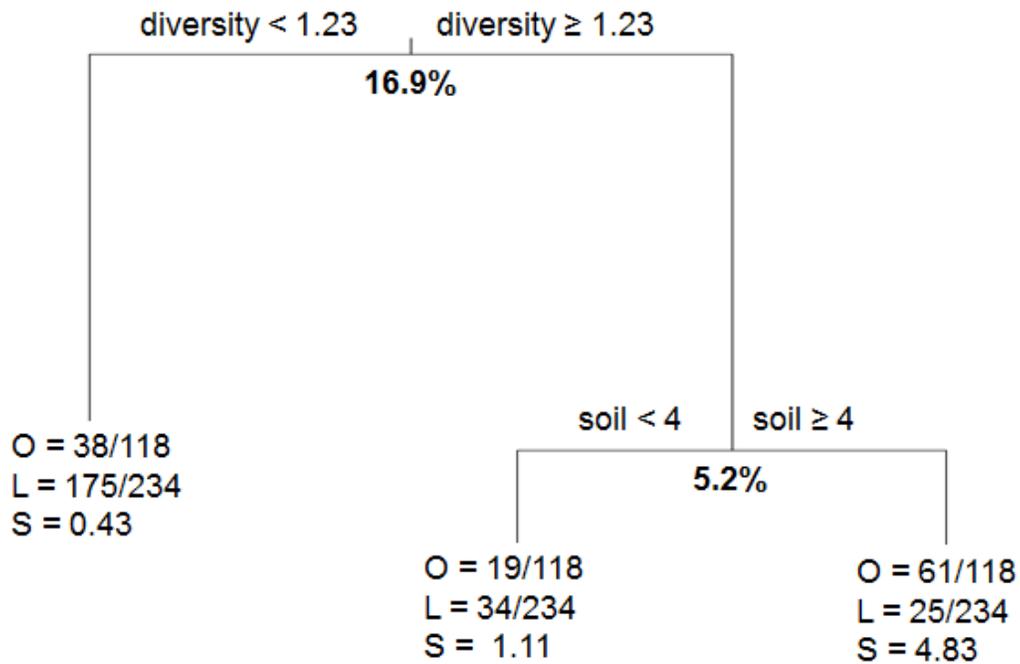


FIGURE 3-4. The classification tree of microhabitat characteristics differentiating lizard occupied sites and random landscape locations. “O” and “L” represents the proportion of all occupied and random landscape microsites observed in a specific branch of the tree respectively. “S” represents the selection ratio for a branch of the tree. Branches with selection ratios >1 are formed by combinations of microsite characteristics selected by lizards more frequently than if sites were selected in proportion to their availability. Variation explained in the dataset by each split is given by percentage at the node of the split. See Table 3-2 for a description of the “diversity” and “soil” variables.

