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HABITAT USE OF THE WESTERN TOAD IN NORTH-CENTRAL ALBERTA AND THE INFLUENCE OF SCALE

by

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Abstract

The western toad (*Anaxyrus boreas,* formerly *Bufo boreas*) is one of many amphibian species considered to be at risk of extinction (COSEWIC status is Special Concern). I examined habitat use patterns of the western toad using several methods to gain a better understanding of its habitat requirements. I examined the relationship between relative abundance of the western toad and two sympatric amphibian species (wood frog, *Lithobates sylvaticus*; and boreal chorus frog, *Pseudacris maculata*) and habitat features at eight scales of spatial extent at 24 wetlands in the Lake Utikuma region of Alberta, Canada. I radio-tracked adult western toads in three study areas in the Aspen Parkland and Boreal regions of north-central Alberta to examine 1) whether patterns of habitat selection change with different scales of spatial extent, spatial resolution, habitat composition, temporal period, and between males and females during the active period, 2) habitat used for hibernation, and 3) factors influencing the timing and nature of movements to hibernation sites.

I found that the abundance of the three amphibian species was best described at different spatial extents and was related to the biology of each species. Resource Selection Function (RSF) models, created using radio-telemetry data, indicated that habitat selection was scale-dependent for western toads; differences in selection were observed among study designs, study areas, time periods, and sexes. Predictive ability did not differ significantly among study designs. However, models that were created using a fine-grained map and home-range spatial extent generally produced models with greater predictive ability than models using a coarse-grained map or population-range extent. During the active season toads selected open habitat types such as wet shrub, disturbed grass, and crop/hay fields. Western toads hibernated terrestrially in pre-existing tunnels and the majority of toads hibernated in forest stands dominated by spruce. Toads used hibernation sites 146–1936 m from breeding ponds and 68% of hibernacula were communal. Arrival at and entry into hibernation sites was influenced by temperature and/or day length; larger toads moved to hibernation sites later in the year. My research results can be used to identify and protect habitat for western toads in Canada.

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List of Symbols, Nomenclature, or Abbreviations

µg	Microgram
AIC	Akaike’s information criteria
ANOVA	Analysis of variance
Avail.	Available
Beta	Coefficient value
C	Celsius
CGHR	Coarse-grained buffered-home-range design
CHL-a	Chlorophyll-a
cm	Centimeter
coef.	Coefficient
COSEWIC	Committee on the status of endangered wildlife in Canada
d	Day
df	Degrees of freedom
DO	Dissolved oxygen
EINP	Elk Island National Park
EOSD	Earth observation for sustainable development
FGHR	Fine-grained buffered-home-range design
FGPR	Fine-grained population-range design
g	Gram
GIS	Geographic information system
GLM	General linear model
GLMM	General linear mixed model

GzLM	Generalized linear model
h	Hour
ha	Hectare
HEAD	Hydrology, ecology and disturbance
IUCN	International union for conservation of nature
km	Kilometer
L	Liter
LSD	Least significant difference
m	Meter
mg	Milligram
Min.	Minimum
mm	Millimeter
mo	month
MRPP	Multi-response permutation procedure
mS	Milli-Siemens
n	Sample size
N	North
NA	Not applicable
NTU	Nephelometric Turbidity Units
P	Probability value
PC	Principle component
PCA	Principle component analysis
pers. comm.	Personal communication

Pre-Hib.	Pre-hibernation
Res	Model residuals
R	Random/available
RSF	Resource selection function
SAV	Submersed aquatic vegetation
SE	Standard error
spp.	Species
SUL	Snout-to-urostyle length
TDS	Total dissolved solids
TM	Thematic mapper
TN	Total nitrogen
TP	Total phosphorus
unpubl.	Unpublished
U	Used
UTM	Universal transverse Mercator
var.	Variance
vs.	Versus
W	West
wk	Week
X_i	Variable of interest
YOY	Young-of-the-Year

Chapter 1. General Introduction

Significant alteration of most ecosystems on Earth has occurred directly or indirectly as a result of increasing human populations and their overexploitation of resources. Alterations have resulted in the loss of suitable habitat for many species, causing population declines to the point where many species are now considered to be at risk of extinction (Baillie, Hilton-Taylor & Stuart, 2004). Most amphibians require both aquatic and terrestrial habitat to complete their life cycle (Trenham & Shaffer, 2005); therefore, this group of vertebrates may be particularly susceptible to habitat alteration since the degradation of either component could result in population declines. Global declines of amphibian populations have been well documented (Houlahan et al., 2000) and habitat loss and degradation are thought to be major causes of these declines (Stuart et al., 2004).

The field of conservation biology has exploded in the past 20 years, with its goals being to 1) investigate and describe biodiversity, 2) understand the effects of human activities on species, communities, and ecosystems, and 3) develop approaches to protect and restore biodiversity (Primack, 2000). Habitat destruction (change in a habitat resulting from pollution or other habitat alterations that makes the habitat unsuitable for the organism), fragmentation (change in landscape structure that results in smaller patch sizes and more edge habitat; Reed et al., 1996), and degradation (change to a habitat that makes it less suitable for an organism even if the dominant structure of the community does not change; Primack, 2000) are major threats to endemic biodiversity (Baillie, Hilton-

Taylor & Stuart, 2004). As a result, investigations of habitat use and critical habitat (defined as habitat that is vital to the survival or recovery of wildlife species; Government of Canada, 2008) have been a major focus for the conservation of species (e.g., Blouin-Demers, Bjorgan & Weatherhead, 2007; Li, Litvak & Clarke, 2007; Gregr et al., 2008).

The western toad (*Anaxyrus boreas*, formerly *Bufo boreas*) is considered to be Near Threatened by the World Conservation Union (IUCN) because drastic population declines have occurred in Colorado, Wyoming, California, and elsewhere (Hammerson, Santos-Barrera & Muths, 2004). In Canada, declines have been reported from the south coast area of British Columbia (Wind & Dupuis, 2002). The western toad has been assigned the status of Special Concern in Canada (COSEWIC, 2009) and Sensitive in Alberta (General Status, Alberta Sustainable Resource Development, 2005), largely as a precautionary measure because of the severe and rapid declines in the United States and lack of information about Canadian populations (Wind & Dupuis, 2002).

These status listings may change in the near future because the taxonomy of the western toad is currently under review. Historical classifications of the *boreas* species group recognized four species (western toad, *A. boreas*; Yosemite toad, *A. canorus*; black toad, *A. exsul*; and Amargosa toad, *A. nelsoni*). The Yosemite, black, and Amargosa toads each have very small distributions in the southwestern US (Davidson & Fellers, 2005; Fellers, 2005; Goebel et al., 2005). The western toad is broadly distributed across western North America (Figure 1-1) and is comprised of two subspecies, the boreal toad (*A. b. boreas*) and the

California toad (*A. b. halophilus*; Muths & Nanjappa, 2005). However, new phylogenetic analyses, based on mtDNA 12S rDNA, cytochrome oxidase I, control region, and restriction sites data, identified three major haplotype clades: northwest, east, and southwest (Goebel et al., 2009). The Northwest clade includes *A. b. boreas, A. b. halophilus*, and *A. canorus* from the middle Rocky Mountains, coastal, and central regions of the west and Pacific Northwest. The Southwest clade includes *A. b. halophilus, A. canorus, A. exsul,* and *A. nelsoni* from California and Nevada. The Eastern clade includes *A. b. boreas* from southern Utah, the southern Rocky Mountains, and north of the Great Basin at the border of Utah and Nevada (Goebel et al., 2009). Samples were not collected from Alberta, but it is assumed that toads from Alberta would fall into the Northwest clade. If the *boreas* species group taxonomy is revised to reflect this new classification, then the status of western toad populations may be changed to provide higher levels of protection for the Eastern clade, for which declines have been most severe (Goebel et al., 2009), and western toads in Alberta may be reassessed to a lower risk category.

The cause of western toad population declines is not known with certainty. Disease appears to be responsible for the drastic declines in the southern Rockies (e.g., chytrid fungus infections, Muths et al., 2003). Carey (1993) suggested that some environmental factors or synergistic effects might be stressing toads, causing suppression of the immune system and making them unable to fight disease. Other suggested threats include spread of the pathogen *Saprolegnia ferax* during fish stocking (Kiesecker, Blaustein & Miller, 2001), ultraviolet radiation

(Blaustein et al., 1994), habitat destruction and degradation (e.g., water retention projects), predation by and competition with exotic species and native species that may be better adapted to altered landscapes, and fishery management activities (Hammerson, Santos-Barrera & Muths, 2004). Urban and agricultural development threaten western toad populations in the south coast of British Columbia through increased road traffic, habitat deterioration, isolation, pesticides, disease, predation or competition associated with exotic bullfrogs (*Lithobates catesbeianus*), and the pathogens and activities of stocked fish (Wind & Dupuis, 2002).

Alberta Sustainable Resource Development is developing guidelines to protect the critical habitat of western toads in parts of Alberta (Boreal/Foothills Sensitive Species Guidelines, unpubl.). However, western toads are very cryptic after they leave breeding congregations at lakes, ponds, and wetlands in late spring and very little is known about their habitat use in Alberta, so identifying critical terrestrial habitat to protect is difficult. To identify habitat that is vital for the survival of a species we must understand its habitat use patterns, fitness associated with different habitat types, and movement abilities. Investigating all of these topics is beyond the scope of this thesis; however, I have taken the first step towards identifying critical habitat for the western toad in Alberta. The goal of my doctoral research was to investigate habitat use of the western toad in north-central Alberta. My research was conducted near the northeastern edge of the western toad's range. Populations near the edge of their range often have lower population sizes, higher extinction rates, and lower adaptability (Bahn, O’Connor & Krohn, 2006); therefore, these populations are more likely to be in need of protection. While examining the patterns of habitat use by western toads, I also examined questions relevant to all ecologists studying the habitat use of an organism: How do spatial and temporal scales, habitat composition, sex of the individual, and method of analysis influence the observed patterns of habitat use.

A common problem with investigating patterns of habitat use is that patterns often change with different scales of spatial extent (Turner, 1989; Wiens, 1989), grain/resolution of the analysis (Hobbs, 2003; Lawler et al., 2004), differing habitat availability (Johnson, 1980; Mysterud & Ims, 1998), and seasons (Schooley, 1994; Arthur et al., 1996), and can differ between males and females (Muths, 2003; Bartelt, Peterson & Klaver, 2004), or between individuals of different age classes (Stamps, 1983; Imansyah et al., 2008). Therefore, it is important that the scales of study are chosen carefully to match the study goals and species of interest. Generalizations about the effect that scale has on habitat selection are few, because of enormous variation in landscapes and patterns of processes influencing resource selection (Boyce, 2006). My research examined western toad habitat use across several spatial scales, study locations, seasons, and between males and females, to try to define patterns broadly in an effort to see how patterns of habitat use change.

Johnson (1980) suggested that habitat selection is a hierarchical process in which our observation of relationships can change along a continuum of spatial scales. One of the basic principles of hierarchy theory is that habitat selection is constrained by the level above and clarified by the level below (Allen & Starr, 1982). Johnson (1980) describes four orders of spatial scale at which habitat selection could be investigated. First-order selection is the geographical range of a species. Second-order selection is the home range of an individual or social group within the geographical range. Third-order selection is the use of various habitat components within the home range by an individual or group. Fourth-order selection is micro-habitat selection, such as the selection of locations with a specific temperature range. In addition, Wiens (1989) suggested that there may be domains of scale, regions of the spatial spectrum over which patterns either do not change or change monotonically. In turn, domains are demarcated by relatively sharp transitions from dominance by one set of factors to dominance by other sets (Wiens 1989). Since habitat selection is often scale-dependent (O'Neill, 1989; Boyce, 2006; Mayor et al., 2009), I investigated habitat selection by western toads across several spatial and temporal scales to gain a better understanding of how they respond to their environment. I investigate second and third order habitat selection of western toads in chapters 2-4, and briefly discuss first order selection here.

Western toads (as the species is currently defined) occur along the Pacific coast from southeastern Alaska to the northwestern parts of Mexico (i.e., Yukon, British Columbia, Washington, Oregon, and California) and east into Alberta, Montana, Wyoming, Idaho, Nevada, Utah, and Colorado, and formerly occurred in northern New Mexico (Hammerson, Santos-Barrera & Muths, 2004; Figure 1-1). They occur at elevations from sea level to 3640 m (Livo & Yeakley, 1997) and occupy a variety of habitats, including boreal forest, temperate forest, shrubland, grassland, desert, montane, arable land, pasture land, and a wide variety of aquatic habitats (Hammerson, Santos-Barrera & Muths, 2004). Western toads are largely terrestrial; they hibernate and forage in terrestrial habitats, but require standing water for the development of eggs and larvae. Their range may be limited in part by precipitation levels and temperature. Western toads are absent from most of the desert in southwestern U.S. (Stebbins, 1985 in Hammerson, Santos-Barrera & Muths, 2004) and also from the arid regions of the Columbia Basin in Washington and the Willamette Valley in Oregon (Leonard et al., 1993 in Wind & Dupuis, 2002). Their eastern range ends approximately where the Great Plains – Palouse Dry Steppe Ecosystem Province begins (Bailey, 1995). In the Yukon, western toads only occur in the southeastern region. They are restricted to valleys with high snowfall and geothermal activity, in which ground freezing is limited and they can burrow below the frost line (Cook, 1977; Mennell, 1997; Smith, Meikle & Roots, 2004).

Western toads occur in the Boreal Forest, Foothills, Rocky Mountain, and Parkland regions of Alberta, but do not occur in the Grasslands or Canadian Shield regions (Alberta Government, 2005; Alberta Sustainable Resource Development (SRD) Fish and Wildlife Management Information System (FWMIS) data). Their range appears to be expanding eastwards in the Boreal Forest and Parkland regions (Alberta SRD FWMIS data) and they can now be found near Cold Lake, Alberta, near the Saskatchewan border (Browne, 2009). The Grassland and Canadian Shield regions are the driest in Alberta (mean annual precipitation 374 mm and 380 mm, respectively vs. 447-798 mm in other regions), but they differ in that the Grasslands region is the hottest region whereas the Canadian Shield is the coldest (mean annual temperature = 4 degrees C and -2.6 degrees C, respectively) in Alberta (Natural Regions Committee, 2006). Precipitation may play a role in the western toad's distribution in Alberta, but a number of other factors could also be contributing. For example, western toads may compete (e.g., for food, or inadvertently for mates) with Canadian toads (*A. hemiophrys*), which overlap in distribution along the eastern edge of the western toad's range in Alberta (Russell & Bauer, 2000). Canadian toads may be better adapted to drier landscapes (e.g., prairies) than western toads.

In Chapter 2 I investigate second-order habitat selection (selection of the home range within the geographical range) by examining the relationship between the relative abundance of the western toad (and two sympatric anuran species) and environmental variables at 24 wetlands in the central mixed-wood subregion of the Boreal Forest region (Alberta Government, 2005), north of Utikuma Lake, AB (Figure 1-2). In that chapter I examine these relationships at a local pond scale, a landscape scale with seven different scales of spatial extent (proportional cover of different vegetation-types within 50-5000 m from the wetland), and relative to geologic landform, to determine how relationships change at differing spatial scales. Inclusion of the wood frog (*Lithobates sylvaticus*) and boreal chorus frog (*Pseudacris maculata*) in this analysis allowed me to compare responses among species and formulate hypotheses as to what biological features influence the strength of the relationship between each spatial extent and anuran abundance for the entire assemblage. Although few studies have examined relationships between amphibian abundance and geologic landform, significant relationships have been found in the US (Wilkins & Peterson, 2000; Russell, Mabee, & Cole, 2004). This variable may be a useful predictor of patterns of abundance for some species that can easily be obtained from maps for most areas. I selected two study areas within the central mixed-wood subregion of the Boreal Forest so that I could compare the results between study areas (Utikuma and a second area farther east near Lac La Biche, termed “Boreal”; Figure 1-2) and identify habitat features that are consistently selected between sites across the region. I chose the Utikuma area specifically because I was able to take part in the Hydrology, Ecology, and Disturbance (HEAD) research project.

In Chapter 3, I examine second- and third-order habitat selection (selection of various habitat components within the home range) of adult western toads during the active season (May-October) at different scales of spatial extent, scales of spatial resolution, habitat composition (i.e., proportions of different land-cover type), temporal periods, and between males and females using resource selection function (RSF) models. I radio-tracked toads to determine locations used on the landscape, and generated random locations within a Geographic Information System (GIS) to determine available habitat locations. I investigate the influence of spatial extent by comparing RSF models that measured available habitat within the population range (second-order selection) and within a 300 m-radius buffer surrounding each location (third-order selection). I compare a third study design that examines third-order selection but differs in resolution of vegetation types to determine how changing the spatial resolution of the GIS habitat map influenced the results and to assess how applicable this publicly available land-cover map is for anuran habitat use investigations.

Conclusions regarding whether a particular habitat component is selected, avoided, or used proportional to its composition are critically dependent upon the array of habitat components that are available to the animal (Johnson, 1980). For this reason, I chose to conduct my radio-telemetry research (Chapters 3 to 5) at three study areas that differed in land-use and occurred in two eco-regions, so that the composition of available habitat types differed (Figure 1-2). I radio-tracked toads at two areas in patches of dry mixed-wood boreal forest in the Parkland region (Alberta Government, 2005); one area is relatively pristine and located in Elk Island National Park, the other is in an agricultural landscape influenced by cattle grazing, cultivation of crops/hay, and rural housing. The third area is in the central mixed-wood subregion of the Boreal Forest region (Alberta Government, 2005) and is influenced by the forestry and oil/gas industries. By choosing a range of study areas, I sought to identify habitat elements that are consistently selected by western toads, and are therefore more likely to define critical habitat for the species in the mixed-wood boreal forest.

Temporal scale is another major consideration in the design of habitat selection studies because selection often changes with season or biological events (Schooley, 1994; Arthur et al., 1996). I expected that western toad habitat selection would differ over the year to meet the needs of reproduction, foraging, and hibernation. In Chapter 3, I divide the active season into three periods for my RSF analyses: May-June, July-August, and September-October, which correspond to the breeding, foraging, and pre-hibernation seasons, respectively. I also examine differences in habitat selection between males and females. I create an RSF model for each study design (n = 3), study area (n = 3), season (n = 3), and sex (n = 2) for a total of 54 RSF models that allow me to directly compare differences among these factors.

Chapters 2 and 3 focus on the active season, and in Chapters 4 and 5 I examine habitat selection and questions related to hibernation. Winter is a critical time period for amphibians and reptiles in cold climates and survival of western toads has been found to be influenced by minimum daily winter air temperatures, snow depth and winter environmental moisture levels (Scherer, Muths & Lambert, 2008). Western toads spend over half of the year in hibernation sites (October to May), so the selection of a good hibernation site is important. Little is known about western toad hibernation sites (but see Mullally, 1952; Campbell, 1970; Jones et al., 1998; Bull, 2006) and no studies have been published on western toad hibernation in Canada. In Chapter 4, I determine (1) locations and describe the physical features of hibernation sites; (2) if western toads hibernate communally; (3) if temperatures at hibernation sites differ from reference sites; (4) whether the distance between breeding ponds and hibernation sites differs between study areas (same as Chapter 3) or between sexes, (5) whether government guidelines for buffers around watercourses would encompass core terrestrial habitat for hibernation; and (6) which land-cover types are selected for hibernation using RSF analyses. My RSF analyses for hibernation habitat examine second-order selection and are similar to those used to examine second order selection during the active season (see FGPR design in Chapter 3).

In Chapter 5, I examine factors affecting the timing and nature of movements to hibernation sites by western toads. I predicted that larger western toads would move to their hibernation sites later than do smaller toads, and move to these sites more directly, along straighter paths. Straight paths indicate oriented movements, while more tortuous movements indicate random search or directed movements with less efficient orientation (Benhamou, 2004). Remaining at foraging grounds later in the year may provide benefits of increased growth, but would also come with increased risk of being trapped away from hibernacula when temperatures drop. In this chapter, I 1) determine if arrival date in the hibernation vicinity or entry date to the hibernation site differs among study areas (same areas as Chapter 3 and 4), years, sex, or with toad size, 2) examine evidence supporting my proposition that larger (likely older) toads are familiar with their landscape and remain at their foraging grounds later in the year than do smaller (likely younger) toads, and 3) determine if the timing of the arrival of toads at and entry into hibernation sites is more strongly correlated with temperature or date (indicating whether physical conditions or innate mechanisms initiate movements). Understanding these kinds of behavior patterns offer insight into the mechanisms behind larger scale patterns of habitat selection and could either be causes or effects of the patterns observed during the pre-hibernation season as documented in Chapter 3. These aspects of behavioral ecology have not been previously investigated for toads.

The overall goal of my doctoral research was to investigate habitat use of the western toad, primarily for conservation applications. However, while investigating the habitat use of the western toad, I also examined general ecological questions on the influence of spatial and temporal scales applicable to anuran habitat selection research. I used different analytical techniques to search for underlying patterns, and I sought mechanisms that could explain the patterns observed. The present thesis is in paper format such that Chapters 2-5 represent manuscripts that have been published in, are accepted for publication by, or will be submitted to peer-reviewed journals in the field of ecology, conservation, or amphibian biology. Chapters 2-5 are co-authored papers; therefore, I have used ‘we/our’ throughout these chapters. Chapter 6 summarizes findings reported in Chapters 2-5.

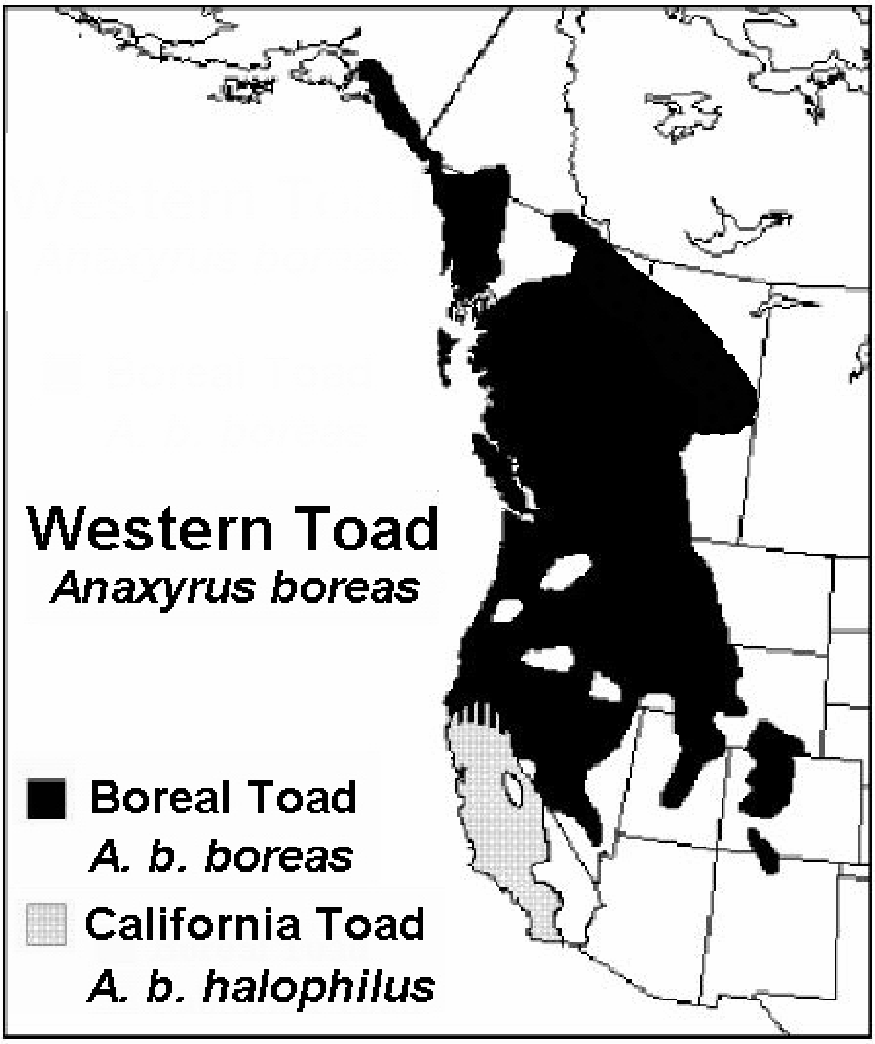

Figure 1-1. North American distribution of the western toad, *Anaxyrus boreas*, indicating the range of the two subspecies, the boreal toad (*A. b. boreas*) and the California toad (*A. b. halophilus*). Modified from Wind and Dupuis (2002).

Figure 1-2. Habitat use of western toads was investigated at four study areas in Alberta, Canada. Amphibian relative abundance surveys were conducted at 24 ponds in the Utikuma study area for analyses in Chapter 2. Western toads were radio-tracked at the Park, Pasture, and Boreal study areas for analyses in Chapters 3 to 5.

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Chapter 2. The Relationship of Amphibian Abundance to Habitat Features Across Spatial Scales in the Boreal Plains[1]

2.1 Introduction

Global declines of amphibian populations have been well documented (Houlahan et al., 2000) and habitat alteration is considered to be a major cause of decline (Stuart et al., 2004). Most amphibians require both aquatic and terrestrial habitat to complete their life cycle (Trenham & Shaffer, 2005); therefore, degradation of either habitat component could result in population declines. Understanding the relationship of a species to its habitat is a prerequisite for making realistic predictions about its response to large- and small-scale habitat change. A common problem with investigating patterns of habitat use is that the perceived patterns often change with different spatial scales of study (Turner, 1989). Several studies examining relationships between richness/abundance of temperate pond-breeding amphibian species and environmental variables at multiple spatial scales have suggested 200 m to 10 km to be appropriate scales for examining relationships between these species and habitat features (e.g., Gibbs, Whiteleather & Schueler, 2005; Herrmann et al., 2005). Suggested spatial scales vary widely among studies, a result that is likely due to differences among species or geographical areas.

We examined the relationship between habitat features and amphibian abundance in boreal Alberta. The boreal plain ecozone covers a vast area of

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western Canada (650 000 km^2); however, relatively little research has examined relationships between amphibians and their habitat here (but see Roberts & Lewin, 1979; Constible, Gregory & Anholt, 2001; Hannon et al., 2002). This region is lightly disturbed, yet is poised for much greater industrial development over the next 20 years (Foote & Krogman, 2006). Alberta Sustainable Resource Development is currently creating industrial development setback distance guidelines so critical habitat for western toad (*Anaxyrus boreas*, formerly *Bufo boreas*) is buffered from disturbances in the boreal region (Boreal/Foothills Sensitive Species Guidelines, unpubl.). However, very little is known about western toad habitat use in the boreal, so identifying critical habitat is difficult. Knowledge of habitat factors that influence anuran abundance over multiple spatial scales may help guide approaches to habitat protection in the near future.

Our objectives were to 1) determine the relative abundance of three anuran species at 24 ponds in boreal Alberta, 2) identify the spatial scale most appropriate for predicting abundance patterns, and 3) examine relationships between anuran relative abundance and habitat features. To meet these objectives, we investigated relevant habitat features for all three anuran species present at our sites in the boreal region of west-central Alberta, Canada: wood frog (*Lithobates sylvaticus*, formerly *Rana sylvatica*), boreal chorus frog (*Pseudacris maculata*), and western toad. Knowledge of the life-history of boreal amphibians is relatively scanty in comparison to amphibians from more southerly regions (Elmberg, 1993). Our study of boreal populations is also novel because we synthesized information across various spatial scales collected as part of a wider ecological and hydrological study of our study area: the Hydrology, Ecology, And Disturbance (HEAD) project. Participating in this project gave us access to an extensive collection of environmental variables that were collected by the group at the 24 study ponds.

2.2 Methods

STUDY SITES

The Hydrology, Ecology, And Disturbance (HEAD) research group is a multi-disciplinary project that collected data at 125 wetlands in the Lake Utikuma region of Alberta, Canada. The goal of HEAD was to be able to predict the response of individual wetlands to disturbances (Hornung, 2003). The wetland sites were approximately 20 km north of Utikuma Lake (56 degrees 00’ – 56 degrees 20’ N, and 115 degrees 20’ – 115 degrees 40’ W), within the central mixed-wood subregion of the boreal forest region (Alberta Government, 2005). For extensive study of geomorphology, hydrology, limnology, submersed vegetation, amphibian and waterfowl habitat quality, the HEAD group selected 24 focal wetlands in a 30-km by 20-km study area. These 24 wetlands were selected from 125 candidate sites because they were deemed to be representative of water-bodies in this region; they varied in size (Table 2-1), and occurred in approximately equal numbers in moraine, outwash, and glaciolacustrine landform types, representative of the region.

Grey luvisols and deep organic peat deposits were the dominant substrate types. All wetlands were relatively shallow, pan-shaped, associated with established floating peat beds, and all had flocculent bottoms (substrate is loosely deposited at the bottom of the wetland and easily suspended; Hornung & Foote, 2006). Common tree species around the 24 wetlands were trembling aspen (*Populus tremuloides*), balsam poplar (*Populus balsamifera*), white spruce (*Picea glauca*), jack pine (*Pinus banksiana*), black spruce (*Picea mariana*), tamarack (*Larix laricina*), and paper birch (*Betula papyrifera*).

STUDY SPECIES

Wood frog and boreal chorus frog are widespread and abundant throughout most of Alberta and are considered to be "secure" (Alberta Government, 2000). The western toad is much less abundant and has a patchy distribution in western and central Alberta (Russell and Bauer, 2000); provincially the species has the general status of "sensitive" (Alberta Government, 2000). These three species are widely distributed in western and northern North America (Stebbins 1985) and are the only amphibians that occur in northwestern Alberta (Russell and Bauer, 2000).

AMPHIBIAN SAMPLING

We conducted seven sets (~every 2 weeks) of visual surveys for amphibians at each of the 24 HEAD research wetlands from May to August 2004. This time period encompassed the peak breeding seasons and periods of metamorph emergence for all three species. Visual surveys were conducted by walking slowly along the wetland perimeter and searching for amphibians within 1 m of each side of the observer. Surveys were conducted for a two-hour period or until the entire perimeter was surveyed. We attempted to capture every amphibian seen. At a few ponds we did not see any chorus frogs or western toads, but heard them calling. To account for their presence, we added one animal to the count for each wetland during each of the first three surveys if one or more individuals were heard calling at that site. We standardized our relative abundance data to numbers of individuals caught·$10h^{-1}$ for each of the three species over the course of the summer (rounded to whole numbers). Each wetland was surveyed regularly throughout the summer, and each was surveyed equally during the breeding and young-of-the-year (YOY) emergence periods.

For all species, we found that the number of captures for a visit to each wetland was related to air temperature (which ranged from 2-29 degrees C, and is also associated with weather and time of day; general linear mixed model (GLMM); R Development Core Team, 2007; $P < 0.05$ for each temperature coefficient). We checked whether mean temperature over all visits varied significantly among wetlands. We found that mean temperatures (range of means = 13-19 degrees C) did not vary significantly among wetlands, indicating that each wetland was sampled equally over the range of temperatures we experienced that summer (one-way ANOVA; SPSS Inc., 1989-2007; $F_{23,144} = 0.616$, $P = 0.912$). Thus, we did not include air temperature in any further analyses. We did not compare relative abundance among species because of potential differences in our ability to detect and capture the three species of anurans.

ENVIRONMENTAL VARIABLES COLLECTION

Local environmental variables

We collected and acquired data for 24 local environmental variables for each wetland (Table 2-1). First, we calculated area and perimeter of each wetland using aerial photographs and Sigma Scan Pro (Systat Software Inc., 1999). Photos from 2000 were used for 21 of the wetlands if available and if they clearly showed wetland edges, otherwise we defaulted to 1986 photos. The wetland edge was considered to be where thick vegetation met open water; this edge was clearly visible from photos and was comparable across years.

We acquired local water chemistry and aquatic flora and fauna data from the HEAD project. The University of Alberta Biogeochemical Analytical Laboratory analyzed water samples (collected 9 June and 30 June 2004) for total nitrogen (TN) and total phosphorus (TP). The average reading from the two sample dates was used for estimates of TN and TP for each wetland. Turbidity, chlorophyll-a (CHL-a), conductivity, water temperature (degrees C), dissolved oxygen (DO), pH, total dissolved solids (TDS), submersed aquatic vegetation (SAV), secchi depth, and wetland depth were randomly sampled at five locations within the open water of each wetland in June 2004. One measurement was taken from each of the five random locations for each variable except turbidity, which had multiple readings (1-4) for each location; the average of these multiple readings was used as the value for that location. In turn, we used the average of the five random points to achieve one value for each variable per wetland for our analyses. SAV was recorded as a categorical count from one to five, one being scant vegetation and five being dense vegetation (see Bayley & Prather, 2003 for details). SAV was collected visually from a small boat.

Aquatic plant density is the proportion of plant volume in an aquatic quadrat sampled. Aquatic plant density could sometimes be > 1 because the full height of emergent vegetation was recorded but quadrat volume was calculated using only water volume. This measure of aquatic vegetation was more detailed than the SAV variable and was collected within 2 m of the wetland edge (where tadpoles are more likely to be), but was collected in 2001 (rather than 2004). Even though this variable was not collected in the same year that we sampled amphibians, we felt that previous pond characteristics were relevant (e.g., Piha, Luoto & Merila, 2007). Please see Hornung & Foote (2006) for a detailed description of the methods of sampling aquatic plant density.

Invertebrates can be competitors of, or predators on, amphibian larvae (Chivers et al., 1999; Mokany, 2007), so we included two estimates of aquatic invertebrate biomass for each wetland: total invertebrates, and predatory invertebrates. Invertebrate biomass was estimated for all 24 wetlands during four systematic surveys conducted between 10 May and 5 September 2001. Three sub-sampling locations were established at each wetland using a stratified random design that was randomly selected along a transect that ran parallel to the wetland shore and was one-third the entire shoreline length. The transect at each wetland was set away from confounding factors such as roads, seismic lines, or oil-well locations. The aquatic/terrestrial interface zone, emergent vegetation zone, and submergent vegetation zone were swept vertically (bottom-up) with two sweeps from each aquatic zone (total of six sweeps) using a standard D-shaped invertebrate dip net (net opening 640 cm^2). Water depth was measured at each sweep location to calculate the volume of water sampled. Invertebrates were identified to the lowest possible taxonomic resolution, which was usually genus, but was sometimes family or species. Biomass was estimated by assigning each individual to a size class and then averaging over the three sampling locations to give an estimate of invertebrate $\text{biomass}\cdot\text{volume}^{-1}\cdot\text{wetland}^{-1}\cdot\text{sampling round}^{-1}$ (see Hornung & Foote, 2006).

We collected data on terrestrial vegetation using a quadrat every 5 m along a 100 m-transect parallel to each wetland's edge. Each quadrat was a 1 m × 10 m rectangle oriented perpendicular to the shoreline and abutting the wetland's edge. We visually estimated percent total vegetation cover, and percent cover and height for the three most dominant plants for each quadrat, then calculated an average percent vegetation cover and median height for each wetland. Dominant vegetation type was categorized into five groups: aquatic plants (e.g., *Carex*, *Typha*), grasses and wildflowers (e.g., *Poa*, *Gypsophila*), shrubs (e.g., *Rhododendron*, *Salix*), conifers (e.g., *Picea*), and deciduous trees (e.g., *Populus*). We calculated the percent cover of each of these vegetation types for each quadrat, then calculated an average percent cover for each category from the 20 samples for each wetland. The vegetation type that had the greatest percent cover average was assigned as the dominant vegetation type for the wetland.

The length and width of all terrestrial woody debris within 10 m of the wetland edge was recorded and proportion of cover calculated. However, we had to estimate the total woody debris for two wetlands. Only one-quarter of the edge was surveyed for one wetland; we assumed the proportion of woody debris was similar around the remainder. The other wetland had too much woody debris to measure. We conservatively assigned this wetland a woody debris proportion cover of 0.01 (twice the amount of the next greatest value). Finally, we recorded the presence or absence of beaver dams or beaver lodges (usually abandoned) on land within 10 m of the entire wetland perimeter. We included this variable because beaver structures are used as hibernation sites by western toad (Chapter 4) and the channels cut by beavers into pond edges provide wet access to forested edges and are used by tadpoles.

Presence of fish was not included as a variable because fish (brook stickleback, *Culaea inconstans*) were only present in two wetlands. Preliminary analysis of our data indicated that the inclusion of fish presence/absence did not increase the explanatory power of our models. Although the abundance of small-bodied fish has previously been found to influence the abundance of anuran amphibians in small boreal lakes in Alberta (Eaton et al. 2005), fish presence did not lead to the exclusion of any amphibian species from these systems or from our wetlands.

Landscape environmental variables

We used a land-cover classification geographical information system (GIS) layer to determine the proportion of cover in various land-class categories within 50, 100, 200, 500, 1000, 2000, and 5000 m buffers from the perimeter of each wetland (Environmental Systems Research Institute, 1999-2004). We chose the seven landscape buffer sizes based on preliminary movement results from radio-tracking western toads in the aspen parkland and boreal regions of Alberta (C. Browne, unpubl. data) and estimates from the literature of dispersal distances for anurans (e.g., Muths, 2003).

The initial land-cover classification was a raster layer (cell size 25 m × 25 m) of 26 land classes created from a Landsat 7 Thematic Mapper (TM) satellite scene taken September 9, 1999 (Ducks Unlimited, 2003). We created buffers around each of the wetlands and used the thematic raster summary to calculate the number of cells of each land class within each buffer area (Beyer, 2004). Because some of our sites were less than 1 km apart, we had overlapping buffers for some sites at the larger landscape scale of spatial extent. To assess the potential effect of compromised independence or spatial autocorrelation, we included our UTM northings and eastings as factors in a curve-fitting regression analysis against the relative abundance data for each species (SPSS Inc., 1989-2007; $P > 0.5$ for all). We found these variables were not significant and excluded them from further analysis.

We identified 15 land classes (consolidated from 20 original classes) within the 5000-m wetland buffers (see Table 2-1) based on those delineated by Ducks Unlimited (2003). We were not able to detect wetlands or other landscape features smaller than the raster layer cell size of 25 m x 25 m.

Landform

We identified the landform type of each site using surficial geology maps created by the Alberta Geological Survey (e.g., Paulen, Pawlowicz & Fenton, 2004). Three geological landform types were represented at our 24 wetlands: outwash plains (n = 7), moraine (n = 10), and glaciolacustrine sites (n = 7). Outwash plains are relatively flat and consist of sands and other fine sediments. Moraines are piles of rocks, silts and sands left behind during glacial retreat. They contain more depressions than the other two landforms. Glaciolacustrine sites are flat areas with clay and extensive peatlands.

DATA ANALYSIS

Our data analysis included two steps for both the local scale and each of the seven landscape scales. Firstly, we incorporated the environmental variables into a Principal Components Analysis (PCA; McCune & Mefford, 1999). Our PCAs accomplished multiple tasks. The analyses simultaneously ran 999 PCAs using randomized data and determined whether the amount of variance explained by the real data for each PC explained significantly more variation than the randomized data (to determine how well the PCs explained the variation in the environmental variable dataset). To help interpret relationships between amphibians and landform type, we also performed a Multi-Response Permutation Procedure (MRPP) on the variables used for each of the eight PCAs with pairwise comparisons to determine whether environmental variables distinguished among the three landform types at each landscape scale of spatial extent. Finally we noted environmental variables showing high correlations ($R^2 >= 0.5$) with the PC axes, so that we could later relate them back to amphibian occurrence data during our second step.

Secondly, for each amphibian species and at each scale of spatial extent, we used the first three PC axis scores as independent variables in a generalized linear model regression analysis (GzLM testing main effects only; R Development Core Team, 2007) against relative abundance data for each wetland. There are two main reasons why we chose our PCA approach rather than directly entering the raw variables in a GzLM. First, many of our variables were correlated and could not be included together in a GzLM, and we did not want to make subjective decisions about which variables were more “important” than others. Second, there were many independent variables that we wanted to test, but only 24 ponds were sampled; therefore, we were limited as to how many variables we could include in our GzLM. By using PCA we reduced the variables to three main axes and, therefore, were able to examine all of the variables simultaneously in one GzLM. Wood frog captures were normally distributed over wetlands, so the regressions assumed a Gaussian distribution and used an identity link function. However, the boreal chorus frog and western toad data included more zeros and small capture values than larger values; data for these species approximated negative binomial distributions. Thus, our regressions for these two species assumed this distribution and used a log-link function. We then compared delta Akaike’s Information Criteria (delta AIC; Burnham & Anderson, 2002) values among spatial scales within each species to determine which set of environmental factors best-explained amphibian relative abundance.

