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Annual migrations of female prairie rattlesnakes, *Crotalus v. viridis*, in Alberta.

by

Dennis Jørgensen

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ABSTRACT

Annual migrations of female prairie rattlesnakes, *Crotalus v. viridis*, in Alberta, Canada.

by

Dennis Jørgensen

September, 2009

Prepared in partial fulfillment of the requirements of the degree of Master of Environmental Design in the Faculty of Environmental Design, The University of Calgary.

Co-supervisors: Dr. C. Cormack Gates and Kevin Lloyd

The purpose of this study was to better understand the migrations of female prairie rattlesnakes, *Crotalus v. viridis*, and how migratory behaviours influence their annual distribution and mortality in southeastern Alberta. I radio-tracked the migrations of 27 females from two den sites in 2004 and 2005. I conducted a posteriori statistical analyses of the radio-tracking data revealing a significant bimodality in the distribution of mean elevation of observed locations making up the annual migration paths of individuals at both study sites. Habitat use was bimodally distributed between individuals using low and high elevation habitats. In conjunction with a GIS plotting annual migration paths and slope I identified two separate habitats occupied by radio-tracked females throughout much of the active season. I termed females occupying exclusively the low elevation habitat in the South Saskatchewan River valley riparian migrants and I termed females occupying primarily high elevation habitat beyond the crest of the river valley during the active season upland migrants. Maximum displacement of riparian migrants from the den

was between 0.47 and 2.6 km, while upland migrants moved between 1.2 and 10 km's from dens. The probability of encountering cultivation was influenced by differential habitat use at one site where upland habitat was almost entirely cultivated but these encounters were not related to a significantly increased probability of mortality of tracked females. This instance of differential habitat use among female prairie rattlesnakes is thought to represent an example of resource polymorphism but potential mechanisms supporting this phenomenon remain unknown.

Key words: *Crotalus viridis viridis*, prairie rattlesnake, migration, elevation, displacement, habitat use, niche, resource polymorphism.

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CHAPTER ONE: GENERAL INTRODUCTION AND THESIS OVERVIEW

BACKGROUND

The first radio-telemetry studies of the annual migrations of prairie rattlesnakes, *Crotalus v. viridis*, in North America were conducted in the mid 1980's in Wyoming (Duvall et al. 1985; King and Duvall 1990). These initial studies analysed both the form and the function of male and non-gravid female spring migrations from over-winter dens to activity ranges where prey and mates are sought (summarized in Table 1). The annual migrations of prairie rattlesnakes involve a seasonal to-and-fro movement of individuals between over-winter dens and active ranges. Individuals leave over-winter dens in the spring and generally return to the same den in the fall. Therefore throughout this document I refer to the outward bound migrations of radio-tracked female prairie rattlesnakes initiated in the spring as spring migrations despite the fact that their outward bound movements may not be completed until summer. Furthermore I refer to their overall movements throughout the active season as annual migrations. The results of previous radio-tracking studies emphasized the long displacement and relatively straight paths followed by individuals during spring migration. A radio-telemetry study of prairie rattlesnakes in Alberta in the 1990's resulted in similar observations of long displacement spring migrations, although the sample consisted of only four rattlesnakes (Didiuk 1999; summarized in Table 1). One of the females tracked in Alberta travelled a straight line distance of approximately 25 km from the over-winter den during spring migration,

engaging in a round trip of 52 km during one active season (Didiuk 1999), which is the longest reported migration of a terrestrial snake in the world.

Three radio-telemetry studies (King 1987; Powell et al. 1998; Parker and Anderson 2007) identified prairie and western rattlesnake populations within which most individuals engaged in long distance spring migrations but some engaged in short distance spring migrations. Tracking prairie rattlesnakes in Wyoming in 1984, King (1987) observed that some animals ($N = 7$) behaved as long distance spring migrants (mean = 4560 ± 964 m (SE)), and engaged in at least one bout of continuous directed movement of more than 500 m/active season, while other apparently healthy individuals were less active and engaged in short distance spring migrations ($N = 2$ males, mean = 437 ± 7.5 m (SE); $N = 2$ non-gravid females, mean = 850 ± 228 m (SE)).