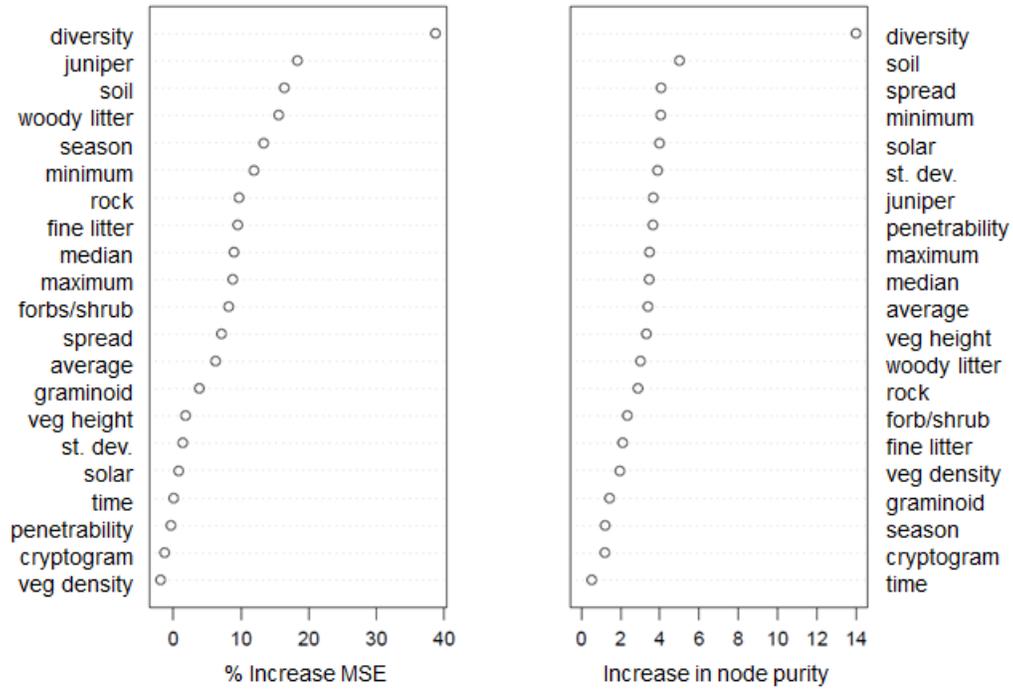


FIGURE 3-5. Variable importance for the CART model comparing lizard occupied sites and random landscape locations. Relative importance can be measured either by the increase in the mean square error (MSE) of the tree (at left) or by the increase in node purity that occurs when a variable is used to make a split in the tree (at right).

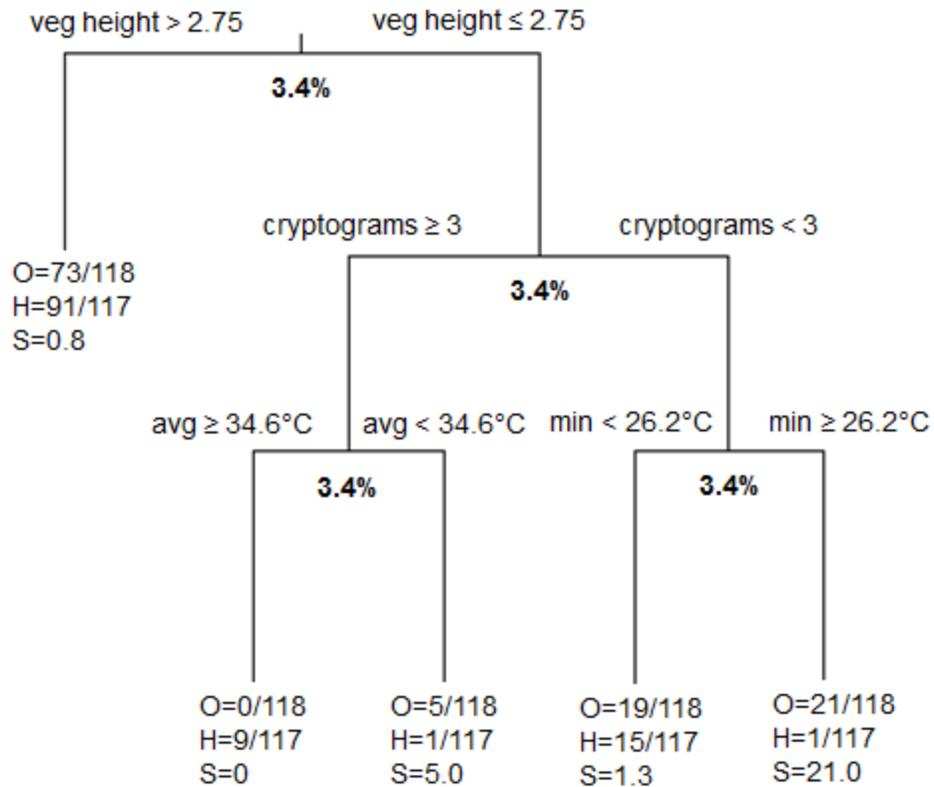


FIGURE 3-6. The classification tree of microhabitat characteristics differentiating lizard occupied sites and paired random sites within a hypothetical home range. “O” and “H” represents the proportion of all lizard and home range microsites observed in a specific branch of the tree, respectively. “S” represents the selection ratio for a branch of the tree. Branches with selection ratios >1 are formed by combinations of microsite characteristics selected by lizards more frequently than if sites were selected in proportion to their availability. Variation explained in the dataset by each split is given by percentage at the node of the split. See Table 3-2 for a description of the variables used in the tree.