To help us interpret our results we used Pearson’s correlations between abundance data and each of the raw environmental variables. We also created partial plots for each significant variable to visually assess our statistical models. We used Cook's distance to determine if any outlier points exhibited a large degree of influence on the parameters for each of our models. We used ANOVA with an LSD post-hoc test (SPSS Inc. 1989-2007) to determine whether differences in amphibian abundances occurred among landform types. Kruskall Wallis tests were used instead of ANOVA when abundance distributions were not normally distributed (SPSS Inc. 1989-2007).

2.3 Results

RELATIVE ABUNDANCE

We caught wood frogs at all 24 wetlands, boreal chorus frogs at 22 sites, and western toads at 20 sites. Mean captures per 10 hours (range) of searching were 26.79 (4 – 60) for wood frog, 9.29 (0 – 70) for boreal chorus frog, and 8.38 (0 – 66) for western toad.

ENVIRONMENTAL VARIABLES AND PCAS

At the local scale, the first PC axis (PC1) was positively correlated with wetland depth, secchi depth, and negatively correlated with DO. PC2 was positively correlated with conductivity, aquatic plant density, and TDS. PC3 was not significant at the local scale (Table 2-2). For the landscape environmental variables, both closed deciduous vegetation and low shrub cover were important environmental variables explaining landscape variation in PC1s of each spatial scale (except the 5000 m scale), mesic herbaceous cover was important in PC2s, and urban cover was important in either PC2s or PC3s (see Table 2-2 for the breakdown of influential environmental variables for the PCs at each spatial scale).

Land cover occurring on the three landform types became more distinct as the scale of measurement increased (Table 2-2). At 50-100 m scales, the moraine sites could be differentiated from the glaciolacustrine sites. At 200-500 m scales, moraine sites were also differentiated from outwash sites. At the 1000 m-scale and larger, all the sites could be grouped by landform (See MRPP results in Table 2-2).

RELATIONSHIPS BETWEEN AMPHBIANS AND ENVIRONMENTAL VARIABLES

We used delta AICs to compare among the regression models: if delta AIC of a model is less than 2, then there is substantial evidence supporting the validity of that model compared to others (Burnham & Anderson, 2002). For wood frog, the best model was decidedly the local one (delta AIC = 0; Table 2-3). The first two factors (PC1 and PC2) had significantly negative coefficients, meaning that wood frogs were more abundant in shallower wetlands with higher DO, and lower conductivity, TDS, and aquatic plant density (Tables 2-2 and 2-3). However, if we compare only among the nested landscape-scale models, the model that best explains the relative abundance of wood frog is the 500 m-scale model (only PC1 was significant; delta AICs = 7.14; Table 2-3). This result indicates that wood frogs are associated with closed deciduous and mixed forest, and are negatively associated with open conifer or low shrub habitat (Tables 2-2 and 2-3). The 1000 m-scale model produced similar results but had a slightly higher AIC value

(Figure 2-1), suggesting that noise, rather than new information, was added at this larger spatial scale.

For boreal chorus frog, the best models described the 1000 and 2000 m scales (PC1 and PC3 were significant; delta AICs = 0 and 1.15 respectively; Table 2-3; Figure 2-1). High relative abundances of boreal chorus frog are therefore associated with closed deciduous forest, mixed forest, and urban habitat. Relative abundances were lower at sites that had higher proportions of open conifer and low shrub habitat (Tables 2-2 and 2-3).

The relative abundance of western toad was best explained by using habitat data representing the 100 m (PC1 significant), followed by 50 m (PC1 significant), and 5000 m-scales (PC1 and PC2 significant; delta AICs = 0, 0.85, and 1.01 respectively; Table 2-3; Figure 2-1). At the smaller landscape scales, western toads were associated with closed deciduous and mixed forest. Relative abundance was positively associated with tall shrub habitat, but showed a negative relationship with low shrub habitat (Tables 2-2 and 2-3). At the 5000 m-scale, relative abundance was again associated with closed deciduous forest, tall shrub habitat, mesic herbaceous cover, and moss. Toads were less abundant at wetlands with higher proportions of surrounding closed or open conifer stands, recently burned sites, pine, low shrubs, and surprisingly, higher coverage by wetlands on the landscape (Tables 2-2 and 2-3).

Based on Pearson correlations, wood frog and western toad abundance and DO were very weakly correlated compared to abundance with pond depth or secchi depth (Table 2-4); therefore, depth was likely driving the relationship between abundance and PC1. Of the local PC2 variables, wood frog abundance showed the strongest correlation with conductivity while chorus frog abundance was more correlated with total dissolved solids; both species were least correlated with aquatic plant density (Table 2-4). At the landscape level, closed deciduous forest showed the strongest correlation with abundance of the PC1 variables for all three species (at the significant spatial scales; Table 2-4).

Partial plots for each of the wood frog models show a relatively even spread of data points (Figure 2-2), suggesting that our regressions did not violate any analytical assumptions. Outliers appear to exist in the chorus frog and western toad partial plots (Figure 2-2), but Cook's distance values for the data points were all less than one, indicating that each of these points does not exhibit a large degree of influence on the parameters, and therefore should be retained in the analysis. The only models with Cook's distance values greater than one were the 200 m wood frog, 200 m western toad, and 1000 m western toad models; we did not change our methodology to adjust these models because we wanted our models to be comparable and consistently analyzed.

RELATIONSHIPS BETWEEN AMPHIBIANS AND LANDFORM

We caught all species at wetlands within each landform from May through August. However, all species displayed higher relative abundances at moraine sites. Wood frogs had greater abundance in moraine sites and lowest abundance in glaciolacustrine sites, but the difference was not statistically significant ($F_{2,21}$ = 2.614, n = 24, P = 0.097). Boreal chorus frogs were significantly more abundant at moraine sites than in either of the other landforms (chi-square$_2$ = 7.55, n = 24, P

= 0.023), and western toads had significantly higher relative abundances at moraine than outwash sites but not glaciolacustrine wetlands (chi-square$_2$ = 6.24, n = 24, P = 0.044; pairwise differences confirmed with a parametric ANOVA using LSD post-hoc tests). The two frog species were caught more often in outwash sites than in glaciolacustrine plains, but the reverse was true for western toad (Figure 2-3).

2.4 Discussion

RELATIVE ABUNDANCE

Capture rates of amphibians (27 wood frogs, 9 boreal chorus frogs, and 8 western toads captured per 10 h of searching) were comparable to those at other sites in our region. Stevens, Paszkowski & Stringer (2006) observed amphibians at comparable rates of 30 wood frogs, 1 chorus frog, and 3 western toads per 10 hours of searching in the boreal foothills region of Alberta. Surveys at 239 wetlands in the Aspen Parkland ecoregion in/near Elk Island National Park, Alberta from May to August 2003 resulted in capture of amphibians at rates of 25 wood frogs, 17 boreal chorus frogs, and 8 western toads per 10 h of searching (C. Browne, unpubl. data). Paszkowski et al. (2002) captured wood frogs at rates of 40 frogs per 10 h of searching along streams in the boreal region of Alberta north of Wandering River; chorus frogs were not observed and western toads were only heard calling at these sites.

SPATIAL SCALE

Our findings support the view that factors at multiple spatial scales influence interpretation of patterns of anuran abundance. The abundance of wood frogs was more strongly related to local variables than to landscape variables, but the reverse was true for boreal chorus frogs and western toads. This suggests that wood frog abundance is more strongly determined by the habitat features of breeding ponds than by the terrestrial habitat used by juveniles and adults for most of the year. Other studies have also found that the quality of breeding habitat was more influential than landscape variables for the wood frog (e.g., Herrmann et al., 2005). The reverse is likely true for chorus frogs and western toads. All three species showed stronger correlations (smaller P-values) with both local and landscape scale PC-axis variables than with landform. The relationship between anuran abundance and landform is interesting because it suggests that we may be able to predict patterns of abundance to some extent based on a very coarse and easy-to-measure environmental variable. Relationships with landform likely reflect correlations between landform type and habitat variables at smaller scales (e.g., deciduous forest cover, conductivity of wetlands) to which amphibians respond directly.

Each of the anuran species in our study responded to environmental variables at different spatial scales among the seven landscape scales that we examined. The wood frog responded most strongly to variables at the 500 m scale, boreal chorus frog at 1000 m, and western toad at the 100 m scale. This result is consistent with the fact that patterns of terrestrial habitat use differ among species (Rittenhouse & Semlitsch, 2007).

The pattern among AIC values and scale of spatial extent for the western toad was different from that of the two frog species. For the most part, frogs responded most strongly to a particular scale of spatial extent (lowest AIC value) and then each larger/smaller spatial scale relative to that focal scale showed a weaker relationship (higher AIC value). Western toad, on the other hand, showed strong relationships to both very small (50 and 100 m) and very large spatial scales (5000 m). We believe this pattern reflects the fact that western toads move between patches of essential habitat for breeding, foraging, and hibernation in their annual cycle, rather than using terrestrial habitat equally radiating from the breeding pond. The area within 100 m of a breeding site is likely important for adult amphibians during the breeding season, YOY when they emerge, and for tadpoles because the immediate landscape influences localized conditions (e.g., shade from canopy, runoff, etc) in nursery wetlands. However, after breeding, adult western toads may move long distances to reach preferred habitat patches (e.g., Muths, 2003: 2324 m). Rittenhouse and Semlitsch (2007) examined the distribution of amphibians during the non-breeding season using kernel density estimation and found that kernel estimates for western toad did not peak near the breeding site; a pattern that also suggests that western toads travel to specific resources that are not evenly distributed on the landscape and not necessarily located near the breeding site.

Wood frog relative abundance was best described by the local scale variables in our study, but of the landscape spatial scales, the model for the 500 m scale was most parsimonious. Wood frog abundance was likely most strongly related to this landscape scale because wood frogs tend to use terrestrial habitat within 500 m of their breeding site (e.g., Rittenhouse & Semlitsch, 2007: 394 m). Boreal chorus frogs in this study responded most strongly to the 1000 m scale. Little is known about the movement abilities/patterns of boreal chorus frogs, but Spencer (1964) examined boreal chorus frog movements in montane Colorado and found that they moved up to 750 m from breeding ponds. Our results suggest that the most explanatory spatial scales identified by models of anuran abundance may be related to the amount of habitat surrounding breeding ponds used during the annual cycle of particular species.

Our results are comparable to other multi-scale studies that have investigated ecologically similar species. The results of Price et al. (2004) for the American toad (*A. americanus*) were similar to our findings for western toad; American toad occurrences were best predicted by variables at the 100 and 3000 m spatial scales (vs. 500 and 1000 m) along the US shores of Lake Michigan and Lake Huron. Price et al. (2004) found that the 500 m scale was best for predicting patterns of abundance for western chorus frogs (*Pseudacris triseriata*). This spatial scale was smaller than those identified by our models for boreal chorus frog; however, the greatest recorded distance from a breeding pond is smaller for the western chorus frog (Kramer, 1973: 213 m) than boreal chorus frog (Spencer, 1964: 750 m) so this disagreement may reflect differences in movement patterns between these two species. Gibbs, Whiteleather and Schueler (2005) found surprisingly large spatial scales (5-10 km) to be most significant for amphibians in New York. Their methodology differed from ours in that they examined changes in presence/absence of amphibians at wetlands over a 21-29 year period. Therefore, extinction-recolonization dynamics would have influenced their dependent variables, whereas our relative abundance values reflected contemporary population dynamics and habitat conditions.

HABITAT RELATIONSHIPS

Local environmental variables

All three species showed significant relationships with local wetland variables (Table 2-3). Wood frog and western toad abundances were negatively related to wetland depth and positively related to dissolved oxygen (Tables 2-2 and 2-3). Shallower wetlands tend to be warmer during the day (Barandun & Reyer, 1997), and both warm temperatures and high oxygen levels facilitate tadpole growth (Collins, 1979; Feder & Moran 1985). For the western toad, Holland (2002) investigated breeding site preference in Colorado and found that water temperature and depth were key variables in relation to site selection, with toads preferring warmer temperatures and waters ≤ 10 cm deep for egg deposition. Conversely, Petranka, Kennedy and Murrey (2003) and Skidds et al. (2007) found wood frogs to be positively associated with pond depth in North Carolina and Rhode Island, respectively; however, the majority of their ponds were temporary, whereas our ponds were permanent. We suspect that wood frogs prefer shallower wetlands provided that wetland hydroperiod is sufficient for larval development. Previous studies have also found positive relationships between dissolved oxygen and presence/abundance (adult or tadpole) or tadpole growth for wood frogs (e.g., Stevens, Paszkowski & Scrimgeour, 2006) and toads of the genus *Anaxyrus* (e.g., Noland & Ultsch, 1981), but others have found no relationship (e.g., Schiesari, 2006).

The relative abundances of wood frog and boreal chorus frog were negatively correlated with conductivity, total dissolved solids, and aquatic plant density (Tables 2-2 and 2-3). Conductivity is often correlated with total dissolved solids, dissolved organic particles, mineral particles, or eutrophication (Pellet, Hoehn & Perrin, 2004). High conductivity could be the result of local soil qualities (e.g., alkaline soils), disturbance, runoff, or increasing concentrations of solutes as water seasonally evaporates and is not replaced (Welch & MacMahon, 2005). Significant negative relationships between conductivity and anuran species richness have also been reported in other studies (e.g., Hecnar & M'Closkey, 1996). Western toads may be more tolerant of water with high ion concentrations than are wood frogs and boreal chorus frogs (toads have been observed to swim across brackish water; Taylor, 1983), which may explain why this species did not show the same negative relationships with local PCA axis 2. We found a negative relationship between frog abundance and aquatic plant density, but others have found positive relationships for the wood frog (e.g., Stevens, Paszkowski & Scrimgeour, 2006). This unexplained result may be an artifact if conductivity is actually driving the relationship between frog abundance and PCA axis 2 (correlations between frog abundance and conductivity are higher than correlations between abundance and aquatic plant density).

Landscape environmental variables

For the spatial scales that most successfully predicted abundance for each species, wood frog, boreal chorus frog, and western toad were positively associated with closed deciduous forest cover and negatively associated with low shrub cover (Tables 2-2 and 2-3). Wood frog and chorus frog also showed a positive relationship with mixed forest and a negative relationship with open conifer cover. Constible, Gregory and Anholt (2001) also found wood frog, but not boreal chorus frog, to be associated with deciduous forest in the boreal region of northeastern Alberta. Other, positive relationships with deciduous and mixed forest cover have been reported for the wood frog, American toad, and spring peeper (*P. crucifer*) in New York State (Gibbs, Whiteleather & Schueler, 2005) and New Brunswick (Waldick, Freedman & Wassersug, 1999).

Terrestrial invertebrate density is positively related to density of understory vegetation, and understory is greater in deciduous than coniferous stands (Willson & Comet, 1996; Ferguson & Berube, 2004). Ferguson and Berube (2004) found that shrub habitat had lower invertebrate abundance than deciduous forest (but still higher than coniferous forest) in the boreal region of northwestern Ontario. Invertebrates are food for frogs and toads; therefore, density of understory vegetation and invertebrates can explain the patterns we observed. If invertebrate abundance in shrub stands is intermediate between that of deciduous and coniferous stands, then shrub stands may offer a habitat of intermediate quality for foraging by amphibians. Furthermore, habitat types with a greater density of understory vegetation could provide more cover to protect amphibians from predation and desiccation.

Chorus frogs showed a positive relationship to urban cover (roads and well pads) at the 1000 m landscape scale (Tables 2-2 and 2-3). We expected either a negative or no relationship with urban habitat for all three amphibian species since increasing traffic volumes can be a serious threat to amphibian populations (Fahrig et al., 1995). However, traffic volumes are relatively low in our study region. The positive relationship between chorus frogs and roads and wells could simply reflect the species' preference for open habitat, or ditching around construction may provide breeding habitat. Eigenbrod et al. (2008) found a similar unexplained positive relationship between traffic density and abundance for wood frog in Ontario, and speculated that features associated with roads, such as ditches, attracted frogs. Alternatively, urban cover may have been related to other variables that influence chorus frog abundance; for example, urban cover was absent from all glaciolacustrine sites and this landform appears to offer poor habitat for the species (i.e., pond conductivity is high and deciduous forest cover is low; Appendix A).

We were surprised that the amount of wetland cover surrounding our ponds was not a significant factor influencing abundance, and in fact, was negatively associated with western toad relative abundance at the 5000 m scale, since wetland connectivity is important for amphibian dispersal (e.g., Elmberg, 1993). We suspect that amphibian abundance in the Utikuma landscape is not limited by the simple number of wetlands, but by local pond conditions and the amount of suitable terrestrial habitat for foraging and hibernation.

Landform

Johnson (1980) suggested that habitat selection is a hierarchical process in which observation of relationships can change along a continuum of spatial scales. One of the basic principles of hierarchy theory is that habitat selection is constrained by the level above and clarified by the level below (Allen & Starr 1982). Based on the hierarchy concept, we believe that the relationships we observed between anuran abundance and landform are the result of correlations with landform and environmental variables at smaller spatial scales (e.g., our local or landscape scale variables) that directly influence anuran abundance. The most parsimonious explanation of why wood frogs and chorus frogs are most abundant at moraine sites and least abundant at glaciolacustrine sites is that deciduous forest cover is significantly more abundant at moraine sites and least abundant at glaciolacustrine sites (Appendix A), and this variable is positively related to frog abundance (Tables 2-2, 2-3, and 2-4). In contrast, viewing western toad abundance in light of associations between our environmental variables and landform types (Appendix A) does not offer a similar clear explanation for why this species should be least abundant at outwash sites.

CONCLUSIONS

We found that environmental variables measured at different spatial scales differ in their ability to predict anuran abundance on the Boreal Plain and that each of three species of anurans responded differently in terms of which spatial scale best predicted abundance. Many researchers assume that most anuran activity occurs within 1 km of wetlands and set their spatial scale of study to this distance (e.g., Knutson et al., 1999). A spatial scale of 1 km would have produced significant models for two of the species in our study, but variables measured at a 1 km scale were not significant for the western toad. Researchers and managers must have knowledge of the biology of species of concern in order to study or conserve populations and communities of these ecologically sensitive animals (Hopkins, 2007). Even in a simple amphibian community, which was characterized by widespread, generalist species, we documented very different responses among species regarding the spatial scales which affected abundances; presumably in a richer community with habitat specialists, these patterns would be even more obvious.

Table 2-1. Local and landscape environmental variables selected for PCA analysis and their means and ranges over all 24 Hydrology, Ecology, and Disturbance research group (HEAD) study wetlands near Lake Utikuma, Alberta, Canada in 2004.

LOCAL VARIABLES	MEAN (RANGE)
Turbidity	6.2 (2.95 – 9.11) NTU (Nephelometric Turbidity Units)
Chlorophyll-a	12.91 (2.93 – 39.05) μg/L
Conductivity	0.138 (0.039 – 0.318) mS/cm
Dissolved oxygen	9.26 (1.36 – 15.48) mg/L
pH	8.94 (7.27 – 9.43)
Water temperature	21 (18 – 25) degrees C
Submersed aquatic vegetation (SAV)	2.55 (1.0 – 3.8)
Wetland depth	67.5 (29.0 – 128.4) cm
Secchi depth	66.8 (29.0 – 128.4) cm
Secchi depth: wetland depth	1.0 (0.9 – 1.0)
Total nitrogen	1993 (923 – 4137) μg/L
Total dissolved solids (TDS)	0.1 (0 – 0.2) g/L
Total phosphorus	72 (29 – 371) μg/L
Invertebrate biomass/volume	8.8 (1.6 – 26.1) mg/L
Predatory invertebrate biomass/volume	2.6 (0.24 – 9.6) mg/L
Aquatic plant density	0.54 (0.20 – 1.07) proportion of plant volume
Woody debris	7.44 x 10^{-4} (0 – 0.01) proportion cover
Dominant vegetation type	aquatic, conifer, deciduous, grass/wildflower, shrub
Beaver structures	0.83 (0 = absent, or 1 = present)
Percent vegetation cover	91.5 (80 – 100) %
Median vegetation height	162.8 (30 – 800) cm
Wetland area	91403 (6 312 – 367774) m^2
Wetland perimeter	1423 (315 – 3070) m

Table 2-1 Continued…

LANDSCAPE VARIABLES (LAND-COVER TYPES)	MEAN (RANGE) % COVER WITHIN A 5000 M RADIUS OF EACH WETLAND
Closed conifer	8 (4 – 14)
Open conifer	26 (12 – 41)
Pine	0.1 (0 – 0.8)
Closed deciduous	26 (10 – 46)
Open deciduous	3.9×10^{-4} ($0 – 5.0 \times 10^{-3}$)
Mixed forest	9 (7 – 10)
Low shrub	5 (2 – 9)
Tall shrub	8 (4 – 12)
Moss	0.3 (0.1 – 0.6)
Mesic herbaceous	5 (2 – 9)
Wet herbaceous	0.2 (0.05 – 0.3)
Urban (roads and well pads)	0.5 (0.1 – 1.2)
Agricultural areas	9.8×10^{-3} (0 – 0.03)
Young stands (burnt)	0.22 (0.04 – 0.44)
Wetlands	12 (2 – 24)
Landform (number of sites)	glaciolacustrine (7), moraine (10), or outwash plain (7)

Table 2-2. Principal Components Analysis using local and landscape scale environmental variables. The variables surround 24 study wetlands at 8 increasing scales of spatial extent (radii, excluding the local scale). The variables listed have a high correlation ($R^2 > 0.5$) with each principal component (PC), and have positive correlations unless marked with a negative sign (-). We also present the amount of variation explained by that PC (% var) and a P-value describing whether the PC explains significantly more variation than 999 PCs using randomized data. Finally, our Multi Response Permutation Procedure (MRPP) shows that when the wetlands were labeled with their landform type, the ability to detect separate landform groups in the PCA scatter-plot is positively correlated with increasing scale of measurement (T-value). The MRPP pairwise comparison results demonstrate which groups can be detected at which spatial scale. * denotes statistical significance at the alpha = 0.05 level.

Scale (m)	PC1 variables	% var	P	PC2 variables	% var	P	PC3 variables	% var	P
Local	•Depth •Secchi •DO(-)	20	0.001 *	•Conductivity •Aquatic plant density •TDS	14	0.008 *	NA	11	0.146
50	•Low shrub(-) •Closed deciduous •Mixed forest •Tall shrub	32	0.001 *	•Open conifer(-)	21	0.002 *	NA	11	0.994
100	•Closed deciduous(-) •Low shrub	28	0.001 *	•Mesic herbaceous	24	0.001 *	NA	12	0.863
200	•Closed deciduous(-) •Open conifer •Low shrub •Mixed forest(-)	27	0.002 *	•Mesic herbaceous	23	0.001 *	NA	14	0.238
500	•Closed deciduous •Low shrub(-) •Open conifer(-) •Mixed forest	33	0.001 *	•Urban(-)	16	0.163	NA	14	0.113
1000	•Closed deciduous •Low shrub(-) •Open conifer(-) •Mixed forest	33	0.001 *	•Wetlands(-)	19	0.005 *	•Urban	14	0.038 *
2000	•Closed deciduous •Low shrub(-)	32	0.001 *	•Mesic herbaceous	28	0.001 *	•Urban	13	0.375
5000	•Wetlands(-) •Moss •Mesic herbaceous •Burnt(-) •Tall shrub •Pine(-)	43	0.001 *	•Closed deciduous(-) •Closed coniferous •Open coniferous •Low shrub	28	0.001 *	•Open deciduous	10	0.987

Table 2-2 Continued…

Scale (m)	Landform MRPP T (P)	
Local	-0.384 (0.288)	landform label does not create groups
50	-1.681 (0.065)	moraine vs. glaciolacustrine
100	-4.658 (0.002*)	moraine vs. glaciolacustrine
200	-5.829 (<0.001*)	moraine vs. glaciolacustrine and moraine vs. outwash
500	-6.384 (<0.001*)	moraine vs. glaciolacustrine and moraine vs. outwash
1000	-6.321 (<0.001*)	all pairwise comparisons
2000	-6.339 (<0.001*)	all pairwise comparisons
5000	-5.806 (<0.001*)	all pairwise comparisons

Table 2-3. Generalized Linear model regression coefficients using the first three principal components (PCs) of a Principal Components Analysis (PCA; environmental variables at 24 study wetlands at 8 increasing scales of spatial extents) as independent variables against relative abundance of the three amphibian species. If the coefficient was significant at the alpha = 0.05 level (denoted by a * next to the PC coefficient P-value), then we note the direction of the coefficient's correlation with the relative abundance data, otherwise 'NA'. We used this information to relate the important environmental variables that describe the PCs to the amphibian relative abundance data. We compared AIC and delta AIC values to determine the spatial extent at which the environmental data best describes the relative abundance for each species. The models for which there is substantial evidence have their delta AIC marked with '§'. A '¤' indicates the best models of the landscape models for the wood frog.

Species	Scale (m)	PC1 coef. P	Coef. direction	PC2 coef. P	Coef. direction	PC3 coef. P	Coef. direction	AIC	Delta AIC
Wood frog	Local	0.033*	-	0.004*	-	0.222	NA	194.48	0 §
	50	0.853	NA	0.088	NA	0.341	NA	204.85	10.36
	100	0.216	NA	0.288	NA	0.109	NA	203.45	8.97
	200	0.072	NA	0.862	NA	0.473	NA	204.87	10.39
	500	0.015*	+	0.521	NA	0.701	NA	201.63	7.15 ¤
	1000	0.043*	+	0.876	NA	0.135	NA	202.12	7.64 ¤
	2000	0.089	NA	0.716	NA	0.353	NA	204.81	10.33
	5000	0.998	NA	0.205	NA	0.390	NA	206.60	12.12
Chorus frog	Local	0.223	NA	0.002*	-	0.019	NA	151.67	6.86
	50	0.987	NA	0.001*	+	0.499	NA	159.25	14.44
	100	0.005*	-	0.003*	+	0.357	NA	155.92	11.11
	200	0.002*	-	0.082	NA	<0.001*	+	150.84	6.03
	500	<0.001*	+	0.004*	-	0.575	NA	148.42	3.61
	1000	<0.001*	+	0.296	NA	<0.001*	+	144.81	0 §
	2000	<0.001*	+	0.649	NA	0.002*	+	145.96	1.15 §
	5000	0.049*	+	0.027*	-	0.010*	+	154.83	10.02
Western toad	Local	0.029*	-	0.166	NA	0.319	NA	153.84	5.48
	50	<0.001*	+	0.343	NA	0.235	NA	149.21	0.85 §
	100	<0.001*	-	0.052	NA	0.105	NA	148.36	0 §
	200	0.040*	-	0.032*	-	0.996	NA	154.00	5.64
	500	0.023*	+	0.001*	+	0.496	NA	150.71	2.35
	1000	0.095	NA	0.138	NA	0.333	NA	157.88	9.52
	2000	0.003*	+	0.026*	+	0.634	NA	153.31	4.95
	5000	0.009*	+	0.001*	-	0.343	NA	149.37	1.01 §

Table 2-4. Pearson correlations between amphibian species abundance and raw environmental variables. Landscape variables were measured at 500 m for the wood frog, 1000 m for the chorus frog, and 100 m for the western toad, the spatial scales at which our anuran abundance data is best described by the environmental variables.

LOCAL VARIABLES	Wood frog	Chorus frog	Western toad
Turbidity	-0.047	0.077	0.149
Chlorophyll-a	0.370	0.085	0.456
Conductivity	-0.548	-0.393	0.200
Dissolved oxygen	0.083	-0.204	0.067
PH	-0.225	-0.421	0.102
Water temperature	0.070	0.091	0.299
Submersed aquatic vegetation (SAV)	0.216	-0.300	0.068
Wetland depth	-0.408	0.011	-0.317
Secchi depth	-0.442	-0.062	-0.316
Secchi depth: wetland depth	-0.146	-0.618	0.116
Total nitrogen	0.087	-0.067	0.584
Total dissolved solids (TDS)	-0.450	-0.559	0.038
Total phosphorus	0.103	0.120	-0.151
Invertebrate biomass/volume	0.047	-0.015	0.016
Predatory invertebrate biomass/volume	0.484	0.381	0.295
Aquatic plant density	-0.465	-0.282	0.245
Woody debris	-0.254	-0.078	-0.063
Beaver structures	-0.506	-0.116	0.071
Percent vegetation cover	0.016	0.349	0.236
Median vegetation height	-0.343	-0.265	-0.033
Wetland area	-0.298	-0.168	-0.092
Wetland perimeter	-0.231	-0.185	-0.175
LANDSCAPE VARIABLES			
Closed conifer	-0.505	-0.366	-0.112
Open conifer	-0.385	-0.344	-0.095
Closed deciduous	0.492	0.417	0.517
Mixed forest	0.422	0.148	0.105
Low shrub	-0.481	-0.304	-0.441
Tall shrub	0.055	0.202	0.044
Moss	0.100	-0.008	-0.241
Mesic herbaceous	-0.189	-0.009	-0.309
Wet herbaceous	0.128	0.315	-0.103
Urban (roads and well pads)	0.137	0.405	-0.077
Agricultural areas	-0.130	-0.163	N/A
Young stands (burnt)	-0.001	0.017	-0.216
Wetlands	-0.275	-0.269	-0.015

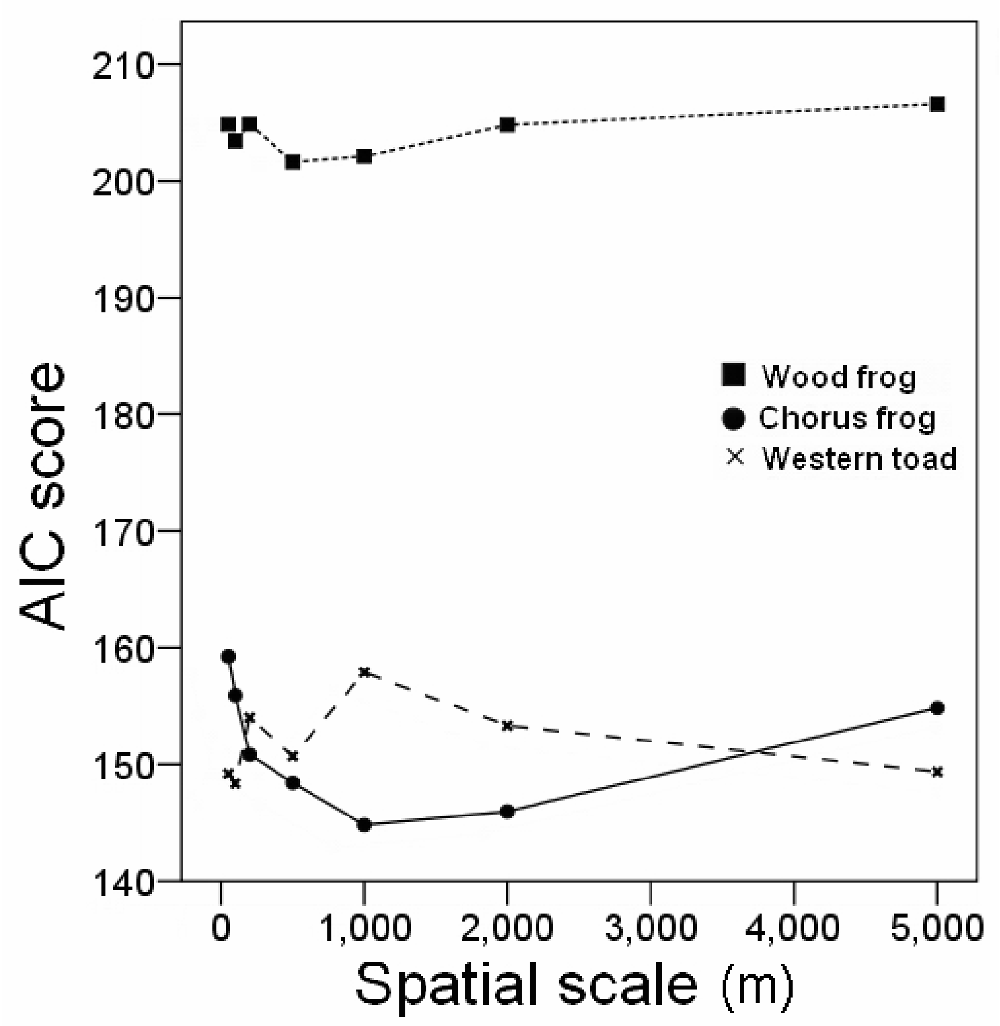

Figure 2-1. Model fit as described by Akaike's Information Criterion (AIC) score for each landscape spatial scale examined.

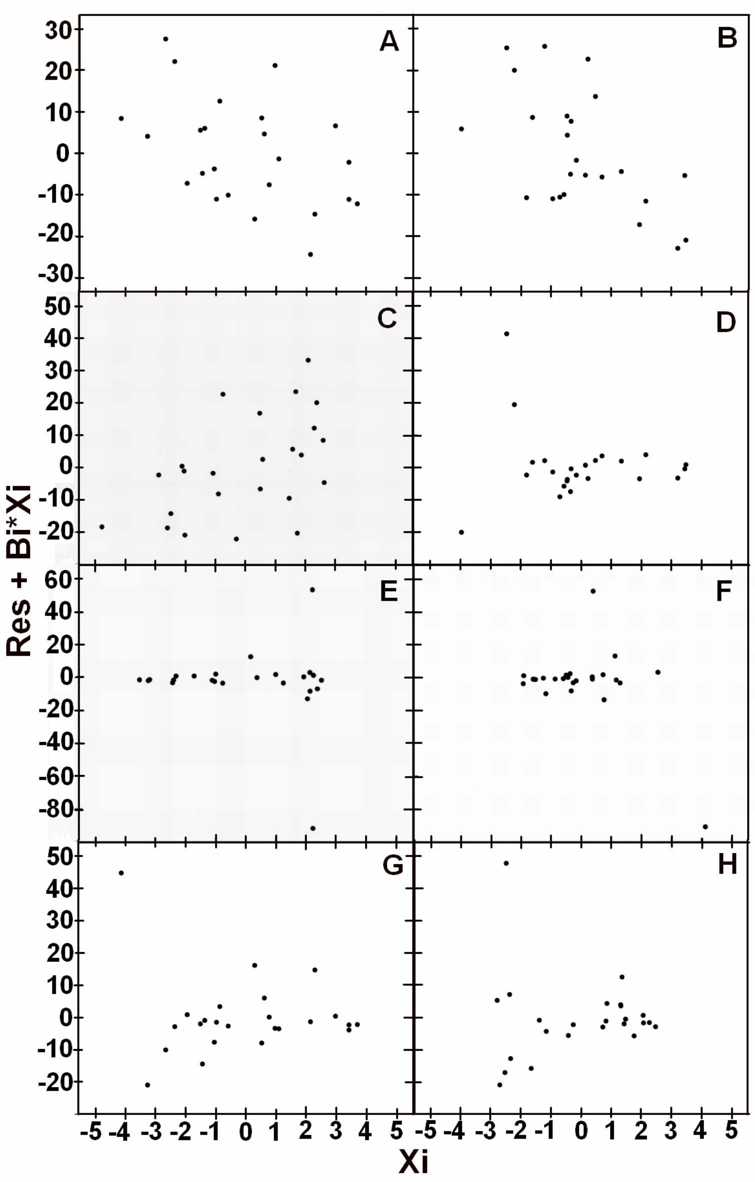

Figure 2-2. Partial plots for significant variables from our Generalized Linear Model analyses. The variable of interest is on the x-axis. The y-axis is (Res + B_i*X_i), where Res = the model residuals, B_i = the coefficient value for the variable of interest and X_i = is the variable of interest. Partial plots are of A) Wood frog local PC1, B) Wood frog local PC2, C) Wood frog 500 m landscape PC1, D) Chorus frog local PC2, E) Chorus frog 1000 m landscape PC1, F) Chorus frog 1000 m landscape PC3, G) Western toad local PC1, and H) Western toad 100 m landscape PC1.

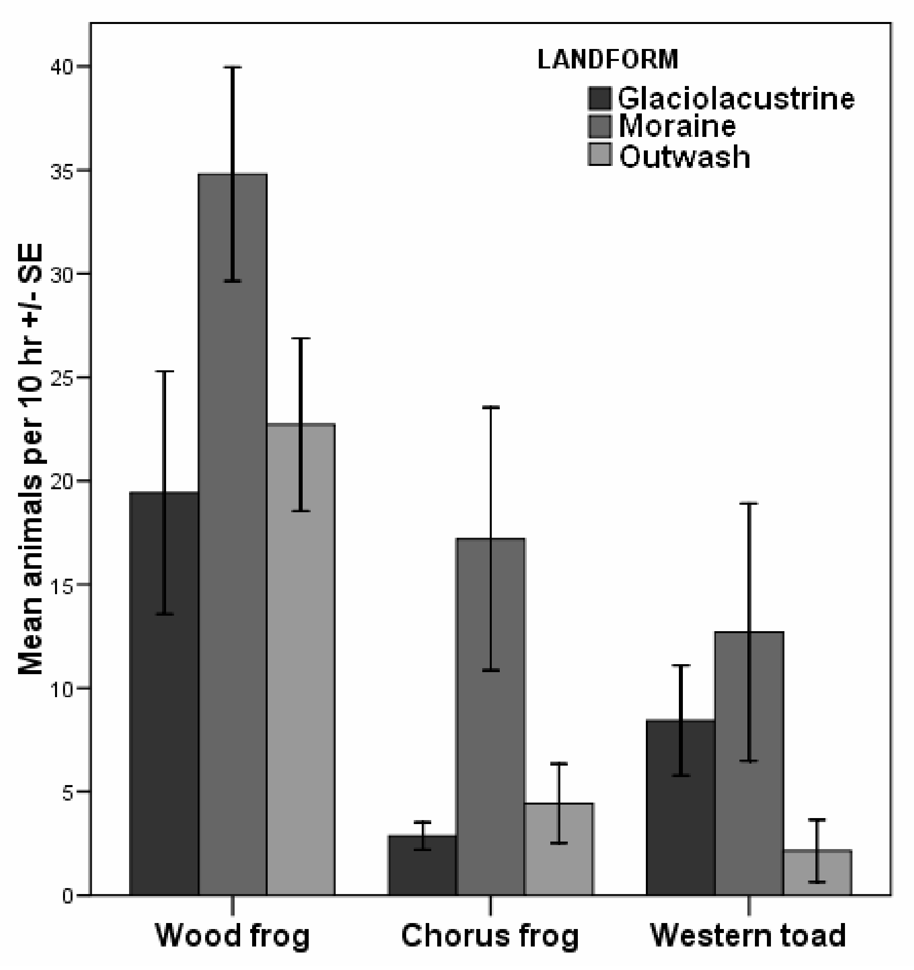

Figure 2-3. Differences among landforms in mean relative abundance of each species.

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Chapter 3. Habitat Selection by Western Toads is Scale Dependent

3.1 Introduction

Understanding patterns of habitat use by animals is necessary for making land management decisions that protect critical habitat for species at risk. However, a common problem with investigating habitat use is that perceived patterns often change with scales of spatial extent (Turner 1989, Wiens 1989), grain or resolution of the analysis (Hobbs 2003, Lawler et al. 2004), habitat composition (Johnson 1980, Mysterud and Ims 1998), season (Schooley 1994, Arthur et al. 1996), sex (Muths 2003, Bartelt et al. 2004), or age classes (Stamps 1983, Imansyah et al. 2008). Therefore, it is important that spatial and temporal frameworks are chosen carefully to match the study goals and species of interest. Generalizations about how scale affects habitat selection are few because of the enormous variation in landscapes, patterns, and processes influencing resource selection (Boyce 2006).

Johnson (1980) proposed that habitat selection is a hierarchical process in which perceived relationships change along a continuum of spatial scales. Habitat selection observed at a given level is constrained by the level above and clarified by the level below (Allen and Starr 1982). Johnson (1980) described four orders of spatial scale at which habitat selection could be investigated, ranging from the selection of the geographical range of the species (first-order selection) to micro-habitat selection (fourth-order selection). Meyer and Thuiller (2006) examined the predictive ability of 1070 resource selection function (RSF, defined as any statistical model that is proportional to the probability of use by a species, Manly et al. 2002) models from 123 published papers and determined that RSFs conducted at the geographical range scale (first-order selection) have had the greatest predictive accuracy, while selection at the scale of the population range (second-order selection) and patches within home ranges (third-order selection) is more difficult to predict.

Studies conducted over large spatial extents are necessary for certain applications, for example, land management; however, increases in extent often require reduction in resolution simply for logistical reasons (Wiens 1989). Coarse map resolution may be adequate for studies of first-order selection, but second or third-order selection may require finer resolution. For example, studies of bird distributions have found that bioclimatic variables predict bird locations well at coarse resolutions (e.g., bird observations recorded on grid maps >= 40 km^2), whereas land-cover and vegetation variables are important at finer resolutions (e.g., grid maps <= 20 km^2; Luoto et al. 2007, Bussche et al. 2008). Few ecological models have tested the relative predictive accuracy of variables measured at different map resolutions (Betts et al. 2006).