In a radio-telemetry study of prairie rattlesnakes in Alberta, Powell et al. (1998) observed two males that migrated 4 and 12 km respectively from the over-winter den, while a non-gravid female moved only 300 m from the den. In a radio-telemetry study of midget-faded rattlesnakes (*Crotalus oreganus concolor*), a western rattlesnake subspecies in Wyoming, Parker and Anderson (2007) observed that few snakes made solely straight-line migrations. Instead most snakes made straight-line movements to and from discrete summer activity ranges where short multidirectional movements occurred, and others made multidirectional movements throughout the active season. Parker and Anderson (2007) suggested the observations of distinct migration patterns in their study represented evidence of behavioural polymorphism. Behavioural polymorphism is defined as the occurrence of two or more discrete forms of behaviour maintained in the same life stage in a single population and not simultaneously expressed in the same individual (West-

Eberhard 1989). Parker and Anderson (2007) speculated that a single movement pattern among individuals composing a population might reduce the likelihood of persistence of that population in response to disturbances affecting their activity range, while the existence of an alternative movement pattern could potentially permit avoidance.

Natural selection can lead to phenotypic differences through either phenotypic plasticity or genetic differentiation (Levins 1968; West-Eberhard 1989; Robinson & Wilson 1994; Orr & Smith 1998; Schluter 2000; Langerhans et al. 2003). Phenotypic plasticity (Stearns 1989) is “the ability of a single genotype to produce more than one alternative form of morphology, physiological state, and/or behaviour in response to environmental conditions” (West-Eberhard 1989). The adaptive plasticity hypothesis postulates that the evolution of phenotypic plasticity provides a mechanism for adaptation to spatially or temporally variable environments (Thompson 1991; Dudley and Schmitt 1996; Schmitt, Dudley and Pigliucci 1999; Agrawal 2001; Ernande and Dieckmann 2004). Disruptive selection is “simultaneous selection for more than one optimal phenotype in a single population”, and is thought to play a major role in the production and maintenance of polymorphisms (Mather 1955; Smith 1990b). When disruptive selection does not result in speciation, and gene flow between morphs is not interrupted, there may be an increase in intraspecific variation.

There is significant theoretical, observational and experimental support for the occurrence and maintenance of resource polymorphisms, within populations of a wide range of unrelated taxa (reviewed by Skulason and Smith 1995). Resource polymorphisms involve “the occurrence of discrete intraspecific morphs showing differential niche use, usually through differences in feeding biology and habitat use”

(Skulason and Smith 1995). Certain ecological conditions are thought to be necessary for more than one phenotype to be optimal in a single population, including limited interspecific competition, significant intraspecific competition, the presence of open or under-exploited niches, and habitat or resource heterogeneity. Under such conditions, resource polymorphisms may permit segregation among habitat types, reducing intraspecific competition and niche overlap by increasing resource partitioning (Schlosser 1987; Schoener 1987; Skulason and Smith 1995; Spina 2000). Even in species-rich environments, resource polymorphisms may arise if particular resources are underused (Skulason and Smith 1995).

Habitat or resource heterogeneity is thought to be necessary for the development of polymorphisms. A substantial component of variability in life histories is imposed on individual genotypes by spatial and temporal variability in the environment (Giesel et al. 1982; Baird et al. 1986; Baird et al. 1987). A number of species in aquatic environments exhibit polymorphisms, possibly because such environments can exhibit great spatial or temporal variability in habitat parameters (Langerhans et al. 2003). As an example of such variability Langerhans et al. (2003) cited differences in resource composition and availability between near-shore, littoral zones and off-shore, open water habitats. Lake Thingvallavatn, Iceland, is known to support four trophic morphs of Arctic charr, *Salvelinus alpinus*, two benthivorous, one planktivorous exploiting pelagic waters, and one piscivorous found in both habitats (Snorrason et al. 1994).

Although fewer resource polymorphisms have been documented in terrestrial systems, studies of polymorphic terrestrial species (e.g. birds and arthropods) have demonstrated the importance of spatial heterogeneity in making alternative resources

available to individuals (e.g. Smith 1990a). The Cocos finch, *Pinaroloxias inornata*, has diversified intraspecifically, with little morphological variation but a variety of stable individual feeding behaviours across several families of birds (Werner 1998 as cited in Skulason and Smith 1995). Among some amphibians (e.g. tiger salamander and spadefoot toad), morphs arise through a phenotype-mediated response to varying densities of conspecifics and food type (Pfennig 1990; Pfennig 1992).

