

COMPARATIVE ECOLOGY OF THREE SYMPATRIC SNAKE SPECIES IN
SOUTHWESTERN SASKATCHEWAN

A Thesis

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by

Laura Elaine Gardiner

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SUPERVISORY AND EXAMINING COMMITTEE

Laura Elaine Gardiner, candidate for the degree of Master of Science in Biology, has presented a thesis titled, ***Comparative Ecology of Three Sympatric Snake Species in Southwestern Saskatchewan***, in an oral examination held on June 28, 2012. The following committee members have found the thesis acceptable in form and content, and that the candidate demonstrated satisfactory knowledge of the subject material.

External Examiner: Dr. Shelley D. Pruss, Parks Canada Agency

Co-Supervisor: *Dr. Christopher Somers, Department of Biology

Co-Supervisor: Dr. Ray Poulin, Adjunct

Committee Member: Dr. Mark Brigham, Department of Biology

Chair of Defense: Dr. Patrick Neary, Faculty of Kinesiology & Health Studies

*Not present at defense

THESIS ABSTRACT

My research focused on the comparative ecology of three sympatric snake species which are of conservation concern in southwestern Saskatchewan: eastern yellow-bellied racers (*Coluber constrictor flaviventris*), a Threatened species in Canada; bullsnakes (*Pituophis catenifer sayi*), Data Deficient, and; prairie rattlesnakes (*Crotalus viridis*), yet to be assessed, but considered a high priority candidate. Few studies on snake ecology have collected data for multiple species at the same site, a factor potentially important for understanding resource partitioning and competition between sympatric species. Furthermore, identifying which resources elicit competition may be critical for the conservation and management of endangered species. I used radio-telemetry, GIS, and multivariate modeling to identify and compare habitat use by racers (n = 33), bullsnakes (n = 16), and rattlesnakes (n = 23) in and around Grasslands National Park, Saskatchewan, Canada. Used and available macrohabitat sites were compared to quantify habitat use by these species. I found that although all species hibernate in communal den sites, during the active season they disperse into different macrohabitats across the landscape. As a result, home ranges were dumbbell-shaped with activity centers near hibernacula and in well-defined areas used in summer, and these centers of activity were connected by narrow corridors. Bullsnakes had the smallest home range (4.6 ± 0.7 ha), while racers (14.2 ± 0.9 ha) and rattlesnakes (13.9 ± 1.5 ha) were similar. Racers strongly selected for riparian areas, bullsnakes tended to inhabit valley grassland habitats, and rattlesnakes tended to be associated with prairie dog colonies. Some rattlesnakes travelled great distances (over 11 km) from the dens compared to the other species (bullsnake maximum = 4 km; racer maximum = 5 km), which may be a result of the macrohabitat

selected being more patchily distributed in the landscape. In addition, I identified microhabitat selection by rattlesnakes which selected for sites with cover (*e.g.* shrubs and burrows) along the edges of prairie dog colonies. The habitat use by the three species I studied is consistent with habitat partitioning during the active season, though overlap does occur at the overwintering sites and in movement between selected macrohabitats. In addition to the general ecological value of my findings, the results of this study will be useful in aiding designation of critical habitat for the eastern yellow-bellied racer and contribute to assessment of bullsnakes and prairie rattlesnakes in Canada.

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DEDICATION

To my mother and father, without whom I would have never developed such an understanding and love for nature; nor would I have achieved as much as I have.

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CHAPTER 1
GENERAL INTRODUCTION

1.1 Habitat Selection in Animals

Selected habitats are a subset of available ones, and the criteria that influence the decision to select for or against particular habitats are a major component of ecological research. Habitat selection involves the consideration of multiple biotic and abiotic factors (Martin 2001), including, but not limited to, environmental conditions (Blouin-Demers and Weatherhead 2001*b*), vegetation structure (Steen et al. 2010), predation risk (Amo et al. 2006, Pietrek et al. 2009, Webb et al. 2009), and proximity to resources such as food or mates (Diller and Wallace 1996, Duvall and Schuett 1997, Blouin-Demers and Weatherhead 2001*a*). Identifying which resources are required by animals is critical to understanding their ecology, and also for the conservation and management of endangered species (Manly et al. 2002). Determining which resources are selected by animals and documenting the availability of those resources, is a common issue for biologists.

Quantifying selection is a challenge for biologists, and often involves identifying habitats used by animals and comparing them to a suite of available habitats (Johnson 1980, Manly et al. 2002, Buskirk and Millspaugh 2006, Thomas and Taylor 2006). The availability of resources in nature is rarely static, therefore used resources should be compared to the currently available resources to accurately measure selection. When resources such as habitat are used disproportionately to their availability, this is defined as selection (Manly et al. 2002). Presumably, animals select (on average) resources that will increase their fitness, and thus high quality habitats will be selected over low quality ones (Manly et al. 2002, Moore and Gillingham 2006, Thomas and Taylor 2006). The term ‘preference’ is often incorrectly used synonymously with ‘selection’, but should

only be used if all resources are equally available to the selector, which is rarely the case in nature (Manly et al. 2002). Documenting disproportional selection of habitats by animals reveals fundamental information about how animals meet their needs for survival, and thus is especially crucial in efforts to preserve species at risk (Manly et al. 2002). The difficulty lies in discerning what should be considered ‘available’ to animals (Buskirk and Millsaugh 2006). Available habitats should be as equally accessible as used habitats, though when first documenting the habitat selection of a species, we rarely understand what limits their access to certain habitats. For spatially distributed habitats, spatial ecology such as movement patterns (Martino et al. 2012) and home range (Kapfer et al. 2008) can be used to determine what is available to a population. The criteria for selection may differ at different spatial scales however, so the scale at which selection is being studied should be considered.

Habitat availability within a landscape may not be equal across multiple spatial scales (Wiens 1989). There is no one single correct spatial scale at which to quantify selection, so multi-scale analyses of habitat selection are becoming more common (Johnson 1980, Law and Dickman 1998, Boyce 2006, Moore and Gillingham 2006, Lagory et al. 2009). Habitat selection occurs in a hierarchical fashion, ranging from a larger, more generalized scale (macrohabitat), to a smaller, more localized scale (microhabitat). Macrohabitat selection occurs when an individual establishes a home range (second-order) within the geographic range of the species (first-order selection, Johnson 1980), while microhabitat selection occurs when an individual bases its movement decisions on the conditions at specific points within their macrohabitat, such as a refuge or foraging site (third-order selection, Johnson 1980). Considering the

difference in home range size (*i.e.* macrohabitat selection) between species, the relative size of macrohabitat versus microhabitat will vary depending on the species of interest. Although critical for effective conservation planning, multi-scale habitat selection remains poorly understood for most wild vertebrates.

1.2 Habitat Selection in Herpetofauna

Herpetiles as a group are underrepresented in the literature in comparison to endothermic vertebrates (*e.g.* birds and mammals). For example, there are far more species of amphibians in the world than mammals, though there are about 10 times the number of papers on mammalian ecology than on amphibians (Shine and Bonnet 2000). Ecological research is therefore massively disproportionate to the taxonomic distribution of terrestrial vertebrate biodiversity. The distribution of research remains unbalanced even within herpetofauna. Though often considered collectively as ‘herpetofauna’, reptiles appear to be in greater danger of global extinction than amphibians, with over four times the number of species at risk (Gibbons et al. 2000).

The amount of research on resource selection of herpetofauna lags behind that of the aforementioned groups for a variety of reasons. Many herpetile species are small, cryptic, elusive, and rarely active, making them difficult to observe. Radio-telemetry becomes a necessity to study habitat use of such groups, but until recently this was difficult due to logistic constraints such as transmitter size. External transmitters such as radio-collars are of little use for certain herpetiles, especially snakes. As such, the need for surgical procedures for implantation of radiotransmitters further complicates research on some herpetofauna. Furthermore, some species are venomous, making them difficult

to handle and risky to study. Snakes are one of the most notorious groups to work with, and the literature reflects this as they receive relatively little consideration compared to other reptiles and amphibians (Toft 1985, Luiselli 2006). Despite these constraints, the need for studies on the ecology of herpetofauna is becoming increasingly urgent, as there are more species of amphibians and reptiles at risk than either birds or mammals (IUCN 2011). Spatial ecology and habitat selection data form the base from which management plans and recovery strategies are delineated. Furthermore, habitat loss is the main contributor to the decline of herpetofauna worldwide (Gibbons et al. 2000, Foley et al. 2005), so studies on the habitat selection of herpetiles, especially snakes, are crucial to the identification of critical habitat and thus the conservation of these species.

1.3 Habitat Selection in Snakes

Habitat selection studies on snakes were uncommon until the early 1990s, albeit with a few exceptions (Fitch and Shirer 1971, Reinert and Kodrich 1982, Weatherhead and Charland 1985). Research on North American snake ecology is particularly sparse regarding habitat selection. With habitat loss being one of the major factors in declining snake species worldwide, a greater understanding of the interactions between these species and their environment is required (Gibbons et al. 2000). Populations at their northern range limits are of particular interest because environmental factors most likely affect their distribution in these areas. The harsh northern climate consisting of shorter summers and longer winters is often accompanied by lower productivity (Harestad and Bunnell 1979). The need to secure enough resources in a less productive environment often results in animals in northern peripheral populations having to travel farther to

satisfy energetic demands than southern populations (Harestad and Bunnell 1979, Arvisais et al. 2002). Kapfer et al. (2008) studied bullsnakes (*Pituophis catenifer sayi*) at the northern periphery of their geographic range in Wisconsin, and found that they had larger movements and home range sizes than previously studied southern populations of the same species. Several snake species exist at the northern extent of their geographic range in southwestern Saskatchewan, but many of these species have not been studied extensively (Martino et al. 2012, Kissner 1996). Furthermore, in Canada, most published studies of snake ecology have focused on non-grassland communities (e.g. Weatherhead and Charland 1985, Blouin-Demers and Weatherhead 2001*a*, 2001*b*, 2001*c*, Harvey and Weatherhead 2006), resulting in a limited understanding of the spatial ecology and habitat use of Canadian grassland snakes.

1.4 Rationale for Studying Saskatchewan Snakes

Due to differences in biotic and abiotic interactions, selection pressures may be different throughout a species' range (Ferguson 2002, Ewert et al. 2005). Animals at the periphery of their geographic range often experience extreme or unique selection pressures which may put these peripheral populations at a greater risk of extinction (Brooks 2000). Southwestern Saskatchewan is home to a community of snakes unique in Canada, consisting of several species at the northern edge of their geographic range. This area may have climatic conditions that approach a threshold of thermal tolerances for these species, making optimal habitat selection crucial to their survival. Several of these species have been studied in the core of their geographic range (the USA), but little attention has been paid to the northern peripheral populations in Canada. Because of

ecological differences associated with latitude and climate, data from southern populations are probably not sufficient on which to base conservation and management decisions in Canada (Cagle 2008).

The Frenchman River Valley of southwestern Saskatchewan is home to various snake species including eastern yellow-bellied racers (*Coluber constrictor flaviventris*), prairie rattlesnakes (*Crotalus viridis*), bullsnakes (*Pituophis catenifer sayi*), western hognose (*Heterodon nasicus*), and plains (*Thamnophis radix*) and terrestrial (*T. elegans*) garter snakes. Unstable slump zones along the slopes of the river valley are a common location for winter hibernation sites for snakes in the area. Snakes are dependent on suitable winter hibernacula for persistence at higher latitudes, and it is common to find more than one species hibernating together at communal hibernation sites in this area; this is likely a response to limited availability of suitable locations for over-wintering. The number and type of snake species occupying hibernacula vary by location, but can be as high as hundreds of individuals (e.g., Gardiner et al. 2011). Eastern yellow-bellied racers have been assessed as a Threatened species in Canada (COSEWIC 2004). Seven hibernacula have been identified as critical habitat for racers in Canada (COSEWIC 2004); the largest den was estimated to contain over 300 racers in 2010 (Gardiner et al. 2010), though this den slumped in 2011 causing a 50% decrease in population size (Gardiner and Sonmor 2011). Little information exists on bullsnakes in Canada, and thus they are currently considered Data Deficient by COSEWIC (COSEWIC 2002). Prairie rattlesnakes have not been assessed by COSEWIC, but they are considered a high priority candidate for assessment (www.cosewic.gc.ca).

Racers and bullsnakes have been studied previously in the Frenchman River Valley (Martino et al. 2012), though information on how their habitat selection relates to other snake species in the community such as rattlesnakes is lacking. Rattlesnakes share winter habitat with racers and bullsnakes in this area, but the differences and similarities in the habitat use of these species during the active season is unknown. In addition, habitat selection of rattlesnakes is of interest in the area due to increasingly frequent interactions with humans due to increasing tourism in the park. Previous studies have focused on the thermal biology (Charland and Gregory 1990, Brown 1991, Graves and Duvall 1993, Shoemaker and Gibbs 2010) and antipredator behaviour (Kissner 1996) of rattlesnakes, rather than their spatial ecology. My research will provide information on the spatial ecology and habitat selection of these species at the northern periphery of their range. In my second chapter I will describe the differences and similarities in habitat use between racers, bullsnakes, and rattlesnakes. Being sympatric species in this area of their range, these species present some interesting research questions such as whether or not the potential for competition exists, at what scale this competition may be occurring, and whether these species are habitat specialists or generalists. These differences may lead to a better understanding of the basic biology of these species, as well as grassland snakes in general. In my third chapter, I will identify microhabitat selection by rattlesnakes, as microhabitat selection has already been identified in racers and bullsnakes (Martino et al. 2012). The results from my study will also contribute to the development of management strategies for these species or for this ecosystem.