Conclusions regarding whether a particular habitat component is selected, avoided, or used in proportion relative to its availability are critically dependent upon the array of habitat options available to an animal and its ability to comprehend its options (Johnson 1980). Also, organisms typically require a mixture of habitat types to fulfill essential needs (e.g., food occurs in a different habitat type than does shelter), thus selection may differ among sites depending on which essential habitat is limited (Mysterud and Ims 1998). The configuration of the landscape can influence home-range size and shape, as individuals must travel farther and with different trajectories depending on the distribution of essential resources (Mysterud and Ims 1998). Likewise needs change seasonally, with age, and with sex; studies of habitat selection that liberally pool data may conceal or confound patterns of habitat use and selection actually experienced by individual animals (Schooley 1994).

RSF analyses are commonly used to examine habitat selection by mammals (e.g., Bleich et al. 2009, Long et al. 2009, Sawyer et al. 2009); however, studies of amphibians and reptiles using this statistical approach are much less common (e.g., a search for the topic “resource selection function” in Web of Science produced 70 articles that were focused as follows: mammals n = 43, birds n = 7, fish n = 5, and statistical methodology n = 15). Amphibian habitat selection studies have commonly examined the relationship between amphibian relative abundance at aquatic breeding sites (since they can be easily detected during this period) and habitat variables measured at or surrounding the wetland (e.g., Waldick et al. 1999, Herrmann et al. 2005, Eigenbrod et al. 2008). Although this approach provides insight into the relationships between amphibians and habitat, many patterns may be masked for temperate pond-breeding amphibians because they have complex life cycles and their habitat needs change year-round (Trenham and Shaffer 2005). Locations recorded year-round are needed to examine seasonal changes in habitat selection. Amphibians tend to be cryptic and difficult to locate in terrestrial environments, but modern radio-transmitters are small enough to be fitted to many amphibian species, and thus allow long-range and temporally extensive tracking.

Our objective was to determine whether perceived patterns of habitat selection change when different scales of spatial extent are employed, scales of spatial resolution differ, habitat composition differs, temporal period changes, and between males and females for a temperate pond-breeding amphibian, the western toad (*Anaxyrus boreas,* formerly *Bufo boreas*). Western toad was an ideal species for our study. Adults are large enough to carry a radio-transmitter (length = 5.1-12.7 cm, Stebbins 2003), so detailed habitat use data can be collected. Western toads have complex life cycles that require aquatic and terrestrial habitat and their habitat use likely changes temporally to meet the needs of breeding, foraging, and hibernation. Female western toads have been found to use locations significantly farther from breeding ponds than have male toads during the foraging period (Muths 2003, Bartelt et al. 2004, Bull 2006, Goates et al. 2007), which suggests that habitat selection may differ between the sexes. The western toad occurs across western North America (Stebbins 2003), so examining how habitat selection changes with changes in land-cover composition will aid in predicting habitat use in other landscapes. Western toad is a species at risk of extinction (COSEWIC status = Special Concern, COSEWIC 2009); we hope our research will identify patterns of habitat selection by western toad so that land managers have better information to apply to protection of habitat for this species.

We use a study approach similar to that of Ciarniello et al. (2007). They used RSF analyses to examine habitat selection by grizzly bears (*Ursus arctos*) and compared models that varied among (1) three spatial extents for the area of available habitat measured (within the study-site, within the home-range, and within predetermined-movement-buffers), (2) two study sites, and (3) between sexes. They found that results were scale-dependent and varied among spatial extents, study sites, and sexes. Although they could not discern one spatial extent to be a consistently better predictor than another, because support for a model was dependent upon the bears' sex and the study site, the within-study-site spatial-extent models had, on average, better predictive ability.

We compared habitat selection at two scales of spatial extent, the population range and buffered-home-range, which are similar to Ciarniello et al.'s (2007) within-study-site and within predetermined-movement-buffers spatial-extents, respectively. Our fine-grained population-range design (FGPR) examined habitat selection within each study site and would be considered a population level design (second-order selection, Johnson 1980) because the extent of each study site was defined using the locations of all toads tracked in this population. Our fine-grained buffered-home-range design (FGHR) examined habitat selection by toads within a predetermined-movement-buffer and would be considered a home-range-level design (third-order selection, Johnson 1980) because toad locations were compared to available habitat locations selected from within individual home ranges. We chose to examine second- and third-order habitat selection because studies conducted at these spatial scales tend to have low predictive accuracy (Meyer and Thuiller 2006), and therefore, are in greater need of research.

We predicted that the FGHR would produce models with greater predictive ability than the FGPR because Compton et al. (2002) suggest that this study design is more appropriate than traditional techniques (i.e., the population-range design) for species with low mobility and large home ranges. We included a third design to examine how changing the spatial resolution of analysis would influence the results. The coarse-grained buffered-home-range design (CGHR) had the same objectives as the FGHR, but used a lower resolution land-cover map (25 m^2 pixel size vs. 0.5 m^2) that is publicly available and covers the forested area of Canada. We predicted that the FGHR would produce models with greater predictive ability than the CGHR because toads are small and sensitive to a variety of abiotic gradients, and thus likely recognize several different habitat types within 25 m^2 areas. Our goal for the CGHR was to access the effectiveness of a lower resolution land-cover map that is publicly available and covers a large geographic area for investigating habitat selection of a temperate pond-breeding amphibian.

Within each of the three designs we created separate RSFs for each of three study sites, three time periods, and for males and females. We sought to identify habitat elements that are consistently selected for by western toads, and are therefore more likely to define critical habitat for the species in at least part of its large range. We conducted our radio-telemetry research at three study locations that differed in land-use and occurred in two eco-regions to examine habitat selection under varying habitat composition choices. We predicted that habitat types selected by toads would vary greatly among study sites, but that certain habitat types would be consistently selected among all three-study sites. We predicted that western toad habitat selection would change over the year, with toads selecting locations close to breeding ponds early in the year, locations close to hibernation sites late in the year, and locations with abundant prey in mid-summer. Therefore, we divided the active period for toads into three different periods: breeding (May-June), foraging (July-August), and pre-hibernation (September-October). We predicted that habitat selection would differ between male and female toads because (1) males remain at breeding ponds longer than do females in the spring, (2) females have been found to select foraging habitat farther from breeding ponds than do males during the summer (Muths 2003, Bartelt et al. 2004, Bull 2006, and Goates et al. 2007), and (3) western toads are sexually dimorphic in size and we found that large toads move to hibernation sites later in the year than small toads (Chapter 5). We predicted that female toads would select open habitat types more often than males, and that males would select habitat types associated with water more often than females, because these relationships have been observed for western toads in the USA (Bartelt et al. 2004, Bull 2006).

3.2 Methods

Study sites

The three study sites were located in north-central Alberta, Canada. The “park site” is an isolated patch of dry mixed-wood boreal forest embedded within the Aspen Parkland natural region and within Elk Island National Park (EINP) (Alberta Government 2005). This site is undeveloped and comprised of forested uplands surrounding shallow lakes and marshes. Forests consist primarily of trembling aspen (*Populus tremuloides*), balsam poplar (*P. balsamifera*), and white spruce (*Picea glauca*), with a hazelnut understory (*Corylus cornuta*). This study site was centered on two shallow lakes (10-20 ha) used by Western Toads for breeding.

The "pasture site", located 3.5 km west of EINP and 10 km from our park site, consists of dry mixed-wood boreal forest converted to agriculture. It supports cattle grazing, cultivation of hay and crops (e.g., wheat, barley, oats, canola, timothy, alfalfa), and rural housing. It contains patches of woods and peatland. Common tree species are trembling aspen, balsam poplar, white spruce, black spruce (*Picea mariana*), paper birch (*Betula papyrifera*), tamarack (*Larix laricina*), and jack pine (*Pinus banksiana*). This study site was centered on four naturalized man-made ponds (0.09-0.4 ha) that were originally created during sand extraction, are currently surrounded by pasture, and are used by western toads for breeding.

The "boreal site" is in the central mixed-wood subregion of the Boreal Forest natural region (Alberta Government 2005), located near Lac La Biche, approximately 150 km north of our park site. This region is influenced by the forestry and oil/gas industries (e.g., seismic lines, pipelines) and comprised mostly of shrub swamps, peatland, upland boreal mixed-wood forest, and forestry cut blocks. Common tree/shrub species are trembling aspen, balsam poplar, white spruce, black spruce, paper birch, tamarack, jack pine, willow (*Salix spp.),* and dwarf birch (*B. nana*). This study site was centered on a small shallow pond (0.07 ha) that is used by western toads for breeding and is located next to a gravel road and in a major utility corridor. A small permanent stream feeds this pond.

We used toad locations (points where toads were located via telemetry) to define the size of the study site at each of the three sites. A circle of available habitat was created for each study site that centered on the main breeding pond or on the midpoint between multiple breeding ponds. The straight-line distance from the breeding pond center to each toad location was calculated. The maximum distance moved by any individual toad in each of the three sites was used as the radius for a circle of available habitat. The maximum distance moved by a toad (and thus the radius of the site) was 983 m for the park site, 1145 m for the pasture, and 2239 m for the boreal site. The resulting study sites encompassed 3.0, 4.1, and 15.7 km^2, respectively.

Radio-telemetry

We captured toads during the active period (May to October) in 2004, 2005, and 2006 either at breeding ponds or opportunistically while tracking other individuals. We worked at the park and pasture sites in 2004, the boreal site in 2005, and the pasture site in 2006. We measured and recorded the snout-urostyle length (SUL to nearest mm), mass (to nearest g), and sex of each toad at the time of capture. Toads captured between May and August were toe-clipped for future identification of recaptured toads that had lost their transmitters and to determine age via skeletochronology (Garrett 2005, Mark 2007).

We followed methods described by Bartelt and Peterson (2000) for attaching radio-transmitters. BD-2, BD-2T, and PD-2 transmitters, weighing 1.0 to 2.3 g, with a minimum battery life of 28 d to 3 mo (Holohil Systems Ltd., Carp, Ontario, Canada), were attached using waist belts made of soft surgical-grade polyethylene tubing (outside diameter = 0.965 mm; CA-63018-667, VWR International, Edmonton, Alberta, Canada) and a large size flyline eyelet (size 9). Transmitters plus belts were always less than 10% of body weight, and mostly less than 5%. We located toads 2-4 times per week. Over the 3 years we radio-tracked a total of 116 Western Toads (54 males and 62 females).

For data analysis, we divided the active period (May-October) into three sequential periods: breeding, foraging, and pre-hibernation. We considered the breeding period to be from May-June, when toads were congregated around breeding ponds. July-August was set as the foraging period, when toads had their greatest annual food intake. Toads moved to their hibernation sites from late August to early October (Chapter 5) and used underground micro-sites more often in September and October, so we considered this to be the pre-hibernation period.

Scales of analysis

We used three different methodologies to compare different spatial scales of analysis. For all spatial scales, the original sites of toad capture were excluded from analysis because such locations may be biased towards sites with greater visibility (e.g., open areas). We excluded points if we were not sure that the toad used the location (e.g., points where only transmitters were found, but toads had escaped, were excluded because a predator or scavenger could have moved the transmitter). Telemetry locations for toads that had entered hibernation sites were not included (we continued to monitor toads for several days to weeks into hibernation). Individual toads that had fewer than four data points were not included. Separate resource selection function (RSF) models were calculated for each study site, time period, and sex. Toad telemetry locations were the "used sites" (1), and randomly generated locations were the "available sites" (0) in our RSF models. All statistics were conducted using SPSS version 15 (SPSS Inc. 1989-2006).

RSF fine-grained population-range design (FGPR)

One goal was to examine patterns of habitat selection on the landscape by toads, so we used a population-level design similar to that of Ciarniello et al.'s (2007) design A. We compared characteristics of areas used by toads to available points drawn throughout each study site. We observed that toads moved up to 391 m/day (straight-line displacement) across land, so theoretically, an individual was able to move from the study site center to anywhere in the study site within 3 days (park and pasture sites) to 6 days (boreal site). As we located toads approximately every 2-5 days, our assumption that any location within our study site was accessible to each toad may not always be valid because our tracking schedule was too frequent to give toads enough time to move anywhere within the study site. Random locations were generated at a mean density of 1 location/1000 m^2 (i.e., 3062 locations in the park, 4119 in the pasture, and 15770 in the boreal site) using Hawth's Tools (Beyer 2004. Hawth's Analysis Tools for ArcGIS. Available online: http://www.spatialecology.com/htools [Accessed 16/10/09]) in ArcGIS 9.1 (ESRI 1999-2004). All toad locations were pooled for analysis within each RSF analysis. An assumption of our statistical analyses is that all data points are independent; however, several locations were recorded for each toad, so these points cannot be considered independent. To control for variation among individuals, toad locations were weighted to equalize sample sizes among animals. A weight value was assigned to each data point by dividing the number of sample points available for the individual with the least number of sample points by the number of sample points available for the individual of interest. For example, if the toad with the fewest data points had 4 locations recorded, each of these locations would be assigned a weight value of 1. For a toad with 10 locations recorded, each of these locations would be assigned a weight value of 0.4 (4/10).

RSF fine-grained buffered-home-range design (FGHR)

The assumption that a toad was able to move to any point within the study site between tracking dates may be unreasonable (Compton et al. 2002), so we created a second set of models using a design employing smaller areas of available habitat, similar to Ciarniello et al.’s (2007) design C. We drew available points from an area within a fixed-size buffer surrounding each location where a toad was recorded. Buffer size was determined by calculating the distance moved between all consecutive locations and taking the mean of the longest 5% of movements for all toads (mean = 300 m +/- 15 SE, n = 2143). We paired each toad location with 10 random points selected within a 300 m-radius buffer from the toad’s previous location. Random locations were generated using Hawth’s Tools in ArcGIS 9.1. We used conditional logistic regression (paired) to compare habitat used to habitat available (Compton et al. 2002).

RSF coarse-grained buffered-home-range design (CGHR)

The CGHR used the same methods as the FGHR, except that we used a coarser-grained land-cover map (see description below) to assign habitat type to used and random points. We used the publicly available Earth Observation for Sustainable Development (EOSD) of forest land-cover map sheets to determine land-cover type for each point.

Geographic information systems data

We created a land-cover geographic information systems (GIS) map of 22 land-cover types (Appendix B) from black and white aerial photographs (taken in 2004 and 2006 for the boreal site, 2005 for the pasture site, and 2001 for EINP) of each of the study sites using ArcGIS 9.2 for the FGPR and FGHR designs. We digitized these at a resolution of 1:1890 (a pixel size of 0.5 m^2 when converted to raster). In addition to land-cover, we included distance to nearest breeding pond and distance to nearest hibernation site in our models in case selection of land-cover type was dependent on the distance from other essential habitat patches. We created a polygon layer for toad breeding ponds by digitizing all known breeding ponds at each study site. A point layer for toad hibernation sites was also created using all known toad hibernation sites (39 sites for 50 radio-tracked toads) at each study site. We are fairly confident that all breeding sites were digitized, but some hibernation sites were likely missed. ArcGIS 9.1 and the habitat maps we created were used to determine the land-cover type, distance to breeding pond, and distance to hibernation site for all toad locations and random points.

We used a map created by Earth Observation for Sustainable Development of forest (EOSD) for our coarse-grained land-cover map (CGHR). This raster layer has 22 land-cover classes, a pixel size of 25 m^2, and was created using Landsat-7 ETM+ data from the year 2000. This map covers the forested areas of Canada, and is free to download (Natural Resources Canada. 2009. Earth Observation for Sustainable Development of forest (ESOD). Available online: http://cfs.nrcan.gc.ca/subsite/eosd/mapping [Accessed 22 July 2009]). Ten of the 22 land-cover types occurred in our study sites (water, exposed land, shrub tall, wetland-treed, wetland-shrub, wetland-herb, herb, coniferous dense, broadleaf dense, mixed-wood dense). Appendix C compares each of these categories to the land-cover types in our fine-grained map. We combined the categories "wetland-treed" and "wetland-shrub" from the coarse-grained map to make it more comparable to our category "wet shrub" in the fine-grained map.

We used ArcGIS 9.1 to determine the land-cover type and distances to essential resources for each point using the coarse-grained map. Because our goal with the CGHR was to determine how applicable our models might be if easily accessible but coarser-grained data were used, we used distance to nearest water and distance to nearest conifer stand instead of distance to nearest breeding pond and distance to nearest hibernation site. Western toads breed in ponds and lakes (Holland 2002), so distance to nearest water would be a reasonable substitute for distance to nearest breeding pond if areas were not ground-truthed to determine breeding sites. Western toads use a variety of land-cover types for hibernation, but the majority of toads at our study sites selected conifer stands (Chapter 4), so we believe that distance to nearest conifer stand could act as a substitute for distance to nearest documented hibernation site.

Model creation and evaluation

We conducted RSF analyses to determine which land-cover types were significantly selected by toads among used land-cover types (Manly et al. 2002). We define the word "selected" as the process by which an animal chose a land-cover type more than would be proportionally expected based on availability, "avoided" as the process in which a animal chose a land-cover type less than would be proportionally expected based on availability, and "used" as when an animal location was recorded in a land-cover type (irrespective of availability). We used generalized linear models (GzLM) with a binomial distribution and logit link function for FGPR and conditional logistic regressions for FGHR and CGHR (SPSS Inc. 1989-2006, Chan 2005).

Land-cover types that were used by toads were considered for entry into the models as binary variables (0 = absent, 1 = present) unless they were only used once for the category of interest (study site, time period, and sex). Deciduous forest was used as the reference land-cover type for all park and pasture models, and conifer forest for the boreal models (unless otherwise noted). The continuous variables "distance to nearest breeding pond" and "distance to nearest hibernation site" were included in all FGPR and FGHR models and "distance to nearest water" and "distance to nearest conifer stand" were included in all CGHR models. The maximum number of step-halvings was set to 30 for all models; we increased this from the default setting of 5 to avoid separation in the data set, which can be a problem with samples that have a high number of parameters relative to sample size (Heinze and Ploner 2003). We tested for collinearity between predictor variables in each model and considered it not to be a concern if correlations between predictor variables were < 0.6. We used alpha = 0.05 to determine statistical significance.

We used five-fold cross-validation to compare the internal consistency of each model following the methods described in Johnson et al. (2006). We used an equal-interval classification to reclassify our RSF maps into 10 equal-interval bins ranked from low- to high-suitability. We then used linear regression to assess fit for each model. Generalized linear models were used to examine adjusted R^2 values for differences in predictive power among study designs, study sites, time periods, and sexes.

3.3 Results

Influence of Spatial Extent

Toads used 17 of the 22 land-cover types that occurred on our fine-grained map; only land-cover types that were inaccessible (building) or provided no overhead cover (railroad, gravel road, paved road, and exposed land) were not used. We could not discern one study design that was consistently a better predictor of selection than another; acceptable and unacceptable models were produced using both designs (Table 3-1). Overall FGHR yielded more highest-ranked models (Table 3-2) and better predictive ability based on mean adjusted R^2 values; however, the difference was not significant (Table 3-3).

Patterns of habitat selection were the same between FGPR and FGHR for most variables (Tables 3-4 and 3-5). However, in two cases we observed an opposite pattern between the FGPR and FGHR for distance measures: 1) foraging boreal males occurred at locations closer to breeding ponds than to random locations in the FGPR model, but occurred at locations farther from breeding ponds than from random locations in the FGHR model, and 2) breeding boreal males occurred at locations closer to hibernation sites than to random locations in the FGPR model, but occurred at locations farther from hibernation sites than from random locations in the FGHR model (Appendix D).

Several models detected selection of certain land-cover types over the reference land-cover using the FGHR (e.g., all pasture and boreal models), whereas these same land-cover types were not significantly selected over the reference land-cover when the FGPR was used (Tables 3-4 and 3-5). In four models, habitat selection was detected using FGPR whereas the same variables were not significantly selected over the reference land-cover using FGHR. Foraging park females and breeding pasture males selected sites closer to hibernation sites, pre-hibernation boreal females selected wet shrub and sites closer to breeding ponds, and foraging boreal females selected tree-dominated cutblocks using the FGPR but not the FGHR.

Distance to nearest breeding pond was a significant variable in 30 of the 36 fine-grained models (Tables 3-4 and 3-5). Selection was greater for locations closer to breeding ponds in all of the significant models except for the FGHR boreal foraging male model (Appendix D). Distance to nearest hibernation site was a significant variable in all FGPR models, with toads selecting locations closer to hibernation sites (Table 3-4; Appendix D). Toads also selected locations closer to hibernation sites in all but three FGHR models (Table 3-5; Appendix D). In total, five models had a reverse trend or non-significant results for the distance to nearest breeding/hibernation variable in the FGHR (Table 3-5).

Influence of Map Resolution

Predictive power did not differ significantly among study designs; however, models that used the coarse-grained map had lower predictive power on average (Table 3-3). In six cases the CGHR models out-performed the FGHR models: breeding park female, pre-hibernation park male, breeding boreal male, foraging boreal male, pre-hibernation boreal male, and pre-hibernation boreal female (Table 3-2).

All nine land-cover types from the coarse-grained map were used by toads. Although some land-cover types were repeatedly selected for (e.g., wet shrub, tall shrub, exposed land) or avoided (e.g., mixed-wood), most showed inconsistent results (Appendix E). Distance to nearest water (surrogate for breeding site) was a significant variable in 13 of the 18 CGHR models (Table 3-6). Toads selected locations closer to water for all significant models (Appendix

D). The five models in which distance to water was not significant were all from the boreal site (Table 3-6). Distance to nearest conifer stand (surrogate for hibernating site) was a significant variable in nine of the 18 CGHR models (Table 3-6). Of the nine significant models, toads selected locations farther from conifer stands in all but the foraging boreal female and foraging boreal male models (Appendix D).

Influence of Habitat Composition

Habitat composition differed greatly among study sites. The three most abundant land-cover types were deciduous forest, marsh, and water at the park site; crop/hay field, pasture, and deciduous forest at the pasture site; and conifer forest, deciduous forest, and mixed-wood forest at the boreal site (Appendix F). Moss, burn, grass dominated clear-cut, and tree dominated cutblock only occurred at the boreal site, and mowed, crop/hay, and pasture only occurred at the pasture site, so these variables could not be compared among study sites. Most land-cover types were used infrequently (Appendix E). Only deciduous forest, conifer forest, wet shrub, and disturbed grass (herbaceous cover in CGHR) occurred in more than half of the models. Some land-cover types that were extensive on the landscape were used frequently (e.g., marsh at the park site, conifer at the boreal site, Appendix G). However, significant selection for a land-cover type occurred more often when it was rare on the landscape and when alternate habitat choices were poor (e.g., conifer forest, marsh, emergent vegetation, and water were selected for in the pasture site). For example, in FGHR at the pasture site, conifer forest was selected by toads in two models, avoided in two models, and not significant in one model compared to deciduous forest, but at the boreal site, where conifer forest was common, it was avoided in two models and not significant in one model compared to deciduous forest.

Although selection for many land-cover types depended on the spatial or temporal scale, some types were repeatedly selected for or avoided among study sites (Appendix E). For example, toads significantly selected for wet shrub habitat in 25 of the 34 models in which it occurred, and only one model showed avoidance of wet shrub (CGHR, boreal pre-hibernation male). Crop/hay fields and pasture habitat only occurred at the pasture site, but toads selected for crop/hay fields in all 10 models in which it occurred and avoided pasture in 6 of the 10 models in which it occurred (Tables 3-4 and 3-5).

There was a significant difference in predictive power among models across study sites (Table 3-3). The park models had lower mean adjusted R^2 values than the pasture or boreal models (Table 3-3).

Temporal Differences

We detected temporal differences in habitat selection. In FGPR and FGHR, wet shrub occurred in 10 of the 12 foraging period models, but only occurred in 6 breeding period models and 6 foraging period models (Tables 3-4 and 3-5). Toads selected for wet shrub in 9 of the 10 foraging period models in which it occurred. The three foraging period models in which wet shrub was not used or selected for were for pasture females (FGPR and FGHR) and pasture males (FGPR). These toads foraged in crop/hay fields (females and males), disturbed grass (females), mowed lawn (males), and emergent vegetation (males). Toads only used water and emergent vegetation habitat during the breeding season, except for foraging pasture males (Tables 3-4 and 3-5). The six models in which distance to nearest breeding pond was not significant were all from the pre-hibernation period (Tables 3-4 and 3-5). For FGPR and FGHR, all foraging period models contained a greater or equal number of significant land-cover variables compared to the corresponding pre-hibernation model (Tables 3-4 and 3-5). Model predictive power did not differ significantly among time periods (Table 3-3).

Differences between Sexes

We detected differences in habitat selection between males and females for some variables. Disturbed grass was selected for in 12 models, all involving female toads exclusively (park foraging; pasture breeding, foraging, and pre-hibernation; and boreal breeding and foraging). For male toads, disturbed grass was either avoided (two models) or not significant (four models) compared to the reference variable (Tables 3-4 and 3-5). The land-cover type, pasture was not significant in any FGPR models except for foraging pasture females (Table 3-4). Only foraging pasture males used water and emergent vegetation habitat outside of the breeding period (Tables 3-4 and 3-5). Model predictive power was significantly greater for females than males (Table 3-3).

3.4 Discussion

Influence of Spatial Extent

Habitat selection studies are abundant in ecology, and it is clear that animals often select different habitat components at different spatial scales (Mayor et al. 2009). We compared two study designs that differed in spatial extent and could not discern one spatial extent that was consistently a better predictor than the other since mean adjusted R^2 values produced from the cross-validation analysis were not significantly different among study designs. The FGHR did have better predictive power (based on mean adjusted R^2 values), which suggests that toads primarily selected for land-cover types based on choices available locally. This outcome agrees with that of Compton et al. (2002) who proposed that paired (conditional) logistic regression is a more appropriate technique than traditional methods (e.g., FGPR) to examine habitat selection for animals with low mobility but relatively large home ranges, such as the wood turtles (*Clemmys insculpta*) that they studied. The FGPR may encompass too large an extent to consider all locations within the study site to be accessible for use between successive observations under most conditions.

We observed patterns that suggest that western toad habitat selection is scale-dependent and follows the principles of hierarchy in that habitat selection is constrained by the level above (FGPR) and clarified by the level below (FGHR) (Allen and Starr 1982). At the larger spatial scale (FGPR) toads must select a home range that contains essential resources (e.g., breeding ponds, hibernation sites) and their habitat selection at this scale is constrained by distance to nearest breeding pond and hibernation site. The smaller spatial scale (FGHR) clarifies patterns of habitat selection; stronger relationships with the land-cover variables were observed at this scale. For example, selection of locations closer to breeding ponds by pre-hibernation boreal females, and of locations closer to hibernation sites by foraging park females and breeding pasture males based on the FGPR, but not the FGHR, suggests that toads are not influenced by these seasonally critical locations as they select habitat within activity areas on a day to day basis, but are constrained by which habitat they can use on the landscape because it must ultimately be within range of these essential features. In turn, land-cover variables appear to be important in a toad’s daily selection of habitat because 23 land-cover variables that were not significant based on the FGPR showed significant selection or avoidance based on the FGHR, whereas only two land-cover variables that were significant based on the FGPR were not significant based on the FGHR. The five models that had a reverse trend or non-significant results for the distance to breeding or hibernation site variables in the FGHR were also the five models that had higher predictive power using the FGPR rather than FGHR (Table 3-2). Locations close to essential resources must be important for western toads, since models that do not show this pattern do not perform well.

Our results show that the scale of spatial extent adopted for analysis can influence the outcomes of habitat selection. In two cases we observed a variable change from significant selection to avoidance between the FGPR and FGHR. In both cases, the reverse trend was observed for a variable (distance to breeding pond or hibernation site) that would be very important for certain periods of the year, but not necessarily important in the daily selection of locations throughout the active period. Boreal males selected habitat closer to breeding ponds and hibernation sites compared to random locations drawn throughout the study site (as shown using the FGPR). However, at the smaller-scale (FGHR) the reverse pattern was observed because boreal males made directed movements to reach their foraging and hibernation sites, and these movements were away from (likely incidentally) the nearest breeding pond and nearest hibernation site, so toads were selecting locations farther from the breeding pond/hibernation site in the 300 m radius circle of available habitat, whereas paired random locations did not display a movement trajectory. We conclude that the FGHR is more appropriate for variables that play a role in the selection of locations within the home range, but that the FGPR is more appropriate for variables that influence the location of the home range on the landscape. Our understanding of western toad habitat selection would be poorer if we had not examined both scales of spatial extent.

Influence of Map Resolution

The fine-grained map (FGHR) produced models with higher predictive power on average than the coarse-grained map (CGHR). We expected this result because toads are small and sensitive to a variety of abiotic gradients, e.g., light, temperature, humidity, stem density, and thus are likely to recognize several different habitat types within 25 m^2 areas (the pixel size of the coarse-grained map). The coarse-grained map homogenizes features and defines each pixel as the land-cover type that covers the greatest area within that pixel. As a result, small discontinuities that are important for toads are less likely to be documented by this map. For example, in the boreal site the breeding ponds and all water bodies within the study site were too small to be detected on the coarse-grained map and the variable, “distance to nearest water” was not significant in five of the six models. The model for breeding boreal females did show significant selection for locations closer to water; however, this result could be misleading because the pattern was created by female toads moving away from their undetected breeding pond (where tracking began) to foraging and hibernation sites and incidentally towards large water bodies located outside of the study site (well beyond the farthest locations visited by those females).

Breeding ponds in the park and pasture sites were larger than in the boreal site, and most were detected on the coarse-grained map. All of the CGHR park and pasture models showed that toads exhibit significant selection for locations closer to water, suggesting that “distance to nearest water” was a good substitute for the variable, “distance to nearest breeding pond” when breeding ponds were large enough to be detected. “Distance to nearest conifer stand” did not appear to be a reliable variable to predict toad habitat selection based on hibernation needs; this variable was not significant in nine of 18 CGHR models. Conifer forest may not be as diagnostic of hibernation habitat as water is of breeding habitat because toads can hibernate in other land-cover types (Chapter 4). Of the nine models in which distance to nearest conifer stand was significant, only the models for foraging boreal female and foraging boreal male indicated selection for locations closer to conifers. A greater percentage of toads using conifer stands for hibernation in the boreal site (79%) than in the pasture (53%) or park (0%) sites (Chapter 4) may explain why only boreal models showed selection for locations closer to conifer forest. Surprisingly, selection for locations closer to conifer stands did not occur during the pre-hibernation period, this variable was not significant for boreal males and showed the reverse trend for boreal females. Similar to the FGHR, the CGHR models detect patterns of directed movement. Many toads in the boreal area made directed movements towards their hibernation sites during the foraging period (C. Browne, unpublished data), which may explain the pattern we observed for forging boreal females and males. By the pre-hibernation period, toads were near hibernation areas (C. Browne, unpublished data) and boreal males selected conifer forest during this period. However, females selected patches of more open habitat (e.g., herbaceous cover).

Another issue with the coarse-grained map was the fact that fewer land-cover types were defined at our study site, so land-cover types that toads use differently were combined, which could distort or mask patterns. For example, the land-cover type herbaceous cover (from the coarse-grained map) included the land-cover types marsh, meadow, disturbed grass, mowed lawn, crop/hay, and pasture (from the fine-grained map). In FGHR models, crop/hay and disturbed grass tended to be selected for, but pasture was avoided (Table 3-5). This could explain the inconsistent patterns we observed for the herbaceous cover type in the coarse-grained models. On the other hand, breaking down land-cover types too finely into categories could also make the results difficult to interpret. Meadow, burn, grass-dominated clear-cuts, tree-dominated cutblocks, and mowed lawn (from the fine-grained map) were rare on the landscape (< 6.3% cover each) and were occasionally used by toads. Since these land-cover types were under-represented, statistically significant selection could occur with a small amount of use, regardless of biological importance.

Although the fine-grained map tended to produce better results, the CGHR actually out-performed the FGHR models in six cases (two park and four boreal models). The park models that had higher predictive power with the coarse-grained map may simply have been the result of low sample size in the FGHR breeding park female and pre-hibernation park male models, causing poor model performance. These two models had sample sizes under 200 in the FGHR, whereas the CGHR had over 100 additional data points in the corresponding models (Tables 3-5 and 3-6). Toads moved farther in the boreal forest and our boreal study site was much larger than either the park or pasture site. We believe that the CGHR performed better than the FGHR for four boreal models because toads were selecting habitat over a larger and coarser spatial scale. The patterns of habitat selection were often different between the FGHR and CGHR, indicating that small patches of certain habitat types may be selected/avoided within larger patches. For example, in the boreal site, pixels identified as wet herbaceous (moss) and wet shrub habitat on the coarse-grained map often contained patches of both of these land-cover types on the fine-grained map. At the coarse-grained scale foraging boreal males selected for wet herbaceous (moss) and wet shrub habitat, but within these habitat types toads likely selected for wet shrub habitat and avoided moss patches because the FGHR showed selection for wet shrub and avoidance of moss.

Although the predictive power of the coarse-grained models was low on average (adjusted R^2 values < 0.6), acceptable models were produced for all but two cases. This result is of interest because the coarse-grained map is publicly available and covers the forested area of Canada. We recommend that researchers take advantage of publicly available land-cover maps, but be aware that these maps may not be at the most appropriate resolution for the study organism or study questions. For western toads, it appears to be important that land-cover types that show opposite patterns (selection vs. avoidance), such as crop/hay fields and pasture, be distinguished as separate categories. We suspect that land-cover maps with fine resolutions (<25 m^2 pixel size) would produce models with greater predictive ability for most amphibian species.

Influence of Habitat Composition

The park models had poor predictive ability compared to the pasture and boreal models, most likely caused by low sample sizes in park models (Table 3-4). We did not have a large enough sample size to properly perform the K-fold cross validation analysis. We chose to include the park site in our analyses, despite the low predictive ability of park models because information on habitat selection by western toads is limited and this additional study site provides useful information.

Land-cover composition differed greatly among study sites (Appendix F). The different choices available to toads at each site played a large role in the land-cover types used. We expected selection to change among study sites because preference may be conditional upon availability, or organisms may have to select for areas that contain a limited resource if favorable combinations of essential habitat patches do not exist (Orians and Wittenberger 1991, Mysterud and Ims 1998). Land-cover types tended to be used more often when abundant on the landscape (e.g., marsh was represented in all park models). This suggests that western toads are somewhat flexible in their habitat use.

Selection or avoidance of deciduous and conifer forest differed among models. Conifer forest appears to be selected for compared to deciduous forest in landscapes where it is relatively rare (e.g., pasture site), but otherwise seems to be avoided by toads during the active period. At a site in northwestern Alberta, we documented a negative relationship between western toad abundance at breeding ponds and percent coverage of conifer stands surrounding these ponds (Browne et al. 2009; Chapter 2). Deciduous forest may be selected over coniferous forest during the active period because deciduous forests have greater understory vegetation and invertebrate densities (Willson and Comet 1996, Ferguson and Berube 2004), which provide cover and food for toads. However, conifer stands are important for toads because they often hibernate there (Chapter 4). Conifer forest may also provide resources not found in certain deciduous forest patches, such as sources of standing water (many conifer stands at our study sites were poorly drained and dominated by black spruce) and refuge (e.g., red-squirrel, *Tamiasciurus hudsonicus,* tunnels), which could explain why toads selected for conifer forest at the pasture site where it was rare on the landscape.

Despite differences in habitat composition among sites, there were some land-cover types that were repeatedly selected. Wet shrub was the most frequently selected land-cover type and it was selected for in all three-study sites. Western toads in Idaho also selected for shrub habitat (Bartelt et al. 2004). Bartelt et al. (2004) found that western toads used terrestrial habitat in ways that allowed them to conserve body water. The low dense structure of shrub and large accumulations of litter and woody debris in shrub habitat may facilitate water conservation in toads, and breaks in the shrub canopy would create areas warmed by the sun (Bartelt et al. 2004). Therefore, shrub habitat would provide the warm, moist conditions preferred by most amphibians (Tracy et al. 1993). Bull (2006) also examined habitat selection by western toads, but found that toads in Oregon used all vegetation types in proportion to their occurrence; however, Bull apparently combined data from five study sites in analyses, which may have masked patterns of selection.

Crop/hay fields and pasture were the most abundant land-cover types at our pasture study site. Toads selected for crop/hay fields but avoided pasture. The pasture at our study site was heavily grazed and provided little cover for toads, or their invertebrate prey. Invertebrate abundance at our pasture study-site was significantly greater in crop/hay fields compared to deciduous or conifer forest, and cattle pasture had lower invertebrate abundance than did deciduous forest (Thompson 2007). Toads likely selected for crop/hay fields because prey was abundant and temperatures would be warmer in the fields compared to the forest, which would facilitate growth (Lilywhite et al. 1973). We do not know whether the toads that used crop/hay fields obtained sufficient moisture from dew or below ground sources, or whether they traveled to water sources from the crop/hay fields regularly. If they had to leave crop/hay fields regularly to obtain water, then the interiors of large crop/hay fields are likely of less value as toad habitat.

Emergent vegetation appears to be selected for depending on the availability of other habitat choices. Emergent vegetation occurred along the edges of breeding ponds at both the park and pasture sites. It was more abundant at the park site (5.1% cover) than pasture site (0.8% cover), but was used more often in the pasture site (e.g., 22% vs. 5% of breeding male locations) and selected for in several pasture models but no park models. The breeding ponds in the park site were surrounded by marsh habitat, whereas the ponds at the pasture site were surrounded by pasture habitat. Pasture habitat contained less vegetative cover, soil moisture, and invertebrate prey (Thompson 2007; C. Browne, unpublished data) than did marsh habitat and appears to be an inferior habitat choice for male toads during the breeding period, because toads at the park site significantly selected marsh but not emergent vegetation, and toads at the pasture site significantly selected emergent vegetation but not pasture.

Temporal Differences

Throughout the active period, toads tended to select for warm, open habitat (i.e., no canopy cover) with abundant prey that should facilitate growth, energy, and fat accumulation for gamete production and over-wintering. This pattern was the most evident during the foraging season; every foraging period model for FGPR and FGHR showed selection for open habitat (e.g., wet shrub, disturbed grass, crop/hay). California toads (*A. b. halophilus*) prefer temperatures between 26-27 degrees C when food is available (Lillywhite et al. 1973); assuming that western toads from Alberta prefer similar temperatures, then the selection of habitat types that allow toads to bask and increase their body temperature would be important for growth because the average mean daily air temperatures at our study sites were much cooler than preferred body temperatures (range: breeding = 11-14 degrees C, foraging = 15-17 degrees C, pre-hibernation = 6-7 degrees C; Environment Canada. 2008. National Climate Data and Information Archive. Available online: http://www.climate.weatheroffice.ec.gc.ca/climateData/canada_e.html [Accessed 7 August 2009]). As expected, temporal differences in habitat selection were detected. During the breeding period, toads selected for locations that were close to breeding ponds (distance to nearest breeding pond was always significant during the breeding period) and they used water and emergent vegetation while they congregated at ponds, but not later in the year. During the pre-hibernation period distance to nearest breeding pond was not a significant variable in six models, indicating that hibernation sites are selected independent of the location of breeding ponds in some circumstances. Selection of certain habitat types became less significant (larger P-values) in several pre-hibernation period models compared to foraging period models, likely because selection of locations close to hibernation sites became more important.

Differences between Sexes

In Colorado, Idaho, Oregon, and Utah, female western toads have been found to travel farther than males to reach their summer foraging grounds from breeding sites (Muths 2003, Bartelt et al. 2004, Bull 2006, and Goates et al. 2007, respectively). Johnson et al. (2007) found this same pattern for gray treefrogs (*Hyla versicolor*). For amphibians, males may remain near breeding ponds to gain a competitive advantage when females arrive to breed in the spring (Bartelt et al. 2004) and females may travel farther than males to reach superior foraging grounds because they require more food and energy to produce eggs (Muths 2003). Johnson et al. (2007) suggest that even if prey densities are uniform, it still may be advantageous for females to move farther from breeding ponds to reduce conspecific competition. Habitat selection differences between males and females may be caused by size differences in sexually dimorphic species. Small individuals may be at greater risk of predation or dehydration, and this can influence the types of habitat they choose or how far they are able to move to reach preferred habitat types (Bartelt et al. 2004).

Bull (2006) radio-tracked western toads during their active period and found that female toads selected more open habitat than males, whereas males were more closely associated with water. We observed patterns consistent with this; for example, disturbed grass was selected for in 12 models for female toads.