Dispersal polymorphisms have also been documented among a variety of terrestrial species, and are one means by which morphs of a single species could access alternative resources or niches in heterogeneous environments (Toonen and Pawlik 2001). Wing polymorphisms in insects are the best known and most well studied type of dispersal polymorphism (Harrison 1980; Roff 1986; Zera and Denno 1997). Many animal species display behavioural polymorphisms that result in dispersal differences among individuals despite morphological similarity (reviewed by Gaines and McClenaghan 1980; Stenseth and Lidicker 1992; Dingle 1996 as cited in Toonen and Pawlik 2001). Both morphological and behavioural dispersal polymorphisms have been studied and shown to have a heritable genetic basis (Dingle 1996) and therefore can be subject to selection. Citing theoretical work (Harrison 1980; McPeck and Holt 1992) Toonen and Pawlik (2001) state that “selection should favour genotypes that can vary their tendency to disperse in habitats that are spatially or temporally variable, or those that remain near their carrying capacity”.

Based on the variety of ecological and environmental conditions thought to promote resource polymorphisms either individually or in combination, it is clear that polymorphisms have the potential to arise in a number of contexts. The ecology of prairie

rattlesnakes and the environment that they occupy in Alberta could support the occurrence of polymorphisms. More specifically, some studies of prairie and western rattlesnakes identified broad variation in displacement and tortuosity of movement paths associated with spring migrations, which could provide opportunities for individuals to access distinct resources or niches in a heterogeneous environment. Prairie rattlesnake over-winter dens in Alberta occur almost exclusively in riparian areas associated with major rivers in southeastern Alberta (Gannon 1978), and both riparian and upland prairie habitats are accessible to migrants. The limited availability of suitable den sites permitting survival over-winter; the occurrence of dens primarily if not exclusively in riparian areas in Alberta; and the limited extent of riparian areas relative to prairie uplands, could contribute to significant intraspecific competition if individuals did not migrate beyond riparian areas. The occurrence of over-winter dens in riparian areas and the presence of adjacent prairie uplands contributes to significant spatial heterogeneity and the availability of two highly distinct habitats.

LAND USE CONTEXT

Temperate grasslands are among the most threatened biomes globally (World Commission on Protected Areas 2002; Henwood 1998a, 1998b). Less than 1.5% (2.5 million acres) of the temperate grasslands in the Northern Great Plains (NGP) ecoregion are managed for biodiversity conservation (Forrest et al. 2004). In Canada, the NGP ecoregion occurs only in Alberta and Saskatchewan. In Alberta only 43% (10.24 million acres) of what was native prairie prior to European settlement remains native (Alberta Prairie Conservation Forum 2000) and in Saskatchewan about 21% (12.77 million acres) of the pre-settlement prairie remains native. In Alberta, pressures contributing to the

reduction of the remaining native prairie include cultivation, agriculture, petroleum and natural gas exploration and development, transportation and access development, and urban and rural development (Coupland 1973; Trottier 1992; Statistics Canada 1996; Diamond 1993; Samson and Knopf 1994; Weins 1996; AEP 1997).

Fragmentation, degradation and loss of native prairie habitat, including riparian areas, upland grasslands and wetlands, have significantly altered the landscape within which endemic plant and animal species exist. As of 1997, 24 of the 31 species at risk in Alberta were reliant on prairie habitats (AEP 1997). About 70% of 230 species at risk in Canada (COSEWIC) are at risk because of loss and degradation of suitable habitat to agricultural impacts (Canada-Manitoba Farm Stewardship Program BMP 2007).

Alberta had over 95,000 km of transportation corridors (e.g., highways, roads, railroads, wellsite roads) in the Grassland Natural Region in 1997 (AEP 1997). Traffic associated with transportation networks (e.g., roads, trails and rights-of way) pose a direct threat of mortality to individual animals crossing them, which can ultimately have consequences for populations (Fahrig et al. 1995). Transportation networks also increase access to and use of formerly remote or inaccessible areas that are potentially sensitive to human activity (Environment Canada 1986).

In Alberta, prairie rattlesnakes were assigned a conservation status of “data deficient” in June 2000 (AESCC 2000), and the species status was to be reassessed within five years using any new information gathered in that time period. This reassessment is currently being undertaken (K. Kissner Pers. Comm.). The species is also listed as “data deficient” federally (COSEWIC 2007), with no time frame set for review of the species federal status, although a draft report is currently being revised (A. Didiuk

Pers. Comm.). The prairie rattlesnake is afforded some protection as a “non-game animal” under the *Alberta Wildlife Act*, which makes it illegal to kill, possess, buy or sell rattlesnakes in Alberta, but a rattlesnake can be killed if it is thought to pose a threat to human safety.