1.5 Study Objectives

1. Describe the differences and similarities of habitat uses by eastern yellow-bellied racers, bullsnakes, and prairie rattlesnakes in southwestern Saskatchewan

2. Identify microhabitat features selected by prairie rattlesnakes in southwestern Saskatchewan

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CHAPTER 2

EVIDENCE OF HABITAT PARTITIONING IN A GRASSLAND SNAKE

COMMUNITY: IMPLICATIONS FOR CONSERVATION

ABSTRACT

The grasslands of southwestern Saskatchewan are home to a variety of snake species at the northern extreme of their geographic range in North America, including the (Threatened) eastern yellow-bellied racer (*Coluber constrictor flaviventris*), the (Data Deficient) bullsnake (*Pituophis catenifer sayi*), and the prairie rattlesnake (*Crotalus viridis*), which is considered a high priority species for status assessment. To aid conservation assessment of these species, we used radio-telemetry, GIS, and multivariate modeling to identify and compare habitat use by racers (n = 33), bullsnakes (n = 16), and prairie rattlesnakes (n = 23) in and around Grasslands National Park, Saskatchewan, Canada. Used and available macrohabitat sites were compared to quantify habitat use. We found that although all three species share hibernacula in the inactive winter season, during the active season they disperse into different macrohabitats across the landscape. As a result, home ranges were dumbbell-shaped with activity centers near hibernacula and in well-defined summer grounds, and these two centers of activity were connected by narrow corridors. Racers strongly selected for riparian areas along streams, bullsnakes selected for valley grassland habitats, and rattlesnakes selected for areas associated with prairie dog colonies. Some rattlesnakes were found to travel great distances (over 11 km) from the dens compared to the other species (bullsnake maximum = 4 km; racer maximum = 5 km), which may be a result of their selected macrohabitat being more patchily distributed in the landscape. Our findings will be useful for designating critical habitat for the eastern yellow-bellied racer and contribute to assessment of bullsnakes and prairie rattlesnakes in Canada.

INTRODUCTION

Habitat selection can have a great effect on the survival and reproductive success of a species. Although critical for effective conservation planning, habitat selection remains poorly understood for most wild vertebrates (Manly et al. 2002). Due to the rapid decline in biodiversity across the globe, identifying critical habitat has become increasingly urgent. Terrestrial ectothermic vertebrates are declining on a global scale (Gibbons et al. 2000), though there is limited published information about their ecology, especially regarding habitat selection. Reptiles are considerably underrepresented due to the current focus on the worldwide amphibian decline. Relative to amphibians, more species of reptiles exist in the world, and are in even greater danger of global extinction (Gibbons et al. 2000). The lack of focus on terrestrial squamates, especially snakes, in the scientific literature may stem from the fact that they can be difficult to work with (Shine and Bonnet 2000). Many species are cryptic, elusive, and venomous, thus potentially dangerous to work with. The conservation of snake species is hindered by the fact that many features of their ecology and natural history are not well known, so research on the interactions between snakes and their environment is needed (Gibbons et al. 2000, Shine and Bonnet 2000).

Studies on habitat selection and niche partitioning in sympatric species have important implications for conservation, as the data will reveal levels of potential competition. Differences in niche selection between similar species reduce interspecific competition allowing ecological equivalents to coexist in equilibrium (Gause 1934). Studies on the community ecology of snakes are rare in general, though there are some notable exceptions (Hirth et al. 1966, Fitch and Shirer 1971, Keller and Heske 2000).

Data on habitat partitioning in snakes are especially scarce and lags behind that of other taxonomic groups such as lizards, birds, and small mammals (Schoener 1974).

Conflicting results have been reported in the few studies that have attempted to document habitat partitioning in snakes, so its level of importance in this group is unknown (Carpenter 1952, Pough 1966, Hebrard and Mushinsky 1978, Keller and Heske 2000).

We examined the movement patterns and macrohabitat use of 3 sympatric snake species at the northern extreme of the mixed grass prairie ecoregion of North America (Canada). This area contains a unique (for Canada) snake community where eastern yellow-bellied racers (*Coluber constrictor flaviventris*), prairie rattlesnakes (*Crotalus viridis*), bullsnakes (*Pituophis catenifer sayi*), western hognose (*Heterodon nasicus*), and plains (*Thamnophis radix*) and terrestrial (*T. elegans*) garter snakes co-exist. Eastern yellow-bellied racers (hereafter racers) are a Threatened species in Canada (COSEWIC 2004), with their range confined to a couple river valleys in southern Saskatchewan and extreme southeastern Alberta (Gardiner et al. 2011). Racers meet the criteria of an Endangered species, but are currently listed as Threatened as the majority of their known range is protected by Grasslands National Park (COSEWIC 2004). Bullsnakes are listed as Data Deficient, as sufficient information does not exist for a proper conservation status assessment to be made (COSEWIC 2002). Prairie rattlesnakes (hereafter rattlesnakes) have yet to be assessed, though they are considered a high priority candidate for assessment due to suspected population declines (Watson and Russell 1997). These three species are vulnerable to extinction in Canada due to habitat loss; they have specific requirements for suitable hibernacula, and are known to exhibit high site fidelity (Ernst and Ernst 2003, COSEWIC 2004, Kapfer et al. 2008, Gardiner and Sonmor 2011).

Although essential for effective conservation planning, little information exists on the spatial ecology and habitat selection of these species (Kapfer et al. 2008, Martino et al. 2012). We identified and compared movement patterns and habitat use between these 3 sympatric species to assist future management decisions regarding these species at the northern extreme of their range.

MATERIALS AND METHODS

Study Area – Research was conducted within and around the West Block of Grasslands National Park (49°10'37"N 107°25'33"W), Saskatchewan, Canada from May to September each year from 2008 to 2011. The west block of Grasslands National Park consists of ~ 49,000 ha of federally protected land in the southwest part of the province. Work was also conducted in a nearby Prairie Farm Rehabilitation Administration (PFRA) community pasture which covers ~ 41,000 ha of federal land northwest of Val Marie. Snakes were captured from three communal dens within the park, in addition to two communal dens in the PFRA community pasture.

The study area is in the northern mixed grass prairie ecoregion and encompasses a large variety of habitats. In terms of macrohabitat, the Frenchman River passes through this region of Saskatchewan, creating unique topography and landscape features. The river valley consists of many steep bluffs and coulees forming upland and lowland areas. Though this area of Saskatchewan has some of the largest remnants of native prairie left in the province, it is highly fragmented by agriculture. With respect to microhabitat, the native plant community of this region typically consists of needle-and-thread (*Stipa comata*), blue grama (*Bouteloua gracilis*), and western wheatgrass (*Agropyron smithii*),

as well as woody species such as sagebrush (*Artemisia* spp.), greasewood (*Sarcobatus vermiculatus*), snowberry (*Symphoricarpos albus*) and creeping juniper (*Juniperus horizontalis*). Burrows are common in the area, created by small mammals such as Richardson's ground squirrels (*Uroditellus richardsonii*), mountain cottontails (*Sylvilagus nuttallii*), American badgers (*Taxidea taxus*) and black-tailed prairie dogs (*Cynomys ludovicianus*).

Study Species – The racer is an elusive, non-venomous snake species with an extremely limited known range on the Canadian prairies (Gardiner et al. 2011). Racers are long, slender, smooth snakes which may exceed 1 m in length, and have a varied diet of insects, amphibians, and small mammals (Ernst and Ernst 2003, COSEWIC 2004). Closely related subspecies of racers to those found in Canada have been studied extensively in the United States (Hirth et al. 1966, Fitch and Shirer 1971, Brown and Parker 1976, Klug et al. 2011a, Klug et al. 2011b), but only one study exists in Canada (Martino et al. 2012). Bullsnares are the largest snake in western Canada; a nonvenomous constrictor capable of reaching over 2 m in length and feed almost exclusively on small mammals (Ernst and Ernst 2003). Little information is available on the habitat requirements of this subspecies (Kapfer et al. 2008), and the size and extent of Canadian populations are completely unknown. Prairie rattlesnakes are a wide-ranging pit-viper capable of reaching over 1.5 m in length with a diet also mainly consisting of small mammals (Hill et al. 2001, Ernst and Ernst 2003). Racers and bullsnares are subject to a variety of threats including habitat loss, potentially isolated populations, geographic dispersal barriers, and anthropogenic disturbance. Rattlesnakes face the same

host of threats, in addition to intensified deliberate persecution and a lower reproductive rate making them potentially more vulnerable to population perturbations (Pendlebury 1977, Watson and Russell 1997, Ernst and Ernst 2003). Few published studies exist on the ecology of the prairie rattlesnakes at the northern extreme of their range (Gannon and Secoy 1984, Gannon and Secoy 1985, Charland and Gregory 1990), none of which focused on their spatial ecology. All three of these species range extensively throughout the United States, though are limited in their Canadian range to southern Saskatchewan and Alberta (Pendlebury 1977, Ernst and Ernst 2003, Gardiner et al. 2011). Little is known about the habitat use of these species at the northern periphery of their geographic range (Kapfer et al. 2008, Martino et al. 2012).

Snake Capture and Tracking - The active season for snakes in Saskatchewan extends from late April until October. Snakes were caught at five different dens during emergence from hibernation using a combination of drift fences with snake traps, opportunistic visual encounters, and road surveys. The majority of snakes were captured by hand at known den sites; or with snake hooks and tubes for rattlesnakes. Individuals were then measured (snout to vent length and tail length), weighed, and sexed (via cloacal probing) (Schaefer 1934). All individuals caught, except small juveniles, were also injected with passive integrated transponders (EIDAP Inc., Sherwood Park, Alberta, Canada) for unique identification. We transported the snakes, housed in individual containers, to the Western College of Veterinary Medicine in Saskatoon. Snakes were surgically implanted with Holohil Systems Ltd. radio-transmitters (model SB-2, mass = 4–5 g, Holohil Systems Ltd., Carp, Ontario, Canada) by veterinarians following previously established

methods (Reinert and Cundall 1982, see Appendix A). We only implanted transmitters in snakes when transmitter mass represented less than or equal to 5% of the snake's body mass and the diameter of the transmitter was less than 50% of the diameter of the snake at the insertion site. Snakes were allowed to recover for 48 hours, as determined by the veterinarians, prior to being released by hand at the site of capture. Snakes carrying transmitters were tracked every 48 hours from May until September. We did not directly approach the snakes to avoid influencing their movements; we either visually confirmed the snake site from a distance, or estimated the snake's location from a short distance (~1-2 m). Universal Transverse Mercator (UTM) coordinates were recorded whenever a snake was located. All methods were approved by the President's Committee on Animal Care at the University of Regina (AUP 09-09).

Movement Patterns Quantification - Movement patterns were quantified using ArcGIS Desktop 10 (ESRI Inc., Redlands, CA). Location points were laid on top of a Digital Elevation Model (DEM) downloaded from Geobase (www.geobase.ca, October 18, 2011). Other layers such as park boundaries, roads, rivers, and prairie dog colonies were also added. Maximum distances moved were determined with the Point Distance tool. Daily movement rates were determined according to previously published methods (Charland and Gregory 1995). Snake location points were first converted into lines using the Points To Lines tool. The total distance (*i.e.* length) of each line was calculated, and divided by the number of days each individual was tracked. Means are presented ± 1 standard error.

GIS analysis of animal movement was supplemented with fractal dimension (fractal D) analysis, which calculates movement path tortuosity (Fractal 5.20, Nams 1996). Fractal D was estimated using the dividers method (Dicke and Burrough 1988), in which the length of the path is measured by walking a pair of dividers along the path dividing it into smaller pieces. Path length is the summation of straight line distances, or steps, between points where the dividers intersect the path. This is done using larger and larger dividers so the slope of a plot containing $\log(\text{path length})$ vs. $\log(\text{step size})$ can be calculated and subtracted from 1, yielding one overall estimate of fractal D over a range of scales. Fractal D lies between 1 (completely straight) and 2 (so tortuous that the complete two-dimensional space is used). Due to the tracking method used in this study (radio-telemetry), movement path tortuosity was measured at a specific scale. As such, it is reported here as a relative measure between species, based on tracking frequency.

Home Range Quantification – Ninety-five percent fixed kernels (ha), and 50% fixed kernels (ha) were calculated to estimate home range size of individuals via the Hawth's Tools extension for ArcMap 9.2 (Beyer 2004). Only individuals tracked over a minimum of 50 days with at least 15 relocations were included in this analysis. The average daily movement rate calculated for each species was used as the smoothing factor to estimate kernel home ranges. Though atypical, this method produces realistic activity centers based on biologically relevant data. Typical automated methods such as least squares cross-validation (LSCVh) and likelihood cross-validation (CVh) have been shown to produce high variability and under-smoothed data, and increasing debate about the

reliability of these methods exists in the literature (Worton 1989, Horne and Garton 2006, Row and Blouin-Demers 2006).