When models for male toads included disturbed grass it was either avoided or not significant compared to the reference variable. The difference in habitat selection could be 1) because female toads are more attracted to habitats that facilitate growth than males are, 2) because males are smaller, which might make them more susceptible to desiccation and restrict their ability to use open habitat, or 3) to reduce conspecific competition (Muths 2003, Bartelt et al. 2004, Johnson et al. 2007).

Pasture habitat was clearly avoided by all toads at the smaller scale of spatial extent (FGHR), but at the larger scale (FGPR) only by females during the foraging period. This difference may be driven by female toads avoiding a habitat type with low prey abundance (Thompson 2007), or female toads using habitat farther from breeding ponds than males (pasture habitat was adjacent to the breeding ponds at this study site). Males selected for habitat close to breeding ponds for a longer period than female toads did; at the pasture site male toads continued to use water and emergent vegetation at their breeding ponds in the foraging period, whereas female toads had all moved upland.

It is not surprising that habitat selection differed between the sexes, since male and female toads have different strategies for increasing reproductive output. Female toads must select habitat that promotes growth because they can produce more eggs if they obtain more energy. Also, larger females are more attractive to male toads than smaller females (Marco et al. 1998). Male toads, however, must balance time spent foraging and attending breeding choruses because both increased size and number of nights spent at breeding choruses increase their chance of reproduction (Gatz 1981; Olson et al. 1986).

The difference in the predictive ability of models for females and males cannot be explained by a difference in sample sizes because sample sizes for the total number of observations (among study sites and temporal periods) were similar between females (n = 910) and males (n = 926). Habitat selection by males may occur at a coarser scale than for females, since the CGHR out-performed the FGHR for all boreal male models. The greater predictive ability of models for female toads may be the result of female toads showing stronger, more consistent patterns of habitat selection, which may have been because female toads often travel farther to reach specific foraging grounds (Muths 2003, Bartelt et al. 2004, Bull 2006, and Goates et al. 2007), they move to foraging grounds sooner than male toads (C. Browne, unpublished data), and stay at foraging grounds later in the year (Chapter 5).

Conclusions

Western toads used a variety of habitat types; only land-cover types that were inaccessible or provided no cover were never used. Throughout the active period, toads selected for habitat that would facilitate growth (warm, open habitat with abundant prey) and/or habitat that provided essential resources (e.g., moisture, shelter, breeding locations). Wet shrub was the most highly selected land-cover type during the active period. This land-cover type was relatively open, so it likely had warm temperatures during the day in the summer, but also had high levels of soil moisture and sources of water that are important for amphibians to avoid desiccation. Habitat selection was scale-dependent and differences in selection were observed among study designs, study sites, time periods, and sexes.

The FGHR produced the best models (highest adjusted R^2 values), suggesting that toads are primarily selecting habitat on a small spatial scale (< 25 m^2) based on the choices available to them in their daily rather than population range. However, the predictive ability of models did not differ significantly among the three study designs; all provided insights on the habitat selection of western toads. The underlying patterns of habitat selection were similar among study designs for most cases. However, opposite patterns (indicating selection vs. avoidance) occurred between FGPR and FGHR in two cases and between the CGHR and fine-grained models several times. These results show that habitat selection patterns are critically dependent upon the spatial scales used for analysis. Changes in resolution (both pixel size and the number of land-cover types identified) had a greater impact on perceived habitat selection choices than changes in spatial extent in our study. The predictive ability of the CGHR was relatively low ($R^2 = 0.584$) and therefore likely of little use for predicting western toad locations. However, by conducting our analyses at different spatial extents, spatial resolutions, study areas, time periods, and between sexes we gained an understanding of how these differences affect perceived selection results. We expect that future studies conducted at additional scales and with additional variables will aid in developing models that can be used over large landscapes to predict high-quality habitat for amphibians.

Our study highlights the importance of scale in habitat selection studies. The study design should be chosen carefully to match research questions and researchers should be sensitive to factors that may affect selection such as habitat composition, season, and sex of the organism. We recommend conducting habitat selection studies at multiple scales to gain a better understanding of how organisms are using their environment.

Table 3-1. Average results from five-fold validation conducted for each model. Linear regression was used to assess model fit. Howlin et al. (2004) was followed to assign each model's predictive ability as "Good", "Acceptable", or "Unacceptable". A good model should have $B_0 = 0$ and $B_1 = 1$.

A. Fine-grained population-range design (FGPR)

Site	Period	Sex	B_0	P	B_1	P	Adjusted R^2	Validation
Park	Breeding	Female	0.055	0.429	0.456	0.250	0.294	Unacceptable
		Male	0.053	0.260	0.466	0.159	0.279	Acceptable
	Foraging	Female	0.040	0.188	0.598	0.008	0.750	Acceptable
		Male	0.062	0.195	0.374	0.216	0.368	Unacceptable
	Pre-hibernation	Female	0.029	0.265	0.848	0.001	0.872	Acceptable
		Male	0.087	0.241	0.130	0.391	0.005	Unacceptable
Pasture	Breeding	Female	0.038	0.144	0.620	0.004	0.825	Acceptable
		Male	0.047	0.052	0.527	<0.001	0.853	Acceptable
	Foraging	Female	0.035	0.372	0.649	0.002	0.760	Acceptable
		Male	0.030	0.240	0.704	0.002	0.831	Acceptable
	Pre-hibernation	Female	0.049	0.191	0.510	0.016	0.644	Acceptable
		Male	0.046	0.178	0.540	0.018	0.711	Acceptable
Boreal	Breeding	Female	0.057	0.093	0.434	0.016	0.653	Acceptable
		Male	0.068	0.029	0.316	0.040	0.551	Acceptable
	Foraging	Female	0.047	0.172	0.526	0.075	0.644	Acceptable
		Male	0.019	0.491	0.813	0.001	0.805	Acceptable
	Pre-hibernation	Female	0.042	0.190	0.578	0.002	0.799	Acceptable
		Male	0.049	0.240	0.507	0.024	0.498	Acceptable

B. Fine-grained buffered-home-range design (FGHR)

Site	Period	Sex	B_0	P	B_1	P	Adjusted R^2	Validation
Park	Breeding	Female	0.001	0.823	0.991	0.009	0.648	Good
		Male	0.002	0.503	0.976	0.049	0.690	Good
	Foraging	Female	0.042	0.462	0.583	0.120	0.380	Unacceptable
		Male	0.066	0.167	0.337	0.255	0.372	Unacceptable
	Pre-hibernation	Female	0.003	0.422	0.971	0.001	0.908	Good
		Male	0.085	0.168	0.146	0.388	0.119	Unacceptable
Pasture	Breeding	Female	0.028	0.082	0.705	<0.001	0.937	Acceptable
		Male	0.039	0.184	0.575	0.001	0.773	Acceptable
	Foraging	Female	0.031	0.329	0.692	0.002	0.765	Acceptable
		Male	0.012	0.548	0.884	<0.001	0.945	Acceptable
	Pre-hibernation	Female	0.017	0.284	0.829	<0.001	0.967	Acceptable
		Male	0.026	0.181	0.742	<0.001	0.940	Acceptable
Boreal	Breeding	Female	0.012	0.727	0.877	0.001	0.851	Good
		Male	0.069	0.049	0.306	0.161	0.272	Unacceptable
	Foraging	Female	0.029	0.294	0.708	0.002	0.795	Acceptable
		Male	-0.064	0.248	1.637	0.001	0.766	Good
	Pre-hibernation	Female	0.028	0.445	0.719	0.042	0.582	Acceptable
		Male	0.020	0.285	0.800	0.030	0.591	Acceptable

C. Coarse-grained buffered-home-range design (CGHR)

Site	Period	Sex	B_0	P	B_1	P	Adjusted R^2	Validation
Park	Breeding	Female	-0.014	0.382	1.136	<0.001	0.983	Acceptable
		Male	0.020	0.535	0.796	0.060	0.635	Acceptable
	Foraging	Female	-0.045	0.542	1.448	0.080	0.369	Acceptable
		Male	-0.058	0.483	1.585	0.114	0.355	Unacceptable
	Pre-hibernation	Female	0.012	0.560	0.876	0.166	0.495	Acceptable
		Male	-0.003	0.352	1.029	0.167	0.490	Acceptable
Pasture	Breeding	Female	0.029	0.326	0.716	0.084	0.617	Acceptable
		Male	0.063	0.335	0.374	0.465	-0.040	Unacceptable
	Foraging	Female	0.034	0.324	0.662	0.039	0.488	Acceptable
		Male	0.020	0.541	0.802	0.031	0.570	Good
	Pre-hibernation	Female	0.015	0.486	0.849	0.121	0.317	Acceptable
		Male	0.015	0.615	0.850	0.004	0.695	Good
Boreal	Breeding	Female	-0.062	0.256	1.627	0.003	0.763	Good
		Male	-0.010	0.468	1.106	0.025	0.607	Acceptable
	Foraging	Female	-0.021	0.654	1.209	0.009	0.618	Good
		Male	0.022	0.300	0.779	0.001	0.781	Acceptable
	Pre-hibernation	Female	-0.028	0.351	1.277	0.001	0.872	Acceptable
		Male	-0.013	0.594	1.129	<0.001	0.895	Good

Table 3-2. Best design of the fine-grained population-range (FGPR), fine-grained buffered-home-range (FGHR), and coarse-grained buffered-home-range (CGHR), based on adjusted R^2 values (1 = highest, 3 = lowest) from five-fold validation.

Site	Period	Sex	FGPR	FGHR	CGHR
Park	Breeding	Female	3	2	1
		Male	3	1	2
	Foraging	Female	1	2	3
		Male	2	1	3
	Pre-hibernation	Female	2	1	3
		Male	3	2	1
Pasture	Breeding	Female	2	1	3
		Male	1	2	3
	Foraging	Female	2	1	3
		Male	2	1	3
	Pre-hibernation	Female	2	1	3
		Male	2	1	3
Boreal	Breeding	Female	3	1	2
		Male	2	3	1
	Foraging	Female	2	1	3
		Male	1	3	2
	Pre-hibernation	Female	2	3	1
		Male	3	2	1
		Total	38	29	41

Table 3-3. Mean adjusted R^2 values from our cross validation analysis calculated for each study design, study site, time period, and sex (A). A generalized linear model indicated that differences in model predictive power (adjusted R^2 values) were significant among study sites and between male and female models but were not significant among study designs or time periods (B).

A.

Category	Sub-category	Mean	SE
Study Design	FGPR	0.619	0.057
	FGHR	0.683	0.060
	CGHR	0.584	0.058
Study Site	Park	0.501	0.064
	Pasture	0.700	0.059
	Boreal	0.686	0.037
Period	Breeding	0.622	0.063
	Foraging	0.631	0.046
	Pre-hibernation	0.633	0.066
Sex	Female	0.689	0.038
	Male	0.569	0.053

B.

Category	Wald Chi-Square	df	P-value
(Intercept)	468.157	1	<0.001
Study Design	2.010	2	0.366
Study Site	9.755	2	0.008
Period	0.030	2	0.985
Sex	4.260	1	0.039

Table 3-4. Resource Selection Functions (RSF) for the fine-grained population-range design (FGPR) were created using generalized linear models in SPSS. Toad presence/absence was the dependent variable. P-values less than 0.05 for land-cover variables indicate significant selection (positive coefficient) or avoidance (negative coefficient) in relation to deciduous for park and pasture sites and to conifer for the boreal site. Pre-Hib. = pre-hibernation.

A. FGPR - Park site.

Period	Sex	Toad n	Random n	Predictor variables	Beta	SE	P-value
Breeding	Female	30	1892	(Constant)	-2.237	0.865	0.010
				Distance to breeding	-0.013	0.006	0.021
				Distance to hibernation	-0.007	0.002	0.002
				Marsh	0.913	0.717	0.203
Breeding	Male*	55	1449	(Constant)	-3.870	0.766	<0.001
				Distance to breeding	-0.022	0.008	0.004
				Distance to hibernation	-0.004	0.001	0.014
				Marsh	2.525	0.743	0.001
				Emergent vegetation	1.849	1.236	0.135
Foraging	Female	68	2009	(Constant)	-0.561	0.410	0.171
				Distance to breeding	-0.006	0.003	0.031
				Distance to hibernation	-0.009	0.002	<0.001
				Wet shrub	1.642	0.418	<0.001
				Marsh	-3.315	1.092	0.002
				Disturbed grass	2.470	0.850	0.004
Foraging	Male	38	1973	(Constant)	-2.254	1.687	0.182
				Distance to breeding	-0.039	0.016	0.013
				Distance to hibernation	-0.005	0.002	0.016
				Wet shrub	4.002	1.407	0.004
				Marsh	0.431	1.522	0.777
Pre-Hib.	Female	27	2023	(Constant)	-3.536	0.729	<0.001
				Distance to breeding	0.000	0.003	0.962
				Distance to hibernation	-0.008	0.003	0.004
				Wet shrub	2.584	0.773	0.001
				Marsh	-0.005	0.850	0.995
				Meadow	3.044	0.982	0.002
Pre-Hib.	Male**	26	718	(Constant)	0.116	0.568	0.839
				Distance to breeding	-0.054	0.021	0.009
				Distance to hibernation	-0.009	0.003	<0.001

*Water was used as the reference variable because only one toad observation occurred in deciduous habitat for the park breeding male model.

** Land-cover types were not examined for pre-hibernation males because all used locations were in marsh habitat except for one location in wet shrub. Only used and random locations within marsh habitat were selected for analysis.

B. FGPR - Pasture site.

Period	Sex	Toad n	Random n	Predictor variables	Beta	SE	P-value
Breeding	Female	210	4047	(Constant)	-1.281	0.479	0.008
				Distance to breeding	-0.008	0.001	<0.001
				Distance to hibernation	-0.005	0.001	<0.001
				Conifer	1.212	0.684	0.076
				Mixed-wood	0.357	0.517	0.490
				Dry shrub	0.368	0.957	0.700
				Wet shrub	2.388	0.680	<0.001
				Marsh	2.294	1.089	0.035
				Disturbed grass	2.428	0.635	<0.001
				Crop/hay	1.613	0.638	0.011
				Pasture	0.055	0.487	0.910
				Emergent vegetation	3.211	0.561	<0.001
				Water	2.604	0.612	<0.001
Breeding	Male	235	3851	(Constant)	-1.097	0.653	0.093
				Distance to breeding	-0.019	0.003	<0.001
				Distance to hibernation	-0.004	0.001	<0.001
				Conifer	2.164	0.910	0.017
				Mixed-wood	0.503	0.742	0.498
				Dry shrub	2.341	0.918	0.011
				Crop/hay	1.932	1.035	0.062
				Pasture	0.901	0.639	0.159
				Emergent vegetation	3.021	0.719	<0.001
				Water	2.947	0.724	<0.001
Foraging	Female	234	3823	(Constant)	-0.723	0.357	0.043
				Distance to breeding	-0.002	0.001	0.035
				Distance to hibernation	-0.010	0.001	<0.001
				Conifer	-0.226	0.601	0.707
				Mixed-wood	-0.237	0.354	0.503
				Disturbed Grass	1.460	0.488	0.003
				Crop/Hay	1.149	0.417	0.006
				Pasture	-0.147	0.497	0.007

B. FGPR - Pasture site. Continued…

Period	Sex	Toad n	Random n	Predictor variables	Beta	SE	P-value
Foraging	Male	194	3962	(Constant)	-1.649	0.367	<0.001
				Distance to breeding	-0.004	0.001	<0.001
				Distance to hibernation	-0.004	0.001	<0.001
				Mixed-wood	0.238	0.392	0.543
				Dry shrub	1.003	0.584	0.086
				Wet shrub	1.161	0.773	0.133
				Disturbed grass	0.204	0.907	0.822
				Mowed lawn	1.985	0.867	0.022
				Crop/hay	0.865	0.439	0.049
				Pasture	-0.634	0.420	0.131
				Emergent vegetation	1.371	0.618	0.026
				Water	0.900	0.827	0.277
Pre-Hib.	Female	100	3871	(Constant)	-0.240	0.507	0.635
				Distance to breeding	-0.005	0.002	0.004
				Distance to hibernation	-0.019	0.003	<0.001
				Conifer	0.013	0.672	0.985
				Mixed-wood	0.683	0.411	0.096
				Dry shrub	-0.117	0.821	0.887
				Disturbed grass	1.500	0.675	0.026
				Crop/hay	1.615	0.680	0.018
				Pasture	-1.387	0.818	0.090
Pre-Hib.	Male	59	1168	(Constant)	2.621	0.935	0.005
				Distance to breeding	-0.005	0.003	0.108
				Distance to hibernation	-0.104	0.019	<0.001
				Conifer	-0.501	0.744	0.500
				Mixed-wood	-0.443	0.583	0.447
				Dry shrub	-0.489	0.888	0.582

C. FGPR - Boreal site.

Period	Sex	Toad n	Random n	Predictor variables	Beta	SE	P-value
Breeding	Female	93	15097	(Constant)	-2.246	0.584	<0.001
				Distance to breeding	-0.004	0.001	<0.001
				Distance to hibernation	-0.008	0.001	<0.001
				Deciduous	1.894	0.722	0.009
				Mixed-wood	1.168	0.862	0.175
				Wet shrub	2.759	0.568	<0.001
				Moss	2.673	0.558	<0.001
				Burn	1.556	0.887	0.079
				Cutblock (treed)	3.526	1.047	0.001
				Disturbed grass	1.916	0.597	0.001
Breeding	Male	143	8784	(Constant)	-1.138	0.415	0.006
				Distance to breeding	-0.010	0.001	<0.001
				Distance to hibernation	-0.002	0.001	0.005
				Wet shrub	2.185	0.380	<0.001
				Moss	2.500	0.413	<0.001
				Clear-cut (grass)	3.132	0.675	<0.001
				Disturbed grass	-0.147	0.534	0.783
				Water	1.264	1.051	0.229
Foraging	Female	84	13482	(Constant)	-2.765	0.583	<0.001
				Distance to breeding	-0.001	0.000	0.002
				Distance to hibernation	-0.013	0.002	<0.001
				Deciduous	2.568	0.545	<0.001
				Wet shrub	2.906	0.507	<0.001
				Moss	0.312	1.269	0.806
				Cutblock (treed)	3.052	0.964	0.002
				Disturbed grass	2.224	0.564	<0.001
Foraging	Male	117	10305	(Constant)	-2.036	0.311	<0.001
				Distance to breeding	-0.002	0.000	<0.001
				Distance to hibernation	-0.003	0.001	<0.001
				Mixed-wood	-0.097	0.426	0.820
				Wet shrub	0.873	0.317	0.006
				Moss	-0.956	0.768	0.213
				Burn	0.197	0.553	0.722
				Clear-cut (grass)	1.021	0.618	0.098
				Disturbed grass	-1.106	0.624	0.076

C. FGPR - Boreal site. Continued…

Period	Sex	Toad n	Random n	Predictor variables	Beta	SE	P-value
Pre-Hib.	Female	64	12825	(Constant)	-1.286	0.415	0.002
				Distance to breeding	-0.001	0.000	0.002
				Distance to hibernation	-0.015	0.002	<0.001
				Deciduous	0.544	0.501	0.277
				Wet shrub	0.961	0.417	0.021
				Moss	0.005	0.779	0.995
				Burn	-0.746	0.801	0.352
				Disturbed grass	-0.291	0.684	0.671
Pre-Hib.	Male	59	7782	(Constant)	-2.054	0.417	<0.001
				Distance to breeding	-0.000	0.000	0.909
				Distance to hibernation	-0.012	0.002	<0.001
				Wet shrub	-1.325	0.836	0.113
				Moss	-0.268	0.832	0.748
				Clear-cut (grass)	1.476	0.643	0.022

Table 3-5. Resource Selection Functions (RSF) for the fine-grained buffered-home-range design (FGHR) were created using conditional logistic regression models in SPSS. P-values less than 0.05 for land-cover variables indicate significant selection (positive coefficient) or avoidance (negative coefficient) in relation to deciduous for park and pasture sites and to conifer for the boreal site. Pre-Hib. = pre-hibernation.

A. FGHR – Park site.

Period	Sex	N	Predictor variables	Beta	SE	P-value
Breeding	Female	191	Distance to breeding	-0.009	0.003	0.001
			Distance to hibernation	-0.012	0.002	<0.001
			Marsh	0.358	0.311	0.251
Breeding	Male*	348	Distance to breeding	-0.026	0.004	<0.001
			Distance to hibernation	-0.006	0.001	<0.001
			Marsh	2.598	0.322	<0.001
			Emergent vegetation	0.734	0.466	0.115
Foraging	Female	489	Distance to breeding	-0.014	0.002	<0.001
			Distance to hibernation	-0.003	0.002	0.082
			Wet shrub	1.013	0.278	<0.001
			Marsh	-3.351	0.371	<0.001
			Disturbed grass	1.652	0.562	0.003
Foraging	Male	239	Distance to breeding	-0.047	0.014	0.001
			Distance to hibernation	-0.007	0.003	0.015
			Wet shrub	2.318	0.849	0.006
			Marsh	-0.926	0.794	0.243
Pre-Hib.	Female	182	Distance to breeding	-0.008	0.003	0.003
			Distance to hibernation	-0.008	0.002	<0.001
			Wet shrub	3.079	0.977	0.002
			Marsh	-0.121	0.296	0.682
			Meadow	1.892	0.833	0.023
Pre-Hib.	Male**	89	Distance to breeding	-0.099	0.042	0.020
			Distance to hibernation	-0.015	0.005	0.004

*Water was used as the reference variable because only one toad observation occurred in deciduous habitat for the park breeding male model.

** Land-cover types were not examined in the pre-hibernation male model because all used locations were in marsh habitat except for one location in wet shrub. Only used and random locations within marsh habitat were selected for analysis.

B. FGHR – Pasture site.

Period	Sex	N	Predictor variables	Beta	SE	P-value
Breeding	Female	2078	Distance to breeding	-0.006	0.001	<0.001
			Distance to hibernation	-0.003	0.001	<0.001
			Conifer	0.607	0.212	0.004
			Mixed-wood	-0.171	0.147	0.245
			Dry shrub	0.327	0.360	0.363
			Wet shrub	2.410	0.368	<0.001
			Marsh	2.487	0.435	<0.001
			Disturbed grass	1.845	0.270	<0.001
			Crop/hay	0.799	0.179	<0.001
			Pasture	-0.659	0.155	<0.001
			Emergent vegetation	2.771	0.295	<0.001
			Water	1.710	0.263	<0.001
Breeding	Male	2258	Distance to breeding	-0.018	0.001	<0.001
			Distance to hibernation	0.000	0.001	0.506
			Conifer	1.685	0.295	<0.001
			Mixed-wood	0.176	0.224	0.433
			Dry shrub	3.307	0.446	<0.001
			Crop/hay	1.975	0.317	<0.001
			Pasture	-0.924	0.225	<0.001
			Emergent vegetation	2.010	0.354	<0.001
			Water	1.506	0.317	<0.001
Foraging	Female	2232	Distance to breeding	-0.005	0.001	<0.001
			Distance to hibernation	-0.006	0.001	<0.001
			Conifer	-0.427	0.162	0.008
			Mixed-wood	-0.188	0.118	0.109
			Disturbed grass	1.112	0.194	<0.001
			Crop/hay	1.080	0.140	<0.001
			Pasture	-1.592	0.162	<0.001
Foraging	Male	1803	Distance to breeding	-0.007	0.001	<0.001
			Distance to hibernation	-0.008	0.001	<0.001
			Mixed-wood	-0.721	0.139	<0.001
			Dry shrub	1.202	0.249	<0.001
			Wet shrub	2.674	0.443	<0.001
			Disturbed grass	-0.456	0.284	0.108
			Mowed lawn	2.295	0.502	<0.001
			Crop/hay	0.952	0.184	<0.001
			Pasture	-1.003	0.168	<0.001
			Emergent vegetation	0.885	0.308	0.004
			Water	0.307	0.339	0.366

B. FGHR – Pasture site. Continued…

Period	Sex	N	Predictor variables	Beta	SE	P-value
Pre-Hib.	Female	949	Distance to breeding	-0.009	0.001	<0.001
			Distance to hibernation	-0.022	0.002	<0.001
			Conifer	0.165	0.308	0.592
			Mixed-wood	0.560	0.226	0.013
			Dry shrub	0.242	0.658	0.713
			Disturbed grass	1.679	0.430	<0.001
			Crop/hay	1.848	0.341	<0.001
			Pasture	-1.962	0.374	<0.001
Pre-Hib.	Male	292	Distance to breeding	-0.002	0.005	0.651
			Distance to hibernation	-0.204	0.056	<0.001
			Conifer	-2.295	1.032	0.026
			Mixed-wood	-2.419	1.026	0.018
			Dry shrub	1.875	14.894	0.900

C. FGHR – Boreal site.

Period	Sex	n	Predictor variables	Beta	SE	P-value
Breeding	Female	893	Distance to breeding	-0.002	0.001	<0.001
			Distance to hibernation	-0.006	0.001	<0.001
			Deciduous	0.992	0.241	<0.001
			Mixed-wood	0.784	0.281	0.005
			Wet shrub	2.419	0.239	<0.001
			Moss	2.984	0.276	<0.001
			Burn	4.321	0.503	<0.001
			Cutblock (treed)	2.929	0.561	<0.001
			Disturbed grass	1.723	0.226	<0.001
Breeding	Male	1158	Distance to breeding	-0.012	0.001	<0.001
			Distance to hibernation	0.006	0.001	<0.001
			Wet shrub	0.651	0.179	<0.001
			Moss	1.569	0.189	<0.001
			Clear-cut (grass)	2.124	0.397	<0.001
			Disturbed grass	-0.894	0.229	<0.001
			Water	0.452	0.517	0.382
Foraging	Female	692	Distance to breeding	-0.002	0.001	0.020
			Distance to hibernation	-0.011	0.001	<0.001
			Deciduous	1.376	0.261	<0.001
			Wet shrub	2.746	0.272	<0.001
			Moss	1.032	0.432	0.017
			Cutblock (treed)	0.285	0.555	0.608
			Disturbed grass	2.196	0.290	<0.001
Foraging	Male	980	Distance to breeding	0.001	0.000	0.005
			Distance to hibernation	-0.004	0.001	<0.001
			Mixed-wood	1.303	0.269	<0.001
			Wet shrub	1.210	0.175	<0.001
			Moss	-1.271	0.246	<0.001
			Burn	-0.460	0.253	0.069
			Clear-cut (grass)	0.601	0.301	0.046
			Disturbed grass	-0.663	0.210	0.002
Pre-Hib.	Female	550	Distance to breeding	0.000	0.001	0.647
			Distance to hibernation	-0.019	0.002	<0.001
			Deciduous	0.362	0.363	0.319
			Wet shrub	0.514	0.317	0.105
			Moss	-0.238	0.573	0.678
			Burn	-2.797	0.698	<0.001
			Disturbed grass	-0.391	0.386	0.311
Pre-Hib.	Male	430	Distance to breeding	0.000	0.001	0.630
			Distance to hibernation	-0.011	0.001	<0.001
			Wet shrub	0.313	0.403	0.438
			Moss	-1.352	0.497	0.006
			Clear-cut (grass)	1.310	0.659	0.047

Table 3-6. Resource Selection Functions (RSF) for the coarse-grained buffered-home-range design (CGHR) were created using conditional logistic regression models in SPSS. P-values less than 0.05 for land-cover variables indicate significant selection (positive coefficient) or avoidance (negative coefficient) in relation to deciduous for park and pasture sites and to conifer for the boreal site. Pre-Hib. = pre-hibernation.

A. CGHR – Park site.

Period	Sex	N	Predictor variables	Beta	SE	P-value
Breeding	Female	294	Distance to water	-0.024	0.004	<0.001
			Distance to conifer	-0.003	0.002	0.151
			Water	-2.690	0.498	<0.001
			Herbaceous cover	-0.658	0.382	0.085
			Conifer	1.833	0.602	0.002
Breeding	Male*	389	Distance to water	-0.016	0.005	0.002
			Distance to conifer	-0.001	0.001	0.333
			Herbaceous cover	-0.837	0.298	0.005
Foraging	Female	592	Distance to water	-0.007	0.002	<0.001
			Distance to conifer	0.007	0.001	<0.001
			Water	-0.621	0.186	0.001
			Herbaceous cover	-1.325	0.187	<0.001
Foraging	Male	278	Distance to water	-0.062	0.015	<0.001
			Distance to conifer	0.010	0.002	<0.001
			Water⊥	-0.362	0.480	0.451
Pre-hib.	Female	145	Distance to water	-0.014	0.003	<0.001
			Distance to conifer	0.013	0.003	<0.001
			Herbaceous cover	-1.282	0.373	0.001
Pre-hib.	Male*	196	Distance to water	-0.113	0.041	0.005
			Distance to conifer	0.001	0.002	0.683
			Herbaceous cover	0.337	0.537	0.531

*Water was used as the reference variable because only one toad observation occurred in deciduous habitat for the park breeding male model and none for the pre-hibernation male model.

⊥The variables "water" and "distance to water" were correlated in this model (r = -0.729). If the variable "distance to water" were omitted, the variable "water" would show a significant positive relationship with toad presence. Dropping the variable "water" from the model does not significantly influence the results for the other two variables.

B. CGHR – Pasture site.

Period	Sex	n	Predictor variables	Beta	SE	P-value
Breeding	Female	2129	Distance to water	-0.005	0.000	<0.001
			Distance to conifer	-0.001	0.001	0.151
			Water	0.749	0.270	0.006
			Wet shrub	0.210	0.171	0.219
			Herbaceous cover	-0.452	0.102	<0.001
			Conifer	-0.296	0.143	0.039
Breeding	Male	2360	Distance to water	-0.008	0.000	<0.001
			Distance to conifer	0.009	0.001	<0.001
			Water	-0.118	0.379	0.756
			Wet shrub	-0.439	0.284	0.122
			Herbaceous cover	0.388	0.164	0.018
			Conifer	1.087	0.194	<0.001
Foraging	Female	2380	Distance to water	-0.003	0.000	<0.001
			Distance to conifer	-0.001	0.001	0.271
			Water	-0.090	0.363	0.805
			Wet shrub	0.718	0.152	<0.001
			Herbaceous cover	-0.359	0.091	<0.001
			Conifer	0.314	0.109	0.004
Foraging	Male	1928	Distance to water	-0.006	0.000	<0.001
			Distance to conifer	0.002	0.001	0.004
			Wet shrub	0.544	0.158	0.001
			Herbaceous cover	-0.412	0.095	<0.001
			Conifer	-0.150	0.133	0.261
Pre-Hib.	Female	987	Distance to water	-0.002	0.001	0.021
			Distance to conifer	-0.001	0.001	0.292
			Wet shrub	0.538	0.256	0.035
			Herbaceous cover	-1.495	0.167	<0.001
			Conifer	0.785	0.177	<0.001
Pre-Hib.	Male	592	Distance to water	-0.007	0.001	<0.001
			Distance to conifer	-0.003	0.001	0.051
			Wet shrub	1.156	0.294	<0.001
			Herbaceous cover	-0.727	0.189	<0.001
			Conifer	-0.802	0.241	0.001

C. CGHR – Boreal site.

Period	Sex	N	Predictor variables	Beta	SE	P-value
Breeding	Female	932	Distance to water	-0.001	0.000	<0.001
			Distance to conifer	0.002	0.002	0.235
			Exposed land	1.138	0.184	<0.001
			Tall shrub	0.929	0.414	0.025
			Wet shrub	-0.003	0.159	0.984
			Wet herbaceous	-0.044	0.196	0.824
			Deciduous	0.031	0.208	0.880
			Mixed-wood	0.219	0.238	0.358
Breeding	Male	1407	Distance to water	0.000	0.000	0.710
			Distance to conifer	0.005	0.002	<0.001
			Exposed land	1.545	0.161	<0.001
			Tall shrub	1.872	0.239	<0.001
			Wet shrub	0.675	0.150	<0.001
			Wet herbaceous	-0.848	0.260	0.001
			Herbaceous cover	0.941	0.327	0.004
			Deciduous	0.861	0.173	<0.001
Foraging	Female	728	Distance to water	0.000	0.001	0.636
			Distance to conifer	-0.006	0.002	0.010
			Wet shrub	0.121	0.173	0.482
			Deciduous	1.396	0.237	<0.001
			Mixed-wood	-0.984	0.263	<0.001
Foraging	Male	1039	Distance to water	0.000	0.000	0.674
			Distance to conifer	-0.012	0.002	<0.001
			Tall shrub	0.614	0.316	0.052
			Wet shrub	0.428	0.134	0.001
			Wet herbaceous	1.154	0.187	<0.001
			Deciduous	0.354	0.211	0.094
			Mixed-wood	-0.209	0.247	0.398
Pre-hib.	Female	584	Distance to water	0.001	0.001	0.343
			Distance to conifer	0.010	0.003	0.001
			Wet shrub	0.512	0.172	0.003
			Herbaceous cover	1.752	0.671	0.009
			Deciduous	0.489	0.269	0.068
			Mixed-wood	-0.745	0.330	0.024
Pre-hib.	Male	547	Distance to water	0.000	0.001	0.483
			Distance to conifer	0.011	0.006	0.058
			Wet shrub	-1.818	0.268	<0.001
			Deciduous	-2.302	0.410	<0.001
			Mixed-wood	-0.610	0.337	0.070

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Chapter 4. Hibernation Sites of Western Toads (*Anaxyrus boreas*): Characterization and Management Implications[2]

4.1 Introduction

The western toad (*Anaxyrus boreas*, formerly *Bufo boreas*) was common historically throughout much of the western United States and Canada (Wind and Dupuis 2002; Corn et al. 2005). Recently, population declines of this species in parts of the U.S. and Canada have warranted its inclusion on the World Conservation Union's (IUCN) Red List of Threatened Species, being accorded near-threatened status (Hammerson, G., G. Santos-Barrera, and E. Muths. 2004. *Bufo boreas*. Available from http://www.iucnredlist.org/details/3179/0. [Accessed 2 July 2008]) and by COSEWIC as being of special concern (COSEWIC 2009). The major threats to this species are believed to be disease (e.g., Kiesecker et al. 2001; Muths et al. 2003), habitat and environmental degradation (e.g., Blaustein et al. 1994; Wind and Dupuis 2002; Hammerson, G., G. Santos-Barrera, and E. Muths. 2004. *op. cit.*), and synergistic effects between these factors where environmental degradation causes stress, immune suppression, and susceptibility to disease (Carey 1993).

Protection of amphibian habitat has focused traditionally on the creation of buffers around breeding ponds or waterways protecting them from disturbance (e.g., Semlitsch and Bodie 2003; Goates et al. 2007). However, buffers are rarely more extensive than 100 m (Lee et al. 2004) and research investigating western

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toad movement patterns indicates that toads use habitat much farther than 100 m from breeding ponds (e.g., mean distance = 652 m, Muths 2003; 814 m, Bartelt et al. 2004; 1968 m, Bull 2006). Research in northwestern Alberta has suggested that western toad abundance in wetland areas is related more strongly to land-cover types surrounding wetlands at a landscape level than the physical or habitat characteristics of the wetland itself (Browne et al. 2009). Terrestrial habitat (for foraging and hibernation) is clearly important for western toads, but wetland buffers are unlikely to protect core habitat (defined as the area that is used by 95% of the population by Crawford and Semlitsch 2007).

Winter is a critical time period for amphibians and reptiles in cold climates, yet current understanding of hibernation requirements for most species is, at best, fragmentary: *A. boreas* is no exception. Survival probability of western toads in Colorado is known to be influenced by minimum daily winter air temperatures, snow depth and winter environmental moisture levels (Scherer et al. 2008). Suitable habitat for hibernation is likely limiting for western toads in the north and at high elevations; for example, in the Yukon the species has only been reported from valleys that receive high snowfall, which prevents deep frost penetration (Cook 1977). The western toad is not a freeze-tolerant species (Mullally 1952; Holzwart and Hall 1984), unlike the wood frog (*Lithobates sylvaticus*; Storey and Storey 1984) and chorus frog (*Pseudacris spp.*; Swanson et al. 1996) that also occur at high latitudes; therefore, toads must find suitable sites below the frost-line for hibernation. Mullally (1952) found western toads in California overwintering in golden-mantled ground squirrel (*Spermophilus* *lateralis*) tunnels at depths of 10-60 cm in October. Campbell (1970) found that western toads in Colorado hibernated communally (but not in physical contact with each other) in underground cavities situated near a spring seep of continuously flowing ground water, and insulated by thick snow cover. At another area in Colorado, Jones et al. (1998) radio-tracked western toads from the active state to entry into hibernation and found that most used golden-mantled ground squirrel burrows, but some individuals used sites near spring seeps, under Engelmann spruce (*Picea engelmannii*), or in clumps of willows (*Salix spp.*). The most northerly study of western toad hibernacula was from Oregon, where Bull (2006) tracked 26 western toads to their hibernation sites and found that they overwintered underground in rodent burrows (red squirrel, *Tamiasciurus hudsonicus*, and possibly ground squirrels, *Spermophilus spp.*), under large rocks, logs or root wads, and in banks adjacent to streams/lakes. Data on hibernation sites for the western toad in Canada are lacking.

We examined habitat selection for hibernacula by western toads at three localities in Alberta, Canada. Our objectives were to determine (1) locations and describe the physical features of hibernation sites; (2) if western toads hibernate communally; (3) if temperatures at hibernation sites differ from those of nearby reference sites; (4) whether the distance between breeding ponds and hibernation sites differs between study areas or between sexes; (5) whether government guidelines for buffers around watercourses would encompass core terrestrial habitat for hibernation; and (6) which land-cover types are selected for hibernation using resource selection function (RSF) analyses.

Our study was exploratory in nature, so we did not formulate *a priori* hypotheses; however, we did make several predictions. We predicted that western toads in Alberta would select rodent burrows or cavities in terrestrial habitat for hibernation, similar to hibernacula described for the species elsewhere, further south in its range (Mullally 1952; Campbell 1970; Jones et al. 1998; Bull 2006). We predicted that the distance between breeding ponds and hibernation sites would differ among study areas located in different ecoregions in Alberta in response to both habitat used locally by toads, and landscape configuration. In Colorado, Idaho, Oregon, and Utah, female western toads have been found to select foraging habitat significantly farther from breeding ponds than do male toads (Muths 2003; Bartelt et al. 2004; Bull 2006; Goates et al. 2007); so we predicted that female toads in Alberta would select hibernation sites farther from breeding ponds than did males, if they select hibernation sites near foraging grounds. Finally, we predicted that buffers designed to protect watercourses would not protect core habitat needed by western toads for hibernation because the most extensive protective buffers are set at 100 m in the province (Alberta Government. 2008. Alberta timber harvest planning and operating ground rules framework for Renewal. Available from http://www.srd.gov.ab.ca/forests/pdf/Annex_4_draft_Jan_15_08Final.pdf [Accessed 2 July 2009]) and previous research has shown that western toads hibernate much farther than 100 m from breeding ponds (range = 180-6230 m, Bull 2006).

4.2 Methods

Study Area.— Our research took place at three study areas in the north-central region of Alberta, Canada; we have designated these as the park area, pasture area, and boreal area. The park area is an isolated patch of dry mixed-wood boreal forest embedded within the Aspen Parkland natural region and located in Elk Island National Park (EINP) (Alberta Government. 2005. 2005 natural regions and subregions of Alberta. Available from http://tpr.alberta.ca/parks/heritageinfocentre/docs/nsr2005_final_letter.pdf. [Accessed 2 July 2009]). This area is undeveloped and comprised mostly of upland forest surrounding shallow lakes and marsh habitat. Forests consist primarily of trembling aspen (*Populus tremuloides*), balsam poplar (*P. balsamifera*), and white spruce (*Picea glauca*), with a hazelnut understory (*Corylus cornuta*). This study area was centered on two shallow lakes (10-20 ha) used by western toads for breeding.

The pasture area consists of dry mixed-wood boreal forest that has been converted to agriculture and is located 3.5 km west of EINP. This area supports cattle grazing, cultivation of hay and crops (e.g., wheat, barley, oats, canola, timothy, alfalfa), and rural housing. It also contains relatively undisturbed woodlots and peatland. Common tree species are trembling aspen, balsam poplar, white spruce, black spruce (*Picea mariana*), paper birch (*Betula papyrifera*), tamarack (*Larix laricina*), and jack pine (*Pinus banksiana*). This study area was centered on four naturalized man-made ponds (0.09-0.4 ha) that were created during sand extraction and are used by western toads for breeding; the surrounding land is used for cattle grazing.