Anecdotal evidence suggests that the number of rattlesnakes in Alberta has declined as a function of road mortality, persecution, agricultural activity and habitat loss and fragmentation (Watson and Russell 1997; Rose 2001; Kissner and Nicholson 2003). Vehicle strikes are a frequent source of snake mortality and have been documented for over half a century (e.g., Van Hyning 1931; Campbell 1956; Pough 1966; Smith and Dodd 2003). Anecdotal evidence and preliminary research in southeastern Alberta (Powell et al. 1998; Didiuk 1999; Joel Nicholson Pers. comm.) has documented frequent mortality of prairie rattlesnakes while crossing roads within annual active ranges. Among prairie rattlesnakes in the northern portion of their range the problem of road mortality is thought to be exacerbated by their annual migrations to locate food and mates (Duvall et al. 1990; King and Duvall 1990; Didiuk 1999).

One of the key phenomena that must be studied to understand the costs and benefits of the changing prairie landscape and human activities on prairie rattlesnakes is the role of annual migrations in determining their distribution during the active season (April to October) in relation to varying habitats and human activities.

PURPOSE

The purpose of this study was to better understand the migratory behaviours of female prairie rattlesnakes and how they influence their annual distribution and mortality in the prairie landscape of south eastern Alberta. The results of previous radio-telemetry

studies demonstrating long and short displacement spring migration patterns were the basis of my interest in the potential for variation in the annual migration patterns of prairie rattlesnakes' to influence their active season distribution on the prairie landscape. I conducted a pilot observational study to examine variation in habitat use and spring migration patterns of female prairie rattlesnakes in Alberta. I thought it possible that access to both riparian and upland habitats and use of varying migration strategies could influence the distribution and mortality of female prairie rattlesnakes during the active season. I conducted a posteriori examination of my radio-tracking data revealing apparent bimodality in mean elevation of habitats used by individuals within study sites during annual migrations. My objectives in this thesis were to analyse apparent differences in habitat use of females on the prairie landscape; to consider associated mortality; to characterize spring migration traits; and to assess whether ontogenetic and life-history characteristics of individuals including initial size-class, reproductive maturity, and reproductive outcomes influence habitat partitioning. The prairie rattlesnake is legally designated as data deficient both provincially and federally pending revision and review of status reports that are currently being updated. This study will contribute significantly to our understanding of factors affecting the conservation status of this species in Alberta.

SPECIFIC QUESTIONS ADDRESSED

Habitat use

Based on a posteriori analyses of the data I posed the questions:

- 1) Is the mean elevation of observed locations occupied during the annual migrations of female prairie rattlesnakes bimodally distributed within sites?

- 2) Is the bimodal distribution of mean elevations occupied during annual migrations related to the use of different habitats?
- 3) How were the habitats occupied by female prairie rattlesnakes defined?
- 4) Do mean squared distances of simulated spring migration paths generated by the site fidelity model account for the observed mean squared distance of spring migration paths of both riparian and upland migrants?
- 5) Do the movement behaviours (maximum displacement, linearity, total observed pathway length) of riparian and upland migrants differ?
- 6) Of the total active season, how much time did riparian and upland migrants occupy spatially separated habitats?
- 7) Is riparian and upland habitat use of radio-tracked female rattlesnakes related to the frequency of encounters with cultivation and are encounters with cultivation related to probability of mortality?
- 8) Differences in migration pattern are sometimes attributed to “differential migration” or differences in the migration patterns of older and younger individuals. Also, some species demonstrating resource polymorphisms differ in growth patterns, which are typically related to ontogenetic niche shifts (e.g. Snorrason et al. 1994) and/or variable migratory behaviors (Skulason and Smith 1995). Are differences in spring migration patterns of female prairie rattlesnakes correlated with differences in initial length and mass, reproductive maturity, annual growth, or reproductive outcomes of annual movements?

Mark-recapture

Using mark-recapture in 2004 and 2005 during departure and return of prairie rattlesnakes from the two focal over-winter den sites at which radio-tracked snakes were captured I estimated the number of adult females. I addressed the questions:

9) What proportion of the estimated overall female population at focal dens was radio-tracked?

10) Do 95% confidence intervals suggest that the predominant habitat use of radio-tracked female prairie rattlesnakes at each den is representative of the larger female population at that den?