One hundred percent minimum convex polygons (MCP; ha) were also calculated to enable comparisons with previous studies via ArcMap 10. Only individuals with at least 10 new locations were included in this analysis, based on previous studies (Himes et al. 2006, Kapfer et al. 2008). Locations were defined as new if they were greater than 20 m from the previous location. Minimum convex polygons, however, are sensitive to sample size, and often overestimate home range size of individuals by producing a rough outline of the total area used (Reed and Douglas 2002). Kernel estimates are a more accurate measure of home range size for species with a discrete number of activity centers, and are more useful for wildlife managers as they produce a probability distribution of habitat use.

All movement and home range comparisons between species were analyzed with one-way ANOVAs and Tukey-Kramer post hoc tests when data met the assumptions of normality and homoscedasticity. When data did not meet the assumptions required for parametric tests, Kruskal-Wallis and Dunn's post hoc tests were used. Statistical tests were performed using GraphPad Prism 5 with an alpha value of 0.05.

Macrohabitat Quantification – I defined macrohabitat as the large-scale environment including broad landscape features that are readily observable, such as vegetation and topography (second-order selection, Johnson 1980). Macrohabitats available to the snakes included: native upland, lowland pasture, hills and slopes, mudflats, crop areas, prairie dog colonies, irrigation areas, open water, roads, and riparian areas. Macrohabitat

was determined at each snake location by visual observation of the surrounding area. These data were then analyzed using ArcGIS Desktop 10. Macrohabitat selection was quantified by determining the proportion of time spent in each macrohabitat type in comparison to the proportion of that macrohabitat available to the snakes. The proportion of each macrohabitat available to the snakes was quantified by creating buffers around each den site from which snakes were tracked. Five kilometer buffers were used to determine macrohabitats available to racers and bullsnakes, while 12 km buffers were used for rattlesnakes. Buffer size was determined based on the maximum distances moved (from their den) by any individual from each species. Though maximum dispersal distances differed between racers and bullsnakes, the same buffer size was used as they remained within a relatively similar distance to the den compared to rattlesnakes. Macrohabitats within the buffers were then traced in ArcMap employing a 2.5 m resolution SPOT image (satellite photo). The Union tool was used to calculate the area of each macrohabitat polygon, and the percentage of each polygon within the buffer was then determined. This value was used as the percent available. The macrohabitat associated with each snake location was determined using the Spatial Join tool. The proportion of time spent in each macrohabitat was calculated and used as the percent used value. Time was used instead of number of relocations as time likely better represents the quality of the selected habitat than number of locations.

RESULTS

Movement and Home Range - A total of 72 snakes from 5 dens were relocated on 1422 occasions over 4 years. The 33 individual racers tracked were relocated a total of 680

times; 415 of these locations were considered new. The 16 individual bullsnakes tracked were relocated a total of 372 times; 130 of these locations were considered new. The 23 individual rattlesnakes tracked were relocated a total of 370 times; 200 of these locations were considered new. The number of new locations per snake varied from 2 to 54 for racers, 2 to 19 for bullsnakes, and 2 to 18 for rattlesnakes.

The average daily movement for racers was 65.3 ± 5.0 m, while rattlesnakes moved 92.0 ± 16.2 m per day. Both species moved further than bullsnakes as documented by Martino et al. (2012) (Figure 1a; $F_{2,69} = 3.61$, $P = 0.032$), although post hoc testing revealed that only rattlesnakes moved significantly further than bullsnakes. The maximum distance racers traveled from their den ranged from 186.9 m to 4993.6 m (mean = 2463.7 ± 223.2 m), while rattlesnakes ranged from 533.6 m to 11,107.1 m (mean = 2812.5 ± 601.2 m). Again, both species appeared to move further than bullsnakes as per Martino et al. (2012), although the differences were not significant (Figure 1b; $F_{2,67} = 2.25$, $P = 0.113$). Movement path tortuosity was greatest for racers (fractal D = 1.14 ± 0.01), while bullsnake (fractal D = 1.11 ± 0.02) and rattlesnake (fractal D = 1.10 ± 0.02) movements were straighter (Figure 1c; $H_2 = 6.05$, $P = 0.048$), although post hoc testing revealed that only rattlesnakes travelled significantly straighter than racers.

Regardless of method, racers and rattlesnakes appeared to have larger home range sizes on average than bullsnakes (Table 1, Figure 2). Using the MCP method, however, home range size did not differ significantly between the three species due to the large amount of variation ($H_2 = 5.31$, $P = 0.070$). Kernel density analysis revealed racers and rattlesnakes have similar home range sizes which differ significantly from bullsnakes (95% KD, $F_{2,43} = 22.86$, $P \leq 0.001$; 50% KD, $F_{2,43} = 24.87$, $P \leq 0.001$). Home ranges

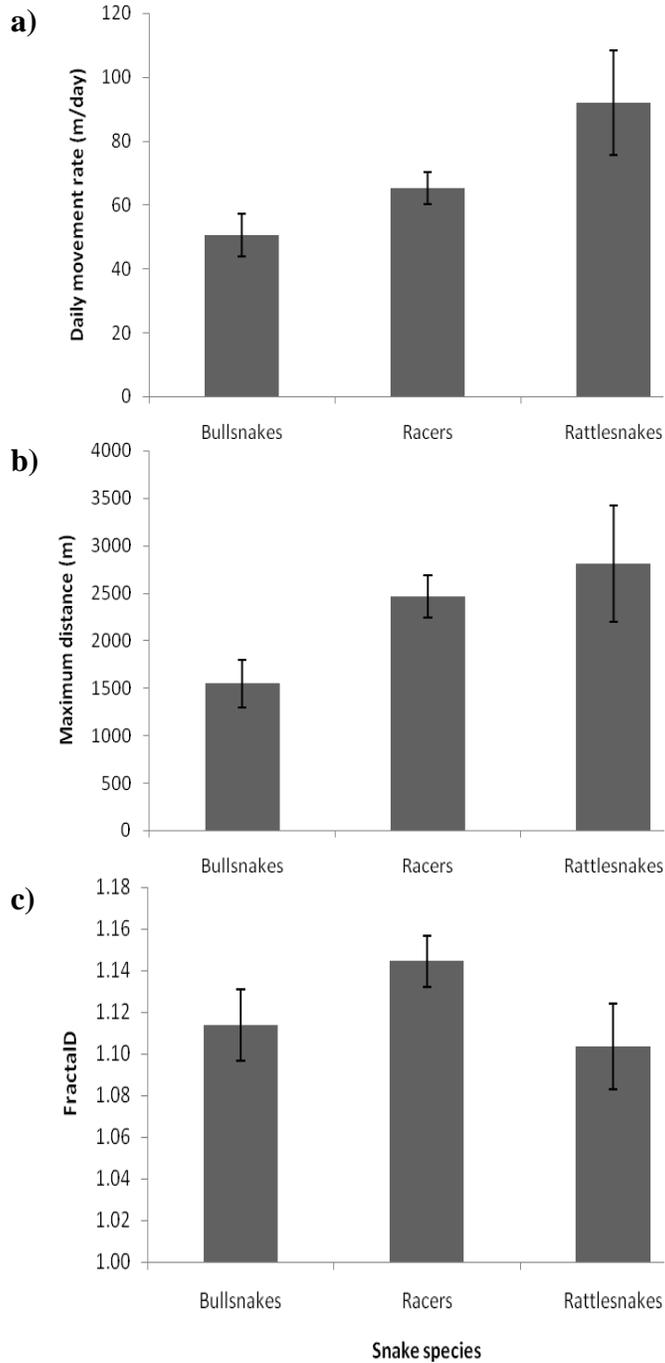


Figure 1. Comparison of daily movement rate (m/day), maximum distance moved from the den (m), and FractalD for sympatric bullsnares, eastern yellow-bellied racers, and prairie rattlesnakes. Bullsnares data are from Martino et al. (2012).

were dumbbell shaped, and thus the kernel results are a more accurate measure of home range size and shape in these species (Figure 3). Home range sizes differed by sex using the MCP method, but not the kernel density method (Table 1). Home range size did not vary significantly with total snake length or number of relocations for any species (data not shown).

Macrohabitat Selection – Racers and rattlesnakes exhibited habitat selection at the landscape scale. Racers used riparian areas 4 times, mudflats 2.5 times, and lowland pasture and hills and slopes almost twice as much as expected based on the availability of these habitats within a 5 km buffer zone around winter dens (Figure 4). Rattlesnakes used prairie dog colonies 11 times, river areas 4 times, and hills and slopes 3 times more than expected (Figure 4). Roads were used according to their availability in the environment by racers and rattlesnakes. In contrast, bullsnakes (Martino et al. 2012) are known to select for roads, lowland pasture, and hills and slopes in the study area (Figure 4). All three species avoid native upland, crop areas, irrigated areas, and open water. Native upland was avoided strongly by racers which used this habitat 18.5 times less than expected. Rattlesnakes strongly avoided crop areas, using them 24 times less than expected based on the availability of these habitats in the environment.

DISCUSSION

Habitat partitioning is occurring with little overlap between these three species despite their communal occurrence at winter hibernacula, which is important to consider when formulating conservation strategies for northern snake communities. Habitat

Table 1. Home range sizes of eastern yellow-bellied racers, prairie rattlesnakes, and bullsnakes calculated using Minimum Convex Polygon (MCP), 95% Kernel, and 50% Kernel Estimates.

Species	MCP (ha)			95% Kernel (ha)	50% Kernel (ha)
	Male	Female	Mean	Mean	Mean
Racers	191.7 ± 67.5	130.2 ± 28.7	159.3 ± 31.7	14.2 ± 0.9	3.0 ± 0.2
Rattlesnakes	78.2 ± 39.9	128.8 ± 74.0	109.3 ± 47.1	13.9 ± 1.5	2.6 ± 0.3
Bullsnakes	-	-	-	4.6 ± 0.7	0.7 ± 0.1

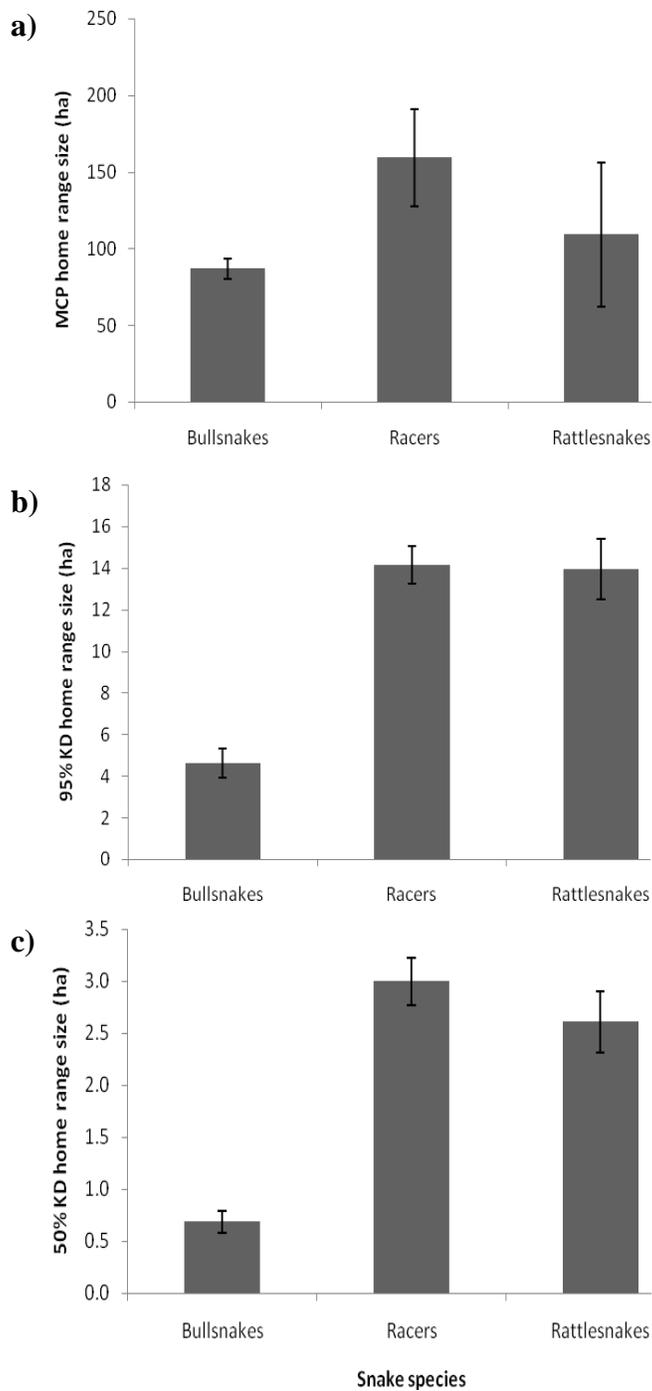


Figure 2. Comparison of home range size (ha) between sympatric bullsnakes, eastern yellow-bellied racers, and prairie rattlesnakes using Minimum Convex Polygon (MCP), 95% Kernel Density (KD), and 50% Kernel Density (KD) techniques. Bullsnares MCP data are from Martino et al. (2012).