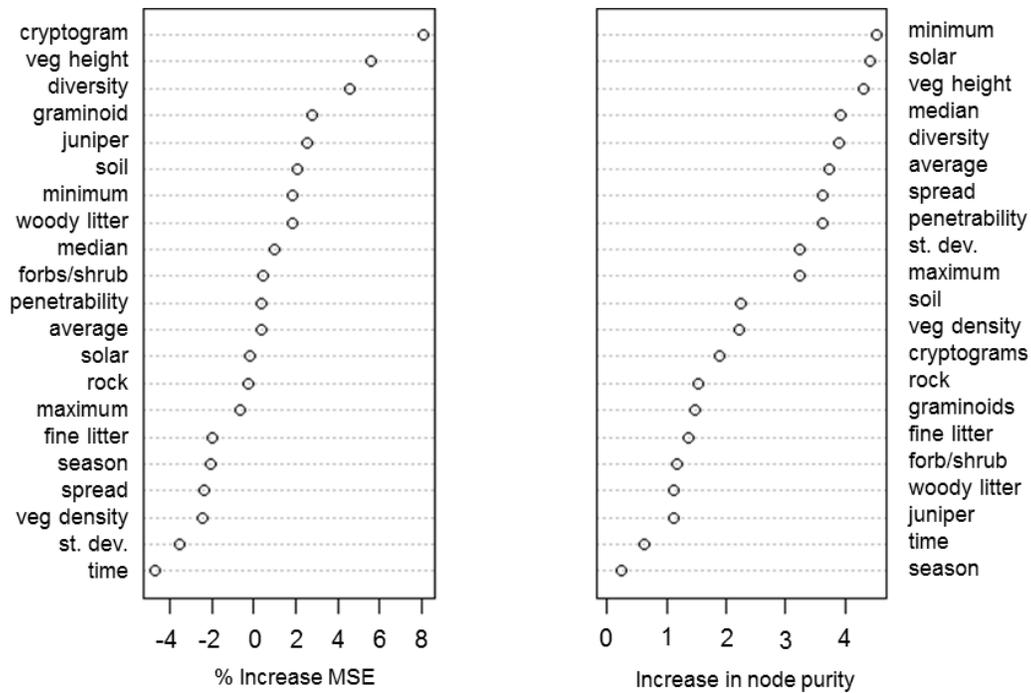


FIGURE 3-7. Variable importance for the CART model comparing lizard occupied sites and paired sites within a hypothetical home range. Relative importance can be measured either by the increase in the mean square error (MSE) of the tree (at left) or by the increase in node purity that occurs when a variable is used to make a split in the tree (at right).

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CHAPTER 4. GENERAL CONCLUSIONS

Prior to this study, little quantitative research had been done to identify the active-season habitat requirements of Greater Short-horned Lizards in Canada. In this thesis, I identified specific habitat characteristics selected by lizards at landscape and micro-scales. Chapter 2 identifies landscape-scale habitat characteristics that can be used to predict relative probability of occurrence, while Chapter 3 demonstrates that Greater Short-Horned lizards select specific combinations of microhabitat features from what is available at 2 scales: the landscape and home range. This multi-scale analysis of habitat selection contributes to our understanding and management of lizard conservation by mapping habitat for Greater Short-horned Lizards and by identifying what micro-scale habitat features are important within the broader landscape. Here, I present a brief research summary followed by a discussion regarding implications of this work relative to defining critical habitat for the species. Lastly, I conclude with recommendations for future *Phrynosoma* surveys.

1. RESEARCH SUMMARY

In Chapter 2: “Defining critical habitat for Greater Short-horned Lizards”, I identified the best landscape-scale predictors and used them to build a spatially-explicit model predicting relative probability of occurrence in Grasslands National Park. Specifically, occurrence of lizards (detections) was best predicted by covariates representing characteristics of the juniper-dune vegetation community, although additional predictors not previously identified included

vegetation patchiness and solar radiation. Occurrence was associated with low vegetation cover, a high degree of vegetation patchiness (quadratic relationship), and a high probability of an erosional vegetation community (quadratic relationship). Contrary to what was expected, lizards selected habitats with low solar radiation. The model is intended to be used to rank areas of habitat value in order of increasing conservation value and subsequently used to inform critical habitat designation for Greater Short-horned Lizards. Ranked habitats were used in concert with estimates of lizard densities to make a habitat-based index of lizard population size in Grasslands National Park. The index of population size can be used for monitoring changes in population size and is therefore an important tool for gauging conservation success of management actions.