APPROACH – LOGIC OF INQUIRY

To address these specific questions I selected two prairie rattlesnake over-winter den sites in the Grasslands Natural Region of southeastern Alberta. I captured and surgically equipped 27 female prairie rattlesnakes with radio transmitters at the two den sites; 12 females at den site A and 15 females at den site B. I radio-tracked female movements during two active seasons (April to October) 2004 and 2005. Preliminary examination of the radio-telemetry data suggested that differences existed among individuals in their use of either exclusively riparian or primarily upland habitats within available habitats adjacent to over-winter dens. Therefore I used the mean elevation of observed locations throughout the active season to explore this potential difference. More specifically, I examined dot plots (suitable for small sample size) of mean elevation for evidence of bimodality, and subsequently analysed these distributions to determine the probability of a normal distribution, to support or refute a bimodal distribution of elevation associated habitat use within study sites. I used two-sample t-tests to determine

whether there was a significant difference between elevations occupied by low elevation migrants and high elevation migrants within sites. I subsequently defined two habitats using GIS-based plots (ArcView 3.2a) of slope in conjunction with annual migration paths of individuals classified as occupying either exclusively riparian or predominantly upland active ranges. I analysed characteristics of movement paths of riparian and upland migrants including maximum displacement, linearity of the observed spring migration path, and total observed pathway length of annual movements. Using the date of arrival and departure of upland migrants to and from upland habitats I calculated the duration of upland activity and the percent of the total active season spent by upland migrants in upland habitat. I used Fisher's exact test to determine whether a relationship existed between riparian and upland habitat use and encounters with cultivation by study site. I also used a Fisher's exact test to determine whether a relationship existed between encounters with cultivation and mortality. I discuss observed mortality and potential costs and benefits of annual habitat use and migration strategies. I recaptured snakes, when possible, at their time of return to the den to measure season-long changes in length and mass and to assess reproductive status. I computed 95% confidence intervals using the Clopper-Pearson exact test for binomial variables to make inferences regarding the proportion of the overall female population at each of the two focal den sites that engaged in riparian and upland migrations. Finally, I discuss key findings, recommendations for management and for future research that might further elucidate conservation needs and priorities for prairie rattlesnake management in Alberta.

THESIS ORGANIZATION

In Chapter 1, I provide background on current knowledge of the annual movements of prairie and western rattlesnakes in the northern portion of their range. I discuss resource polymorphisms and the conditions that are thought to promote or maintain them. I consider the land use context within which the study was conducted and the conservation status of prairie rattlesnakes in Alberta and how it is thought to have changed in response to human activities and modifications. I describe the methods used to determine whether annual migrations are contributing to habitat partitioning among prairie rattlesnakes in Alberta.

In Chapter 2, I determined whether annual habitat use and migration patterns contribute to habitat partitioning among radio-tracked females in two populations of prairie rattlesnakes in southeastern Alberta. I defined habitat boundaries based on annual migration paths and a GIS including elevation and slope grid layers. I determined which movement variables are most closely associated with individuals occupying riparian and upland habitats. I calculated the percent of the active season spent in upland habitats by upland migrant radio-tracked females. I considered whether habitat use among radio-tracked female rattlesnakes is related to encounters with cultivation and whether such encounters contribute to increased probability of mortality. I assessed whether morphometric and reproductive characteristics of individuals including initial size-class, reproductive maturity, and reproductive outcomes are associated with habitat preference. Finally, I speculate on potential explanations for the observed distribution of riparian and upland migrants between study sites.

In Chapter 3, I summarize the key findings of this study and discuss implications of habitat partitioning and migration patterns for the conservation of prairie rattlesnakes, discussing potential costs and benefits of human activities and human modified landscapes within the rattlesnakes range in southeastern Alberta. I also propose future research to further elucidate needs and priorities for prairie rattlesnake conservation in Alberta.

CHAPTER TWO: ANNUAL MIGRATIONS AND HABITAT USE OF RADIO-TRACKED FEMALE PRAIRIE RATTLESNAKES IN ALBERTA

INTRODUCTION

In temperate regions occupied by snakes, sub-freezing ambient temperatures oblige them to hibernate in subterranean dens over-winter (Gregory 1984). The limited availability and distribution of thermally suitable hibernation sites permitting survival of snakes (Gregory 1974, Aleksuk 1976) separates hibernaculae from annual activity ranges where prey or other required resources (e.g., mates) are sought when temperatures permit activity (Gregory et al. 1987). Migration occurs when resources (e.g., food, shelter and mates) required by an animal are spatially or temporally separated or transitory, thus requiring movement to exploit resources (Baker 1978; Semlitsch 1985; Pilliod et al. 2002;