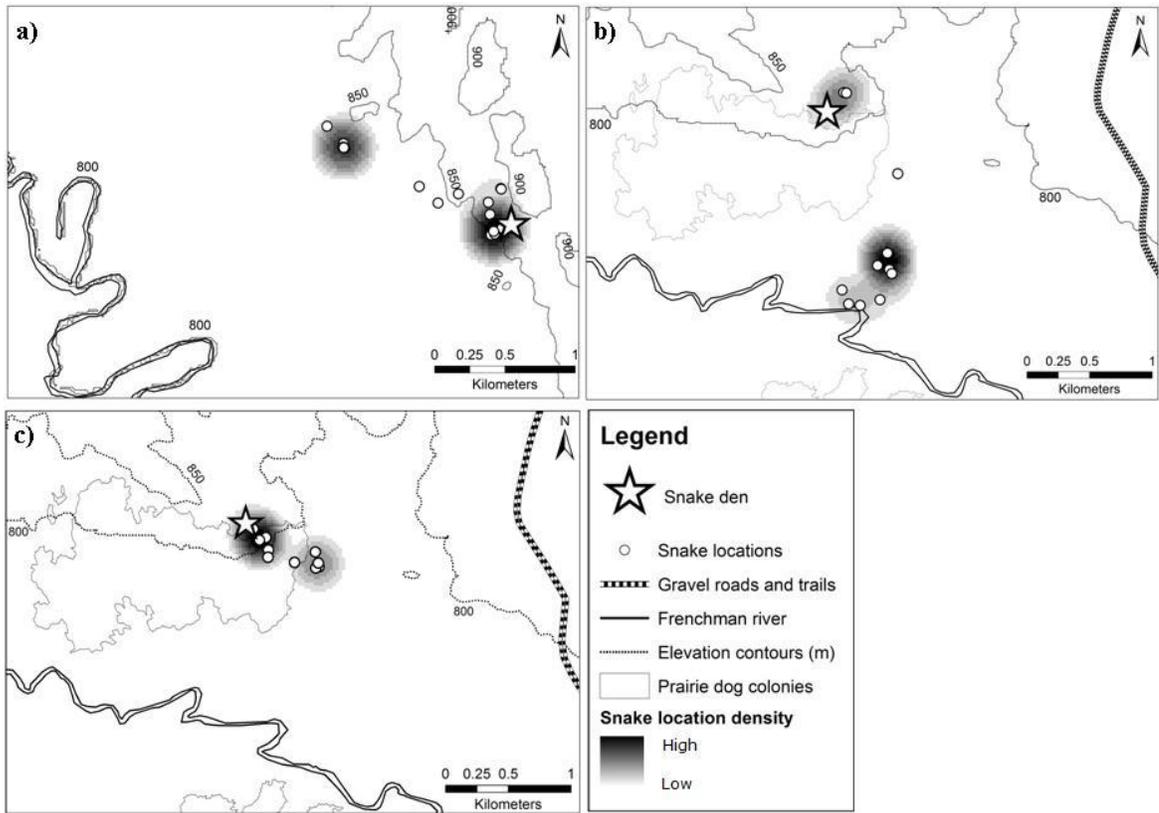


Figure 3. Kernel Density maps of home range shape of representative individuals of sympatric bullsnakes (a), eastern yellow-bellied racers (b), and prairie rattlesnakes (c).

partitioning reduces competition for resources allowing the existence of sympatric species (Gause 1934), though partitioning can occur at different scales. At the geographic scale, racers, bullsnakes, and rattlesnakes overlap in range in this area, though they select different macrohabitats at the landscape scale. Habitat partitioning at this scale has been previously documented in snakes. Keller and Heske (2000) documented habitat partitioning in a snake community in east-central Illinois. Black rat snakes (*Elaphe obsoleta obsoleta*), fox snakes (*E. vulpina vulpina*), and blue racers (*Coluber constrictor foxii*) hibernated communally, although they dispersed into forested habitats, prairies and old fields respectively during the active season. Communal hibernation followed by differential habitat selection during the summer suggests habitat partitioning varies on a temporal scale as well, with partitioning occurring only during the active season when species may compete for resources such as food or nesting sites. Habitat partitioning is not well documented in snakes, but this trend suggests management strategies for a snake community in which most species hibernate, must take into account the various summer habitats required by the different species, in addition to the communal dens.

Summer habitats used by snake species may or may not be site specific. Plummer and Congdon (1994) documented that blue racers in South Carolina were located in shrubby habitats and thickets 50% of the time, forested areas 25% of the time, and grassland 25% of the time, though they did not compare use to availability. These results differ from Keller and Heske (2000), who reported blue racers using open fields rather than shrubs and forests. We found that bullsnakes select mostly for valley grassland habitats, while Kapfer et al. (2008) reported northern populations of bullsnakes using open bluff habitats. These site-specific differences in habitat selection by the same

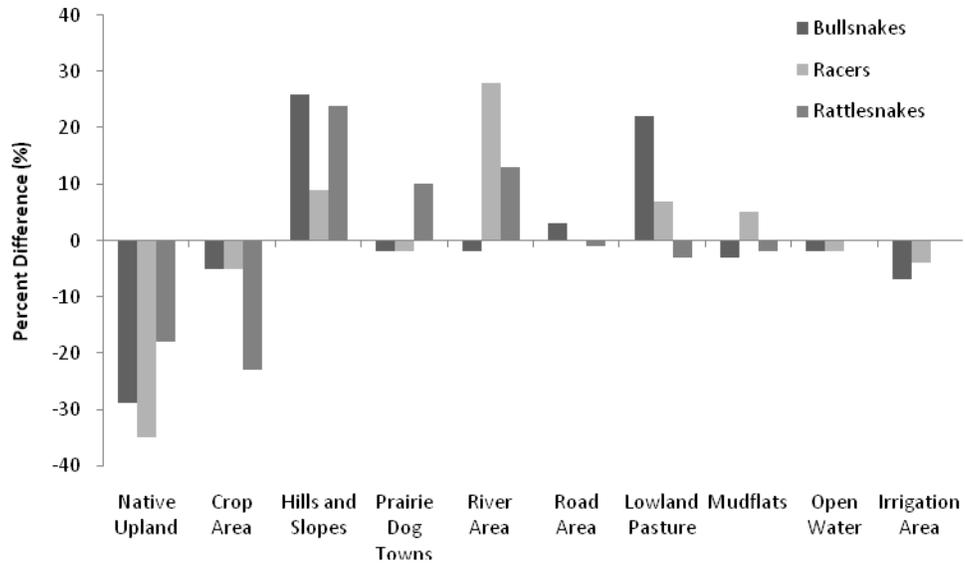


Figure 4. Percent difference (%) between the proportion of landscape types used by versus available to bullsnares, eastern yellow-bellied racers, and prairie rattlesnakes. Bullsnares data are from Martino et al. (2012). Positive values indicate the degree to which habitat was used more frequently than expected based on availability, while negative values indicate the degree to which habitat was avoided.

species may be a result of the available habitats in the area. The various species that make up the local community may also be a factor with respect to summer habitat selection. As habitat partitioning likely reduces competition, and allows the existence of sympatric species (Gause 1934), snakes may adjust their habitat use in response to the other species present in the community. Whether differential habitat use by the same species in different communities is the result of: 1) the available habitats, 2) community composition, or 3) a combination of both must be understood before critical habitat can be identified for differing northern snake communities.

The different movement patterns we recorded for the three species reflect the relative distances of the selected macrohabitats from the hibernacula. Racers likely moved further from the den than bullsnakes because riparian areas were further from the den sites than lowland pastures. The long-distance, straight-line movements we recorded for rattlesnakes may be explained by the patchily distributed prairie dog colonies they selected for (Duvall et al. 1985, Duvall et al. 1990). In Wyoming, prairie rattlesnakes are known to move lengthy, straight-line distances between patchily distributed demes of deer mice (Duvall et al. 1985). This trend suggests that prairie rattlesnakes move in response to the distribution of their selected prey relative to the locally available small mammal species, which are known to make up the majority of their diet (Hill et al. 2001). Rattlesnakes in our study could be further classified into two movement classes: 1) remain in close proximity to the den, or 2) disperse large distances (*i.e.* sitters and rovers respectively, Sokolowski 1998), with few individuals employing an intermediate strategy. The classification of prairie rattlesnakes into 2 movement types has previously been undertaken (Duvall and Schuett 1997), which suggests this phenomenon is a consistent

attribute. Duvall and Schuett (1997), however, suggest that male rattlesnakes are the individuals that make the straight-line movements to increase mating success, though we observed long-distance directed movements equally in both sexes, so our data do not support this hypothesis. Dispersing individuals may maintain gene flow between populations, although if this were the case, then the reason why this phenomenon is not observed in racers and bullsnakes (or is at least less obvious) is unclear. Regardless, critical habitat will likely have to be identified separately for sitting versus roving rattlesnakes.

Home ranges were dumbbell-shaped for all species with activity centers concentrated around winter and summer habitats, connected by movement corridors. Kernel density analysis is therefore a much more accurate estimator of home range shape and size of these species, as has been found for other species of snakes (Reed and Douglas 2002, Rodríguez-Robles 2003). Snakes at the northern periphery of their geographic range are tied to winter hibernation sites, which may or may not be in close proximity to adequate summer habitats. Therefore the distance between winter and summer grounds for snakes may vary. Although racers did not travel nearly as far from the den as rattlesnakes, kernel density analysis revealed their home range sizes to be similar. This is because the activity centers were similar in size, while the length of the movement corridor between the winter and summer grounds for the two species differed. The distance between the winter and summer grounds varied more within rattlesnakes due to the two movement strategies exhibited by this species (*i.e.* sitters and rovers). These distinct movement patterns were the cause of the variation seen in the average daily movement rate, maximum distance moved from the den, and MCP home range size

for rattlesnakes as well. In contrast, bullsnakes had concentrated activity centers closer to the den relative to the other species; again, likely reflecting their selection of a macrohabitat within close proximity to the den sites. All three species therefore vary in the length of their movement corridors, further suggesting they select distinct summer habitats.

MANAGEMENT IMPLICATIONS

Habitat differences between species during the active season should be considered when making management decisions regarding hibernating snake populations. Small reserves around communal hibernacula have been identified as insufficient to protect snakes during the active season (Martino et al. 2012, Williams et al. 2012), and our results show that identifying summer grounds will likely require species-specific considerations. Martino et al. (2012) suggested that simply creating management buffers around dens would likely not be sufficient to include summer grounds in northern snake populations, and they further suggested that this can be mitigated by either defining much larger den buffers or identifying a corridor system linking smaller protected areas surrounding winter and summer habitats. Our results show the home ranges of these northern grassland snakes are indeed dumbbell-shaped, and thus management considerations must include the den area, corridors and the summering grounds. Habitat use during the active season differs by snake species and thus conservation strategies must incorporate these differences. For example, racers strongly avoid prairie dog colonies, though these areas are heavily used by rattlesnakes. Management decisions should therefore consider the snake community by identifying all species present in the

community, and their summer habitat requirements. Furthermore, corridors connecting winter and summer grounds may not be the shortest path between the two. For example, if a prairie dog colony is located between the two activity centers for racers, they appear to take a longer route to avoid this habitat type. Habitat barriers (natural and anthropogenic) must therefore also be considered when identifying an effective corridor system.

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CHAPTER 3
MICROHABITAT SELECTION BY PRAIRIE RATTLESNAKES IN
SOUTHWESTERN SASKATCHEWAN

ABSTRACT

Prairie rattlesnakes (*Crotalus viridis*) range extensively throughout the United States, but are becoming a species of conservation concern in Canada due to suspected population declines. Data on the habitat selection by prairie rattlesnakes are required to inform management strategies and recovery plans. We used radio-telemetry and generalized linear mixed models to identify habitat use by prairie rattlesnakes (7 males, 16 females) in and around Grasslands National Park, Saskatchewan, Canada. Eight habitat variables were compared between used and available microhabitat sites to quantify microhabitat selection by this species. We found that prairie rattlesnakes select for specific sites (*i.e.* within 1 m) with shrub cover and burrows, and avoid bare ground. Shrub cover was 2-fold higher at used habitat sites compared to available sites, while bare ground showed the opposite trend. In addition, two-thirds of individuals were located within 1 m of a burrow. This implies that retreat sites are important in microhabitat selection by this species. Retreat sites were important components of microhabitat selection regardless of the habitat they selected at the larger landscape scale. None of the habitat variables measured were significant predictors of rattlesnake microhabitat selection at a 10 m scale, indicating rattlesnakes select habitat at a fine level. Microhabitat selection did not differ significantly between males and females.

INTRODUCTION

Habitat selection studies on snakes were uncommon before the early 1990s, though there are some exceptions (Fitch and Shirer, 1971; Reinert and Kodrich, 1982; Weatherhead and Charland, 1985). Even since, research on North American snake ecology is limited, especially with regards to habitat selection. Habitat loss is one of the major factors in declining snake diversity worldwide, therefore identifying critical habitat for snakes is becoming increasingly urgent (Gibbons et al., 2000). Populations at northern range limits are of particular interest because environmental factors most likely affect snake distribution in these areas. Northern range limits likely have climatic conditions that approach a threshold of thermal tolerances for snakes, making optimal habitat selection crucial to their survival.

Southwestern Saskatchewan is home to a snake community consisting of several species at the northern edge of their geographic range, including the prairie rattlesnake. The prairie rattlesnake ranges quite extensively throughout the United States, but is becoming a species of conservation concern in Canada due to suspected population declines (Watson and Russell, 1997). Data on the ecology of prairie rattlesnakes are required for a comprehensive conservation status assessment to be made. The majority of studies on habitat selection of prairie rattlesnakes have been done on southern populations in the core of their geographic range (Fitch, 1949; Hirth et al., 1966; Duvall et al., 1985; Macartney et al., 1988; King and Duvall, 1990; Reed and Douglas, 2002), but because of ecological differences associated with latitude and climate, data from southern populations are probably not sufficient on which to base conservation and management decisions in Canada (Cagle, 2008). A limited number of studies have been

done on the ecology of prairie rattlesnakes at the northern extreme of their range (Gannon and Secoy, 1985; Charland and Gregory, 1990), but these focused on thermal ecology with little to no reference to the structural characteristics of habitat use.