My research in Chapter 3: “Do Greater Short-horned Lizards select hot spots or are other microsite characteristics more important?” measured whether Greater Short-horned Lizards select warm over cooler microhabitats, or whether other factors, such as composition or structure of vegetation cover contribute more to microhabitat selection. I found that micro-thermal habitat characteristics were not good predictors of lizard microhabitat selection at the landscape scale. Rather, when comparing lizard occupied microsites and random landscape microsites, I found that lizards selected sites with a high diversity of cover types. In highly diverse microsites, lizards selected for high amounts of bare soils as a component of the diverse cover. When I compared microsites selected by lizards and microsites within a random home range, I found that selection within the home range was highest for microsites with short vegetation, low cryptogram cover

(ground cover of mosses and lichens), and warm minimum surface temperatures. Selection was also strong for microsites with short vegetation, higher cryptogram cover, and cool average soil surface temperatures at the home range scale. No support was found distinguishing microsite locations between random home range and landscape sites. Greater Short-horned Lizards are not necessarily limited by the availability of heat at a microsite scale during the active season. This finding indicates that other limiting factors impact lizard populations, such as those relating to hibernation mortality. More research is required to ensure that appropriate year-round habitat is protected for this species.

2. CRITICAL HABITAT IMPLICATIONS

The goal from the onset of this thesis research was to identify habitat characteristics important for the survival and recovery of Greater Short-horned Lizards. One practical result of this research is to provide an evidence-based designation of critical habitat in the upcoming recovery strategy. That goal has been realized by the use of a model similar to the one presented in Chapter 2 in a draft designation of critical habitat for the Saskatchewan portion of the lizards' range.

In the draft designation, the reclassified model serves to outline the shape of occupied patches that capture a high proportion (70%) of known occurrences. Patches where lizards have not been observed in recent surveys are not included in the draft designation. While protecting high-density occupied habitats will contribute to the species long-term persistence on the landscape, there are three

potential problems that arise from combining the model with an occurrence-based approach.

First, some of the patches excluded due to an absence of lizard observations may in fact be occupied, but no survey effort has been made within that patch, or the patch was surveyed but not with sufficient search effort to detect lizard occupancy. Surveys of the study area were not designed with the goal of determining detection probability or patch-based occupancy. Without estimates of detection probability, it is not possible to determine how many visits to a site or how much search effort is required within a habitat patch to say with confidence that the patch is unoccupied (Durso et al. 2011). If potentially occupied patches are considered unoccupied for the purposes of delineating critical habitat, a portion of suitable occupied habitat may be excluded from protection.

Alternatively, the excluded habitat patches may represent habitat that is suitable but currently unoccupied. By using recent lizard observations for identifying habitat patches for critical habitat protection, occupancy status is based on a narrow window of time. Suitable habitat patches may be temporarily unoccupied due to stochastic extinction (Hanski 1994). Therefore, habitat patches that may be important for metapopulation dynamics would be excluded from critical habitat. These patches may represent important recolonization or translocation habitat that can become occupied in the future (Cornelisse 2013). Such additional protected habitat may be important for the recovery of a declining population.

A third problem with using an occupied-based patch approach to designating critical habitat for Greater Short-horned Lizards arises from the spatial arrangement of lizards across the landscape. The reclassified model demonstrates that lizards occur in low densities over a wide range of habitat conditions. While these areas may have a low density of lizards, they may contain a significant portion of the lizard population due to the large area they encompass. Restricting critical habitat to high-density occupied habitat may result in excluding a large proportion of individuals from habitat protection.

Chapter 3 (microhabitat selection) has not been expressly incorporated into the draft definition of critical habitat. However, small-scale habitat selection may be useful for identifying activities that are considered likely to destroy critical habitat. Cover type diversity was an important factor identifying microhabitat selection for Greater Short-horned Lizards; therefore, preserving cover type diversity should be a priority in occupied areas. Threats to cover type diversity may include construction activities and invasion of non-native plants such as yellow sweet clover (*Melilotus officinalis*), which, as a nitrogen-fixer, may have a considerable effect on vegetation composition and structure in badland plant communities (Van Riper and Larson 2009). Common public uses of Grasslands National Park unlikely to impact microsite cover type diversity include light trail activities, dispersed off-trail hiking, horseback traffic, and backcountry camping.

3. SURVEY RECOMMENDATIONS

Several aspects of the survey conducted in this research were novel to Greater Short-horned Lizard surveys in Canada and proved beneficial in identifying selected habitat characteristics. Based on my experiences conducting lizard surveys in Grasslands National Park, I recommend the following methods be considered for future *Phrynosoma* surveys in Canada.