The boreal area is in the central mixed-wood subregion of the Boreal Forest natural region (Alberta Government. 2005. *op. cit.*), located north of Lac La Biche approximately 150 km north of our park area. This region is influenced by the forestry and oil/gas industries (e.g., seismic lines, pipelines) and is comprised mostly of shrub swamps, peatland, upland boreal mixed-wood forest, and forestry cut blocks. Common tree/shrub species are trembling aspen, balsam poplar, white spruce, black spruce, paper birch, tamarack, jack pine, willow, and dwarf birch (*B. nana*). This study site was centered on a small shallow pond (0.07 ha) that is used by western toads for breeding and is located next to a gravel road and in a major utility corridor. A small permanent stream feeds this pond.

Land-cover features were measured using ArcGIS 9.2 (ESRI, Redlands California, USA) within a 2 km radius of the center of each study area (the main breeding pond, or the midpoint between the main breeding ponds), encompassing an area of 12.56 km^2 per study area (Fig. 4-1).

Radio-telemetry.—We captured toads during the active season (May to October) in 2004, 2005, and 2006 while they were breeding at ponds or opportunistically while tracking other individuals. We radio-tagged the majority of female toads encountered at breeding ponds. Large numbers of males congregated to breed (e.g., we observed 28 males at the boreal area on 21 May 2005 and 41 males at the pasture area on 15 May 2006), so fewer than half of the males observed were radio-tagged. We measured and recorded the snout-urostyle length (SUL) to nearest mm, mass to nearest g, and sex of each toad at the time of capture. Toads captured between May and August received toe-clips for identification of recaptured toads that lost their transmitters. Clipped toes were also used by other researchers to determine age via skeletochronology (Garrett 2005; Mark 2007).

We radio-tracked adult toads for 1 w to 5 mo prior to hibernation to locate hibernation sites. We followed methods described by Bartelt and Peterson (2000) for attaching radio-transmitters. BD-2, BD-2T, and PD-2 transmitters, weighing 1.0 to 2.3 g and having minimum battery life of 28 d to 3 mo (Holohil Systems Ltd., Carp, Ontario, Canada), were attached using a waist belt made of soft surgical-grade polyethylene tubing (outside diameter = 0.965 mm; CA-63018-667, VWR International, Edmonton, Alberta, Canada) and a large size flyline eyelet (size 9). All transmitters/belts were less than 10% of body weight and most were less than 5%. We located toads 2-4 times per week. During the 3 years, we radio-tracked a total of 116 western toads (54 males and 62 females) and followed 50 to their hibernation sites (21 males and 29 females; Table 4-1).

Physical features of hibernation sites.**—**We measured physical features of each hibernaculum located, and assigned each a category (e.g., peat hummock, natural crevasses, sandy soil). We excavated each hibernation site between 3-23 October in each year of the study to measure the physical features in the hibernaculum and to capture the toad to remove its transmitter. We recorded soil texture, soil percent organic composition, soil percent moisture, soil pH, canopy cover, toad depth below surface, depth to water table (if encountered when excavating the toad), tunnel width, and dominant plant taxa surrounding a site (See Appendices H and I for details). After excavation, the site was restored as closely as possible to its original condition. Each hibernaculum excavation and restoration was completed within 1 day.

Communal use of hibernation sites.**—**We recorded the number of toads encountered in each hibernation site. Sites were confirmed to be communal hibernacula if more than one toad was observed. The number of communal hibernacula were likely underestimated because we did not disturb hibernation sites more than necessary to remove the tracked toad.

We used a Kruskal-Wallis test (SPSS Inc., Chicago, Illinois, USA) to determine if the number of toads per hibernaculum differed among study areas. We compared the distribution of the number of toads per hibernaculum to a Poisson distribution using a Kolmogorov-Smirnov Z test (SPSS Inc., Chicago, Illinois, USA) to determine if the distribution of toads was random among hibernating sites. We used alpha = 0.05 to establish significance for all statistical tests.

Temperature loggers in hibernation sites.**—**At the boreal study area in fall 2005, we placed temperature data loggers (HOBO Temperature (degrees C) 1996 Onset Computer Corp., Bourne, MA, USA) in four toad hibernation sites and four reference sites (paired with hibernation sites) on 8 October; data loggers recorded temperatures every 3.5 h until 28 May 2006. We selected reference sites that appeared visually similar to the hibernation site (e.g., peat mounds of similar size, similar soil types) and that were located in close proximity to the corresponding hibernation site (average = 23 m between hibernation and paired reference site, range = 12-31 m). We buried data loggers to the same depth that the toads occupied in their hibernaculum at the paired hibernation site (Table 4-2). The maximum number of consecutive days below 0, -1.5, and -5.2 degrees C were tallied. We examined the days below -1.5 and -5.2 degrees C because this is the temperature range that Swanson et al. (1996) report ice crystallization to occur in the tissues of other toad species (*A. cognatus* and *A. woodhousei*). We used a paired *t*-test (SPSS Inc., Chicago, Illinois, USA) to determine if minimum winter temperatures were significantly different between the four paired hibernation and reference sites. We used a Kolmogorov-Smirnov test to determine if data were normally distributed for all parametric tests.

Distances moved from breeding ponds to hibernation sites.**—**We compared distances moved from breeding pond to hibernation site between the pasture area and boreal area and between males and females using general linear models (GLMs; SPSS Inc., Chicago, Illinois, USA). We defined distances moved from breeding pond to hibernation site as the straight-line distance between the two points. The park area was not included in this analysis because only one toad was tracked from breeding to hibernation site.

***Watercourse protective buffers.*—**We determined the distance between each hibernation site and the closest open water body using ArcGIS 9.1, aerial photographs, and ground-truthing. We then assessed each point to determine which ones would be protected based on the Alberta Timber Harvest Ground Rules (Alberta Government. 2008. *op. cit.*).

***Resource Selection Functions.*—**We created a land-cover geographic information systems (GIS) map of 22 land-cover types from aerial photographs of each study area using ArcGIS 9.2. We digitized these at a resolution of 1:1890, which was the finest resolution possible from the available aerial photographs. We determined the number of toad hibernation sites in each land-cover type using the land-cover map and UTM coordinates for each hibernaculum, and calculated the proportion of use for each land-cover type. We calculated available habitat for each area using ArcGIS 9.2. We considered available habitat to be any habitat within 2 km of the study-area center. Selection indices for each land-cover type were calculated by dividing the proportion of toads using the land-cover type for hibernation in a study area (number of toads in the land-cover type divided by the total number of toads) by the proportion of available habitat (area of land-cover type divided by the total area for the study area) (Manly et al. 2002).

We conducted a Resource Selection Function (RSF) analysis to determine whether the land-cover types with the highest selection indices were selected significantly more often for hibernation than other land-cover types used by western toads. Random locations were generated for each study area at a mean density of 1 location/1000 m^2 using Hawth's Tools (Beyer H.L. 2004. Hawth's Analysis Tools for ArcGIS. Available from http://www.spatialecology.com/htools. [Accessed 2 July 2009]) in ArcGIS 9.2. Random locations that fell within land-cover types used by toads for hibernation (7765, 2622, and 6266 locations for the park, pasture, and boreal areas, respectively) were used as available habitat points. We used logistic regression (SPSS Inc., Chicago, Illinois, USA) to determine which of the designated land-cover types were most strongly selected by toads (Manly et al. 2002). Land-cover types that were used by toads were considered for entry into the models as binary variables (0 = absent, 1 = present). Three land-cover types were used for hibernation in the park area, three in the boreal area, and four at the pasture area (Table 4-3). Deciduous forest was used as the reference land-cover type for all park and pasture models and conifer forest for the boreal models; therefore, these were withheld from the respective models.

4.3 Results

Physical features of hibernation sites.**—**As predicted, all toads selected pre-existing tunnels or cavities for hibernation. Seven types of hibernation sites were used (Table 4-4) and all were terrestrial. However, we cannot be certain that toads did not enter the ground water later in the winter because the water table was as little as 33 cm below surface (3 cm below recorded toad locations) at some hibernation sites (Appendix H).

Peat hummocks consisted of mounds of peat and moss. Cavities in these hummocks appeared to originate as rotted tree stumps. All peat hummocks were found in treed peatlands and one site was in a burnt treed peatland. Dominant tree species were black spruce and white spruce at the pasture area and black spruce and tamarack at the boreal area.

Toads used both abandoned and active red squirrel middens, as well as squirrel tunnels. Locations associated with squirrels in the boreal area occurred in treed peatland habitat with black spruce and tamarack as the dominant tree species. Pasture locations associated with squirrels occurred in coniferous or mixed forest with black spruce or white spruce as the dominant tree; trembling aspen, balsam poplar, and tamarack occurred at some locations. Red squirrel tunnels were distinguished from Richardson ground squirrel (*Spermophilus richardsonii*) tunnels based on the habitat type in which they occurred (coniferous or mixed forests vs. pasture or agricultural fields) and observations of red squirrels around the sites.

Underground crevasses were used by eight toads at two sites, one in the park and the other in the pasture area. These sites appeared to be ponds that had dried and the bed cracked, forming crevasses. Crevasses were more than 2 m deep, 2-5 cm wide, and extended many meters horizontally. The surface layer of the crevasse soil was hard, dark brown, organic soil with an underlying layer of grey Gleysol. The park site was located in an upland grassy meadow and the pasture site was located within an open deciduous forest stand with an extensive shrub layer.

Three toads hibernated in cavities under white spruce trees and three under black spruce trees. These locations were all within the pasture area and were situated in treed peatlands, coniferous forests, and mixed forests which could include tamarack or *Populus* species.

Root channels were cavities left by rotted tree roots. These occurred in deciduous or mixed forests (pasture area) and in wet shrub habitat (boreal area), with the dominant tree/shrub species in both areas being paper birch and white spruce. Aspen and alder (*Alnus spp.*) were also present at some sites.

Abandoned American beaver (*Castor canadensis*) lodges used for hibernation were adjacent to streams (pasture area) or lakes (park area). The two lodges along streams were located in the bank and bore abundant shrub cover (e.g., trembling aspen; red-osier dogwood, *Cornus stolonifera*; rose, *Rosa acicularis*). The lodge adjacent to the lake was a log pile surrounded by marsh.

Muskrat (*Ondatra zibethicus*) tunnels used for hibernation were at the edges of shallow lakes in the park area. These tunnels ran from deciduous forest, through marsh, and into lakes. One toad’s hibernation site was in aspen forest 20 m from the lake, the other two were in the marsh 10-15 m from the lake.

Communal use of hibernation sites.—Communal hibernation was confirmed for 68% of the radio-tracked toads across the three study areas. Communal hibernacula contained up to 29 toads; however, sites with two to five toads were most common (Fig. 4-2). The number of toads per hibernaculum did not differ significantly among study areas (Kruskal-Wallis chi-square = 2.396, df = 2, P =

0.302). The distribution of the number of additional toads per hibernaculum was significantly different from a Poisson distribution (Z = 2.529, n = 50, P < 0.001; Fig. 4-2), indicating that toads were not distributed randomly amongst appropriate hibernation sites.

Males and females, and adults and juveniles (including young-of-the-year), were found together. We found toads clustered in physical contact with each other at some sites, but at other sites individuals were not touching. Inactive toads aroused quickly when disturbed. In three cases, toads that we captured at a particular breeding pond in the spring entered the same hibernation site. Of the toads captured at the breeding pond in the boreal area, two pairs of males each shared a communal hibernaculum; these hibernacula were located 1020 m and 661 m from the breeding pond. A male and two females from the pasture area moved 368 m from their breeding pond to a common hibernation site.

Temperature loggers in hibernation sites.—Temperatures varied little throughout the day at some sites, but at other sites fluctuations occurred in response to above ground-temperatures (Fig. 4-3). The minimum temperatures in the hibernation sites examined all fell below –1.5 degrees C at some point during winter (Table 4-2). Only two hibernation sites and one reference site experienced temperatures below –5.2 degrees C (Table 4-2). The distribution of minimum temperatures from all monitored sites was not significantly different from a normal distribution (Z = 0.689, n = 8, P = 0.729), so parametric statistics could be used. Minimum temperatures were not significantly different between hibernation and reference sites (t = 1.572, df = 3, P = 0.214).

Distances moved from breeding ponds to hibernation sites.**—**We tracked 28 individuals (15 males and 13 females) for the active season, from breeding ponds to hibernation sites (Table 4-1). Toads moved farther between breeding and hibernation sites in the boreal area (mean = 1086 m +/- 128 SE, 95% CI = 835-1337 m, range = 220-1936 m, n = 14) than they did in the pasture area (mean = 373 m +/- 39 SE, 95% CI = 297-449 m, range = 146-682 m, n = 13). Parametric statistics were used because the distribution of distances moved was not significantly different from a normal distribution (Z = 0.922, n = 27, P = 0.363). There was a significant difference in distances moved between the pasture and boreal areas but not between sexes (Table 4-5).

Watercourse protective buffers.**—**All toad hibernation sites at the park area were located within 100 m of a lake. At the boreal area, one hibernation site was located within 30 m of a small permanent stream (channel width 0.7-5 m) and another was located within 60 m of a large permanent stream (channel width > 5 m), whereas all other hibernation sites (90% of toads tracked) were located beyond the watercourse protective buffer. At the pasture area, three toads hibernated within 30 m of a small permanent stream, but all other hibernation sites (84% of toads tracked) were located over 100 m from water.

Resource Selection Functions.**—**Toads first captured in September or October within 25 m of another radio-tracked toad with which they eventually hibernated (two from the boreal area in 2005 and five from the park area in 2004) were excluded from analyses because these observations were not independent; i.e., these late-season toads were encountered only because they congregated near hibernacula which we had already located via radio-tracked toads. All land-cover types used for hibernation had selection index values greater than one, indicating that they were selected at rates greater than their relative availability, except for deciduous forest in the park area, which was used at lower rates than its occurrence on the landscape (Table 4-3).

Of the land-cover types used for hibernation in the park area, dry meadow was significantly selected compared to deciduous forest (the reference land-cover; Table 4-6). Conifer forest and dry shrubland were significantly selected compared to deciduous forest in the pasture area (Table 4-6). Of the land-cover types used for hibernation in the boreal area, none showed significant selection or avoidance compared to conifer forest (Table 4-6).

4.4 Discussion

Physical features of hibernation sites.**—**Our study is the first known to locate and describe, in detail, hibernation sites for the western toad in Canada, or any amphibian at these latitudes in North America. Western toads in our study areas hibernated terrestrially and selected pre-existing tunnels or cavities. This is consistent with observations from other parts of the species' range (Mullally

1952; Campbell 1970; Jones et al. 1998; Bull 2006). Sandy patches were common at our study areas, but none of our toads dug into the sand or loose soil, unlike the situation for Canadian toads (*A. hemiophrys*; Breckenridge and Tester 1961; Kuyt 1991) and natterjack toads (*Epidalea calamita*; Denton and Beebee 1993; Bosman et al. 1996). The tubercles on the hind-feet (used for digging) of the western toad are much smaller and softer than those of the Canadian toad (Wayne Roberts, pers. comm.); therefore, western toads are likely less effective at burrowing.

Unlike western toads from Colorado (Jones et al. 1998) and California (Mullally 1952), toads in Alberta did not use ground squirrel tunnels for hibernation, even though ground squirrel tunnels were abundant at our pasture site and were commonly used by toads during the spring and summer (~15% of all locations during radio-tracking). One toad occupied a ground squirrel tunnel 25 m from his breeding pond for the entire foraging season, but moved 446 m to a coniferous forest in early September to hibernate. Most of the ground squirrel tunnels were located in open areas with sandy soil, so perhaps these areas were too cold, dry, or poorly insulated for toad hibernation.

Some of the toads in our study were found hibernating in locations where the water table was close to the surface (e.g., 33 cm). Since some species of toads are known to continue to burrow throughout the winter to stay below the frost line (Tester and Breckenridge 1964a) we cannot be sure that toads did not enter ground water later in the season. We did not measure how deep the frost-line penetrated the substrate at these sites, but peat-lands in northern Alberta can freeze up to 80 cm deep (Kevin Devito, pers. comm.). Western toads have never been observed hibernating in water, but some of the sites where we observed toads appeared likely to freeze down to the water table. Cavities were present in the ground at some of these sites, which would have allowed toads to easily move deeper, if they were able to hibernate in water. In Sweden, Hagstrom (1982) discovered that common toads (*Bufo bufo*; typically a terrestrial hibernator) hibernate on land or in water, with the preferred location being dependent on local conditions. Therefore, toads from northern climates may have different adaptations for hibernation than do populations farther south.

***Communal use of hibernation sites.*—**Toads may hibernate communally because suitable hibernation sites are limited or because there are benefits to aggregation (e.g., predator defense, as a predator may sample only one individual in a group of toads, as this genus is known to be toxic; Licht and Low 1968). We propose that suitable sites for communal toad hibernation are uncommon across the study landscapes, as toads traveled long distances from their breeding ponds to reach hibernacula (range = 146–1936 m). Also, pairs of radio-tracked toads shared hibernation sites on three occasions, suggesting that sites are locally limited and that communal hibernation is not simply a by-product of large population size. Tester and Breckenridge (1964b) also suspected that communally-hibernating Canadian toads were selecting sites based on physical characteristics, independent of the presence of other toads. Although an earlier study of hibernacula in Oregon did not document communal hibernation (Bull 2006), communal hibernacula occurred at all of our study areas.

Temperature loggers in hibernation sites.**—**The temperature loggers that were placed in hibernation and reference sites in the boreal area from 8 October 2005 to 28 May 2006 showed that hibernation sites were not significantly warmer in winter than the paired references sites. Reference sites were in close proximity to the paired hibernation site (range 12-31 m between hibernation site and paired reference site) and appeared similar based on visual examination (e.g., peat mounds of similar size, similar soil types). Therefore, other variables (e.g., soil moisture, water-table level, presence of tunnels, cavity size) may also play a role in the selection of hibernacula. Toads are not freeze-tolerant and have been reported to die at temperatures between –1.5 to –5.2 degrees C (Swanson et al. 1996). The tissue crystallization temperature depends on substrate moisture; toads freeze at higher sub-zero temperatures on wet substrate because inoculative freezing occurs (Swanson et al. 1996). Temperatures at two of our hibernation sites fell well below this range (–8.38 and –9.46 degrees C). These hibernacula were below –5.2 degrees C for over 0.5 d (Table 4-2); therefore, any toads that remained at this location likely did not survive, since Mullally (1952) observed *A. b. halophilus* to freeze overnight at –2 degrees C. We suspect that the toads in these sites dug into the soft organic soil to keep below the frost line; however, we did not attempt to relocate toads, so we cannot rule out mortality. Alternatively, *A. b. boreas* may have greater tolerance to freezing temperatures. We are not aware of any studies that have examined temperature tolerance of western toads in the northern part of their range.

***Distances moved from breeding ponds to hibernation sites.*—**Toads from the boreal area moved significantly farther from breeding ponds to reach hibernation sites compared to toads from the pasture area, which suggests that toad movements are not fixed, but are labile in response to the configuration of the landscape. The majority (16 of 19) of toads at the pasture area hibernated in a woodlot located relatively close to breeding ponds (50-900 m depending on the location within woodlot and breeding ponds). The landscape of the pasture area was dominated by agriculture (67%), which was never used by toads for hibernation and presumably was unsuitable. Bull (2006) also examined distances toads moved between breeding ponds and hibernation sites in Oregon; toads at her sites, which were located in mountainous, coniferous forest, moved much farther than ours (mean = 1968 m, range = 180-6230 m, n = 26). Martin (2008) radio-tracked the closely related Yosemite toad (*A. canorus*) in the Sierra Nevada Mountains of California; the mean distance between breeding ponds and hibernation sites for these toads (mean = 194 m, range = 142-235 m, n = 3) was less than ours (mean = 717 m, range = 13-1936 m, n = 28).

We found no difference in distances moved from breeding ponds to hibernation sites between males and females, similar to Huste et al.'s (2006) results for the natterjack toad. Female western toads have been found to travel farther than males to reach their summer foraging grounds from breeding sites in the western US (Muths 2003; Bartelt et al. 2004; Bull 2006; Goates et al. 2007). Muths (2003) suggested that females travel farther than males to reach foraging grounds because they require more food and energy to produce eggs. We suspect that the reason we found no difference between the sexes in distances moved to reach hibernation sites from breeding ponds was that males and females require similar, specific conditions for overwintering and appropriate sites are uncommon and unrelated to foraging habitat. Consistent with this hypothesis, Johnson et al. (2007) found that overwintering sites of male and female gray treefrog (*Hyla versicolor*) were located similar distances from the breeding pond, but during the foraging season females moved significantly farther from the breeding pond than did males.

Watercourse protective buffers.—Hibernation sites of western toads are very difficult to locate in the field, so hibernaculum protection depends on protecting suitable habitat near water-bodies or known breeding ponds. Small permanent streams (channel width 0.7-5 m), large permanent streams (channel width > 5 m), and lakes are present in our study areas; these watercourses are assigned protective forested buffers of 30, 60, and 100 m, respectively (Alberta Government. 2008. *op. cit.*). All toad hibernation sites at the park area received *de facto* protection because they are located in a National Park; however, they were also located within the range of 100 m watercourse buffers. In contrast, at the boreal and pasture areas, 90% and 84% of toads tracked, respectively, hibernated outside of buffers. Thus, current regulations prescribing watercourse buffers in Alberta do not protect the core terrestrial habitat required for hibernation at our boreal or pasture areas.

A wetland-based approach of protecting a buffer of terrestrial habitat surrounding all breeding ponds is also unrealistic for the western toad because very wide buffers of 449 m and 1337 m (95% upper confidence limits for the distance between breeding pond and hibernation site) would be needed to protect core terrestrial habitat for the pasture and boreal areas, respectively. These distances are larger than the mean maximum distance of 368 m recommended by Semlitsch and Bodie (2003) for core terrestrial habitat of anurans. A different approach to managing habitat is clearly needed for the western toad (e.g., identification of critical habitat patches for protection of a population).

***Resource Selection Functions.*—**Toads were found to hibernate in a variety of natural land-cover types, but did not hibernate in any human-altered land-cover types (e.g., agricultural fields, forestry cut-blocks, residential yards, roadsides). Human-altered land-cover occurred in all of our areas and dominated the pasture area (4.3% of park, 73.2% of pasture, 12.5% of boreal). Natural sites have less bare ground and more vegetative structure (higher densities of vegetative stems in the understory, trees in the canopy, and woody debris), which provides insulation from wind and low temperatures (Dolby and Grubb 1999), and traps blowing snow to provide further insulation (Ross et al. 1968).

Deciduous forest was the only land-cover type, that was used for hibernation by toads, that had selection indices <1 (indicating that it was used but less than proportionately available); deciduous forest was weakly selected at the pasture area, used below proportional availability at the park area, and not used at all at the boreal area. Therefore, deciduous forest appears to be poor habitat for hibernation in these areas. Structures selected as hibernation sites by toads (Table 4-4) were uncommon in deciduous stands (dominated by Trembling Aspen); aspen forest also tends to be less insulated from cold winter temperatures than do spruce stands (Balland et al. 2006). However, toads may select deciduous forest for hibernation in landscapes dominated by land-cover types completely unsuitable for hibernation, such as those found in the pasture area.

Conifer forest was the most strongly selected of the land-cover types used for hibernation at the pasture area. Fifty-three percent of tracked toads in this area hibernated in coniferous forest, dominated by black spruce or white spruce, despite its scarcity on the landscape (0.9%). We suspect that toads selected conifer forests for hibernation because of differences in frost depth and availability of suitable microhabitat (e.g., tunnels). Balland et al. (2006) compared winter frost depth among jack pine, black spruce, and aspen stands in central Saskatchewan. They showed that frost depth was related to the amount of thermal insulation (from plants and peat) on the ground and that frost penetrated deepest in jack pine stands and least in black spruce stands. Peat hummocks, red squirrel tunnels, and cavities under spruce trees (the structures used by 71% of toads at the pasture area) were associated with conifer forests.

Dry shrubland was the other land-cover type that was selected compared to deciduous forest at the pasture area. The selection value for dry shrubland was large, even though only two hibernation sites occurred in it, because this land-cover type was rare (0.8% cover). Similar to the dry shrubland habitat at the pasture area, dry meadow habitat at the park area showed selection because it was rare and one hibernaculum occurred in a meadow (Table 4-3).

Conifer forest, wet shrubland, and a patch of burnt forest (originally black spruce/tamarack stands) were the land-cover types used in the boreal area. The wet shrubland and burn land-covers had higher selection values than conifer forest because they were rare on the landscape, but selection of these land-cover types was not significantly greater than conifer forest because the vast majority of toads (79%) hibernated in black spruce/tamarack stands.

Conclusions.—Our results suggest that hibernation sites for western toads are limited in their availability in two ecoregions within its Canadian range: RSF analyses showed significant selection of certain land-cover types, toads moved long distances to reach hibernation sites, and communal hibernation was common. The destruction or degradation of small patches of terrestrial habitat could translate into large negative impacts on populations even if breeding wetlands remained intact. Our research also highlights the importance of conducting species-specific, region-specific studies to manage habitat for species at risk, since general guidelines (e.g., Semlitsch and Bodie 2003) will not adequately protect all species at all localities. As it is unrealistic to institute prescriptive procedures to create protective buffers surrounding ponds that are large enough to encompass hibernation sites for the western toad, we hope that land managers will use our results to identify habitat that is likely suitable for hibernation. We suggest that patches of spruce-dominated conifer forest, with complex habitat structure that creates subterranean spaces and insulation on the ground, be protected for western toads in north-central Alberta. Other habitat types should be recognized as providing suitable conditions for hibernation if appropriate microhabitat features are present (e.g., crevasse and root systems, beaver and muskrat structures).

Table 4-1. The number of western toads (*Anaxyrus boreas*) radio-tracked to hibernation sites at each area per year and the number of toads tracked the entire season (from breeding pond to hibernation sites).

	Tracked to hibernation		Located breeding and hibernation sites	
Year/Area	Male	Female	Male	Female
2004 park	5	5	1	0
2004 pasture	0	2	0	2
2005 boreal	10	11	8	6
2006 pasture	6	11	6	5

Table 4-2. Temperatures experienced in hibernation sites and paired reference sites during winter of 2005/2006 in our boreal area near Lac La Biche, Alberta. Temperatures were recorded every 3.5 h from 8 October 2005 to 28 May 2006.

Toad ID	Hibernation or Reference	Shelter type	Depth (cm)	Temperature (degrees C)			Consecutive days below x degrees C		
				Min.	Mean	SE	0	-1.5	-5.2
BRO	Hibernation	Red squirrel midden tunnel	45	-2.44	0.05	0.024	176	0.7	0
BRO	Reference	Organic soil under spruce tree	45	-1.06	-0.12	0.022	154	0	0
DAR	Hibernation	Peat hummock with cavities	53	-2.40	-0.24	0.027	149	4.7	0
DAR	Reference	Peat hummock without cavities	53	-3.37	-0.50	0.036	176	22.2	0
MEA	Hibernation	Burnt peat hummock with cavities	47	-8.38	-0.72	0.033	191	10.7	0.6
MEA	Reference	Burnt peat hummock with cavities	47	-1.40	0.21	0.030	163	0	0
MU	Hibernation	Peat hummock with cavities	62	-9.46	-1.20	0.051	175	41.9	3.2
MU	Reference	Peat hummock with cavities	62	-6.31	-0.45	0.046	150	21.7	0.7

Table 4-3. Proportional use of each land-cover type occupied by 43 hibernating western toads (*Anaxyrus boreas*), available land-cover (proportion within 2 km of the breeding site), and selection indices for each study area, A) Park (n = 5), B) Pasture (n = 19), and C) Boreal (n = 19). Larger values for the selection index indicate land-cover types that were selected most strongly relative to availability. Selection index values between 0 and 1 indicate land-cover types that were used but less than proportionately available.

A) Park (n = 5)

Land-cover type	Available	Used	Selection Index	Standardized Selection Index
Dry meadow	0.015	0.2	13.00	0.76
Marsh/wet meadow	0.165	0.6	3.63	0.21
Deciduous forest †	0.440	0.2	0.45	0.03
Mowed lawn	<0.001	0	0	0
Building	<0.001	0	0	0
Paved surface	0.001	0	0	0
Gravel road	0.004	0	0	0
Conifer forest ‡	0.013	0	0	0
Pasture/sparsely vegetated	0.018	0	0	0
Disturbed grassland	0.020	0	0	0
Wet shrubland	0.039	0	0	0
Dry shrubland	0.040	0	0	0
Emergent vegetation	0.052	0	0	0
Mixed-wood forest ℓ	0.092	0	0	0
Water	0.100	0	0	0

B) Pasture (n = 19)

Land-cover type	Available	Used	Selection Index	Standardized Selection Index
Conifer forest ‡	0.009	0.53	58.89	0.76
Dry shrubland	0.008	0.11	13.41	0.17
Mixed-wood forest ℓ	0.037	0.16	4.32	0.06
Deciduous forest †	0.154	0.21	1.36	0.02
Building	0.002	0	0	0
Paved surface	0.004	0	0	0
Dry meadow	0.006	0	0	0
Exposed soil	0.006	0	0	0
Mowed lawn	0.008	0	0	0
Gravel road	0.009	0	0	0
Water	0.009	0	0	0
Emergent vegetation	0.010	0	0	0
Wet shrubland	0.011	0	0	0
Marsh/wet meadow	0.024	0	0	0
Disturbed grassland	0.035	0	0	0
Pasture/sparsely vegetated	0.140	0	0	0
Crop field/ hay field	0.528	0	0	0

C) Boreal (n = 19)

Land-cover type	Available	Used	Selection Index	Standardized Selection Index
Burn	0.015	0.05	3.62	0.42
Wet shrubland	0.048	0.16	3.27	0.38
Conifer forest ‡	0.435	0.79	1.82	0.21
Dry meadow	0.001	0	0	0
Mixed-wood forest	0.002	0	0	0
Railway	0.002	0	0	0
Gravel road	0.005	0	0	0
Clear-cut (grass dominated)	0.006	0	0	0
Water	0.006	0	0	0
Dry shrubland	0.007	0	0	0
Marsh/wet meadow	0.015	0	0	0
Moss/peat wetland	0.033	0	0	0
Cut-block (tree/shrub)	0.051	0	0	0
Disturbed grassland	0.061	0	0	0
Mixed-wood forest ℓ	0.098	0	0	0
Deciduous forest †	0.216	0	0	0

† Deciduous forests were defined as having > 80% deciduous trees.

‡ Coniferous forests have > 80% conifer trees.

ℓ Mixed-wood forest have > 20% of both deciduous and coniferous trees.

Table 4-4. Hibernation sites used by western toads (*Anaxyrus boreas*) in north-central Alberta.

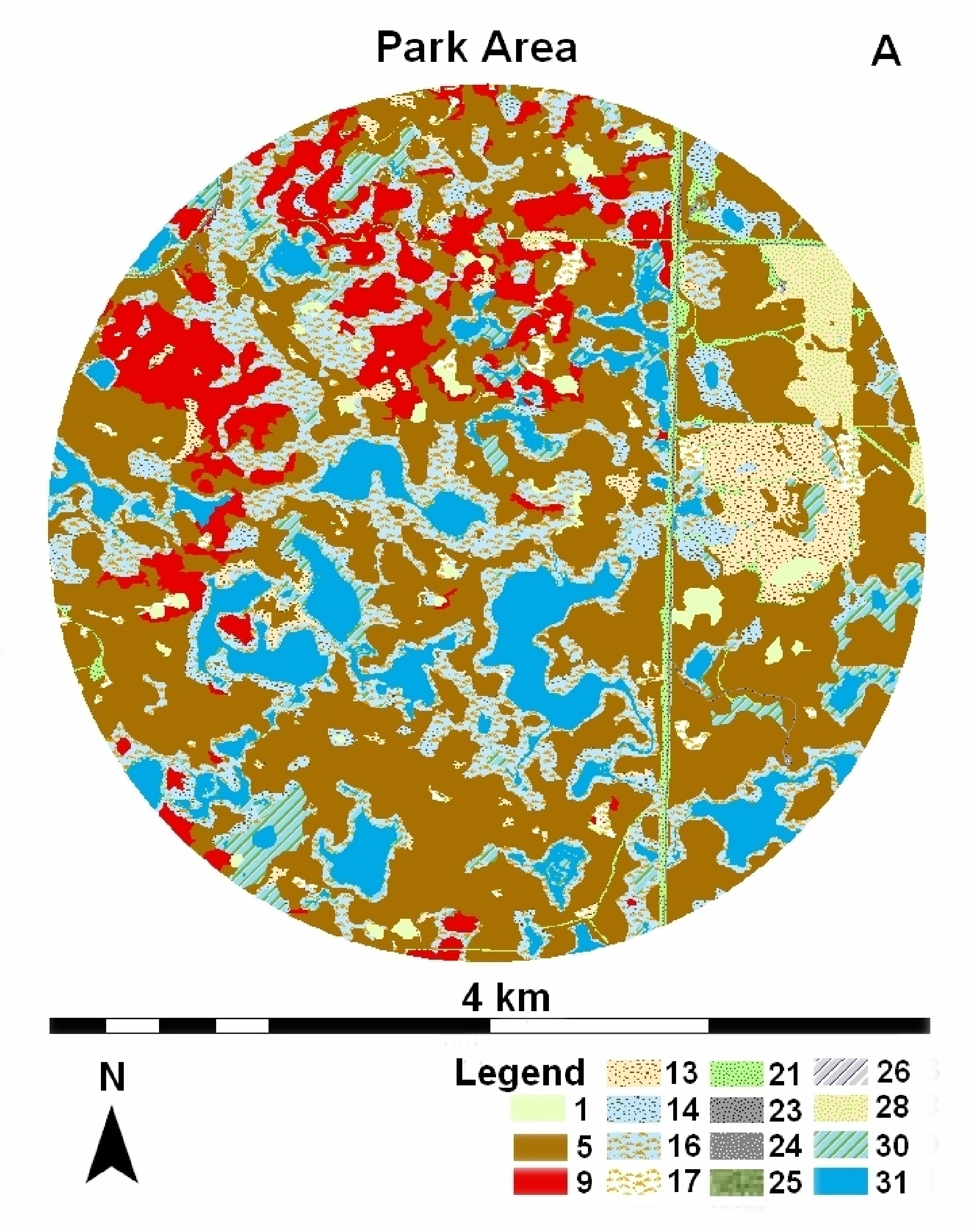
Hibernation structure type	2004 Park	2004 Pasture	2005 Boreal	2006 Pasture
Cavities in peat hummocks	0	0	14	1
Red squirrel middens	0	2	4	3
Natural crevasses	6	0	0	2
Cavities under spruce trees	0	0	0	6
Decayed root channels	0	0	3	2
Abandoned beaver lodges	1	0	0	3
Muskrat tunnels	3	0	0	0

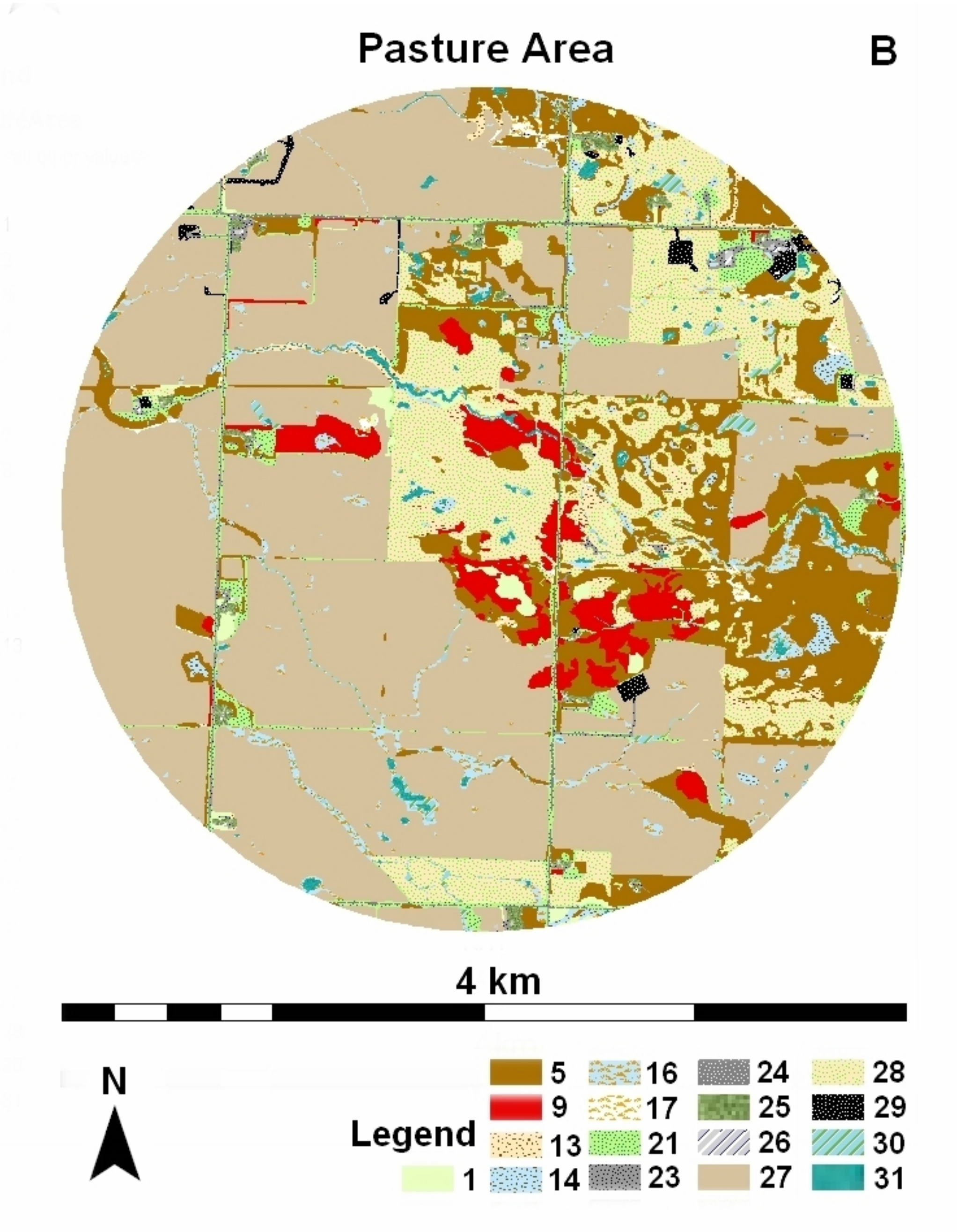
Table 4-5. Results of a general linear model examining the influence of study area and sex on the straight-line distances moved by western toads between breeding ponds and hibernation sites.

Source	df	F	P-value
Model	3	8.625	0.001
Intercept	1	102.715	<0.001
Study area	1	23.974	<0.001
Sex	1	0.460	0.504
Study area * Sex	1	0.209	0.652
Total	27		

Table 4-6. Resource Selection Function models examining whether land-cover types were significantly selected by western toads (*Anaxyrus boreas*) compared to reference land-cover types: deciduous forest in the park (n = 5) and pasture (n = 19) areas, and conifer forest in the boreal area (n = 19). P-values less than 0.05 indicate significant selection (positive coefficient) or avoidance (negative coefficient) in relation to the reference land-cover variable.