We examined microhabitat selection of prairie rattlesnakes in southwestern Saskatchewan, Canada, near the northern limit of their geographic range in North America. Microhabitat selection was quantified using a paired used versus availability design, where identical microhabitat measurements were taken at used and available sites for comparison. Resource selection function modeling was then used to create a model to predict suitable habitat. Developing a microhabitat selection model for prairie rattlesnakes at the northern periphery of their range allows us to identify suitable habitat, which will be pertinent to conducting an accurate conservation status assessment.

MATERIALS AND METHODS

Study Area – The study was conducted within the West Block of Grasslands National Park (49°18'83"N 107°59'52"W), Saskatchewan from May to September in 2010 and 2011. The west block of Grasslands National Park is approximately 49,000 hectares of federally protected land in southwestern Saskatchewan. This area is in the northern mixed grass prairie ecoregion and encompasses a large variety of grassland and agricultural habitats, including some of the largest remnants of native prairie left in the province. In terms of macrohabitat, the Frenchman River passes through this region creating many steep bluffs and coulees dividing upland and lowland areas. With respect to microhabitat, the native plant community of this region typically consists of needle-and-thread (*Stipa comata*), blue grama (*Bouteloua gracilis*), and western wheatgrass (*Agropyron smithii*),

as well as woody species such as sagebrush (*Artemisia* spp.), winterfat (*Erotia lanata*), greasewood (*Sarcobatus vermiculatus*), wolfwillow (*Elaeagnus commutate*), snowberry (*Symphoricarpos albus*) and creeping juniper (*Juniperus horizontalis*). Burrows are common in the area, created by small mammals such as Richardson's ground squirrels (*Uroditellus richardsonii*), mountain cottontails (*Sylvilagus nuttallii*), American badgers (*Taxidea taxus*) and black-tailed prairie dogs (*Cynomys ludovicianus*).

Study Species – Prairie rattlesnakes are a wide-ranging pit-viper capable of reaching over 1.5 m in length (Ernst and Ernst, 2003). They have an extensive range in the United States, but within Canada are confined to southern Saskatchewan and Alberta (Pendlebury, 1977). They face the same host of threats as other snake species in the area including habitat loss, geographic dispersal barriers, and anthropogenic disturbance, in addition to deliberate persecution and a lower reproductive rate (Gannon and Secoy 1984) making them potentially more vulnerable to population perturbations (Pendlebury, 1977; Watson and Russell, 1997). Prairie rattlesnakes have not been assessed by COSEWIC, but they are considered a high priority candidate for assessment due to suspected population declines (www.cosewic.gc.ca, February 15, 2012).

Snake Capture and Tracking - The active season for rattlesnakes in Saskatchewan extends from April until October. Snakes were caught with snake hooks and tubes during emergence from hibernation at two known hibernacula, through opportunistic visual encounters, and through road surveys. Individuals were then measured (snout to vent length and tail length), weighed, and sexed (via cloacal probing) (Schaefer, 1934). All

individuals caught, except small juveniles, were also injected with passive integrated transponders (EIDAP Inc., Sherwood Park, Alberta, Canada) for unique identification. Snakes were then transported in individual containers to the Western College of Veterinary Medicine in Saskatoon and surgically implanted with Holohil Systems Ltd. radio-transmitters (model SB-2, mass = 4–5 g, Holohil Systems Ltd., Carp, Ontario, Canada) by veterinarians following previously established methods (Reinert and Cundall 1982, see Appendix A). We only implanted snakes when the mass of the transmitter was less than or equal to 5% of the snake's body mass and the diameter of the transmitter was less than 50% of the diameter of the snake at the insertion site. Snakes were allowed to recover post surgery for 48 hours prior to release at the capture site. One death did occur post surgery, which was determined to be an anesthetic death by the veterinarians based on a post mortum.

Using radio-telemetry, 23 individual rattlesnakes (7 males, 16 females) were tracked approximately every 48 hours from May until September. We did not directly approach the snakes to avoid influencing their movements; we either visually confirmed the snake site from a distance, or estimated the snake's location from a short distance (~1-2 m). Habitat selection was quantified with a paired used versus availability design (Buskirk and Millspaugh, 2006; design 4 in Thomas and Taylor, 2006), where used and available habitat sites were compared using a suite of habitat variables selected from previously published studies on snake habitat selection (Harrell and Fuhlendorf, 2002; Harvey and Weatherhead, 2006; Moore and Gillingham, 2006; Wisler et al., 2008; Martino et al., 2012). The exact snake location was considered the used site, while a location 50 m from the used site, in the direction of the snake's previous location, was

considered the available site. When a snake was located, Universal Transverse Mercator (UTM) coordinates were recorded. Whether the snake was in the same spot (<2 m from previous location), same area (<20 m from previous location), or a new area (>20 m from previous location) was also recorded. Flagging tape was then used to mark the snake's current location so habitat variables could be measured at a later date (within a few days), minimizing disturbance to the snake. All methods were approved by the President's Committee on Animal Care at the University of Regina (AUP 09-09).

Microhabitat Quantification - I defined microhabitat as the small-scale environment consisting of physical and ecological characteristics that may distinguish it from its immediate surroundings (third-order selection, Johnson, 1980). Identical microhabitat measurements were taken at 190 used and 190 available sites for comparison. I measured 8 habitat variables including percent grass, percent bare ground, percent forb cover, percent shrub cover, vegetation density (using a Robel pole measurement), maximum vegetation height, distance to nearest burrow, and distance to nearest shrub (Harvey and Weatherhead, 2006; Moore and Gillingham, 2006; Wisler et al., 2008; Martino et al., 2012). Rattlesnake microhabitat was measured when an individual was found in a new area only. A location was defined as new if it was greater than 20 m from the previous location. A 50x50 cm Daubenmire frame was placed directly on the new location with each side facing a cardinal direction (Daubenmire, 1959). The %grass, forb, shrub, and bare ground within the quadrat were estimated to the nearest 5%. Maximum vegetation height was measured to the nearest cm within the quadrat, while Robel pole measurements of vegetation density (Robel et al., 1970) were recorded in each cardinal

direction and averaged. Distance to nearest burrow and distance to nearest shrub were measured (± 1 m), and then categorized based on whether the burrow or shrub was 0-1 m, 2-5 m, or ≥ 6 m from the snake site. The same measurements were undertaken at locations 10 m in each cardinal direction from the snake site to determine whether snakes were selecting habitat at a fine scale level (snake site specific), or at a more general, local level (10 m radius from snake site). Local measurements were averaged between the cardinal directions to obtain a single local value for each habitat variable.

Microhabitat data were analyzed using resource selection function modeling (Manly et al., 2002; Boyce, 2006; Johnson et al., 2006; Martino et al., 2012). Resource selection functions are defined as any function proportional to the probability of use of a resource unit by an organism (Manly et al., 2002). To determine if any of the habitat variables selected affect the probability of rattlesnakes selecting microhabitat sites, I used models which compare these microhabitat characteristics between sites used by snakes and those available to them (Martino et al., 2012). None of the 8 microhabitat variables chosen were highly correlated ($r < 0.7$), so all of the variables were included in the analysis. Data were pooled for both sexes in the analysis, as microhabitat selection did not differ significantly between male and female rattlesnakes. I used generalized linear mixed models (mixed-effects logistic regressions; PROC GLIMMIX; SAS Institute, 2008) to model the microhabitat data, which allowed me to control for repeated measurements from the same individuals, as well as an unequal number of observations between individuals (Gillies et al., 2006). Snake ID and den were defined as random effects to extend the scope of inference to the entire rattlesnake population (Gillies et al., 2006; Bolker et al., 2008). A linear relationship was assumed in the modeling procedure,

which is standard when little is known about the ecology of a species. Microhabitat variables were analyzed individually in univariate models first, and only significant variables ($P < 0.05$) were included in the top multivariate model. Means are presented ± 1 standard error.

RESULTS

Rattlesnakes exhibited selection at the microhabitat level. The top model that explained the differences between snake locations at the site specific level and random available sites included percent bare ground, percent shrub cover, vegetation density, maximum vegetation height, and distance to nearest burrow (Table 1). Percent shrub cover and proximity to burrow positively affected the probability of use by rattlesnakes, while percent bare ground had a negative effect. Vegetation density and maximum vegetation height were not important predictors of microhabitat use by rattlesnakes. These two variables were included in the top model as they positively affected habitat use by rattlesnakes in the univariate models, though they did not prove significant in the multivariate model. Mean percent bare ground at available sites was 1.5 times greater than at sites used by rattlesnakes (Fig. 1a). Based on the linear predictive model, increasing the amount of bare ground decreased the probability of use by rattlesnakes (Fig. 1b). Mean percent shrub cover at sites used by rattlesnakes was approximately twice that found at random available sites (Fig. 2a). The predicted probability of habitat use by rattlesnakes increased as the amount of shrub cover increased (Fig. 2b). Rattlesnakes were found in close proximity (0-1 m) to burrows most frequently, near burrows (2-5 m) less frequently, and away from burrows (≥ 6 m) least frequently (Fig. 3a). The model

predicted the probability of a rattlesnake using habitat within 0-1 m of a burrow as the highest, with a decreasing probability of habitat use with increasing distance from a burrow (Fig. 3b). For the local analysis (10 m in each cardinal direction from the used or available site), none of the habitat variables were significant predictors of microhabitat selection by rattlesnakes at the local level.

DISCUSSION

Rattlesnakes selected for shrub cover and burrows, and less bare ground at the site-specific level, which likely indicates retreat sites are important for this species. Retreat sites were important components of microhabitat selection regardless of the broader landscape being occupied. None of the habitat variables we measured were significant predictors of rattlesnake microhabitat selection at the local scale (10 m radius from snake site), indicating rattlesnakes select habitat at a site-specific level. The association between rattlesnakes and retreat sites is consistent with the habitat selection described for bullsnakes and racers in this area (Martino et al., 2012) as well as more southerly areas (Moriarty, 1991; Plummer and Congdon, 1994). Removal of retreat sites has also been shown to cause population declines in broad-headed snakes (*Hoplocephalus bungaroides*, Webb and Shine, 2000), providing further evidence that suitable retreat sites are critical for snakes regardless of species or location.

Terrestrial squamates often select microhabitat based on thermal qualities (Blouin-Demers and Weatherhead, 2001; Shoemaker and Gibbs, 2010; Lelievre et al., 2011); though it appears less important for tropical species (Shine and Madsen, 1996). Temperature is critical for various reptilian functions including ecdysis, embryonic

Table 1. Top generalized linear mixed model explaining prairie rattlesnake microhabitat selection at the site specific level. For categorical variables (Distance to burrow), category 3 was a reference value (what the other 2 categories were compared to) with a value of 0 in the analysis and is not included in the table.

Effect	Estimate	Standard Error	<i>F</i> Value	<i>P</i> Value
Percent bare ground	-0.02466	0.007384	11.15	0.0009
Percent shrub	0.02976	0.006332	22.09	<0.0001
Vegetation density	0.00166	0.015730	0.01	0.9159
Vegetation height	0.00207	0.007783	0.07	0.7908
Distance to burrow				
Cat 1	3.28460	0.467000	18.45	<0.0001
Cat 2	0.53000	0.367000		