Annual migrations in temperate regions of both North America and Europe have been observed among snake species including but not limited to Red-sided garter snakes (*Thamnophis sirtalis parietalis*; Gregory and Stewart 1975; Aleksuk 1976; Larsen 1987), Western yellow-bellied racers (*Coluber constrictor mormon*; Hirth et al. 1969; Brown and Parker 1976), Desert striped whipsnakes (*Masticophis t. taeniatus*; Hirth et al. 1969), Common European adders (*Vipera berus*; Viitanen 1967; Prestt 1971) and nearctic *Crotalus* spp. (Klauber 1972) including Sidewinders (*Crotalus cerastes*; Secor 1994) and Timber rattlesnakes (*Crotalus horridus*; Brown et al. 1982). In contrast some snake species movements in temperate regions are short and erratic (e.g. Blanchard and Finster 1933; Hirth et al. 1969; Fitch and Shirer 1971; Lawson 1994).

Annual migration of prairie rattlesnakes (*Crotalus v. viridis*) and western rattlesnakes (*Crotalus oreganus* spp.) is well documented (Fitch 1949; Woodbury 1951;

Hirth et al. 1969; Klauber 1972; Parker and Brown 1974; Gannon 1980; Ludlow 1981; Diller and Wallace 1984; Gannon and Secoy 1985; King 1987; Duvall et al. 1990; King and Duvall 1990; Powell et al. 1998; Didiuk 1999; Ashton 2003, Jenkins and Peterson 2005, Parker and Anderson 2007). Male and non-gravid female prairie rattlesnakes radio-tracked in Alberta have been documented to migrate further than any other terrestrial snake species in the world (maximum displacement, up to 25 km; Didiuk 1999). The prairie rattlesnake hibernates throughout its range in North America (Figure 1), and generally demonstrates high fidelity to winter den sites (Gregory 1982, 1984). They disperse from hibernaculae in spring to active ranges where they feed and adults mate, returning to the same hibernaculum in the fall to over-winter, a necessity which results in both spatial and temporal separation of required resources (i.e., prey, mates and hibernaculae).

Unlike amphibians that must typically migrate to and from aquatic breeding habitats, reptile breeding biology does not generally require migration for reproductive purposes, and reptile migrations are much more likely to be based upon foraging behaviour (Russell et al. 2005). A primary function of prairie rattlesnake migrations is to locate prey patches (e.g., Duvall et al. 1990). The movements of non-gravid females are focused on locating prey throughout the active season, while those of males are focused on locating prey until mature females become sexually receptive in late summer (July and August), then sexually mature males stop feeding and begin searching exclusively for mates (King and Duvall 1990; Duvall and Schuett 1997). Similar to the females of many reptile species (Brown 1991; Brana, Gonzales & Barahona 1992; Doughty & Shine 1997; Madsen & Shine 1999) and most viperid snakes (Madsen and Shine 1992, Brown 1993,

Martin 1993), female prairie rattlesnakes reproduce infrequently (less-than-annually) and are capital breeders meaning that stored resources constitute the primary energy source for reproduction (Blem 1981; Lourdais et al. 2002). As capital breeders, body fat reserves are critical to reproduction in female rattlesnakes (Aldridge, 1979; Galligan and Dunson, 1979; Blem 1982; Diller and Wallace 1984; Macartney and Gregory 1988; Charland and Gregory 1989; Brown 1991). It is believed that in a given year female vipers do not initiate vitellogenesis (i.e. follicle development) unless they have accumulated sufficient energy stores to reach a high body condition threshold (Naulleau and Bonnet 1996).

The adaptive significance of migration and the relative effectiveness of varying spring migration strategies of communally denning snakes have been the subject of discussion and research (Hirth et al. 1969; Brown and Parker 1976; Duvall et al. 1985; King 1987; Duvall et al. 1990; King and Duvall 1990; Duvall et al. 1997; Duvall and Schuett 1997). Duvall et al. (1997) hypothesized that the search strategies of individuals should reflect selection pressure for search paths that maximize the location of prey patches whose position and profitability are unknown because the location of resource units (e.g., prey patches) sought by prairie rattlesnakes in Wyoming may change unpredictably from year to year. Based on simulation modelling they determined that search paths approximating a straight line generated large numbers of encounters with resources that were both clustered and widely dispersed (Duvall et al. 1990; King and Duvall 1990). Based on the results of their simulation experiments (Duvall et al. 1997), and consistent observations of fixed-bearing migrations among prairie rattlesnakes radio-tracked in Wyoming (Duvall et al. 1985, King and Duvall 1990, Duvall et al. 1990),