Study Area	Variable	Coefficient	SE	Odds ratio	P-value
Park	(Constant)	-8.616	1.000		<0.001
	Dry meadow	3.541	1.416	34.5	0.012
	Marsh	2.071	1.155	7.9	0.073
Pasture	(Constant)	-6.185	0.501		<0.001
	Conifer forest	3.708	0.599	40.8	<0.001
	Dry shrubland	2.233	0.872	9.3	0.010
	Mixed-wood forest	1.156	0.766	3.2	0.131
Boreal	(Constant)	-5.904	0.259		<0.001
	Wet shrubland	0.622	0.634	1.9	0.326
	Burn	0.705	1.036	2.0	0.496


Park Area
A
4 km
N
Legend
13
21
26
1
14
23
28
5
16
24
30
9
17
25
31


Pasture Area
B
4 km
N
Legend
5
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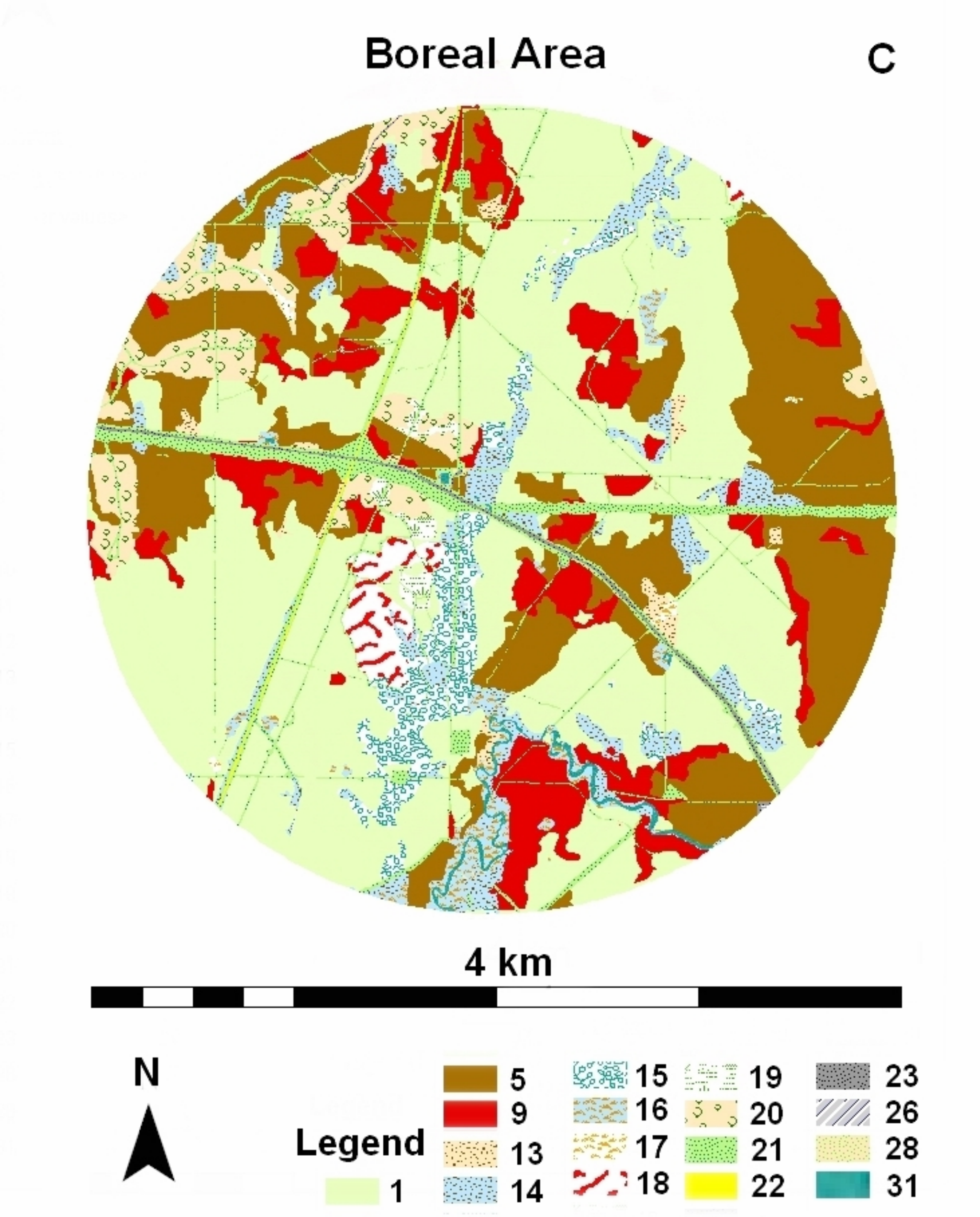
31


Boreal Area
C
4 km
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Legend
1
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23
26
28
31

Figure 4-1. Land-cover maps created in ArcGIS for each of our study areas: (A) Park; (B) Pasture; and (C) Boreal. Land-cover types are: 1 = conifer forest; 5 = deciduous forest; 9 = mixed-wood forest; 13 = dry shrubland; 14 = wet shrubland; 15 = moss; 16 = marsh; 17 = dry meadow; 18 = burn; 19 = clear-cut (grass dominated); 20 = cut-block (tree dominated); 21 = disturbed grassland; 22 = railway; 23 = gravel road; 24 = paved surface; 25 = mowed lawn; 26 = building; 27 = crop field/ hay field; 28 = pasture; 29 = exposed soil; 30 = emergent vegetation; and 31 = water.

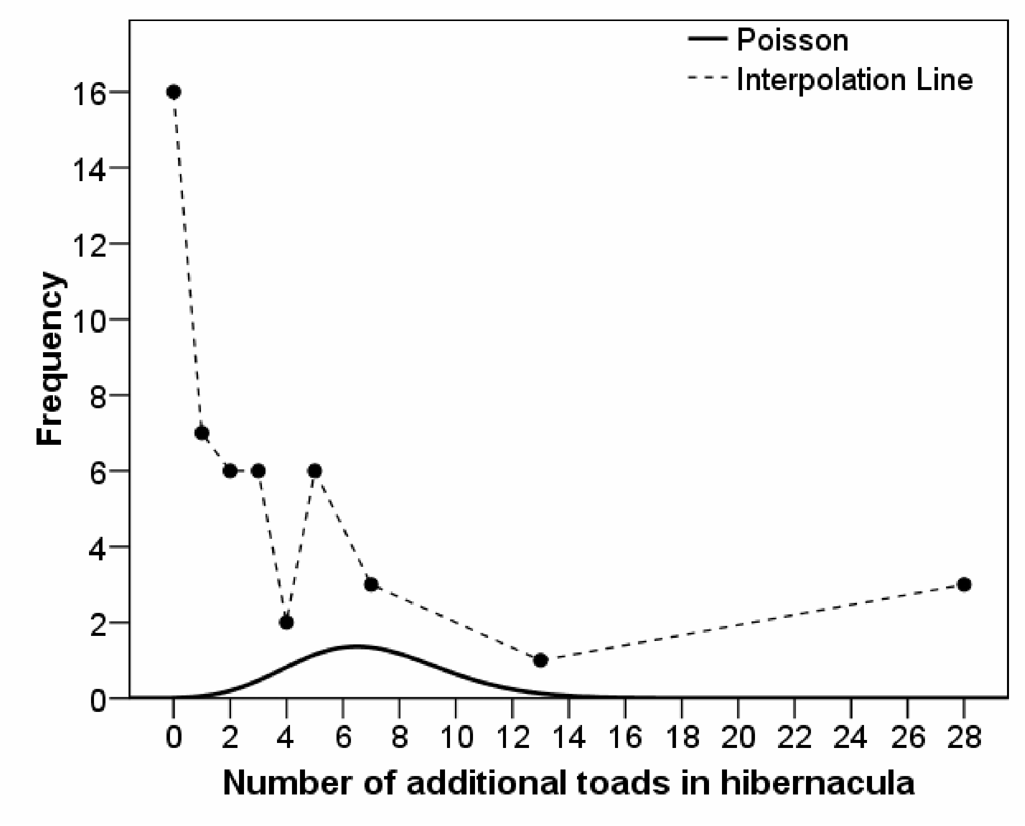

Figure 4-2. The distribution of the number of western toads (*Anaxyrus boreas*) per hibernaculum (in addition to the radio-tracked individual) differs from a Poisson distribution, indicating that toads were not distributed randomly amongst appropriate hibernation sites.

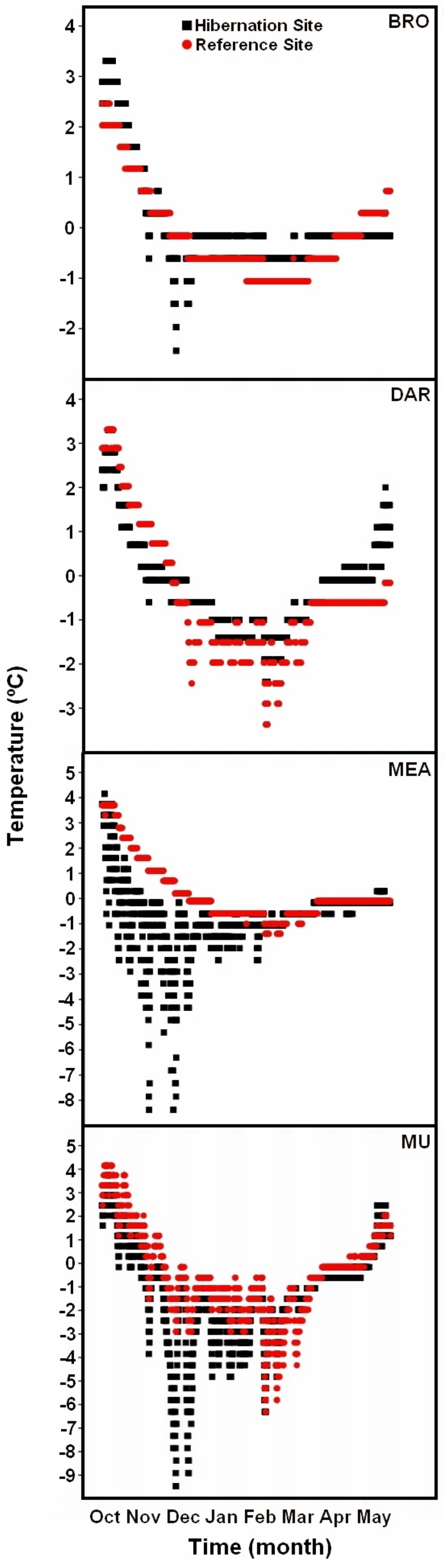

Figure 4-3. Temperatures recorded by data loggers every 3.5 h at four hibernation sites and reference sites in the boreal area from 8 October 2005 until 28 May 2006. Toad ID is listed in the top right of each panel.

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Chapter 5. Factors Affecting the Timing of Movements to Hibernation Sites by Western Toads[3]

5.1 Introduction

In northern localities, toads (family Bufonidae) spend up to 7 months in hibernation. Site selection and factors affecting movements to hibernation sites are likely very important for overwinter survival. Surprisingly, little research has investigated behavior associated with hibernation compared to breeding, and the factors influencing timing of movements to hibernation sites by toads have not been investigated. Changes in temperature are an important cue for reptiles to move into hibernation sites (Nussear et al., 2007; Sexton and Hunt, 1980). Photoperiod is also an important cue for ectotherms, and unlike temperature, which can fluctuate dramatically, photoperiod reliably reflects seasonal changes (Lutterschmidt et al., 2006). Reduced foraging opportunities and precipitation events have also been proposed as cues that may trigger hibernation in reptiles (Gregory, 1982).

The western toad (*Anaxyrus boreas,* formerly *Bufo boreas*) is a wide-ranging North American species, occurring from California to southern Alaska (Hammerson et al., 2004). Mullally (1952) reported that western toads in California were very sensitive to light levels and also temperature; he noted that western toads became active at the same time each evening and if temperatures fell below 3 degrees C, toads took shelter. Campbell (1970) noted that western

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toads in Colorado began to move to their hibernacula in late August and early September and most had entered their hibernacula by October. We suspect that toads generally use temperature and/or photoperiod as cues for the initiation of movement to hibernation sites.

Kelleher and Tester (1969) found that Canadian toads (*A. hemiophrys*) in Minnesota hibernated communally and displayed fidelity to hibernation sites. Adults may have greater site fidelity or homing ability than do juveniles, as 97.1% of adult toads returned to their specific hibernation site compared to only 89.8% of juveniles (Kelleher and Tester, 1969). Breckenridge and Tester (1961) studied Canadian toads at this same area and reported that large adults tended to hibernate earlier, and adult toads entered hibernacula earlier than young of the year; however, they did not investigate what influenced these differences in hibernation timing. One of us (C.L.B.) suspected that larger western toads moved to their hibernation sites later than smaller toads and moved to these sites more directly, along straighter paths (based on observations from radio-telemetry). We hypothesized that older (larger) toads are familiar with their landscape and locations of suitable hibernacula and may maximize their fitness by remaining at good foraging grounds as late in the year as possible.

Our objectives were to 1) determine if arrival date to the hibernation vicinity or entry date to the hibernation site differ among study areas, years, sex, or with toad size, 2) examine evidence supporting our hypothesis that larger (likely older) toads are familiar with their landscape and remain at their foraging grounds later in the year than do smaller (likely younger) toads, and 3) determine if the timing of the arrival of toads at and entry into hibernation sites is more strongly correlated with temperature or date. Our study is unique because it is the first detailed investigation to examine these questions for any amphibian.

5.2 Methods

Study Area

Our research took place at three study areas in the north-central region of Alberta, Canada. The “park” area was located in Elk Island National Park (53.675 N, -112.792 W) in an isolated patch of dry mixed-wood boreal forest in the Aspen Parkland natural region (Alberta Government, 2005). This area was relatively pristine and mostly comprised of upland forest surrounding shallow lakes and marsh habitat. Western toads bred in these lakes. Forests consisted primarily of aspen (*Populus tremuloides*), balsam poplar (*Populus balsamifera*), and white spruce (*Picea glauca*), with a hazelnut understory (*Corylus cornuta*).

The “pasture” area was located adjacent to Elk Island National Park (53.704 N, -112.931 W) and consisted of dry mixed-wood boreal forest that had been converted to agriculture. This area supported cattle grazing, cultivation of crops and hay (e.g., wheat, barley, oats, canola, timothy, alfalfa), and rural housing. It also contained relatively undisturbed woodlots and peatland. Western toads bred in naturalized man-made ponds that were originally created during sand extraction; the surrounding land was used for cattle grazing. Common tree species were trembling aspen, balsam poplar, white spruce, black spruce (*Picea* *mariana*), paper birch (*Betula papyrifera*), tamarack (*Larix laricina*), and jack pine (*Pinus banksiana*).

The “boreal” area was located north of Lac La Biche (55.052 N, -111.704 W) in the central mixed-wood subregion of the Boreal Forest natural region (Alberta Government, 2005). This region was moderately altered by the forestry and oil/gas industries, and mostly comprised of shrub swamps, peatland, upland boreal mixed-wood forest, and forestry cut blocks. Western toads bred in a small shallow pond that formed next to a gravel road and in a major utility corridor. A small permanent stream fed this pond. Common tree/shrub species were trembling aspen, balsam poplar, white spruce, black spruce, paper birch, tamarack, jack pine, willow (*Salix spp.*), and dwarf birch (*B. nana*).

Radio-telemetry

We captured toads during the active season (May to October) in 2004, 2005, and 2006 either while they were breeding at ponds or opportunistically while tracking other individuals. We measured and recorded the snout-urostyle length (SUL to nearest mm), weight (to nearest g), and sex of each toad at the time of capture. Toads captured between May and August were toe-clipped for future identification of recaptured toads that had lost their transmitters.

We radio-tracked adult toads for 1 wk to 5 months prior to hibernation to enable location of their hibernation sites. We followed the methods described by Bartelt and Peterson (2000) for attaching radio-transmitters. Holohil BD-2, BD-2T, and PD-2 transmitters (Holohil Systems Ltd., Carp, Ontario, Canada), weighing 1.0-2.3 g (minimum battery life 28 d to 3 months), were attached using a waist belt made of soft surgical grade polyethylene tubing (outside diameter = 0.965 mm; VWR International, CA-63018-667) and a large size flyline eyelet (size 9; the Fishin' Hole, Edmonton, Alberta, Canada). All transmitters/belts were less than 10% of body weight, and most were less than 5%. We located toads 2-4 times/wk.

Over 3 years, we radio-tracked a total of 116 western toads and were able to follow 49 to hibernation sites (Table 5-1). Toads moved up to 2239 m (straight-line distance) from their initial capture point. We suspected a toad was in its hibernation site if it remained underground in the same site for over 1 week (in September or October), or if it was found underground with other toads (communal hibernacula). Toads were often active in their hibernation sites and would move up to 7 m through tunnels underground if we disturbed the ground by digging. However, it was rare (only four toads) to observe a toad above ground again after it had entered its eventual hibernation site. We continued to track individuals until we were confident that all toads were in their hibernation sites. We concluded that all individuals were in their hibernation sites by 14 October in 2004; a heavy snow fell on 15 October 2004 that lasted through the winter. In 2005, all toads were in hibernation sites by 3 October and the ground was beginning to freeze by this time. In 2006, all toads were in hibernation sites by 10 October.

Timing of Hibernation

We examined the date of arrival at the hibernation vicinity and date of entry into the hibernation site in relation to study area, year, sex, and size of toads. We considered the date of arrival to be when a toad was located within 25 m of its eventual hibernation site and remained within 25 m. Entry date was when a toad entered its eventual hibernation site and remained below ground. Because exact arrival/entry dates would have fallen between when we first observed a toad in the vicinity/below ground and the previous tracking encounter, we estimated all arrival/entry dates as the mid-point between the date when the toad was found in the vicinity of, or within, its hibernaculum and the date of the previous sighting.

We tested all data for normality using Kolmogorov-Smirnov one-sample tests for normality. We then used general linear models (GLM) to test whether dependent variables (date of arrival, date of entry, distance between mid-September location and hibernation site, and straightness of movements) differed among study areas and years, if so, we ran analyses separately by area or year, respectively, for that dependent variable.

We used GLMs to determine if there were any differences in arrival or entry dates for toads of different sex or SUL. Sample size was slightly smaller for the arrival data than entry data (Table 5-1) because some of the toads were caught < 25 m from their hibernation site so arrival date was not known. SUL was not recorded for one male toad from the park area, so this individual was dropped from analyses involving SUL.

To determine if larger toads made longer, straighter movements late in the season in traveling from foraging grounds to hibernation sites, we compared SUL to the straight-line distance between a toad's location in mid-September (September 15, or the closest date to September 15) and its hibernation site (assuming that large distances were associated with toads that remained at foraging grounds and small distances were associated with toads already moving towards hibernacula). Mid-September was chosen because this date captured a range of behaviors; 32% of toads had arrived in the vicinity of their hibernacula, but many were moving or still at foraging grounds. We also compared SUL to the straightness of movements to hibernation sites in mid-September (assuming that straighter paths indicate directed movements to known locations). We quantified straightness of movements using a straightness index (Straightness = D/L; D = beeline distance, L = sum of move lengths), where a value of 1 indicates a completely straight line and values close to 0 have many turns (Benhamou, 2004). In both cases we examined relationships with GLMs.

We obtained data on temperature from Environment Canada from the Elk Island National Park (2004 and 2006) and Lac La Biche (2005) weather stations (Environment Canada, 2002*a*). Mean minimum temperature was calculated for each week using daily minimum temperature values. We used a generalized linear model to examine the relationship between cumulative number of toads having arrived at/entered into hibernation sites and week of the year (a surrogate for day length) and mean minimum temperature for each week. We used the Akaike information criterion (AIC) to determine whether the cumulative number of toads arrived/entered was best predicted by date or minimum temperature. Correlations between week of the year and temperature were examined using Pearson correlations.

All statistical analyses were computed using SPSS version 16 (SPSS Inc., 1989-2007).

5.3 Results

The dependent variables (date of arrival, date of entry, distance between mid-September location and hibernation site, and straightness of movements) did not differ significantly from a normal distribution (Kolmogorov-Smirnov: Z = 1.037, n = 41, P = 0.233; Z = 0.751, n = 49, P = 0.625; Z = 1.210, n = 41, P = 0.107; Z = 1.163, n = 41, P = 0.134, respectively).

Mean date of arrival at the hibernation site did not differ significantly among study areas or years ($F_{3,41}$ = 1.902, P = 0.146; Table 5-2). However, the timing of entry was significantly different among study area-years ($F_{3,49}$ = 9.050, P < 0.001; Table 5-2). Toads entered hibernation sites significantly earlier at the boreal area in 2005 than at the park and pasture areas in 2004, and pasture area in 2006 (Tukey post hoc test: P < 0.05). We found no difference among area-years for distance between mid-September location and hibernation site ($F_{3,41}$ = 1.752, P = 0.173) and straightness of movements ($F_{3,41}$ = 1.811, P = 0.162).

Males arrived in the vicinity of their hibernacula earlier than females (mean Julian day = 256 +/- 3.12 SE, range = 239-276, n = 16 vs. mean Julian day = 267 +/- 2.48 SE, range = 240-283, n = 25). However, toads are sexually dimorphic with respect to body size (females larger than males) and a GLM indicated that arrival date was significantly related to SUL and not sex when both were considered simultaneously ($F_{2,41}$ = 11.7, $P < 0.001$, SUL: $P = 0.001$, Sex: $P = 0.138$; Figure 5-1). Sex and SUL did not influence entry dates in 2004 ($F_{2,11}$ = 1.346, $P = 0.313$), 2005 ($F_{2,20}$ = 0.681, $P = 0.519$), or 2006 ($F_{2,17}$ = 0.136, $P = 0.874$).

For all areas combined, large toads were located significantly farther from their hibernation sites in mid-September ($F_{1,41}$ = 7.206, $P = 0.011$; Figure 5-2) and moved along straighter paths to reach their hibernation sites ($F_{1,41}$ = 10.414, $P = 0.003$; Figure 5-3).

Minimum and maximum temperatures were compared with arrival and entry dates for each year (Figure 5-4). Average temperatures in September were lowest in 2004 and highest in 2006 (Table 5-3). In 2004, week of the year was a better predictor than temperature for both arrival and entry date at the two Aspen Parkland areas (Table 5-4). Temperature and week of the year were correlated in 2004 at the Aspen Parkland areas ($r = -0.771$), but less so than in other years. In 2005 at the boreal area, temperature was slightly better than week of the year at predicting arrival date (Table 5-4), but the two variables were highly correlated ($r = -0.991$). The best model for entry date at the boreal area in 2005 was the model that included both temperature and week of the year (Table 5-4). In 2006 at the pasture area, temperature and week of the year were highly correlated with each other ($r = -0.966$) and both produced significant models for arrival and entry dates with similar AIC scores (Table 5-4).

5.4 Discussion

Toads arrived in their hibernation vicinity gradually from 27 August to 10 October and arrival dates did not differ among areas or years. This date range was very similar to that reported by Campbell (1970) for western toads in Colorado; Campbell reported that toads began moving to their hibernation sites in the last week of August and first two weeks of September, and by October most had entered hibernacula. In Oregon, western toads arrived at overwintering sites between 16 September and 10 November in 2002-2005 (Bull, 2006).

Entry into hibernation sites was significantly earlier in 2005 at the boreal area (beginning 31 August) than in the Aspen Parkland areas in either 2004 or 2006 (beginning 26 and 15 September, respectively). Earlier hibernation at the boreal area was expected because this location is farther north than the other two areas and tends to be colder in September (Environment Canada, 2002*b*). Average temperatures in September were actually lower in 2004 at the Aspen Parkland areas than 2005 in the boreal, but a warm period (temperatures above 20 degrees C) occurred during the last week of September 2004, which likely delayed hibernation. Although temperature appears to be the main factor controlling the timing of entry into hibernation sites, we cannot rule out a role for photoperiod in triggering hibernation.

If photoperiod plays a large role in timing of movements to hibernacula, this could potentially be a future conservation concern if global climate change continues; if fall temperatures change significantly, then toads may arrive at their hibernation sites too early (missing out on foraging opportunities) or too late (risk of freezing). Extra foraging time may be especially important in mild years, since energy reserves are depleted more rapidly during milder winters, which can cause higher rates of overwinter mortality (Reading, 2007). We attempted to determine whether arrival and entry dates at hibernacula were more tightly related to temperature or week of the year; however, these two variables were highly correlated and we could not determine which was the “master factor”.

Male toads arrived at their hibernation vicinity earlier than female toads; however, when SUL was taken into consideration it became clear that this pattern was an artifact of females being larger on average than males. Smaller toads arrived in their hibernation vicinity earlier than large toads, regardless of sex. This pattern is the reverse of that observed by Breckenridge and Tester (1961) for Canadian toads in Minnesota; they reported that large adults tend to hibernate earlier, and adult toads enter hibernacula earlier than young of the year. Breckenridge and Tester (1961) do not offer an explanation for their observation. However, as noted earlier, Kelleher and Tester (1969) reported that adult Canadian toads from this same area accurately homed to their hibernation sites more frequently than juveniles, so perhaps it takes longer for young toads to select a hibernation site than more experienced individuals. Alternatively, additional foraging time may be more critical for small toads since their reserves are smaller, which could also result in smaller toads entering hibernacula later than large toads.

Western toads at our Aspen Parkland areas have been found to live up to 8 years, and large toads tend to be older (Garrett, 2005). We suspect that at our study areas, larger western toads are older individuals that are familiar with their landscape and locations of suitable hibernacula and that these individuals choose to move to their hibernation vicinity later in the season so they can maximize their fitness by remaining at good foraging grounds as late in the year as possible. It is not known when in the year western toads stop feeding to prepare for winter; however, Lillywhite et al. (1973) found that young California toads (*A. b. halophilus*) were still feeding in early September because stomach contents of 50 individuals contained partially digested invertebrate material. California toads in lab experiments stop feeding when held at low temperatures (14 degrees C) for prolonged periods (Lillywhite et al., 1973). Preest and Pough (1989) reported body temperatures between 16.4-29 degrees C for active American toads (*A. americanus*) in New York State. Maximum daily temperatures were often above 16 degrees C in September at our study area (Figure 5-4), so toads were likely still able to forage, at least during the warmer periods of the month. We found that larger toads were significantly farther from their hibernation sites in mid-September and larger toads moved along straighter paths to their hibernation sites, which supports our initial predictions based on qualitative observations. In addition to knowledge of their landscape, larger toads may be able to remain at foraging grounds later in the season because their larger bodies lose heat more slowly and protect them if they are caught away from their hibernacula during a cold snap.

Conclusions

Efficient timing of movements to hibernation sites may be critical for toads to maximize time spent on good foraging grounds but also ensure arrival at hibernation locations before temperatures become too cold for movement. Arrival date in the hibernation vicinity was similar among study areas, separated by up to 170 km, but smaller toads arrived earlier. Entry date into hibernation sites was similar for toads of all sizes, but was significantly earlier at our most northern area and was significantly related to temperature and/or the highly correlated variable: week of the year. Our data show that larger (likely older) toads move to hibernation sites later in the year and move along straighter paths to reach these sites, suggesting that these individuals know their landscape.

Table 5-1. The number of toads radio-tracked to determine date of arrival at the hibernation vicinity, hibernation entry date, and the number of individuals tracked from mid-September to hibernation.

Year/study area	Male arrival	Female arrival	Male entry	Female entry	Male mid-Sept	Female mid-Sept
2004 pasture	0	2	0	2	0	2
2004 park	2	2	5	5	2	2
2005 boreal	8	10	9	11	9	9
2006 pasture	6	11	6	11	6	11

Table 5-2. Julian dates of the arrival of toads at and their entry into hibernation sites.

	Arrival				Entry			
	n	Mean	SE	Range	n	Mean	SE	Range
Pasture 2004	2	280	3.00	277-283	2	284	6.50	277-290
Park 2004	4	254	8.68	244-280	10	278	2.54	260-289
Boreal 2005	18	261	2.35	239-276	20	265	1.83	243-276
Pasture 2006	17	264	3.62	241-283	17	274	1.57	258-283

Table 5-3. Average mean, minimum, and maximum daily temperatures for September at Aspen Parkland areas in 2004 and 2006 and boreal area in 2005.

Year	Temperature (degrees C)		
	Mean (SE)	Minimum (SE)	Maximum (SE)
2004	9.0 (0.68)	3.0 (0.60)	14.9 (0.94)
2005	9.5 (0.51)	3.8 (0.55)	15.3 (0.71)
2006	11.7 (0.93)	5.0 (0.54)	18.2 (1.49)

Table 5-4. Results of Generalized Linear Models examining the influence of mean minimum temperature and week of the year on the cumulative number of toads A) arriving at hibernation sites, and B) entering hibernation sites.

A) Arrival

Year	Independent variables	AIC	Wald chi-square	P-value
2004	Temperature	27.622	2.336	0.126
	Week	19.593	22.400	<0.001
	Temperature and	19.025	3.102	0.078
	Week		24.812	<0.001
2005	Temperature	29.585	80.928	<0.001
	Week	31.656	55.560	<0.001
	Temperature and	31.366	2.789	0.095
	Week		0.224	0.636
2006	Temperature	33.687	46.460	<0.001
	Week	33.778	45.771	<0.001
	Temperature and	34.875	0.964	0.326
	Week		0.862	0.353

B) Entry

Year	Independent variables	AIC	Wald chi-square	P-value
2004	Temperature	43.544	4.430	0.035
	Week	32.682	46.950	<0.001
	Temperature and	33.329	1.492	0.222
	Week		33.084	<0.001
2005	Temperature	29.991	75.713	<0.001
	Week	34.042	35.601	<0.001
	Temperature and	25.226	30.392	<0.001
	Week		12.528	<0.001
2006	Temperature	40.040	28.298	<0.001
	Week	41.036	23.617	<0.001
	Temperature and	41.942	1.185	0.276
	Week		0.099	0.752

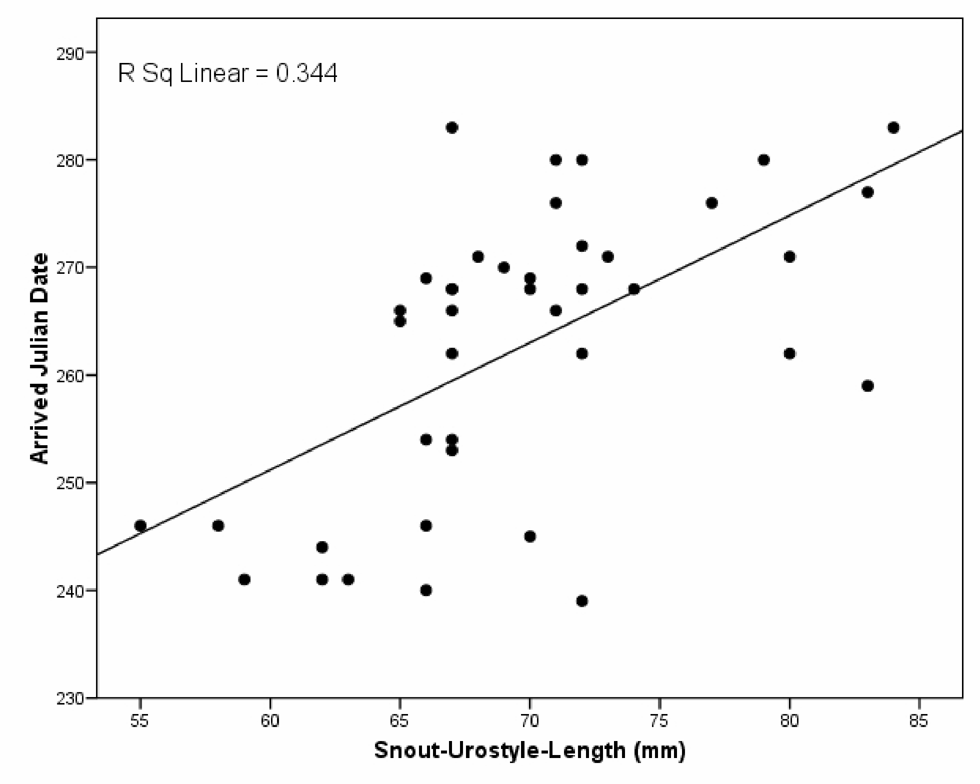

Figure 5-1. Large western toads arrived at the vicinity of hibernation sites significantly later than small toads. A linear regression trendline was fitted through the data using SPSS (SPSS Inc. 1989-2007).

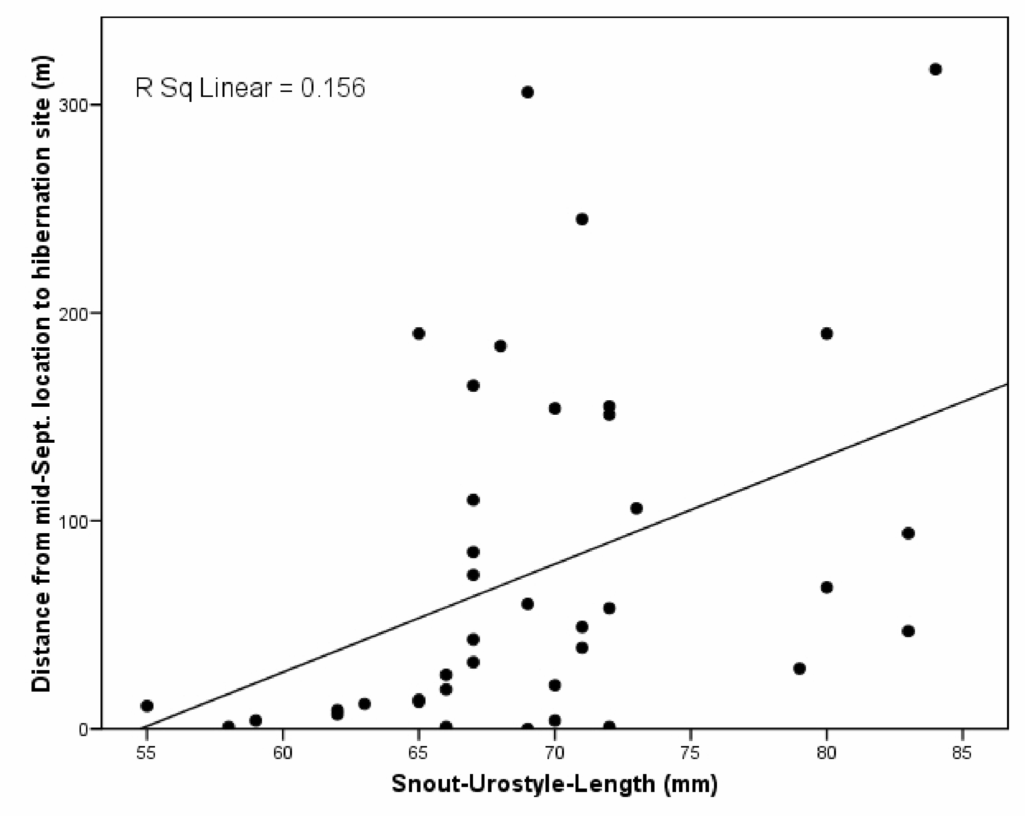

Figure 5-2. Large toads were farther from hibernation sites in mid-September than were small toads. A linear regression trendline was fitted through the data using SPSS (SPSS Inc. 1989-2007).

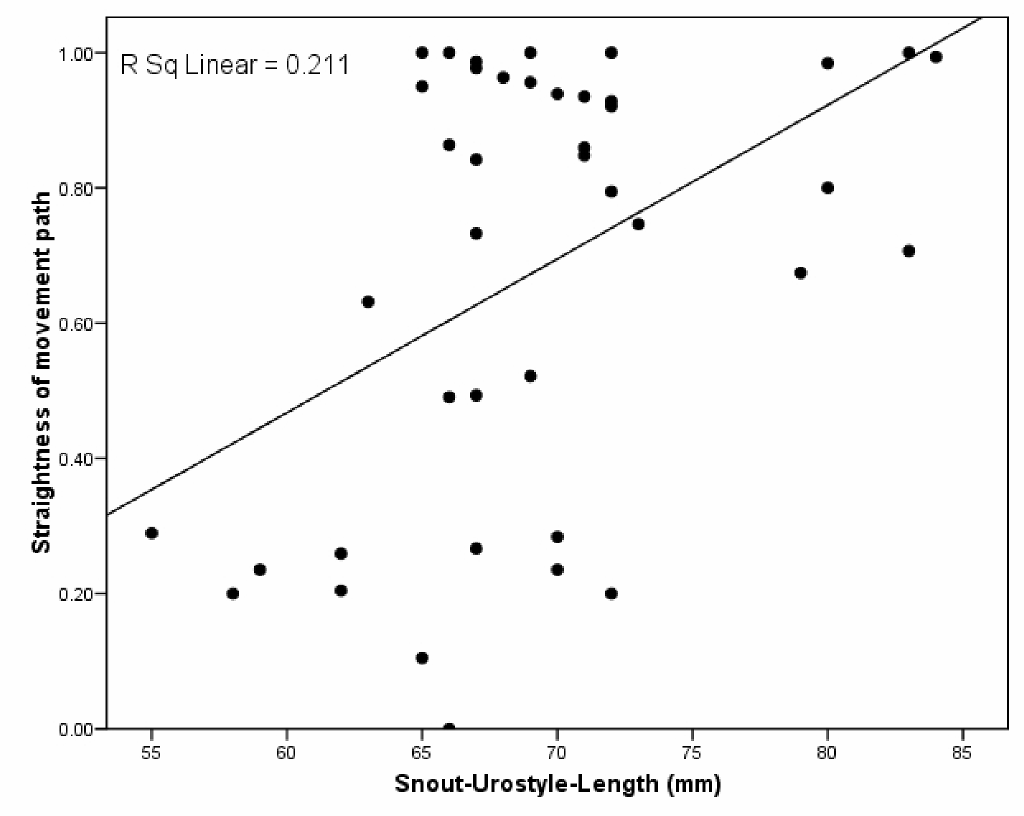

Figure 5-3. Large toads moving to hibernation sites from their locations in mid-September followed straighter paths than did small toads. A linear regression trendline was fitted through the data using SPSS (SPSS Inc. 1989-2007).

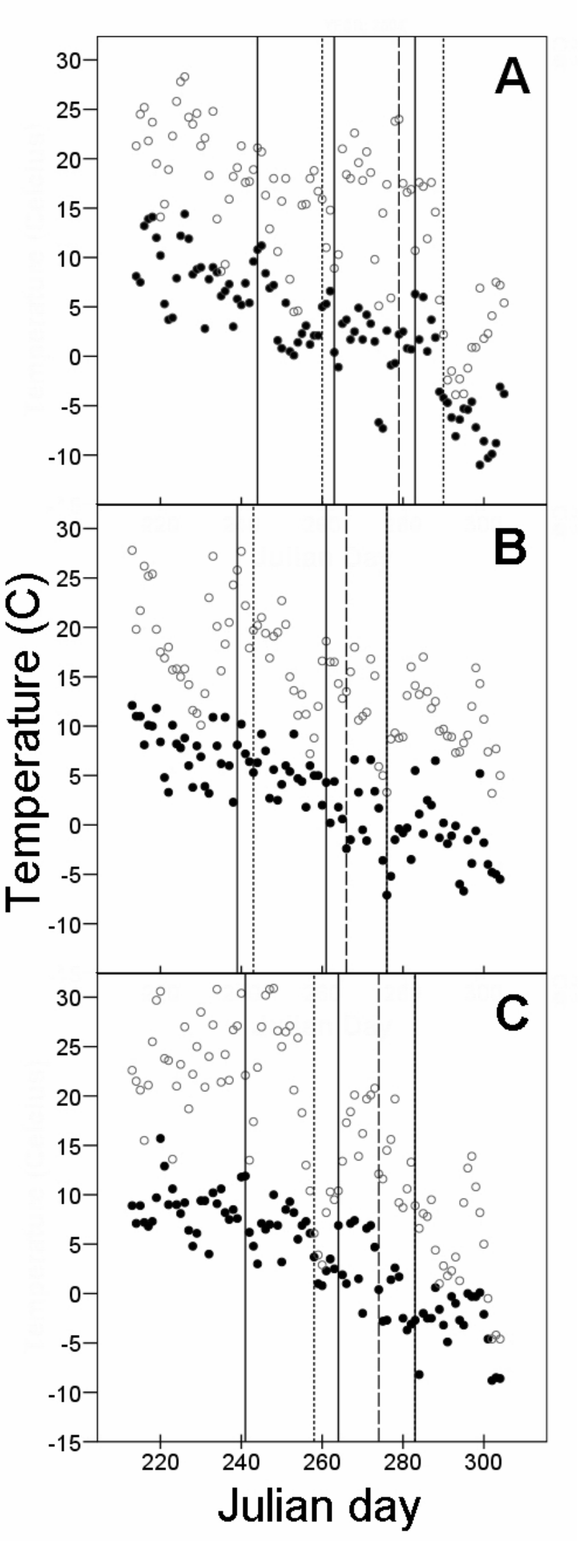

Figure 5-4. Minimum and maximum daily temperatures (degrees C) from August to October. Solid circles indicate minimum daily temperatures and hollow circles are maximum daily temperatures. Solid vertical lines indicate earliest, mean, and latest arrival dates. Dashed lines indicate earliest, mean, and latest entry dates (note: latest arrival and entry dates overlap in 2005 and 2006). Toads were tracked until day 297 in park and pasture areas in 2004 (A), 276 in boreal area in 2005 (B), and 285 in pasture area in 2006 (C).

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Chapter 6. General Conclusions

Habitat alteration has been identified as a major factor responsible for the global declines of amphibian populations (Stuart et al., 2004). Amphibians may be more susceptible to habitat alteration than other vertebrates because they require both aquatic and terrestrial habitat to complete their life cycle (Trenham & Shaffer, 2005). The western toad (*Anaxyrus boreas*) is one of many amphibian species at risk of extinction (status = Special Concern in Canada; COSEWIC, 2009). Habitat use by western toads had not previously been investigated in Alberta, Canada. Determining the habitat requirements of a species is fundamental to effective conservation (Luck, 2002).

My doctoral research focused on the general question: What habitat types are selected by western toads in north-central Alberta? To gain a better understanding of underlying habitat selection by western toads, I examined this question across several different spatial and temporal scales, employing different analytical techniques, and looked for mechanisms that could explain the patterns that I observed. My observations of the influence of spatial and temporal scales, and different analytical techniques are likely applicable to many amphibian species.