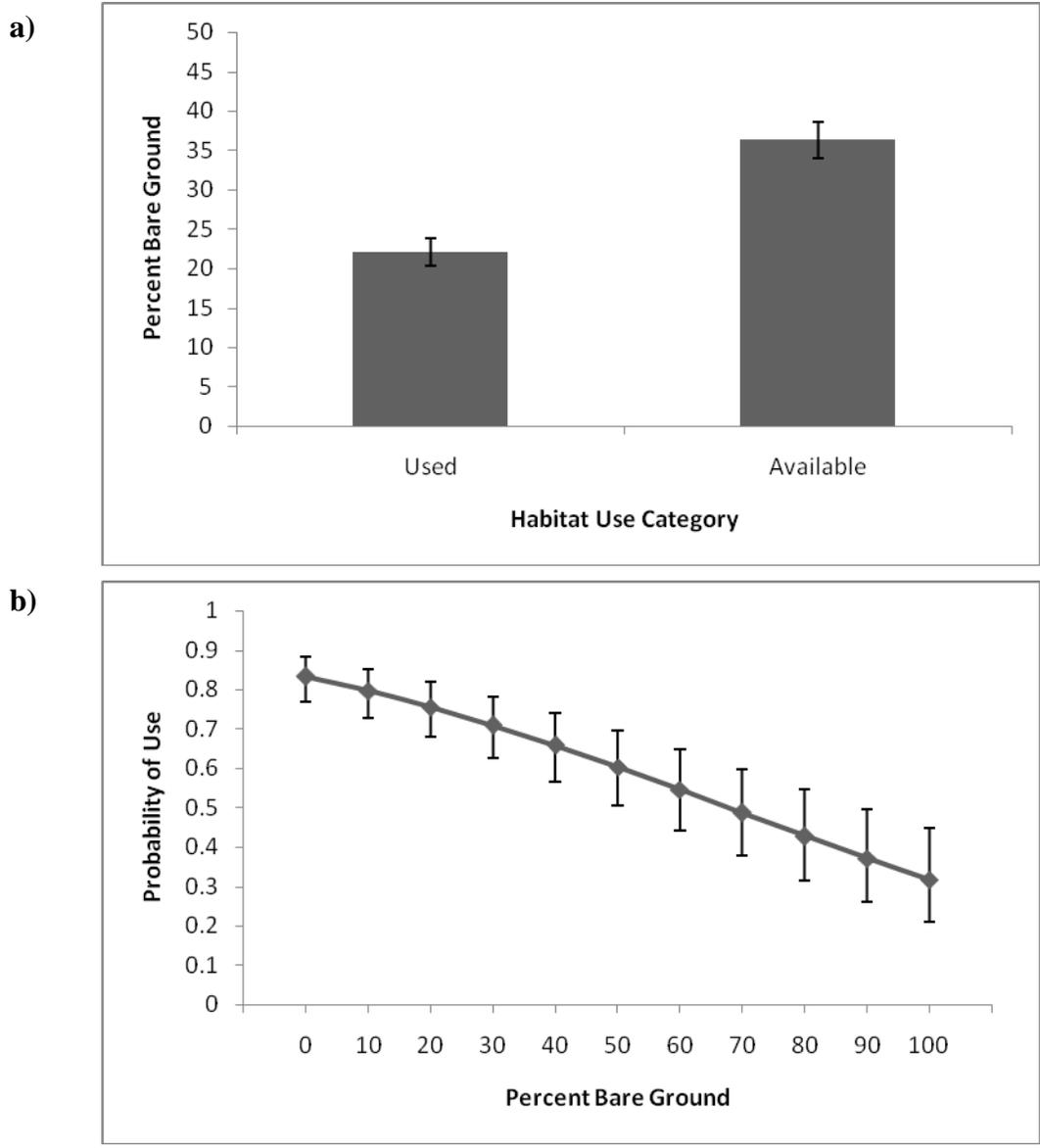


Figure 1. Mean percent bare ground at sites used by versus available to prairie rattlesnakes (a), and the predicted probability of habitat use by prairie rattlesnakes at varying amounts of bare ground (b).

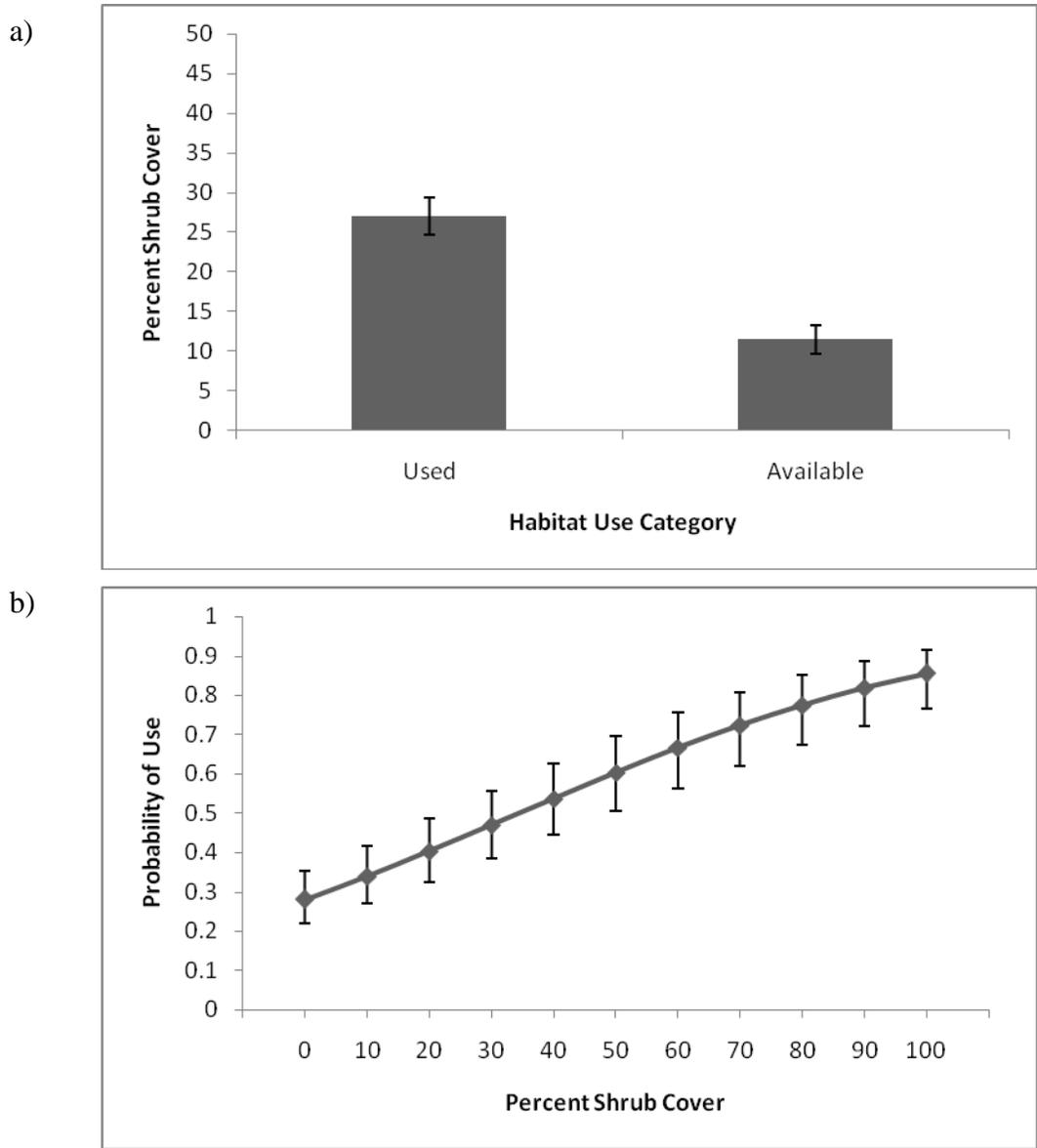


Figure 2. Mean percent shrub cover at sites used by versus available to prairie rattlesnakes (a) and predicted probability of habitat use by prairie rattlesnakes at varying amounts of shrub cover (b).

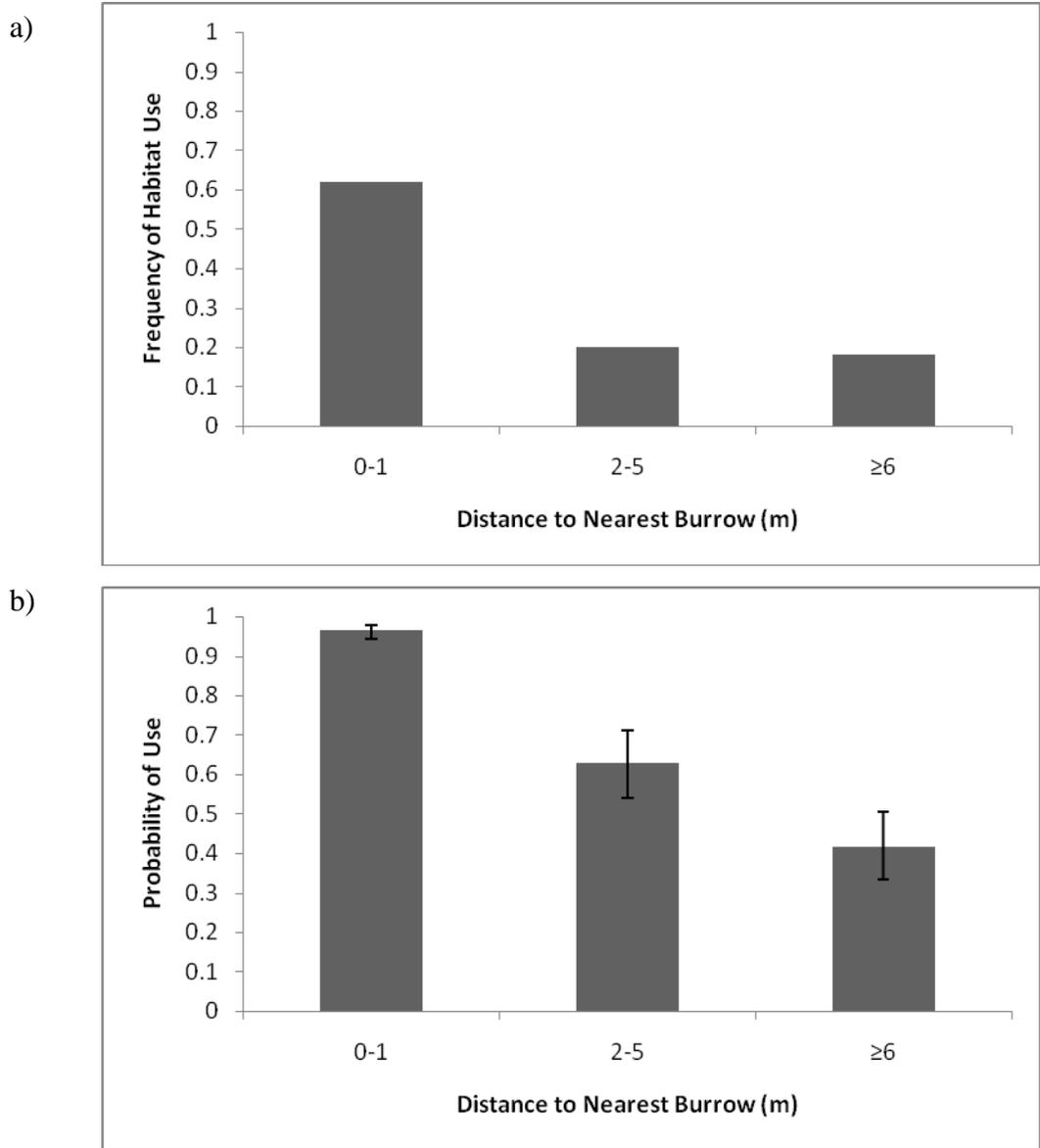


Figure 3. Relative frequency (a) and predicted probability (b) of habitat use by prairie rattlesnakes at (0-1 m), near (2-5 m), or away (≥ 6 m) from burrows.

development, digestion, locomotion, and recovery from injury. Species that exist in warmer climates are likely able to thermoregulate more efficiently, or spend less time thermoregulating than snakes living in colder climates. Furthermore, species living in northern temperate climates experience both hot and cold extremes making thermoregulation an even greater challenge. The northern extreme of their range likely presents a thermally challenging environment for prairie rattlesnakes, so retreat sites such as burrows and shrubs are likely important for thermoregulation (Huey et al. 1989). In addition, a large portion of the diet of prairie rattlesnakes is known to consist of small burrowing mammals (Hill et al., 2001); therefore burrows likely serve as foraging sites as well. Since small mammals often create burrows at the base of shrubs, as roots provide infrastructure keeping the burrow from collapsing, shrubs may also provide access to prey in addition to cover from predators and thermal benefits.

Rattlesnakes rely on cryptic coloration and pattern to avoid detection by predators, especially when sufficient cover is present (Ernst and Ernst, 2003). Predators of rattlesnakes in our study area include hawks (*Buteo* spp.), eagles (*Aquila chrysaetos*), great horned owls (*Bubo virginianus*), badgers (*Taxidea taxus*), coyotes (*Canis latrans*) and foxes (*Vulpes vulpes*). Retreat sites consisting of burrows or shrubs, or a combination thereof, are likely important to reduce detection by these predators. Since distance to the nearest shrub was not a significant predictor of microhabitat use by rattlesnakes but shrub cover was important in site selection, the characteristics of the shrubs themselves must be important in the habitat selection process. The significance of shrub cover indicates that the amount of cover provided by the shrub is a determining factor in their selection, which may differ between various species of shrubs; making this likely to be an anti-

predator strategy. Identifying and measuring these characteristics will determine which shrub species rattlesnakes are specifically selecting for, which could then be incorporated in management plans for the species.

Beyond providing cover from predators, burrows may also serve as primary nesting habitat for rattlesnakes in our study area. Burrows provide a relatively constant temperature (Huey et al. 1989), and embryonic development in snakes is critically dependent on temperature (Burger and Zappalorti, 1988; Weatherhead et al., 1998; Ji and Du, 2001; O'Donnell and Arnold, 2005). In viviparous snakes such as the prairie rattlesnake, embryonic development is affected by temperature specifically during the gestation period (Graves and Duvall, 1993; Ji and Du, 2001; O'Donnell and Arnold, 2005). Pregnant prairie rattlesnakes are known to behaviourally modify body temperature during gestation and select microhabitat based on ambient temperature during this period (Graves and Duvall, 1993). Burrows are likely desirable nesting sites due to their thermal quality, especially in a thermally challenging environment such as the northern periphery of a geographic range.

In summary, retreat sites are a vital component of microhabitat for prairie rattlesnakes. In the northern mixed grass prairie ecoregion, shrubs and burrows make suitable retreat sites. In this area, burrows are commonly created by small mammals such as Richardson's ground squirrels, mountain cottontails, badgers and black-tailed prairie dogs. Rattlesnakes cannot dig their own burrows, and thus are dependent on these species to create sites that can serve as retreats. In addition, shrubs available for retreat sites include sagebrush, winterfat, greasewood, wolfwillow, snowberry and creeping juniper.