Most importantly, GPS track logs should be used to quantify search effort and document the area searched. Quantifying search effort made identification of selected habitats possible. Also, GPS can be used to ensure that the desired area was covered in a survey and help searchers maintain the target search speed (2-3 km/h).

Secondly, a survey methodology that maximizes observations should be used. In my experience, a random meander survey methodology resulted in high numbers of lizard observations despite their low density on the landscape. Using this approach, high amounts of survey effort could be made in habitats that experienced observers identified as “good” habitat. Such allocation of survey effort effectively resulted in a stratified survey design, with additional effort made in areas that were likely to be suitable habitat. Some type of stratified search effort is necessary to maximize observations when individuals are generally rare on the landscape. In future surveys, I recommend an adaptive sampling survey design that employs additional search effort in some habitats while not relying on observer experience to identify what habitats require additional effort, particularly when knowledge of the complete distribution of the species in the area is the goal

(Walker 2012; Maxwell et al. 2012). One type of adaptive sampling, time-constrained adaptive sampling, was found to nearly double the number of observations per hour compared to linear transects in a survey of a small cryptic tortoise (*Pyxis arachnoides*) in Madagascar (Walker 2012). Locating the animal triggers additional search effort, allowing search effort to be targeted to high-quality habitats without relying on observer experience. Such a survey design would be ideal for Greater Short-horned Lizards, since surveys are frequently plagued by low numbers of observations. In order to rectify this problem, surveys for Greater Short-horned lizards could consist of a predetermined start point, end point, and general direction of travel to ensure the study area is adequately covered. Observers would be free to meander to a certain extent, but be restricted by the start and end points. When a lizard or a sign of a lizard (e.g. scat) is observed, a specified amount of time-limited additional search effort would occur in the adjacent area. By combining a transect approach, random meanders, and time-constrained adaptive sampling, the number of lizards observed per unit effort should be maximized and the true distribution of the species identified.

4. LIMITATIONS AND RECOMMENDED RESEARCH

While this thesis research makes a valuable contribution to identifying critical habitat for Greater Short-horned Lizards in Canada, further questions remain. One knowledge gap hindering conservation is selection for hibernation habitat. Most research has focused on habitat use during the active season (Powell et al. 1998; James 2002; and Chapter 2 and 3 of this thesis, the exception being research by

Mathies and Martin 2008). However, range-limiting factors are possibly related to winter climate and its effect on hibernation mortality at the northern range extent (Powell and Russell 1994, 1996). For example, in winters with low snow cover, lizards overwintering on steep slopes with limited accumulation of snow may become cold enough to contribute to mortality (Powell and Russell 1996). Hibernation habitat characteristics are an important factor identifying high-quality habitat for other extreme northern reptiles, such as the eastern Massasauga rattlesnake (*Sistrurus catenatus catenatus*, Harvey and Weatherhead 2006) and it would be expected to also be important for Greater Short-horned Lizards in Canada.

Hibernation mortality may have a particularly large impact on neonate survival. During a mild winter with heavy snow cover, a large proportion of the year's young may survive, contributing to a rapid population increase. Conversely, during periods of severe winter weather, hibernation mortality may drastically increase for neonates, contributing to population stagnation and eventual decline. In addition to climate, the condition of neonates entering hibernation may significantly impact their overwinter mortality (Iraeta et al. 2008). Year-to-year population fluctuations were not examined in this study, but may contribute to perceived declines in population size when surveys are conducted infrequently, as they are with Greater Short-horned Lizards in Saskatchewan and Alberta (James 2002).

A related avenue for future research would be examination of habitat quality for both the active-season and hibernation, rather than assuming that selected habitat

represents quality habitat. High-quality habitats contribute to demographic growth, where births exceed mortality (Delibes et al. 2001). Indicators of habitat quality for Greater Short-horned Lizards may include number of young per female (fecundity) or measurements of active season and hibernation season mortality. In Chapter 2 of this thesis, I assumed that there are no site-specific effects on mortality or reproductive success. Therefore high densities of lizards were considered indicative of high-quality habitat. However, high densities of animals are not necessarily an indicator of high-quality habitat if high densities of animals in these areas are not reproductively successful (Delibes et al. 2001). I did not attempt to measure indicators of habitat quality due to the difficulty in identifying sources of mortality and measuring reproductive success for a small, cryptic animal such as the Greater Short-horned Lizard. More directed research on this and the other questions could help address knowledge and data gaps for this species at risk.

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