Duvall and Schuett (1997), hypothesized that fixed-bearing orientation by prairie rattlesnakes might contribute to increased search efficiency while seeking prey and mates. Duvall and Schuett (1997) found that movement paths approaching a straight line resulted in greater reproductive success among male prairie rattlesnakes seeking mates. They equated straighter movement paths with greater search efficiency. Zollner and Lima (1999) used computer simulations to compare the effectiveness of several search rules for landscape-level search for habitat in idealized landscapes (uniform, random or clumped patches). Their simulations suggested that the best non-systematic search paths were nearly straight (vector (r) greater than or equal to 0.9), but usually not completely straight. Nearly straight searchers were much less likely than completely straight searchers to leave the landscape they were searching, and were simultaneously likely to avoid much of the redundant search inherent in less correlated random walks. Optimal path straightness was strongly influenced by patch density, mortality risk, and energy reserve levels, but landscape configuration was of limited influence. The success of exhaustive systematic searches surpassed nearly straight-line random walks when animals had considerable perceptual range.

Three radio-telemetry studies of prairie or western rattlesnake (King 1987; Powell et al. 1998; Parker and Anderson 2007) identified populations within which some individuals engaged in long distance migrations and others engaged in short distance migrations. Tracking prairie rattlesnakes in Wyoming in 1984, King (1987) observed that some animals ($N = 7$) behaved as long distance spring migrants (mean = 4560 ± 964 m (SE)), and engaged in at least one bout of continuous directed movement of more than 500 m/active season, while other apparently healthy individuals were less active and

engaged in short distance spring migrations ($N = 2$ males, mean = 437 ± 7.5 m (SE); $N = 2$ non-gravid females, mean = 850 ± 228 m (SE)). In another radio-telemetry study of prairie rattlesnakes in Alberta, Powell et al. (1998) observed two males that migrated 4 and 12 km respectively from the over-winter den, while a non-gravid female moved only 300 m from the den. In a radio-telemetry study of midget-faded rattlesnakes (*Crotalus oreganus concolor*), a western rattlesnake subspecies in Wyoming, Parker and Anderson (2007) observed that few snakes made solely straight-line movements. Instead most snakes made straight-line movements to and from discrete summer activity ranges where short multidirectional movements occurred, and others made multidirectional movements throughout the active season. Parker and Anderson (2007) suggested these observations of distinct movement patterns represented evidence of behavioural polymorphism.

Behavioural polymorphism is defined as the occurrence of two or more discrete forms of behaviour maintained in the same life stage in a single population and not simultaneously expressed in the same individual (West-Eberhard 1989). Parker and Anderson (2007) speculated that a single movement pattern might limit the ability of individuals to adapt to disturbances within their activity range, and the existence of an alternative movement pattern could enhance the persistence of individuals and hence populations in response to disturbance. Parker and Anderson (2007) did not cite phenotypic plasticity as a potential explanation, a possibility that cannot be ruled out.

The limited number of radio-telemetric studies of prairie rattlesnakes, the relative lack of inter-annual comparisons of individuals movements, their restricted geographical distribution and their relatively small sample sizes, demonstrate that we have incomplete knowledge of the potential variation in annual habitat use and spring migration patterns

between individuals, sexes, size-classes, years and populations. Greater knowledge of the variation in annual habitat use and spring migration patterns occurring among rattlesnakes in Alberta will provide a stronger foundation upon which to assess the distribution of prairie rattlesnakes and associated benefits and risks of human activities and modifications during the active season in southeastern Alberta.

In this observational study I examined whether annual habitat partitioning and differing spring migration patterns exist among females from two populations of prairie rattlesnakes in southeastern Alberta. Based on identified habitat use categories I conducted a rudimentary examination of any associated differences in variables typically used to characterize their migrations (e.g. maximum displacement, linearity). I tested whether differential habitat use is related to site specific encounters with cultivation and whether encounters with cultivation are related to altered mortality rates. I examined whether differential habitat use is correlated with varying size-class, reproductive maturity and reproductive outcomes. I believe that prairie rattlesnakes provide an excellent model for examining why differential habitat use and spring migration patterns might exist within species considering that communal denning results in all subjects occupying the same initial location, thereby presumably providing exposure to equivalent initial conditions, resources and choices.