Suitable habitat for prairie rattlesnakes will likely contain these species, which should be considered when formulating management strategies for prairie rattlesnakes.

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CHAPTER 4

SYNTHESIS AND SUGGESTIONS FOR FUTURE RESEARCH

4.1 Synthesis

Habitat loss is thought to be one of the major causes of snake diversity declines in the world, so the identification of critical habitat for species at risk is important for their preservation (Gibbons et al. 2000, Foley et al. 2005). Research on North American snake ecology is limited, particularly regarding habitat selection. In Canada, most published studies of snake ecology have focused on non-grassland communities (e.g. Weatherhead and Charland 1985, Blouin-Demers and Weatherhead 2001*a*, 2001*b*, 2001*c*, Harvey and Weatherhead 2006), resulting in a limited understanding of the spatial ecology and habitat use of Canadian grassland snakes. The purpose of my research was to identify and compare habitat selection by racers, bullsnakes, and rattlesnakes in a grassland community at the northern limit of the geographic range of the species. Additionally, I aimed to determine microhabitat selection by rattlesnakes. These three species are vulnerable to extinction in Canada due to habitat loss; they have specific requirements for suitable hibernacula in this area of their range, and are known to exhibit high site fidelity (Ernst and Ernst 2003, COSEWIC 2004, Kapfer et al. 2008, Gardiner and Sonmor 2011). Although essential for effective conservation planning, little information exists on the spatial ecology and habitat selection of these species at the northern limit of their range (Kapfer et al. 2008, Martino et al. 2012). Being sympatric species in my study area, they also lend themselves to being able to address some interesting ecological questions, such as whether or not resource competition exists, and at what scale this competition may be occurring. My research provides information on the habitat use of these species at the northern periphery of their geographic range.

Chapter 2 compares the movement patterns, home range, and macrohabitat selection of sympatric racers, bullsnakes, and rattlesnakes. They exist communally at overwintering (*i.e.* den) sites, but disperse into different macrohabitats during the active season. Rattlesnakes were found to move farthest from the dens, followed by racers, and then bullsnakes. Rattlesnakes could be further divided into two movement groups; sitters and rovers (Sokolowski 1998). Sitters remained in relatively close proximity to the den while rovers dispersed large distances; greater than 11 km in more than one instance. Rattlesnakes also moved in much straighter paths than racers, while bullsnakes exhibited an intermediate strategy. These movement patterns are most likely the result of their macrohabitat selection. In this area of their range, these species rely on slump-based, upland hibernacula to survive the harsh winters (Mackay 1987, Macartney and Weichel 1993, Gardiner and Sonmor 2011). All three species were found to avoid upland areas, and descend into lowlands following emergence from hibernation. All three species also exhibited a slight positive selection for hills and slopes, which likely reflects their unavoidable descent across this macrohabitat type from the den sites. Bullsnakes selected valley grassland habitats, which exist at the base of the hills on which the dens are situated. Racers were found to select for riparian areas, which exist along the middle of the river valley. Lastly, rattlesnakes were found to be associated with prairie dog colonies, which are patchily distributed throughout the landscape. Snakes are known to travel long distances when they require patchily distributed resources, which is likely the case for prairie rattlesnakes (Duvall et al. 1985, Duvall et al. 1990; Duvall and Schuett 1997). The different movement patterns in these three species therefore likely reflect the relative distances of the macrohabitats I identified from den sites in this area.

Home range sizes also differed between the three species, although the method of analysis had an effect on this difference. MCPs revealed that racers have the largest home range size, followed by rattlesnakes, and then bullsnakes. Based on the maximum distances moved by these species, these results were contrary to what was expected. MCPs of rattlesnake ranges, however, were long and narrow due to their direct movement patterns, while the tortuous movements of racers gave their ranges a polygon shape. In contrast, kernel densities revealed that racers and rattlesnakes have very similar home range sizes, while bullsnake home ranges are much smaller (less than half). Kernel density is a more accurate estimator of home range size for species with discrete activity centers, like snakes (Reed and Douglas 2002). Racers and rattlesnakes have similar-sized activity centers around their winter and summer grounds, but the movement corridors connecting the two are much larger for dispersing rattlesnakes.

For racers specifically, the distance from the den site to the river affected the distance between winter- and summer-ground kernels, providing further evidence that the distance of selected macrohabitats from the den affects snake movement patterns. Kernels representing summer grounds were much closer to the den (wintering grounds) if the den was closer to a riparian area. Some dens had apparent obstacles to racer movement between the den and the river, so snakes would have to take a longer route. A prairie dog colony acted as an obstacle in one instance, and anthropogenic barriers were observed at dens outside the park. Habitat selection is therefore just as important within the movement corridor, and obstacles (natural or anthropogenic) have an effect on snake movement.

Chapter 3 describes microhabitat selection by prairie rattlesnakes, and I found that they select for habitat with little bare ground, the presence of shrub cover, and close proximity to burrows. Collectively, these results indicate that retreat sites are important habitat features. The association between snakes and retreat sites has been reported in previous studies (Moriarty 1991, Plummer and Congdon 1994), including racers and bullsnakes in our study area (Martino et al. 2012). Retreat sites are likely important for protection from predators, as well as thermoregulation (Huey et al. 1989, Blouin-Demers and Weatherhead 2001*a*, Lelievre et al. 2011). Small burrowing mammals are known to make up the majority of the diet of bullsnakes (Rodríguez-Robles 2002) and rattlesnakes (Hill et al. 2001), so burrows are likely important as a source of prey for these two species. At the macrohabitat level, rattlesnakes were found to select for prairie dog colonies (see Chapter 2), but the microhabitat results revealed a selection against bare ground. This may be the result of rattlesnakes selecting edge habitats.

In the field, rattlesnakes were often found around the edge of prairie dog colonies. These areas often contain large sagebrush and greasewood shrubs, which likely serve as a source of cover as shrub cover was found to be selected for by rattlesnakes. The prairie dog colonies are likely a major source of prey, as well as a source of abundant burrows for thermoregulatory purposes. Predators have been shown to increase their foraging efficiency by concentrating their activity along habitat edges (Yahner 1988, Paton 1994), and the association of snakes with habitat edges has been previously documented (Durner and Gates 1993, Blouin-Demers and Weatherhead 2001*c*). Habitat edges also provide a range of microclimates which likely benefits thermoregulation, a critical component of habitat selection for ectothermic vertebrates such as snakes (Blouin-Demers and

Weatherhead 2001*a*, 2001*c*). A large prairie dog colony exists between the Snake Pit den and the river. Racers were found to avoid prairie dog colonies, and at this site would clearly go around the edge of the colony to reach the river. The potential therefore exists for racers and rattlesnakes to be competing for retreat sites associated with shrubs in this area. Further study is required to determine if differential selection is occurring between snake species regarding the shrubs they select for.

4.2 Conclusions

The differential habitat use I reported is consistent with habitat partitioning between the three species during the summer, although overlap does occur at the overwintering sites and during the movement between selected macrohabitats. During the active season, bullsnakes selected for valley grassland habitats, racers selected for riparian areas, and rattlesnakes tended to be associated with prairie dog colonies. As a result, racers travel further from the den on average than bullsnakes, while rattlesnakes are variable; though rattlesnakes travel in much straighter paths than racers. Home range size also differed between species, though kernel density was a more accurate measure of home range shape. Home ranges were dumbbell-shaped with activity centers near hibernacula and in well-defined summer grounds, and these centers of activity were connected by narrow corridors. Bullsnakes had the smallest home range, while racers and rattlesnakes were similar; though racer kernels were much closer together on average. Data on microhabitat selection already exist for racers and bullsnakes (Martino et al. 2012), so my study fills a knowledge gap on rattlesnakes. Rattlesnakes selected for decreased bare ground, increased shrub cover, and close proximity to burrows. On the

macrohabitat level, rattlesnakes were often seen along the edges of prairie dog colonies. Collectively, these data indicate selection for retreat sites along the edges of prairie dog colonies, which is likely due to optimal foraging and the thermoregulatory opportunities presented by habitat edges.

4.3 Conservation Implications

Few studies of snakes have examined the ecology of multiple species simultaneously at the same site, which is important for understanding resource partitioning and competition between sympatric species. Management decisions regarding one species may affect another, although the extent of the effect cannot be known if the interactions between sympatric species are not well understood. Martino et al. (2012) proposed that den buffers will likely not include summer grounds in northern snake populations, which must be compensated for by either defining much larger den buffers or identifying a corridor system linking smaller protected areas surrounding winter and summer habitats. According to my results, buffers would have to be up to 12 km in radius to include all three of the snake species studied, which may be unrealistic in many locations. Identifying a corridor system is likely more realistic, though protected summer habitats, unlike the communal winter dens, will differ depending on which species conservation strategies target. Racers for instance require riparian habitat, bullsnakes require valley grassland habitats, and rattlesnakes require prairie dog colonies. Racers and bullsnakes completely avoid prairie dog colonies, but they are clearly not disadvantageous for all snake species. Habitat use differences between species during the

active season should therefore be considered when making management decisions regarding hibernating snake communities.

Regardless of the macrohabitat selected at the landscape scale, retreat sites appear to be important for all three species (This study; Martino et al. 2012). In addition, rattlesnakes select habitats found along the edges of prairie dog colonies, so managing the amount of edge habitat could be important in the management of this snake species. Management plans regarding rattlesnakes should also consider prairie dogs (*Cynomys ludovicianus*), or other colonial small burrowing mammals such as Richardson's ground squirrels (*Urocitellus richardsonii*). Since racers and bullsnakes avoid prairie dog colonies, they likely depend on the burrows made by other mammals. Questions remain regarding the specific species of shrub each snake species may be selecting for, as well as characteristics of retreat burrows.

4.4 Suggestions for Future Research

An interesting and important direction for future research would be to study the factors affecting snake movement corridors. My data suggest that the distance between the den and the selected macrohabitat type may affect the dispersal distance. For instance, if a den is situated in close proximity to the macrohabitat types selected during the active season, snakes will have to travel a short distance to the summer grounds compared to areas with dens further away. Tracking snakes from more dens which exist at varying distances from macrohabitats known to be selected by snakes could be used to test this idea. Some individuals may still disperse great distances (*e.g.* roving rattlesnakes), however, which is likely important for maintaining gene flow and genetic diversity

among populations. Studying movement corridors of dispersing individuals is therefore equally important as studying those of individuals that stay within close proximity to the den. Features of the corridors to be measured could include topography, vegetation type and cover, physical barriers (natural and anthropogenic), and human disturbance. The results could then be used to identify and protect movement corridors for snakes in fragmented habitats.

With respect to movement, my data also suggest racers and bullsnakes may include dispersing individuals as well as rattlesnakes. Histograms of the maximum distance moved from the den by each species suggest a bimodal distribution likely representing the two movement groups (*i.e.* sitters and rovers) identified for rattlesnakes in Chapter 2 (Figure 1). Biologically this makes sense, as gene flow between den sites and genetic diversity of the species likely depend on dispersal by individuals. The groups are just less obvious for racers and bullsnakes, as roving individuals in these species do not appear to disperse as far as rattlesnakes. The majority of individuals of all three species stayed within 2500 m of the den sites, with a limited number of individuals dispersing beyond this distance. Dispersing individuals appear to make up a relatively smaller proportion of the population, although whether this is due to the difficulty of dispersing in fragmented habitats or the difficulty of tracking these individuals (resulting in their exclusion from analyses) is uncertain. Sample size therefore greatly affects the shape of the histogram, with racers ($n = 33$, Figure 1b) exhibiting the clearest bimodal distribution, and bullsnakes ($n = 16$, Figure 1a) less so. Tracking more individuals, especially bullsnakes, is needed to assess this theory. Future research could also be

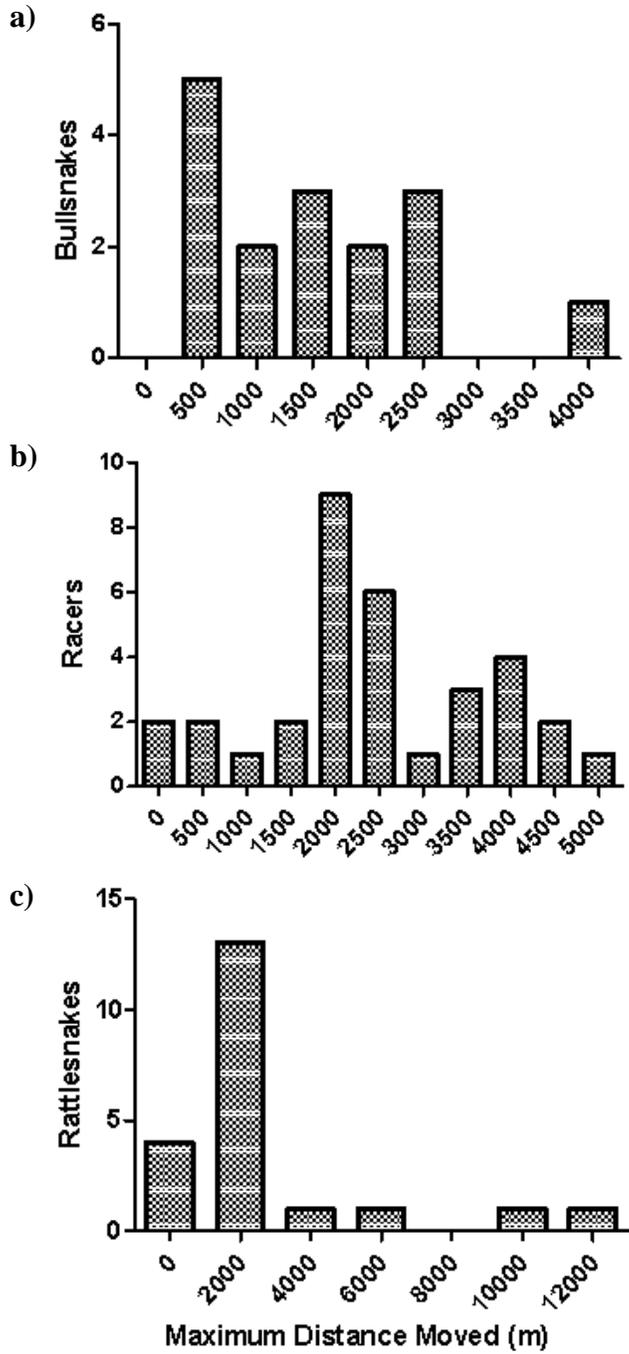


Figure 1. Histograms of maximum distance (m) moved from den sites by sympatric bullsnakes (a), eastern yellow-bellied racers (b), and prairie rattlesnakes (c).

undertaken to assess why roving individuals of the three species disperse different distances. If the reason for dispersing is in fact to maintain gene flow between den sites (which is also uncertain), then why racers disperse 5 km while rattlesnakes disperse over 11 km would be an interesting question to address with important conservation implications.