In Chapter 2, I investigated the relationship between anuran relative abundance at wetlands and environmental variables measured both at wetland sites and in the surrounding landscape. In Chapters 3 and 4, I reported results from radio-tracking toads and used Resource Selection Functions (RSF) to determine habitat types selected by animals during the active period and for hibernation, respectively. Although I examined land-cover types associated with western toad use in all three of these chapters, I did not necessarily expect to find the same result among chapters. Relative abundance data (Chapter 2) likely reflects the health of a population and the overall habitat quality of the landscape for the population. However, correlations between relative abundance and landscape patterns do not necessarily mean that individuals use the land-cover types that are highly correlated with abundance. Radio-tracking reveals which land-cover types are actually used by individuals. RSF models can be created using radio-telemetry data and random points collected from a defined area of available habitat to determine which habitat types are selected. I assume that habitat types selected are high-quality habitat (promoting survival and growth) because preferences for environments should parallel their quality (i.e., organisms should respond positively to environments in which their fitness is good; Orians & Wittenberger, 1991). For example, toads selected for warm, open habitat types that would facilitate growth during the active season and selected for spruce stands for hibernation, which likely provide good thermal insulation that would facilitate survival through the winter. However, my analyses do not measure fitness associated with each habitat type, so I cannot distinguish high-quality habitat from habitat types that are attractive sinks (habitat types preferred by individuals that result in low survival or reproductive success; Delibes, Gaona & Ferraras, 2001). However, by comparing the results among my analyses I was able to compare patterns and determine what features western toads consistently select. For example, western toads were positively associated with deciduous forest during the active season in the central mixed-wood subregion of the Boreal Forest. Relative abundance of western toads was positively associated with deciduous forest cover at the Utikuma study area (Chapter 2) and RSF models showed that female toads selected deciduous forest during the breeding and foraging period at my boreal study area north of Lac La Biche (Chapter 3). Wet shrub habitat was selected by radio-tracked toads in 25 of 34 RSF models during the active season (Chapter 3) and was also used by hibernating toads at the boreal area (Chapter 4). At my pasture study area in the Aspen Parkland, toads selected for crop/hay fields but avoided pasture for all three temporal periods during the active season (Chapter 3). My thesis research advances our current knowledge of the habitat use patterns of western toads.

The Influence of Scale

Research investigating relationships between habitat features and the abundance and distribution of species has been a major focus in ecology (Orians & Wittenberger, 1991; Rosenzweig, 1991; Luck, 2002). Habitat selection research is extremely complicated because perceived selection often changes with scales of spatial extent (Turner, 1989; Wiens, 1989), grain or resolution of the analysis (Hobbs, 2003; Lawler et al., 2004), habitat composition (Johnson, 1980; Mysterud & Ims, 1998), season (Schooley, 1994; Arthur et al., 1996), sex (Muths, 2003; Bartelt, Peterson & Klaver, 2004), or age class (Stamps, 1983; Imansyah et al., 2008). The possible scales across which ecological systems may be investigated form a continuum (Morris, 1987; Wiens, Rotenberry & Van Horn, 1987). Because changes in scale can influence the patterns retrieved, conclusions about habitat selection may only be valid at the scale at which they are examined (Mayor et al., 2009). Interpreting differences in an organism's habitat selection among studies is complex because many components (e.g., spatial scale, duration, methodology, sample sizes, or analytical procedures) can influence the results (Wiens, Rotenberry & Van Horn, 1987). I examined the influence of spatial scale in Chapters 2 and 3.

In Chapter 2, I examined the relationship between the relative abundance of the western toad (and two sympatric anuran species) and environmental variables at 24 wetlands north of Utikuma Lake, AB using 23 pond variables and 15 landscape variables at seven scales of spatial extent (50, 100, 200, 500, 1000, 2000, and 5000 m). For the most part, the wood frog (*Lithobates sylvaticus*) and boreal chorus frog (*Pseudacris maculata*) responded most strongly to a particular scale of spatial extent and then each subsequent scale larger or smaller than the focal scale showed a weaker relationship. Western toad, on the other hand, showed strong relationships to variables measured at both very small (50 and 100 m) and very large (5000 m) spatial extents. This bimodal pattern observed with western toads may reflect the fact that western toads move between patches of essential habitat for breeding, foraging, and hibernation in their annual cycle, rather than using terrestrial habitat surrounding the breeding pond equitably. Rittenhouse and Semlitsch (2007) examined the distribution of amphibians during the non-breeding season using kernel density estimation and found that kernel estimates for western toad did not peak near the breeding site; a pattern that also suggests that western toads travel to specific resources that are not evenly distributed on the landscape and not necessarily located near the breeding site.

I found that the abundance of each species was best described by different scales of spatial extent (Chapter 2). The wood frog responded most strongly overall to local pond variables, but at the landscape level, responded most strongly to variables measured at the 500 m scale. The boreal chorus frog responded strongest to landscape variables measured at the 1000 m scale, and western toads at the 100 m scale. Wood frogs tend to use terrestrial habitat within 500 m of their breeding site (e.g., Rittenhouse & Semlitsch, 2007 reported maximum movements of 394 m). Only one published study has examined boreal chorus frog movements; Spencer (1964) found that boreal chorus frogs moved up to 750 m from breeding ponds. My results suggest that the spatial scales identified by models of anuran abundance that are most explanatory may be related to the extent of habitat surrounding breeding ponds used during the annual cycle of a particular species.

In Chapter 3, I compared differences in habitat selection among three study designs that varied in spatial extent and resolution, three study areas, three temporal periods within the active period for toads, and between males and females by creating separate RSF models for each category. Differences in selection were observed among study designs, study areas, time periods, and sexes, indicating that habitat selection for western toads is dependent on the spatial and temporal scale, composition of vegetation and other landscape features, and also differs between males and females. Previous research has suggested that patterns of habitat selection are more likely to change among spatial scales in heterogeneous landscapes (e.g., montane landscapes) where organisms perceive differences among patches compared to homogeneous landscapes (e.g., tundra landscape) (Kotliar & Wiens, 1990; Boyce, 2006). I would consider my landscapes to be heterogeneous in nature, since more than one land-cover type on the fine-grained map would often occur within one pixel of the coarse-grained map (e.g., patches of both wet shrub and moss habitat on the fine-grained map were often contained within pixels of moss habitat on the coarse-grained map), which may explain why I observed different patterns of habitat selection among spatial scales.

I used five-fold cross-validation to determine the predictive performance of each RSF model in Chapter 3. Although patterns of habitat selection differed, the predictive ability of the model did not differ significantly among study designs (fine-grained population range, FGPR; fine-grained buffered-home-range, FGHR; and coarse-grained buffered-home-range, CGHR) or temporal periods (breeding, foraging, and pre-hibernation) indicating that each of these spatial and temporal scales provided information on habitat selection by western toads at the scale examined. Predictive ability differed among study areas and sexes. Models for habitat in Elk Island National Park had poor predictive ability compared to those for the pasture area in the Aspen Parkland and the boreal study area. The park models had low sample sizes, so the difference likely reflects a weakness in my study rather than regional differences. The difference in the predictive ability of the model between females and males cannot be explained as easily; sample sizes were similar between females and males. Females may have shown stronger, more consistent patterns of habitat selection because female toads often travel farther to reach specific foraging grounds (Muths, 2003; Bartelt, Peterson & Klaver, 2004; Bull, 2006, Goates, Hatch & Eggett, 2007, and C. Browne, unpubl. data), they move to foraging grounds sooner than male toads (C. Browne, unpubl. data), and stay at foraging grounds later in the year (Chapter 5).

Although predictive ability did not differ significantly among study designs, the FGHR had the greatest predictive ability and the CGHR had the least. This suggests that toads recognize several different habitat types within 25 m^2 areas (the pixel size of the coarse-grained map). Another factor that may have contributed to the lower predictive ability of the CGHR design is that different land-cover types recognized on the fine-grained map were often amalgamated into one land-cover type on the coarse-grained map (e.g., marsh, meadow, disturbed grass, mowed lawn, crop/hay, and pasture from the fine-grained map were combined into herbaceous cover). Toads tended to select for some of these habitat types (e.g., crop/hay) and avoid others (e.g., pasture), which could explain why the land-cover herbaceous cover showed inconsistent patterns of selection and avoidance by western toads among models using the CGHR.

I recommend that land-managers or researchers wishing to identify high-quality habitat for amphibians be cautious about using publicly available land-cover maps since these may not provide sufficient resolution. I agree with other researchers that studies examining habitat selection should be conducted at several spatial scales, preferably structured as a nested hierarchy (Allen & Starr, 1982; Maurer, 1985; Wiens, Rotenberry & Van Horn, 1987). It is believed that habitat selection is constrained by the level above and clarified by the level below, so examining the level above and below the spatial scale of interest may reveal mechanisms that explain or constrain the patterns of habitat selection observed (Allen & Starr, 1982).

Habitat Use and Conservation

Adult western toads congregate at breeding ponds to lay their eggs from April to June in Alberta, but spend the majority of their life in terrestrial habitat (Russell & Bauer, 2000; personal observation). Anuran presence/absence surveys typically focus on wetlands because breeding vocalizations and high densities of individuals make detection easier (e.g., Crump & Scott, 1994; Shirose et al., 1997). Toads are very cryptic during their foraging period and move underground for hibernation, which makes detection very difficult or impossible. Alberta Sustainable Resources Development recommends setback distances of 50 m and 100 m from breeding pond edges for low and medium disturbance activities, respectively, during the breeding period (May 15 – June 15) and during metamorph dispersal (July 15 – August 15), and 300 m year-round for high disturbance activities (Boreal/Foothills Sensitive Species Guidelines, unpubl.). They also recommend setback distance of 50 m and 100 m from hibernation sites for medium and high disturbance activities, respectively, from September-April, and 50 m year-round for high disturbances (Boreal/Foothills Sensitive Species Guidelines, unpubl.). However, hibernation sites are nearly impossible to locate in the field, so they likely receive no protection from this guideline. My research indicates that most toads hibernate more than 300 m from their breeding ponds (Chapter 4), so an alternative method for protecting western toad hibernation sites in Alberta is clearly needed. I suggest locating toad populations using visual and call surveys around wetlands during the breeding period, then protecting patches of habitat surrounding breeding ponds based on my habitat selection results (Chapter 4).

My research strongly suggests that hibernation sites are limited for western toads in Alberta: RSF analyses showed significant selection for certain land-cover types (and selection differed from foraging habitat), toads moved long distances to reach hibernation sites (range = 146-1936 m), and communal hibernation was common (Chapter 4). Toads used cavities in peat hummocks, red-squirrel middens, natural crevasses, decayed root channels, cavities under spruce trees, abandoned beaver lodges, and muskrat tunnels for hibernation. These micro-sites occurred in deciduous forest, conifer forest, mixed-wood forest, dry shrubland, wet shrubland, marsh, dry meadow, and burned forest. Habitat selection depended on the array of habitat components available to the animal and differed among study areas. Overall, toads showed strong selection for conifer stands for hibernation. Toads moved farther to reach hibernation sites at the boreal area (mean = 1086 m +/- 128 SE) compared to the pasture area (mean = 373 m +/- 39 SE). Differences in movement distances were likely the result of differences in landscape configuration (the arrangement of habitat patches on the landscape); however, it is not clear whether toads moved farther in the boreal area because hibernation sites were limited close to the breeding pond or because the boreal landscape facilitated movement by toads (e.g., higher levels of soil moisture, more small water bodies).

The importance of ponds for reproduction, and of hibernation sites for surviving the harsh Canadian winters is clear, but foraging habitat for western toads has received less attention. Habitat used by the western toad during the foraging period is not currently protected in Alberta, so my first goal in Chapter 3 was to determine if toads selected certain land-cover types during the foraging season or if they simply used habitat in proportion to its availability in an area that encompassed breeding ponds and hibernation sites. All of my RSF models describing toad occurrence during the foraging season showed selection for certain land-cover types (Chapter 3). Toads selected for open habitat types (e.g., wet shrub, disturbed grass, crop/hay) that likely provided warm temperatures (in the summer) and abundant prey that would facilitate growth. Female toads showed a stronger selection for open habitat compared to males (Chapter 3). Females may require greater caloric intake in order to produce a clutch of eggs (Muths, 2003), males may be restricted in their ability to use open habitat because their smaller size may make them more susceptible to desiccation (Bartelt, Peterson & Klaver, 2004), or males and females may select different habitat types to reduce conspecific competition (Johnson, Knouft & Semlitsch, 2007).

Results from Chapter 5 also indicate that foraging grounds are important for western toads. I found that larger toads move to hibernation sites later in the year and move along straighter paths to reach sites. I hypothesize that larger toads are remaining at their foraging grounds as late in the year as possible in order to maximize their growth, and are able to stay in these areas longer than are small toads because they are older individuals that are familiar with their landscape and locations of suitable hibernacula. In addition to knowledge of their landscape, larger toads may be able to remain at foraging grounds later in the season because their larger bodies lose heat more slowly and would buffer them if they were caught away from their hibernacula during a cold snap.

Toads selected for warm, open habitat with abundant prey that would facilitate growth during the breeding season and pre-hibernation season; however, habitat selection differed slightly from that displayed in the foraging season (Chapter 3). During the breeding season, toads strongly selected for locations that were close to breeding ponds and they used water and emergent vegetation while they congregated at ponds for breeding, but not later in the year (Chapter 3). During the pre-hibernation season selection of certain habitat types became less significant (e.g., deciduous forest, wet shrub, moss, and disturbed grass all had larger P-values during the pre-hibernation season compared to the foraging season for boreal females using the FGHR design) as selection of locations close to hibernation sites became the driving factor (Chapter 3).

At my Utikuma study area, I found that western toad relative abundance was positively associated with deciduous forest cover and negatively associated with low shrub cover on PC1 in an ordination I conducted at the 100 m scale (Chapter 2). At the 5000 m scale, western toad abundance was positively associated with moss, mesic herbaceous, and tall shrub on PC1, and deciduous forest on PC2, and negatively associated with wetlands, burned areas, and pine stands on PC1, and coniferous forest and low shrub cover on PC2 (Chapter 2). Patterns were consistent between Chapters 2 and 3 for several land-cover types; for example, toads were generally associated with tall shrub, moss, and mesic herbaceous cover (i.e., dry meadow, disturbed grass, grass-dominated clear-cut).

The selection or avoidance of deciduous forest, conifer forest, and wetlands changed seasonally and differed among study areas in Chapters 3 and 4. Western toads selected conifer forest for hibernation habitat in the pasture study area, used it proportionally to its availability in the boreal area, and did not use conifer forest in the park area (Chapter 4). RSFs for the breeding period often show selection of wetland habitat types (e.g., marsh, emergent vegetation, water) for the park and pasture study areas, but not for the boreal area (Chapter 3). Deciduous forest was selected over coniferous forest during the active season for several models in the boreal study area, but only by pre-hibernation pasture males in the Aspen Parkland (Chapter 3). In Chapter 2, western toad relative abundance was positively associated with deciduous forest and negatively associated with conifer forest and wetlands. The results from Chapter 2 are similar to those I found at the boreal study area from radio-tracked toads, which suggests that habitat selection differs between the central mixed-wood Boreal Forest and Aspen Parkland regions. Deciduous forest may be selected over coniferous forest during the active period because deciduous forests have more understory vegetation and support greater invertebrate densities (Willson & Comet, 1996; Ferguson & Berube, 2004), which provide, respectively, cover and food for toads. Conifer forest is important for hibernation (Chapter 4) and wetlands are important for breeding, but these habitat types were not positively associated with toad abundance/occurrence in the Boreal Forest (Chapters 2, 3, and 4), so they must not be limiting. Comparing the results from Chapter 2 to those of Chapters 3 and 4, the relative abundance of western toads at the 24 wetlands in the Utikuma area appears to reflect abundant foraging habitat, which suggests that high-quality foraging habitat is important for western toads in the Utikuma region. Alternatively, differences in habitat use patterns as reported in Chapter 2, and Chapters 3 and 4 may reflect differences in habitat use between adult and juvenile toads because toads of all age classes were included in the relative abundance counts in the Utikuma area, but only adult toads could be radio-tracked.

Habitat use of the western toad changes year-round to meet the needs of reproduction, foraging, and hibernation. Specific habitat types were selected for during each of these periods, which show that toads distinguish among habitat patches and do not use terrestrial habitat in patterns that reflect simple availability. I recommend that land-managers wishing to protect habitat for the western toad in Alberta protect a mixture of land-cover types that provide habitat for the breeding season (e.g., ponds, emergent vegetation, marsh), foraging season (e.g., grasslands, shrub), and hibernation (e.g., conifer forest).

For an example of specific recommendations for the study areas at which I radio-tracked toads, I would suggest that land managers avoid adding habitat types that provide no overhead cover (railroad, gravel road, paved road, and exposed land) and restore these areas to other habitat types, if possible. Pasture habitat was avoided by toads and covered a large area surrounding the breeding ponds at my pasture study area in the Aspen Parkland. Vegetation was sparse in pasture habitat and likely did not provide enough overhead cover for toads and/or their prey. Vegetation was sparse in the pasture habitat because the soil was sandy and cattle were allowed to graze during the summer each year. To improve the habitat quality of this pasture for toads, I would recommend that cattle grazing be reduced (e.g., not permitted until September when toads are beginning to move to hibernation sites).

Future Research

My research provides new information on habitat types selected during the active season and for hibernation by western toads in north-central Alberta. However, habitat selection differed among my study areas, so the applicability of my models for predicting western toad habitat use outside of my study areas is likely limited. Development of a model that can be used to predict high-quality habitat for western toads beyond the study areas in which it was created would be a very useful tool for land-managers; therefore, more research at additional study areas to test and refine my models would be a useful endeavor for future research. Inclusion of a function in these models that accounts for the relative abundance of each land-cover type on the landscape, and that gives additional weight to essential habitat types that may be limited, may be worthy of exploration. Determining individual fitness (survival, growth, and reproductive success of the individual) associated with use of different land-cover types would be useful for determining high-quality habitat for western toads. Although it is often assumed that individuals will select habitat types that maximize their fitness, there is a wide range of ecological processes that may prevent individuals from always using the highest-quality habitat (McLoughlin et al., 2006). For example, toads may select crop/hay habitat because it provides warm temperatures and abundant prey, but are insensitive to the mortality risk that occurs during crop/hay harvest. Determining individual fitness associated with different habitat types will facilitate understanding the patterns of habitat use and will help managers protect the correct habitat types to maintain healthy western toad populations.

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Appendices

Appendix A. Mean (SE) of local and landscape (measured at the 500 m scale) environmental variables and dependent variables (anuran abundance) among the landform types glaciolacustrine (n = 7), moraine (n = 10), and outwash (n = 7) for 24 wetlands at the Utikuma area in Chapter 2. Units for each variable are listed in Table 2-1. Kruskal-Wallis tests were conducted to determine if significant differences existed among landform types for each variable. Significant differences were not found unless indicated by a * ($P < 0.05$), ** ($P < 0.01$), or *** ($P < 0.001$).

LOCAL VARIABLES	Glaciolacustrine	Moraine	Outwash
Turbidity	5.23 (0.55)	6.15 (0.62)	7.24 (0.30)
Chlorophyll-a	11.35 (3.52)	16.48 (3.80)	9.37 (2.79)
Conductivity*	0.20 (0.03)	0.12 (0.02)	0.11 (0.02)
Dissolved oxygen	7.37 (2.06)	10.00 (1.47)	10.09 (1.45)
PH	9.01 (0.16)	9.02 (0.16)	8.77 (0.31)
Water temperature	20.78 (0.86)	21.52 (0.43)	20.08 (0.55)
Submersed aquatic vegetation (SAV)	2.33 (0.39)	2.50 (0.26)	2.86 (0.33)
Wetland depth	72.19 (5.97)	59.40 (9.72)	74.43 (11.7)
Secchi depth	72.19 (5.97)	58.24 (9.25)	73.49 (11.4)
Secchi depth: wetland depth	1.00 (0.00)	0.99 (0.01)	0.99 (0.01)
Total nitrogen	2272 (157)	2032 (187)	1656 (169)
Total dissolved solids (TDS)	0.13 (0.02)	0.09 (0.01)	0.09 (0.01)
Total phosphorus	73.01 (10.7)	81.72 (32.29)	58.01 (11.5)
Invertebrate biomass/volume*	11.22 (2.67)	9.80 (1.91)	4.81 (0.83)
Predatory invertebrate biomass/volume**	1.43 (0.18)	4.16 (0.78)	1.72 (0.53)
Aquatic plant density**	0.74 (0.09)	0.52 (0.05)	0.36 (0.05)
Woody debris	0.75 (0.21)	155.7 (106)	32.10 (14.35)
Beaver structures	0.86 (0.14)	0.70 (0.15)	1.00 (0.00)
Percent vegetation cover	88.61 (2.73)	94.55 (1.76)	90.14 (3.06)
Median vegetation height	150.0 (39.0)	175.5 (74.9)	157.5 (82.9)
Wetland area	88177 (18044)	63083 (20084)	135086 (59563)
Wetland perimeter	1282 (101)	1228 (201)	1841 (394)

Appendix A Continued…

LANDSCAPE VARIABLES	Glaciolacustrine	Moraine	Outwash
Closed conifer*	0.081 (0.022)	0.035 (0.007)	0.062 (0.012)
Open conifer**	0.443 (0.050)	0.142 (0.017)	0.279 (0.055)
Closed deciduous**	0.099 (0.031)	0.484 (0.035)	0.256 (0.085)
Mixed forest	0.061 (0.010)	0.102 (0.009)	0.079 (0.020)
Low shrub*	0.090 (0.013)	0.031 (0.005)	0.077 (0.022)
Tall shrub	0.113 (0.021)	0.113 (0.013)	0.092 (0.020)
Moss	0.006 (0.002)	0.005 (0.001)	0.003 (0.001)
Mesic herbaceous	0.062 (0.012)	0.033 (0.005)	0.058 (0.018)
Wet herbaceous	0.001 (0.000)	0.004 (0.002)	0.001 (<0.001)
Urban (roads and well pads)	0	0.008 (0.004)	0.011 (0.004)
Agricultural areas	0	<0.001 (<0.001)	0.001 (<0.001)
Young stands (burnt)	0.002 (0.001)	0.003 (0.001)	0.005 (0.001)
Wetlands	0.043 (0.018)	0.040 (0.012)	0.076 (0.033)
DEPENDENT VARIABLES			
Wood frog	19.43 (5.86)	34.80 (5.16)	22.71 (4.17)
Chorus frog*	2.86 (0.67)	17.20 (6.34)	4.43 (1.91)
Western toad*	8.43 (2.66)	12.70 (6.21)	2.14 (1.50)

Appendix B. Descriptions of each land-cover type from the fine-grained map used in Chapters 3 and 4.

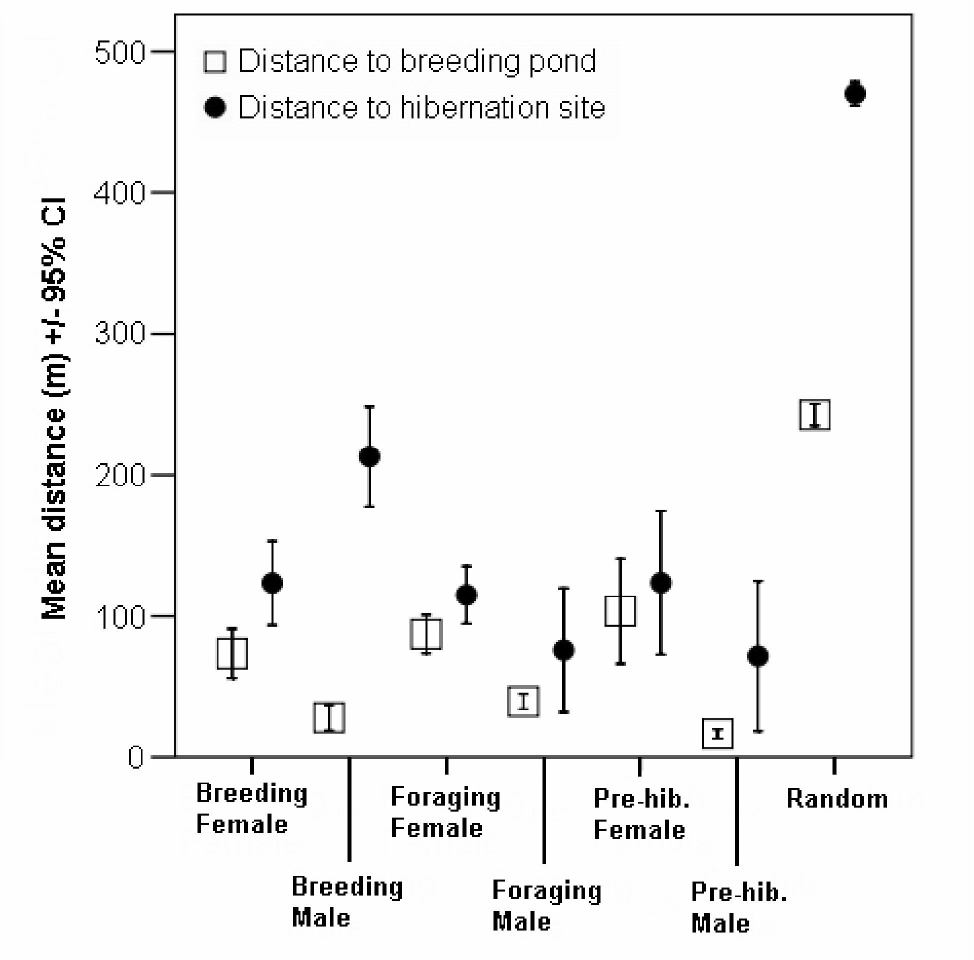
Land-cover type	Description
Conifer	Tree cover of 6-100% crown closure with over 80% of trees being conifer.
Deciduous	Tree cover of 6-100% crown closure with over 80% of trees being deciduous.
Mixed-wood	Tree cover of 6-100% crown closure with over 20% of both conifer and deciduous trees.
Dry shrub	Shrub cover of 6-100% with a dry to moderately well drained substratum.
Wet shrub	Shrub cover of 6-100% with a poorly drained to flooded substratum.
Moss	Less than 6% tree/shrub cover. Ground is predominately covered by mosses/bryophytes.
Marsh	Less than 6% tree/shrub cover. Ground is predominately covered by graminoids. Substratum is poorly drained.
Dry meadow	Less than 6% tree/shrub cover. Ground is predominately covered by graminoids. Substratum is dry to moderately well drained.
Burn	Burn/partial burn.
Clear-cut grass dominated	Clearcut/partial cut. Ground is predominately covered by graminoids.
Cutblock tree/shrub dominated	Clearcut/partial cut. Ground is predominately covered by shrubs or young trees.
Disturbed grass	Roadsides, cutlines, pipelines, utility corridors, or any other human modified landscape with the ground predominately covered by graminoids.
Railway	Railway.
Gravel surface	Gravel surface.
Paved surface	Paved surface.
Mowed lawn	Graminoid surface cover that is mowed several times/year.
Building	Building.
Crop/hay field	Cultivated farmland growing hay or crops.
Pasture	Cattle pasture.
Exposed soil	Non-vegetated soil (e.g., roads through farm-fields)
Emergent vegetation	Aquatic habitat with emergent vegetation.
Water	Water with submersed or no vegetation.

Appendix C. Land-cover categories in the fine-grained map and the equivalent categories in the coarse-grained map used in Chapter 3.

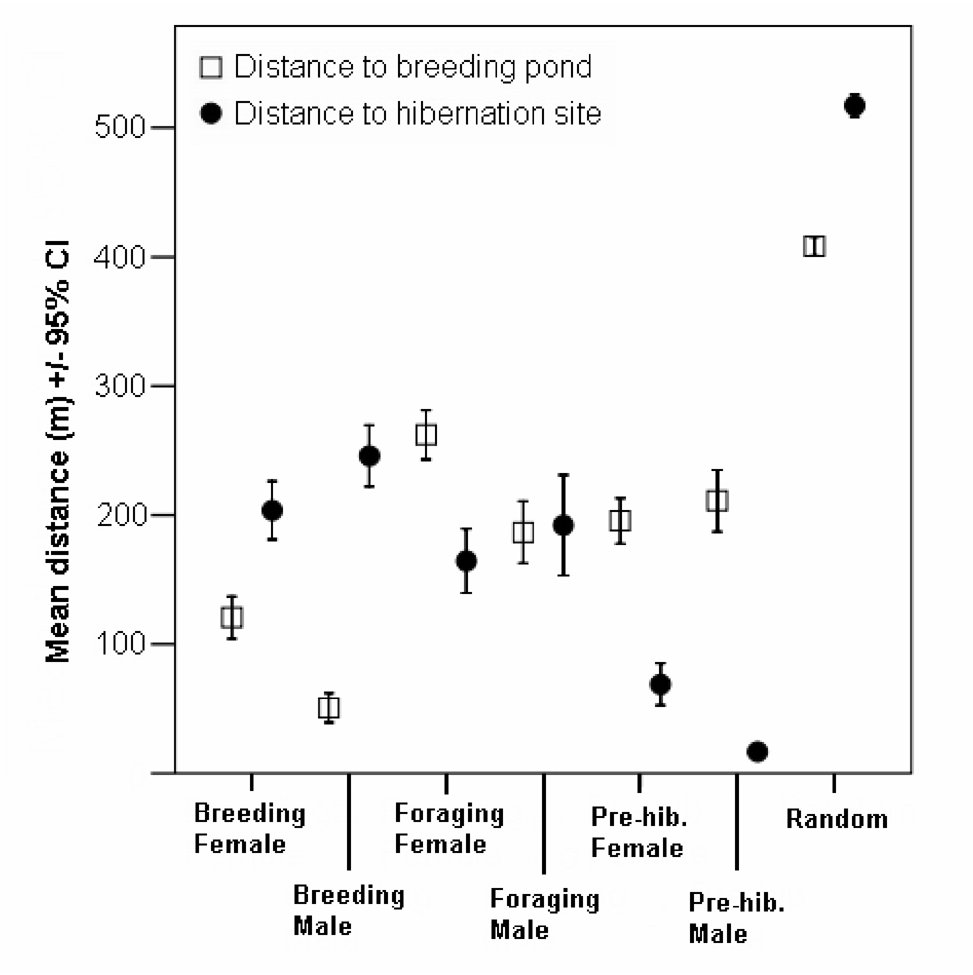
Fine-grained map	Coarse-grained map
Conifer	Coniferous dense
Deciduous	Broadleaf dense
Mixed-wood	Mixed-wood dense
Dry shrub	Shrub tall
Wet shrub	Wetland-treed; Wetland-shrub
Moss	Wetland-herb
Marsh	Herbaceous cover
Dry meadow	Herbaceous cover
Burn	Exposed land
Clear-cut grass dominated	Exposed land; Herbaceous cover; other
Cutblock tree/shrub dominated	Exposed land; other
Disturbed grass	Herbaceous cover
Railway	Exposed land
Gravel surface	Exposed land
Paved surface	Exposed land
Mowed lawn	Herbaceous cover
Building	Exposed land
Crop/hay field	Herbaceous cover
Pasture	Herbaceous cover
Exposed soil	Exposed land
Emergent vegetation	Water; Herbaceous cover; other
Water	Water

Appendix D. Mean distance (m) +/- 95% CI of western toad (*Anaxyrus boreas*) locations to nearest breeding pond and hibernation site or to nearest water and conifer stand were compared to random locations in Chapter 3. Western toad locations were collected using radio-telemetry at three study sites (Park, Pasture, and Boreal) in north-central Alberta. Random locations were drawn from throughout the study area for the fine-grained population-range design (FGPR) models. Within the FGPR, one set of random locations was drawn for each study area and compared to the six sets of use locations that varied among seasons and sex. For the fine-grained buffered-home-range design (FGHR) and coarse-grained buffered-home-range design (CGHR) models, 10 random locations were drawn from within a 300 m-radius buffer from the toad's previous location, for each use location. Locations used by toads (U) were compared to randomly generated locations that represented available choices (R). Pre-hib. = Pre-hibernation.