Another direction for future research could be to determine the types of shrubs and burrows snakes are selecting for when choosing a retreat site, and why. Structural characteristics such as shrub species, volume, and cover could be important, including the amount of litter depth underneath the shrub. Structural characteristics of burrows such as size, depth, location, and aspect in addition to the internal microclimate could also be measured. A variety of burrows exist in the mixed grass prairie ecoregion due to the various burrowing mammals that live there, which presents an opportunity for choice. Rattlesnakes are mostly associated with prairie dog burrows, though racers and bullsnakes also depend on burrowing mammals which exist in riparian and lowland pasture habitats respectively. In areas of their range where prairie dogs do not occur, rattlesnakes must depend on other burrowing mammals such as Richardson's ground squirrels. Further study is required to determine which burrowing mammals the snakes depend on, and should be considered when constructing management plans.

Within species, habitat selection may differ between different age and reproductive classes. Habitat selection of juvenile snakes is not well understood in general, which likely reflects the difficulty of tracking snakes which are too small to fit a radio-transmitter. Furthermore, snakes at northern latitudes may not reproduce every year. Viviparous snakes like rattlesnakes are known to reproduce biennially in Wyoming

(Graves and Duvall 1993), and may only reproduce every 4 years in the extreme north of their range (Ernst and Ernst 2003). During reproductive years, snakes may select different habitat, especially females which require a specific thermal environment for embryonic development. Retreat site selection should be a key focus for future study, as sufficient retreats must be available for a viable population to exist. Furthermore, the thermal quality of nesting habitat likely differs for oviparous and viviparous snakes, as viviparous snakes can relocate the embryos if conditions become unfavourable. As both oviparous and viviparous snake species exist at our study site, future work could compare the thermal environment of nest sites between these species. After the eggs are laid, or young are born, snakes may select different habitat as they prepare for hibernation, so temporal habitat selection may be important as well. Temporal shifts in habitat selection by snakes are documented in the literature (Weatherhead and Charland 1985, Plummer and Congdon 1994), although this is likely site-dependent, as conflicting evidence exists (Keller and Heske 2000).

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APPENDICES

APPENDIX A – Modified surgical protocol for implantation of radio-transmitters

Surgical procedures for coelomic implants followed those developed specifically for snakes, which have been the standard procedures for herpetologists for the last 27 years (Reinert and Cundal 1982). All surgeries were performed by a licensed DVM and the anesthesia was performed by a licensed DVM. Dr. Dennilyn Parker from the University of Saskatchewan's Western College of Veterinary Medicine successfully performed 18 of these surgeries two years prior to the project.

As recommended by the Canadian Council on Animal Care (CCAC), the diameter of the transmitter was no greater than 50% of the diameter of the snake, and the mass of the transmitters was less than or equal to 5% of the snake's body mass. The transmitters used were 14 mm in length, 9.5 mm in diameter and weighed 3.8 g (Holohil Systems Ltd., Model SB-2 – 5 month battery life – see <http://www.holohil.com/snake.htm>). Thus, the smallest snake acceptable for use with a radio-transmitter was approximately 19 mm in diameter and 76 g (Note: of the seven adult yellow-bellied racers captured in 2007, the average mass was 129 g). However, based on observations in 2008, we built in an additional safe guard for size, and will require that the smallest snakes selected for surgery be 85 grams or larger. The manufacturer encapsulates each transmitter with multiple layers of a biologically inert butyl rubber compound to prevent tissue reactions. The stranded stainless steel whip antenna is 30 cm long and is encapsulated with a clear Teflon coating, with a blunt tip to minimize any risk of penetration of the skin. Clear silicone tubing reinforces the base of the antenna to the transmitter. Transmitters are soaked in a cold Savlon bath prior to surgery.

Surgeries were conducted under sterile surgical conditions. Ten to fifteen minutes before induction, the snake was given an injection of buprenorphine at a dose of 0.01mg/kg IM. After the 10-15 minutes had passed, the snake was placed in a plexi-glass dosing chamber with a heating pad beneath. Isoflurane was used as the general anaesthetic. Typically, the snake was placed in the dosing chamber and left to settle and to allow its body temperature to rise to increase respiration rate. Isoflurane was delivered via a precision vapourizer in a Bain circuit. The snake was 'tanked down' in the induction chamber with oxygen flow at 1-2 L/min and the vapourizer set at 5%. Once the righting reflex was lost, the snake was removed from the chamber and intubated with an uncuffed endotracheal tube. The tube was secured to the lower jaw with tape. Venomous snakes were maintained with a mask. Anesthesia was maintained with the vapourizer set at 2-3% or higher as needed and an oxygen flow of approximately 1 L/min.

The snake was stretched out on a heating pad and a Doppler probe was placed over the heart to measure heart rate. Oral mucous membrane colour was also monitored throughout the surgery. The incision site was located and bupivacaine was administered subcutaneously at the incision site up to a maximum dose of 0.2mg/kg. Alternatively, this drug could be administered as a 'splash block' to the site after the incision has been made. Any gross debris was washed from the surface of the snake. The surgical site was then prepared by scrubbing with chlorhexidine gluconate soap and alcohol with 3 applications each moving from head to tail. The surgical site was then draped either with sterile cloth surgical drapes, or with sterile transparent adhesive drapes. The surgeon did a surgical scrub and wore sterile surgical gloves.

A 2-3 cm lateral incision was made at mid-body at scale rows 2-3. The fasciae

were teased apart to create a good exposure of the base of the ribs which were then lifted up to create a tunnel (pocket) under the rib cage while avoiding tearing of the peritoneum. The transmitter was inserted into the pocket. A small opening was made in the rib musculature to pull the antennae wire through to the exterior of the ribs. The ribs were then moved back in place over the transmitter. An olive-tipped cannula was inserted under the skin at the incision site and directed posteriorly toward the tail where a small incision was made to access the tip of the cannula once inserted. The transmitter antenna wire was inserted into the cannula and out its end, and the cannula containing the antenna wire was withdrawn from the small incision. This process was repeated twice more such that the antenna wire was completely under the lateral skin of the snake posterior of the transmitter location. During this process any minor bleeding from cut capillaries was flushed with saline to maintain visibility. The incision site for the transmitter was closed with 3-0 PDS sutures in a horizontal mattress pattern, and the small cannula/antenna wire incisions were closed with simple interrupted sutures. The incisions sites were cleaned with sterile saline, dried with gauze, and spray bandage was applied.

After completion of surgery, a dose of meloxicam was given at 0.2mg/kg IM. Then the vapourizer was turned off and oxygen was delivered for at least 5 minutes, or until the snake moved spontaneously. When significant muscle tone returned, the snake was moved to an adjacent plastic tub for recovery. A heating pad was provided, and a fan was operated at the top of the pan on low speed to dispel anaesthetic gas as the snake recovered. A pan of water was provided and the snake was monitored continuously for the first 30 minutes to observe respirations, and regularly thereafter until release (1 to 3 days later).

APPENDIX B

Table 1. Capture and relocation data for snakes radio-tracked in this study.

Year	Species	Snake ID	Sex	Den	Relocations	Days Tracked
2008	Racer	YBR003	M	PFRA1	51	114
2008	Racer	YBR004	M	PFRA1	33	114
2008	Bullsnake	BS006	F	PFRA1	45	109
2008	Bullsnake	BS003	F	PFRA1	8	114
2008	Bullsnake	BS005	F	PFRA1	31	108
2008	Bullsnake	BS011	M	PFRA1	50	103
2008	Bullsnake	BS002	M	PFRA1	11	34
2008	Bullsnake	BS009	M	PFRA1	24	107
2008	Bullsnake	BS007	M	PFRA1	41	107
2008	Bullsnake	BS008	M	PFRA1	26	114
2008	Bullsnake	BS004	M	PFRA1	11	30
2008	Bullsnake	BS012	M	PFRA1	30	103
2008	Bullsnake	BS010	M	PFRA1	39	92
2009	Racer	DLR08	F	DebLes	39	113
2009	Racer	DLR11	F	DebLes	22	83
2009	Racer	GR01	F	Gergovia	5	10
2009	Racer	GR02	F	Gergovia	2	6
2009	Racer	GR05	F	Gergovia	9	56
2009	Racer	GR06	F	Gergovia	6	53
2009	Racer	SPR07	M	SnakePit	40	137
2009	Racer	SPR08	M	SnakePit	42	137
2009	Racer	SPR09	M	SnakePit	28	117
2009	Racer	SPR10	M	SnakePit	38	128
2009	Racer	SPR12	M	SnakePit	38	137
2009	Racer	SPR15	F	SnakePit	19	58
2009	Racer	SPR17	M	SnakePit	21	103
2009	Racer	SPR19	F	SnakePit	15	47
2009	Racer	SPR21	F	SnakePit	35	126
2009	Racer	SPR22	M	SnakePit	37	129
2009	Racer	SPR26	F	SnakePit	31	90
2009	Bullsnake	DLB01	F	DebLes	19	63
2009	Bullsnake	DLB02	F	DebLes	12	50
2009	Bullsnake	DLB03	F	DebLes	16	55
2009	Bullsnake	DLB04	M	DebLes	11	74
2009	Bullsnake	GB01	F	Gergovia	3	14

2010	Racer	SPRAC034	F	SnakePit	4	12
2010	Racer	SPRAC013	F	SnakePit	17	151
2010	Racer	SPRAC012	F	SnakePit	19	151
2010	Racer	SPRAC006	F	SnakePit	21	88
2010	Racer	SPRAC031	F	SnakePit	17	92
2010	Racer	SPRAC011	F	SnakePit	4	13
2010	Racer	SPRAC029	F	SnakePit	11	92
2010	Racer	SPRAC018	F	SnakePit	11	53
2010	Racer	SPRAC030	F	SnakePit	13	50
2010	Racer	SPRAC015	F	SnakePit	21	151
2010	Racer	SPRAC028	F	SnakePit	8	70
2010	Racer	SPRAC033	F	SnakePit	13	96
2010	Racer	SPRAC017	F	SnakePit	24	151
2010	Racer	SPRAC001	F	SnakePit	18	151
2010	Rattlesnake	SPPRS001	F	SnakePit	8	24
2010	Rattlesnake	SPPRS004	F	SnakePit	30	151
2010	Rattlesnake	SPPRS003	F	SnakePit	30	151
2010	Rattlesnake	SPPRS002	M	SnakePit	23	151
2010	Rattlesnake	SPPRS005	F	SnakePit	5	13
2010	Rattlesnake	SPPRS006	M	Unknown	13	33
2011	Rattlesnake	SPPRS020	F	SnakePit	5	23
2011	Rattlesnake	SPPRS017	F	SnakePit	32	90
2011	Rattlesnake	SPPRS013	F	SnakePit	19	57
2011	Rattlesnake	SPPRS021	M	SnakePit	5	120
2011	Rattlesnake	SPPRS022	F	SnakePit	28	83
2011	Rattlesnake	KPRS001	F	Kornfeld	9	24
2011	Rattlesnake	SPPRS012	F	SnakePit	4	18
2011	Rattlesnake	SPPRS015	F	SnakePit	6	13
2011	Rattlesnake	SPPRS019	M	SnakePit	17	79
2011	Rattlesnake	KPRS002	F	Kornfeld	28	120
2011	Rattlesnake	SPPRS016	F	SnakePit	22	83
2011	Rattlesnake	KPRS004	M	Kornfeld	31	75
2011	Rattlesnake	KPRS003	F	Kornfeld	15	62
2011	Rattlesnake	KPRS006	F	Kornfeld	7	21
2011	Rattlesnake	SPPRS018	F	SnakePit	29	90
2011	Rattlesnake	KPRS005	M	Kornfeld	16	106
2011	Rattlesnake	RPRS001	M	Unknown	12	17