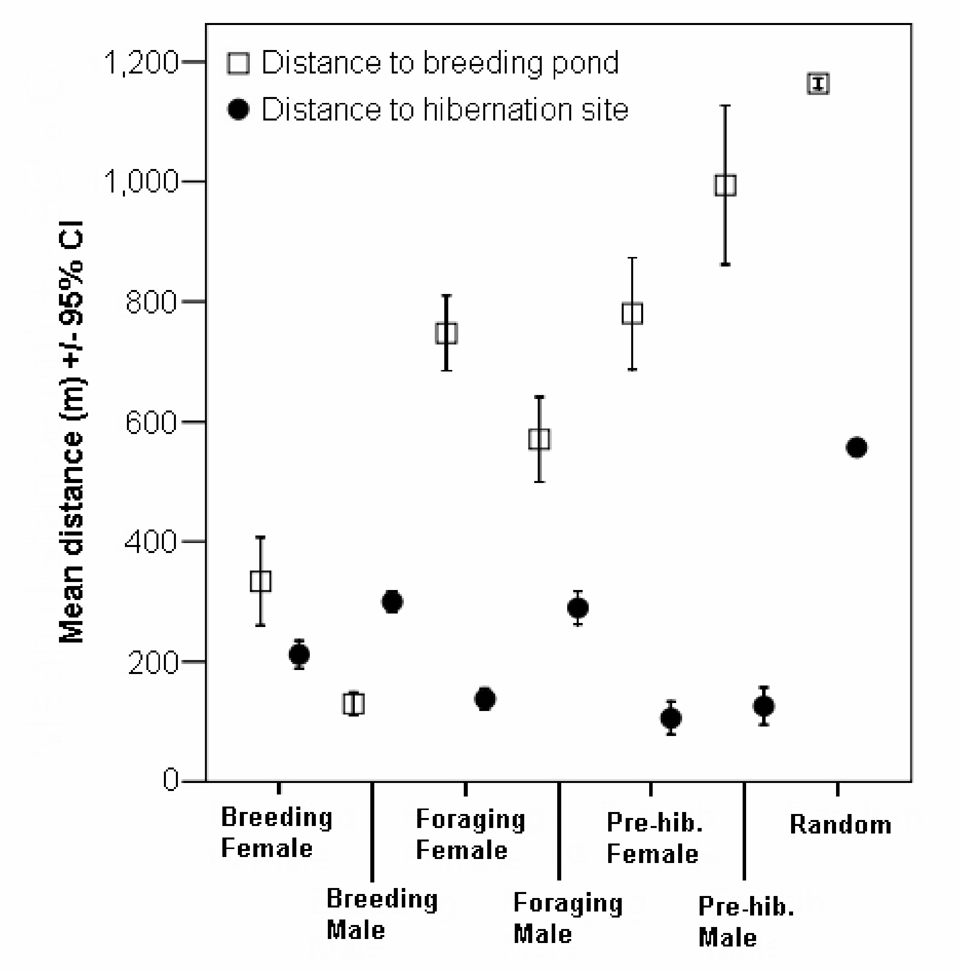
A. Park FGPR

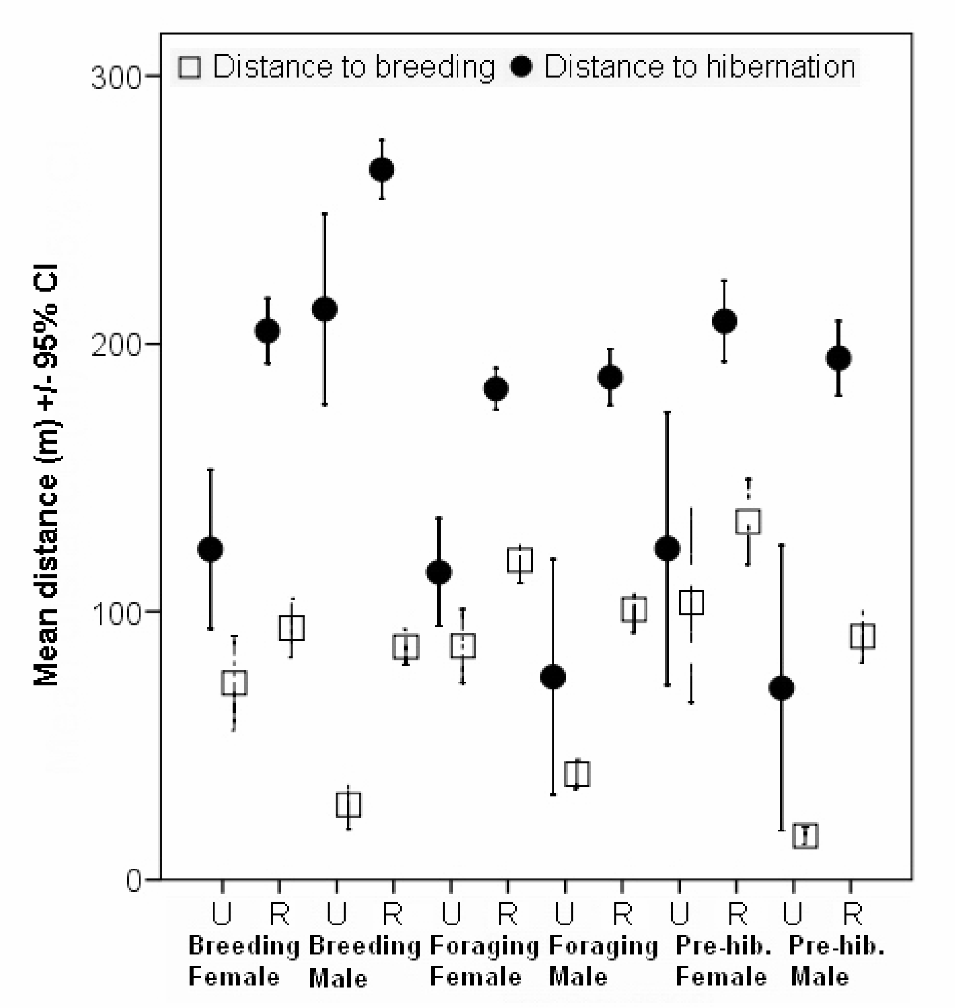


B. Pasture FGPR

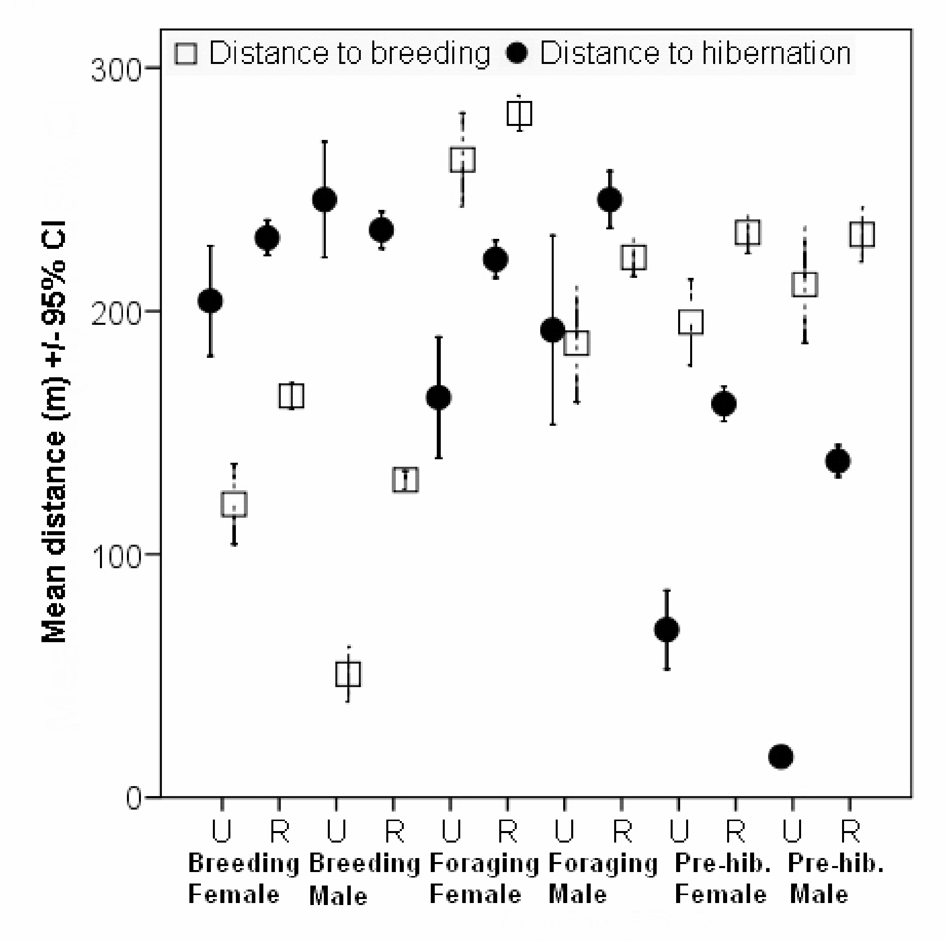


C. Boreal FGPR

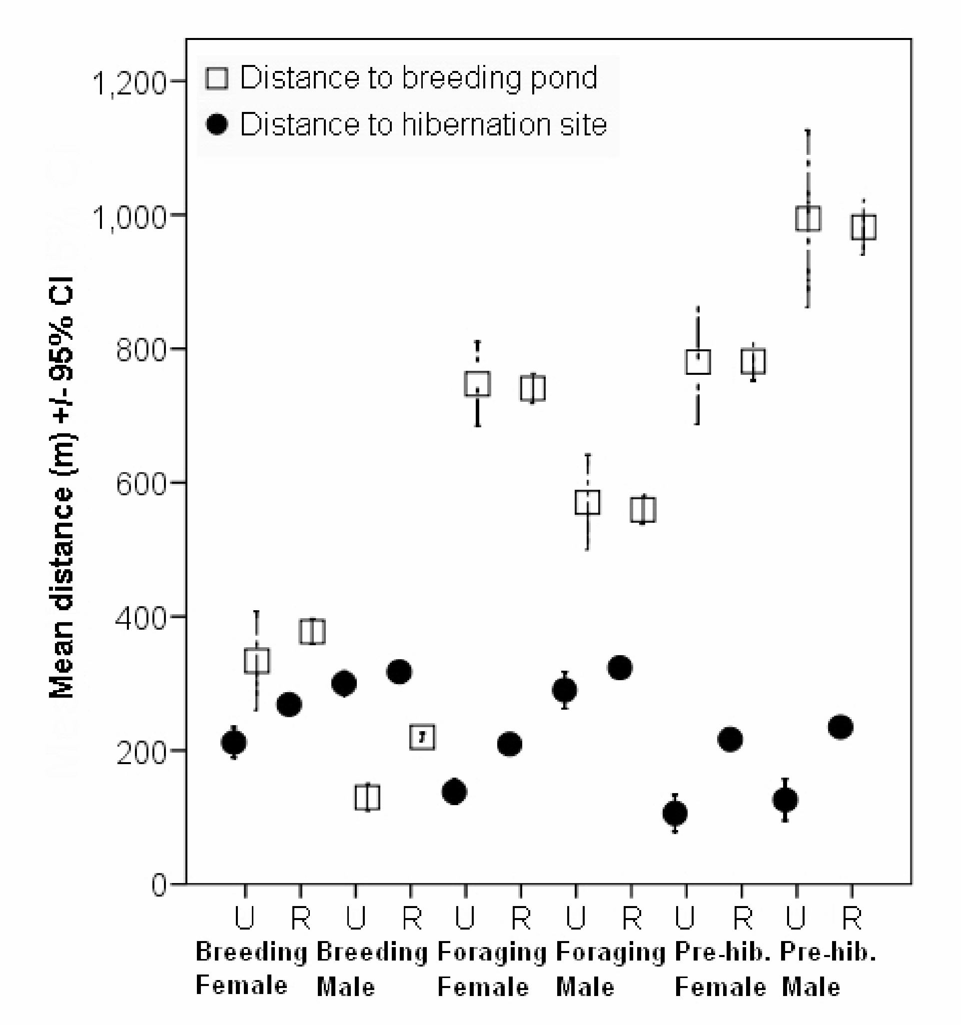


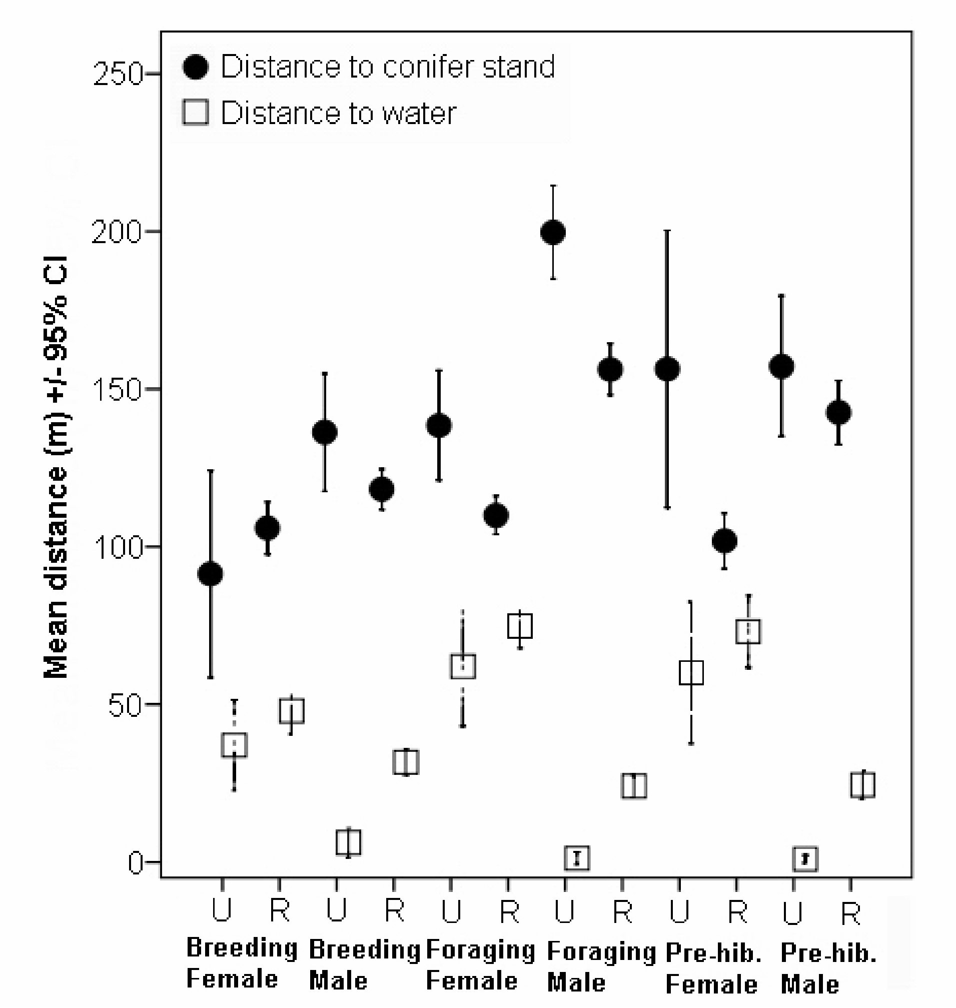

☐ Distance to breeding
● Distance to hibernation
Mean distance (m) +/- 95% CI
300
200
100
0
U
R
U
R
U
R
U
R
U
R
U
R
Breeding Female
Breeding Male
Foraging Female
Foraging Male
Pre-hib. Female
Pre-hib. Male

E. Pasture FGHR

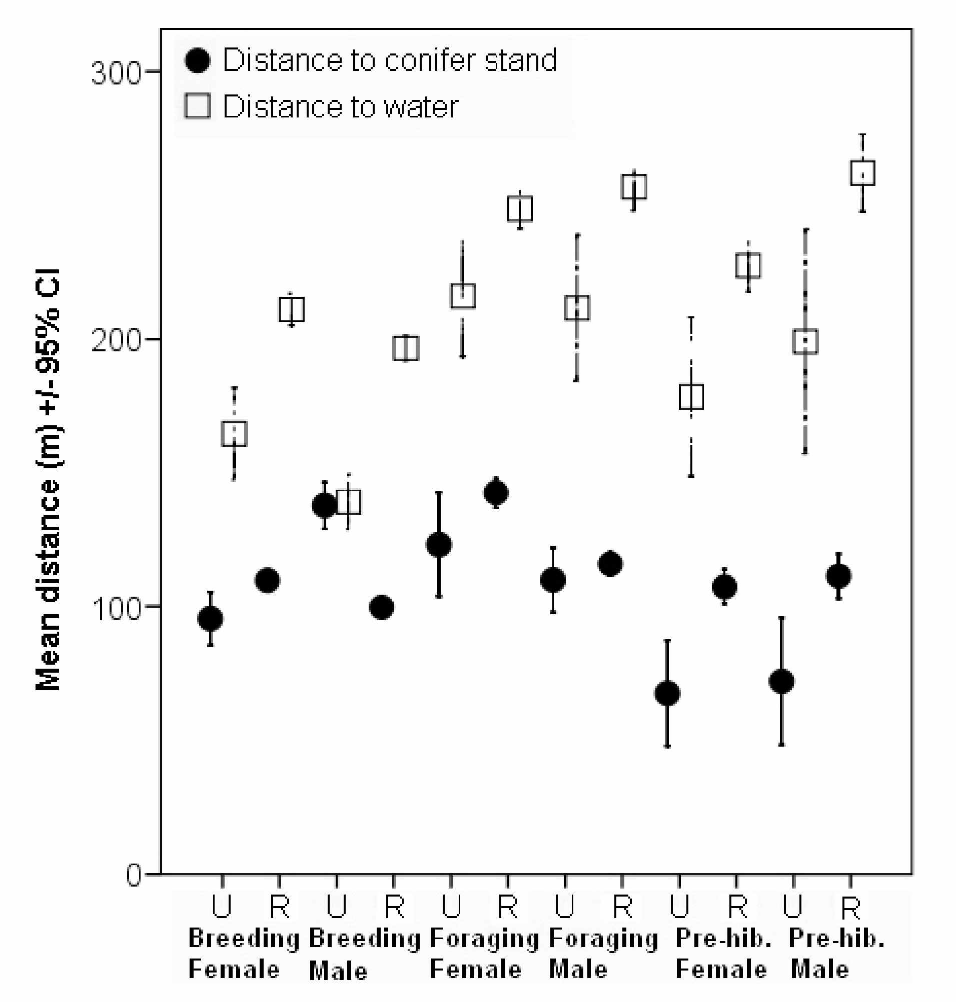


F. Boreal FGHR

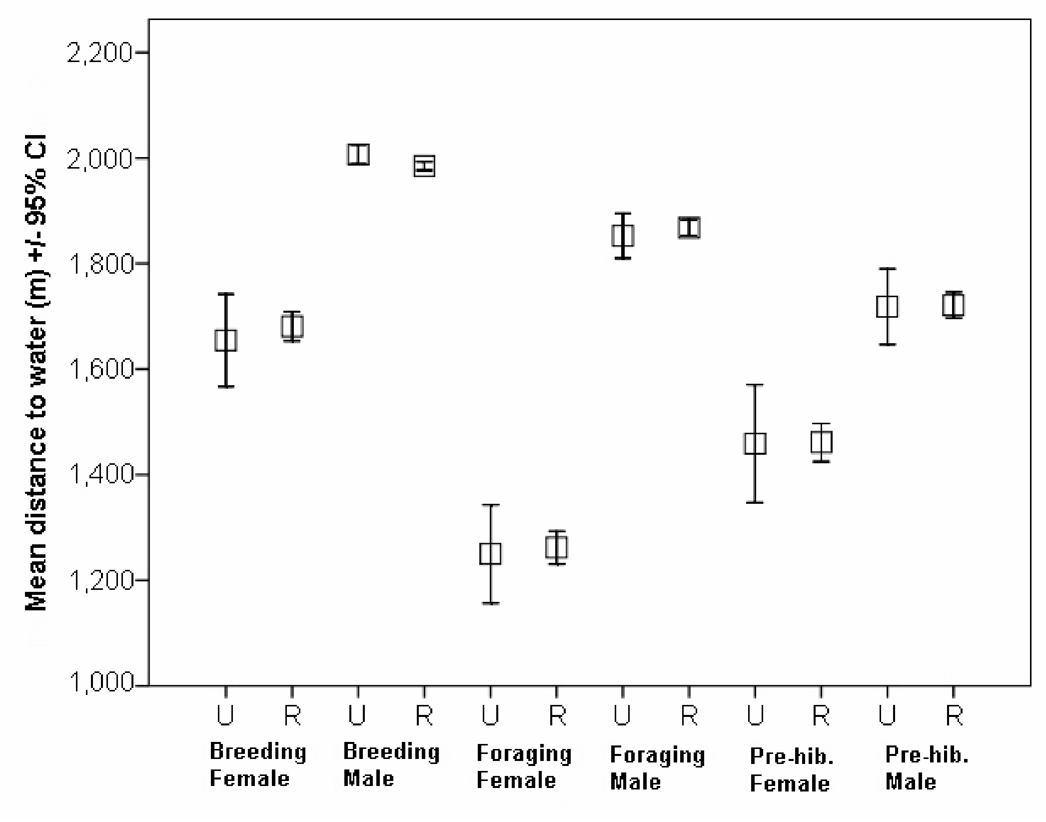



● Distance to conifer stand
☐ Distance to water
Mean distance (m) +/- 95% CI
0
50
100
150
200
250
U
R
U
R
U
R
U
R
U
R
U
R
Breeding Female
Breeding Male
Foraging Female
Foraging Male
Pre-hib. Female
Pre-hib. Male

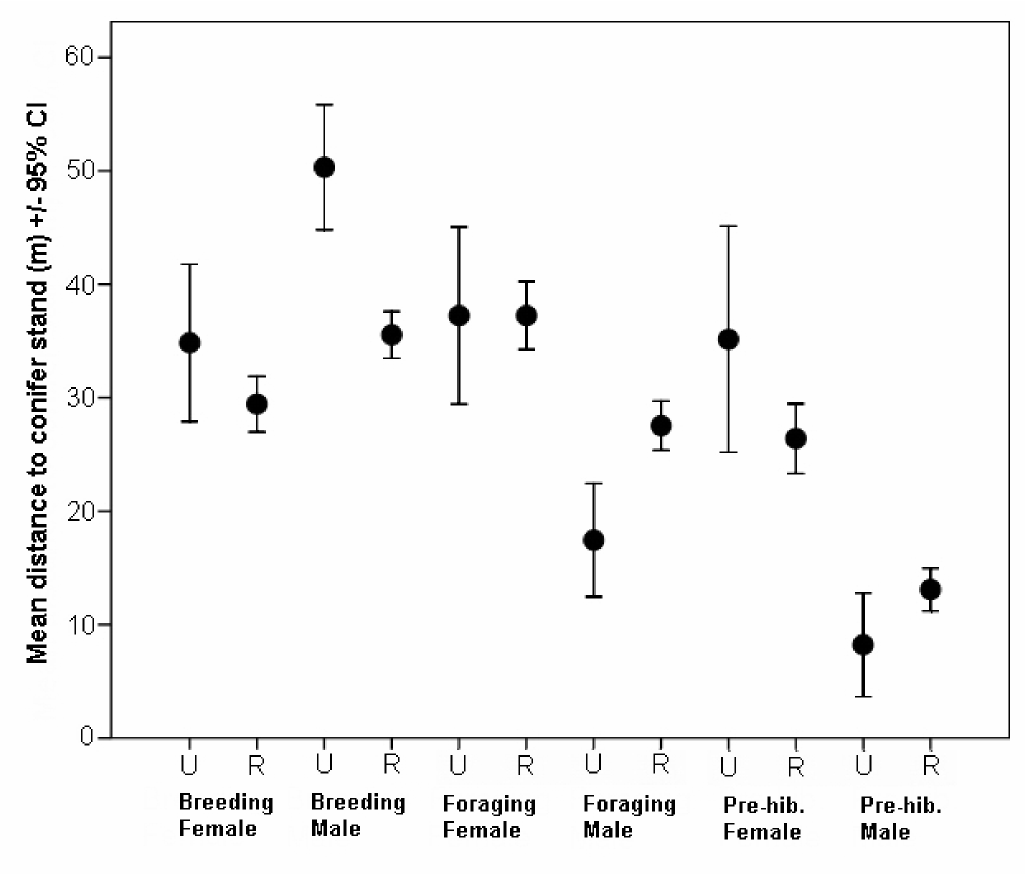
H. Pasture CGHR



I. Boreal CGHR
a) Mean distance to water



I. Boreal CGHR
b) Mean distance to conifer stand



Appendix E. Summary of the number of Resource Selection Function (RSF) models in Chapter 3 that each land-cover variable was selected for, used but avoided, not significantly different from the reference variable, used as the reference variable, or not used (either because the land-cover type was not available or it was avoided) by western toads (*Anaxyrus boreas*) that were radio-tracked at three study sites (Park, Pasture, and Boreal) in north-central Alberta.

A. Fine-grained population-range design (FGPR)

	Selected	Used but Avoided	Not significant	Reference	Not used by toads
Conifer	1		4	6	7
Deciduous	2		1	11	4
Mixed-wood			8		10
Dry shrub	1		4		13
Wet shrub	9		2		7
Moss	2		4		12
Marsh	2	1	3	1	11
Dry meadow	1				17
Burn			3		15
Clear-cut grass dominated	2		1		15
Cutblock tree/shrub dominated	2				16
Disturbed grass	6		4		8
Mowed lawn	1				17
Crop/hay field	4		1		13
Pasture		1	4		13
Emergent vegetation	3		1		14
Water	2		2		14

B. Fine-grained buffered-home-range design (FGHR)

	Selected	Used but Avoided	Not significant	Reference	Not used by toads
Conifer	2	2	1	6	7
Deciduous	2		1	11	4
Mixed-wood	3	2	3		10
Dry shrub	2		3		13
Wet shrub	9		2		7
Moss	3	2	1		12
Marsh	2	1	3	1	11
Dry meadow	1				17
Burn	1	1	1		15
Clear-cut grass dominated	3				15
Cutblock tree/shrub dominated	1		1		16
Disturbed grass	6	2	2		8
Mowed lawn	1		1		16
Crop/hay field	5				13
Pasture		5			13
Emergent vegetation	3		1		14
Water	2		2		14

C. Coarse-grained buffered-home-range design (CGHR)

	Selected	Used but Avoided	Not significant	Reference	Not used by toads
Conifer	4	2	1	6	5
Deciduous	2	1	3	10	2
Mixed-wood		2	3		13
Tall shrub	2		1		15
Wet shrub	7	1	4		6
Wet herbaceous	1	1	1		15
Herbaceous cover	3	8	2		5
Exposed land	2				16
Water	1	2	3	2	10

Appendix F. Proportion of each land-cover type at each study site (Park, Pasture, and Boreal) that western toads (*Anaxyrus boreas*) were radio-tracked at in north-central Alberta for the fine-grained population-range design (FGPR) models in Chapter 3.

Land-cover type	Park	Pasture	Boreal
Conifer	0.016	0.016	0.412
Deciduous	0.397	0.158	0.249
Mixed-wood	0.052	0.099	0.089
Dry shrub	0.015	0.012	0.006
Wet shrub	0.032	0.010	0.047
Moss	0	0	0.026
Marsh	0.224	0.014	0.015
Dry meadow	0.017	0.003	0.001
Burn	0	0	0.017
Clear-cut grass dominated	0	0	0.005
Cutblock tree/shrub dominated	0	0	0.062
Disturbed grass	0.010	0.028	0.055
Railway	0	0	0.001
Gravel surface	0.003	0.004	0.006
Paved surface	0	0.003	0
Mowed lawn	0	0.004	0
Building	0	0.001	<0.001
Crop/hay field	0	0.411	0
Pasture/sparsely vegetated	0	0.213	<0.001
Exposed soil	0	0.004	0
Emergent vegetation	0.051	0.008	<0.001
Water	0.182	0.011	0.007

Appendix G. Proportion of locations used by western toads (*Anaxyrus boreas*) radio-tracked at the Park, Pasture, and Boreal study sites in north-central Alberta and proportion available for each land-cover type in Chapter 3. Proportion of available land-cover was calculated from throughout the study area for the fine-grained population-range design (FGPR) models. For the fine-grained buffered-home-range design (FGHR) and coarse-grained buffered-home-range design (CGHR) models, proportion of available land-cover was calculated from random locations drawn from within a 300 m-radius buffer from the toad's previous location; 10 random locations were drawn for each use location. Pre-hib. = Pre-hibernation.

A. Park FGPR

Land-cover type	Breeding Female	Breeding Male	Foraging Female	Foraging Male	Pre-hib. Female	Pre-hib. Male	Available
Sample size (n)	31	56	68	39	27	27	
Conifer	0	0	0	0	0	0	0.016
Deciduous	0.29	0.018	0.559	0.103	0.333	0	0.397
Mixed-wood	0	0	0	0	0	0	0.052
Dry shrub	0	0	0	0	0	0	0.015
Wet shrub	0	0	0.382	0.59	0.148	0.037	0.032
Moss	0	0	0	0	0	0	0
Marsh	0.677	0.786	0.029	0.282	0.333	0.963	0.224
Dry meadow	0	0	0	0	0.185	0	0.017
Burn	0	0	0	0	0	0	0
Clear-cut grass dominated	0	0	0	0	0	0	0
Cutblock tree/shrub dominated	0	0	0	0	0	0	0
Disturbed grass	0	0	0.029	0	0	0	0.01
Railway	0	0	0	0	0	0	0
Gravel surface	0	0	0	0	0	0	0.003
Paved surface	0	0	0	0	0	0	0
Mowed lawn	0	0	0	0	0	0	0
Building	0	0	0	0	0	0	0
Crop/hay field	0	0	0	0	0	0	0
Pasture/sparsely vegetated	0	0	0	0	0	0	0
Exposed soil	0	0	0	0	0	0	0
Emergent vegetation	0	0.053	0	0.026	0	0	0.051
Water	0.032	0.143	0	0	0	0	0.182

B. Pasture FGPR

Land-cover type	Breeding Female	Breeding Male	Foraging Female	Foraging Male	Pre-hib. Female	Pre-hib. Male	Available
Sample size (n)	213	236	238	195	100	60	
Conifer	0.047	0.034	0.046	0.005	0.070	0.067	0.016
Deciduous	0.099	0.034	0.189	0.205	0.200	0.467	0.158
Mixed-wood	0.117	0.068	0.197	0.169	0.410	0.300	0.099
Dry shrub	0.014	0.042	0	0.062	0.040	0.150	0.012
Wet shrub	0.066	0	0	0.021	0	0	0.010
Moss	0	0	0	0	0	0	0
Marsh	0.023	0	0	0	0	0	0.014
Dry meadow	0	0	0	0	0	0	0.003
Burn	0	0	0	0	0	0	0
Clear-cut grass dominated	0	0	0	0	0	0	0
Cutblock tree/shrub dominated	0	0	0	0	0	0	0
Disturbed grass	0.066	0.004	0.105	0.026	0.090	0.017	0.028
Railway	0	0	0	0	0	0	0
Gravel surface	0	0	0	0	0	0	0.004
Paved surface	0	0	0	0	0	0	0.003
Mowed lawn	0	0	0.008	0.041	0	0	0.004
Building	0	0	0	0	0	0	0.001
Crop/hay field	0.099	0.021	0.387	0.185	0.150	0	0.411
Pasture/sparsely vegetated	0.174	0.360	0.063	0.200	0.040	0	0.213
Exposed soil	0	0	0	0	0	0	0.004
Emergent vegetation	0.183	0.220	0.004	0.067	0	0	0.008
Water	0.113	0.216	0	0.021	0	0	0.011

C. Boreal FGPR

Land-cover type	Breeding Female	Breeding Male	Foraging Female	Foraging Male	Pre-hib. Female	Pre-hib. Male	Available
Sample size (n)	94	143	85	118	64	59	
Conifer	0.106	0.112	0.118	0.508	0.516	0.881	0.412
Deciduous	0.085	0	0.212	0.000	0.125	0	0.249
Mixed-wood	0.043	0	0.012	0.119	0	0	0.089
Dry shrub	0	0	0	0	0	0	0.006
Wet shrub	0.213	0.497	0.400	0.203	0.188	0.034	0.047
Moss	0.309	0.280	0.024	0.025	0.047	0.034	0.026
Marsh	0	0	0	0	0	0	0.015
Dry meadow	0	0	0	0	0	0	0.001
Burn	0.043	0	0	0.051	0.047	0	0.017
Clear-cut grass dominated	0	0.035	0	0.042	0	0.051	0.005
Cutblock tree/shrub dominated	0.021	0.000	0.024	0.008	0	0	0.062
Disturbed grass	0.170	0.063	0.212	0.042	0.078	0	0.055
Railway	0	0	0	0	0	0	0.001
Gravel surface	0	0	0	0	0	0	0.006
Paved surface	0	0	0	0	0	0	0
Mowed lawn	0	0	0	0	0	0	0
Building	0	0	0	0	0	0	<0.001
Crop/hay field	0	0	0	0	0	0	0
Pasture/sparsely vegetated	0	0	0	0	0	0	<0.001
Exposed soil	0	0	0	0	0	0	0
Emergent vegetation	0	0	0	0	0	0	<0.001
Water	0.011	0.014	0	0	0	0	0.007

D. Park FGHR

Land-cover type	Breeding Female		Breeding Male		Foraging Female		Foraging Male		Pre-hib. Female		Pre-hib. Male	
	Used	Avail.	Used	Avail.	Used	Avail.	Used	Avail.	Used	Avail.	Used	Avail.
Sample size (n)	31	310	56	560	68	680	39	390	27	270	27	270
Conifer	0	0.016	0	0.005	0	0.012	0	0.003	0	0.022	0	0
Deciduous	0.290	0.297	0.018	0.318	0.559	0.351	0.103	0.326	0.333	0.356	0	0.307
Mixed-wood	0	0.016	0	0.013	0	0.009	0	0.021	0	0.011	0	0.022
Dry shrub	0	0.006	0	0.004	0	0.004	0	0	0	0.011	0	0
Wet shrub	0	0.013	0	0.011	0.382	0.057	0.590	0.023	0.148	0.033	0.037	0.007
Moss	0	0	0	0	0	0	0	0	0	0	0	0
Marsh	0.677	0.342	0.786	0.371	0.029	0.296	0.282	0.282	0.333	0.274	0.963	0.333
Dry meadow	0	0.013	0	0.016	0	0.004	0	0.010	0.185	0.011	0	0.004
Burn	0	0	0	0	0	0	0	0	0	0	0	0
Clear-cut grass dominated	0	0	0	0	0	0	0	0	0	0	0	0
Cutblock tree/shrub dominated	0	0	0	0	0	0	0	0	0	0	0	0
Disturbed grass	0	0	0	0	0.029	0.015	0	0	0	0.022	0	0
Railway	0	0	0	0	0	0	0	0	0	0	0	0
Gravel surface	0	0	0	0	0	0.001	0	0	0	0.004	0	0
Paved surface	0	0	0	0	0	0	0	0	0	0	0	0
Mowed lawn	0	0	0	0	0	0	0	0	0	0	0	0
Building	0	0	0	0	0	0	0	0	0	0	0	0
Crop/hay field	0	0	0	0	0	0	0	0	0	0	0	0
Pasture/sparsely vegetated	0	0	0	0	0	0	0	0	0	0	0	0
Exposed soil	0	0	0	0	0	0	0	0	0	0	0	0
Emergent vegetation	0	0.035	0.054	0.052	0	0.046	0.026	0.092	0	0.067	0	0.052
Water	0.032	0.261	0.143	0.211	0	0.204	0	0.244	0	0.189	0	0.274

E. Pasture FGHR

Land-cover type	Breeding Female		Breeding Male		Foraging Female		Foraging Male		Pre-hib. Female		Pre-hib. Male	
	Used	Avail.	Used	Avail.	Used	Avail.	Used	Avail.	Used	Avail.	Used	Avail.
Sample size (n)	213	2130	236	2360	238	2380	195	1950	100	1000	60	600
Conifer	0.047	0.031	0.034	0.029	0.046	0.055	0.005	0.048	0.070	0.044	0.067	0.053
Deciduous	0.099	0.124	0.034	0.094	0.189	0.162	0.205	0.143	0.200	0.174	0.467	0.217
Mixed-wood	0.117	0.161	0.068	0.182	0.197	0.161	0.169	0.179	0.410	0.236	0.300	0.210
Dry shrub	0.014	0.014	0.042	0.008	0	0.011	0.062	0.021	0.040	0.013	0.150	0.020
Wet shrub	0.066	0.008	0	0.007	0	0.002	0.021	0.009	0	0.007	0	0.008
Moss	0	0	0	0	0	0	0	0	0	0	0	0
Marsh	0.023	0.005	0	0.002	0	0.005	0	0.004	0	0.001	0	0.002
Dry meadow	0	0.002	0	0.003	0	0.006	0	0.006	0	0.006	0	0.013
Burn	0	0	0	0	0	0	0	0	0	0	0	0
Clear-cut grass dominated	0	0	0	0	0	0	0	0	0	0	0	0
Cutblock tree/shrub dominated	0	0	0	0	0	0	0	0	0	0	0	0
Disturbed grass	0.066	0.020	0.004	0.015	0.105	0.021	0.026	0.022	0.090	0.022	0.017	0.027
Railway	0	0	0	0	0	0	0	0	0	0	0	0
Gravel surface	0	0.002	0	0	0	0.003	0	0.004	0	0.001	0	0.002
Paved surface	0	0.006	0	0.010	0	0.007	0	0.006	0	0.009	0	0.005
Mowed lawn	0	0	0	0	0.008	0.003	0.041	0.003	0	0.003	0	0
Building	0	0	0	0	0	0	0	0	0	0.001	0	0
Crop/hay field	0.099	0.135	0.021	0.049	0.387	0.334	0.185	0.181	0.150	0.200	0	0.172
Pasture/sparsely vegetated	0.174	0.467	0.360	0.572	0.063	0.217	0.200	0.347	0.040	0.260	0	0.262
Exposed soil	0	0	0	0.001	0	0.001	0	0.003	0	0	0	0.002
Emergent vegetation	0.183	0.010	0.220	0.011	0.004	0.008	0.067	0.011	0	0.010	0	0.005
Water	0.113	0.016	0.216	0.016	0	0.003	0.021	0.014	0	0.013	0	0.003

F. Boreal FGHR

Land-cover type	Breeding Female		Breeding Male		Foraging Female		Foraging Male		Pre-hib. Female		Pre-hib. Male	
	Used	Avail.	Used	Avail.	Used	Avail.	Used	Avail.	Used	Avail.	Used	Avail.
Sample size (n)	94	940	143	1430	85	850	118	1180	64	640	59	590
Conifer	0.106	0.352	0.112	0.310	0.118	0.305	0.508	0.442	0.516	0.392	0.881	0.610
Deciduous	0.085	0.152	0	0.073	0.212	0.235	0	0.108	0.125	0.180	0	0.054
Mixed-wood	0.043	0.080	0	0.015	0.012	0.100	0.119	0.048	0	0.113	0	0.080
Dry shrub	0	0.002	0	0.003	0	0.006	0	0.007	0	0.006	0	0.002
Wet shrub	0.213	0.118	0.497	0.203	0.400	0.104	0.203	0.086	0.188	0.105	0.034	0.047
Moss	0.309	0.085	0.280	0.115	0.024	0.069	0.025	0.087	0.047	0.045	0.034	0.059
Marsh	0	0.005	0	0.003	0	0.002	0	0.003	0	0.002	0	0
Dry meadow	0	0	0	0	0	0	0	0	0	0	0	0
Burn	0.043	0.012	0	0.013	0	0.051	0.051	0.059	0.047	0.050	0	0.063
Clear-cut grass dominated	0	0.018	0.035	0.020	0	0.011	0.042	0.025	0	0.011	0.051	0.012
Cutblock tree/shrub dominated	0.021	0.014	0	0.054	0.024	0.019	0.008	0.027	0	0.005	0	0.005
Disturbed grass	0.170	0.147	0.063	0.155	0.212	0.094	0.042	0.092	0.078	0.088	0	0.061
Railway	0	0	0	0	0	0	0	0.001	0	0	0	0
Gravel surface	0	0.013	0	0.029	0	0.004	0	0.013	0	0.005	0	0.002
Paved surface	0	0	0	0	0	0	0	0	0	0	0	0
Mowed lawn	0	0	0	0	0	0	0	0	0	0	0	0
Building	0	0	0	0	0	0	0	0	0	0	0	0
Crop/hay field	0	0	0	0	0	0	0	0	0	0	0	0
Pasture/sparsely vegetated	0	0	0	0	0	0	0	0	0	0	0	0
Exposed soil	0	0	0	0	0	0	0	0	0	0	0	0
Emergent vegetation	0	0	0	0	0	0	0	0	0	0	0	0
Water	0.011	0.002	0.014	0.007	0	0.001	0	0.003	0	0	0	0.005

Land-cover type	Breeding Female		Breeding Male		Foraging Female		Foraging Male		Pre-hib. Female		Pre-hib. Male	
	Used	Avail.	Used	Avail.	Used	Avail.	Used	Avail.	Used	Avail.	Used	Avail.
Sample size (n)	31	310	56	560	68	680	39	390	27	270	27	270
Conifer	0.097	0.019	0	0.036	0	0.053	0	0.005	0	0.033	0	0.022
Deciduous	0.194	0.197	0.018	0.188	0.485	0.284	0.077	0.210	0.667	0.300	0	0.196
Mixed-wood	0	0	0	0	0	0	0	0	0	0	0	0
Tall shrub	0	0	0	0	0	0	0	0	0	0	0	0
Wet shrub	0	0.052	0.018	0.059	0.015	0.063	0	0.049	0	0.067	0	0.056
Wet herbaceous	0	0	0	0	0	0	0	0	0	0	0	0
Herbaceous cover	0.419	0.268	0.143	0.225	0.132	0.296	0	0.233	0.296	0.256	0.148	0.252
Exposed land	0	0	0	0	0	0	0	0	0	0	0	0
Water	0.290	0.465	0.821	0.493	0.368	0.304	0.923	0.503	0.037	0.344	0.852	0.474

H. Pasture CGHR

Land-cover type	Breeding Female		Breeding Male		Foraging Female		Foraging Male		Pre-hib. Female		Pre-hib. Male	
	Used	Avail.	Used	Avail.	Used	Avail.	Used	Avail.	Used	Avail.	Used	Avail.
Sample size (n)	213	2130	236	2360	238	2380	195	1950	100	1000	60	600
Conifer	0.099	0.085	0.089	0.083	0.202	0.121	0.128	0.098	0.360	0.116	0.150	0.113
Deciduous	0.169	0.151	0.034	0.100	0.214	0.198	0.195	0.166	0.300	0.213	0.283	0.218
Mixed-wood	0	0	0	0	0	0	0	0	0	0	0	0
Tall shrub	0	0	0	0	0	0	0	0	0	0	0	0
Wet shrub	0.061	0.035	0.013	0.035	0.084	0.040	0.108	0.044	0.080	0.036	0.200	0.035
Wet herbaceous	0	0	0	0	0	0	0	0	0	0	0	0
Herbaceous cover	0.610	0.719	0.856	0.771	0.492	0.634	0.569	0.680	0.260	0.622	0.367	0.620
Exposed land	0	0	0	0	0	0	0	0	0	0	0	0
Water	0.061	0.009	0.008	0.010	0.008	0.007	0	0.009	0	0.013	0	0.013

I. Boreal CGHR

Land-cover type	Breeding Female		Breeding Male		Foraging Female		Foraging Male		Pre-hib. Female		Pre-hib. Male	
	Used	Avail.	Used	Avail.	Used	Avail.	Used	Avail.	Used	Avail.	Used	Avail.
Sample size (n)	94	940	143	1430	85	850	118	1180	64	640	59	590
Conifer	0.255	0.321	0.098	0.271	0.306	0.288	0.373	0.390	0.344	0.441	0.780	0.554
Deciduous	0.181	0.185	0.189	0.166	0.459	0.275	0.119	0.135	0.297	0.206	0.034	0.085
Mixed-wood	0.053	0.049	0	0.016	0.035	0.131	0.059	0.084	0.063	0.117	0.102	0.071
Tall shrub	0.021	0.016	0.098	0.030	0	0.004	0.025	0.022	0	0.005	0	0.003
Wet shrub	0.160	0.215	0.224	0.248	0.188	0.172	0.271	0.203	0.234	0.158	0.085	0.217
Wet herbaceous	0.074	0.091	0.021	0.097	0.012	0.091	0.136	0.058	0.016	0.052	0	0.044
Herbaceous cover	0	0.009	0.021	0.017	0	0.013	0.008	0.009	0.047	0.006	0	0
Exposed land	0.255	0.114	0.350	0.155	0	0.027	0.008	0.099	0	0.016	0	0.025
Water	0	0	0	0	0	0	0	0	0	0	0	0

Appendix H. Physical characteristics of different types of hibernacula from three study sites in north-central Alberta in Chapter 4. Soil texture was determined using the soil texture triangle (NASA's Goddard Space Flight Center. 2002. Soil texture – to determine soil texture. Available from http://soil.gsfc.nasa.gov/pvg/texture2.htm. [Accessed 2 July 2009].). Soil textures are organic (O), organic/needles (O/N), clay loam (CL), sandy loam (SL), loamy sand (LS), loam (L), sandy clay loam (SCL), silt loam (SiL). Percent organic composition of the soil was determined using the 'direct estimation of organic matter by loss-on-ignition' method (Ravindranath, N.H., and M. Ostwald. 2007. Carbon Inventory Methods Handbook for Greenhouse Gas Inventory, Carbon Mitigation and Roundwood Production Projects. Springer, Netherlands.). Percent moisture and pH of the soil were determined using a pH/soil moisture reader (Kelway). Canopy cover was measured using a spherical densiometer; measurements were taken at waist height and the average of four readings (facing each of the four cardinal directions) was used. Soil moisture, pH, and canopy cover were not recorded in 2004.

	Peat hummock	Squirrel midden	Crevasse	Spruce cavity	Root channel	Beaver lodge	Muskrat tunnel
N	15	9	8	6	5	4	3
Soil textures	O	O, O/N	O	O, O/N	O	O, CL, SL, LS	L, SCL, SiL
Mean (range) % organic of soil	86 (74–96)	81 (66–97)	86 (71–89)	75 (64–84)	76 (57–84)	9 (2–18)	7 (3–12)
Mean (range) % moisture of soil	58 (40–71)	66 (45–100)	73 (65–80)	62 (30–75)	54 (30–70)	60	NA
Mean (range) soil pH	6.7 (6.4–7.0)	6.6 (6–7)	7 (6.9–7.1)	6.9 (6.6–7)	6.9 (6.7–7)	7 (6.9–7)	NA
Mean (range) % canopy cover	42 (8–77)	80 (53–95)	13 (4–22)	76 (47–95)	28 (3–56)	33 (15–42)	NA
Mean (range) depth of toad below surface (cm)	44 (30–70)	38 (30–50)	~80 (~20–100)	47 (30–70)	39 (25–53)	79 (35–130)	31 (30–34)
Depth to water table (cm)	>= 33	>= 40	NA	NA	>= 38	NA	NA
Tunnel/cavity width (cm)	6.5 to 100	4 to 15	2 to 5	>= 10	>= 15	10 to 40	9

Appendix I. Dominant plant taxa recorded in the immediate vicinity of western toad (*Anaxyrus boreas*) hibernation sites (listed in approximate order of abundance) at three study sites in north-central Alberta in Chapter 4.

Type	Site	Under-story vegetation
Peat hummock	Boreal	Labrador tea (*Rhododendron groenlandicum*), lingonberry (*Vaccinium vitis-idaea*), grass (family Poaceae), horsetail (*Equisetum spp.*), false Soloman's seal (*Maianthemum spp.*), currant (*Ribes spp.*), kidney leaf violet (*Viola renifolia*), raspberry (*Rubus idaeus*), and red-osier dogwood (*Cornus stolonifera*).
	Pasture	Labrador tea.
Red squirrel midden	Boreal	No vegetation at three sites. Labrador tea, lingonberry, and horsetail at one site.
	Pasture	Sparse vegetation. Bunchberry (*C. canadensis*), raspberry, and grass on some locations.
Natural crevasse	Park	Grass, stinging nettle (*Urtica dioica*), and raspberry.
	Pasture	Grass, stinging nettle, and raspberry.
Spruce cavity	Pasture	Grass, kidney leaf violet and Labrador tea.
Root channel	Boreal	Grass, raspberry, current, sweet-scented bedstraw (*Galium triflorum*), and horsetail.
	Pasture	Grass and bunchberry.
Beaver lodge	Park	Stinging nettle, hemp-nettle (*Galeopsis tetrahit*), and grass.
	Pasture	Aspen (*Populus tremuloides*), red-osier dogwood, rose (*Rosa acicularis*), bracted honeysuckle (*Lonicera involucrata*), snowberry (*Symphoricarpos spp.*), and horsetail.
Muskrat tunnel	Park	Hazelnut (*Corylus cornuta*), grass, and willow (*Salix spp.*) at some or all of the sites.