METHODS

Study area

I tracked the annual movements of 27 female prairie rattlesnakes over a two year period (2004-2005) from two hibernacula within the South Saskatchewan River

watershed near Medicine Hat, Alberta (50° 1' N; 110° 43' W). I defined a hibernaculum as a network of fissures and mammal burrows presumed to be connected, separate and distinct from other such networks, from which prairie rattlesnakes would emerge and disperse in the spring and return in the fall to over-winter. One hibernaculum (den site A) was located approximately 20 km north of Medicine Hat. The surrounding area was principally a public land grazing disposition consisting primarily of native dry mixed-grass prairie, and a small amount of privately owned cultivated land. Significant gas development has also occurred in this area. I sampled another hibernaculum (den site B) at a second site approximately 13 km west of Medicine Hat. The river valley in which this hibernaculum was located was a combination of privately owned and public land characterized by native dry mixed-grass prairie subject to cattle grazing, while the adjacent upland was almost entirely privately owned cultivated land (dry land and irrigation farming) with some tame pasture and rural residential development. The two den sites are approximately 28 km apart (Figure 1).

Radio-telemetry

Males exhibit migratory, foraging and mate-searching movements during the active season that might have confounded the detection of patterns. I selected non-gravid female prairie rattlesnakes as the subjects for this study because they are thought to engage strictly in migratory and foraging movements during the active season. I monitored the movements of 27 non-gravid female prairie rattlesnakes using radio-telemetry over two active seasons (late April to early October 2004 and 2005), 12 at den site A (4 in 2004; 8 in 2005) and 15 at den site B (8 in 2004; 7 in 2005).

Veterinary surgeons performed radio-transmitter implantations at the Calgary Zoo Animal Health Centre under aseptic conditions (Appendix I). I held snakes in a controlled environment for 24 hours following surgery, and then released them at the den where I had captured them. I received approval for all surgical and handling procedures under the University of Calgary, Certification of Animal Care #BI2004-024 (2004-2006); Alberta Sustainable Resource Development Collection Licences #118 (2004-2005) and #20372 (2005-2006); and Alberta Sustainable Resource Development Research Permits #15383 (2004-2005) and #20390 (2005-2006).

Once the radio-equipped snakes began to move away from hibernacula in spring, I recorded locations on a daily basis or as weather permitted (1 to 3 day intervals) throughout the 2004 or 2005 active season (late April to October). I used A Garmin™ 12XL GPS unit to record the coordinates (UTM, NAD 83) of snake locations. I downloaded coordinates from GPS units using OziExplorer GIS mapping software (Version 3.95.4g, D & L Software Pty Ltd. Australia). I exported location data from OziExplorer to ArcView 3.2a (ESRI 2000) for analysis.

Of the 12 females radio-tagged at site A, I did not track two females (one mortality (rattlesnake ID: CC) and one signal-loss (rattlesnake ID: C)) for a sufficient duration to characterize their migrations, resulting in the characterization of the observed migrations of 10 females. Of the 15 females radio-tagged at site B, I did not locate one female with sufficient frequency to include in analyses because she swam across the South Saskatchewan River hindering regular relocation (rattlesnake ID: Y), resulting in the characterization of 14 females observed movement paths. Therefore, I located twenty

four snakes once every one to three days during the active season, or until death, permitting me to completely analyse their movement patterns.

I collected tracking data for four females in both 2004 and 2005. To avoid issues of non-independence of samples I used only the first season of movement data to calculate summary statistics for three of these females (Table 3, rattlesnake ID: D, G and M). The fourth female was gravid in the first season so I used only the second season of movement data to calculate summary statistics on spring migration and annual movements (Table 3, rattlesnake ID: K). I tracked five rattlesnakes that were killed during annual movements for most of an active season and I included their data in calculations of movement statistics (Table 3, rattlesnake ID: F, J, P, Q, U). I did not include one other rattlesnake killed prior to commencing spring migration in calculations of movement statistics (rattlesnake ID: CC).

Habitat use

I conducted a posteriori examination of the migration paths of radio-tracked females, plotting them in ArcView 3.2a including a Digital Elevation Map (DEM, 25 metre grid, Alberta Environment and Space Imaging LLC 2000) and a slope grid derived from the DEM revealing that some individuals remained within the South Saskatchewan River valley throughout the active season while other individuals' annual activity ranges included adjacent uplands. To examine the distribution of the mean elevation of observed locations of individual radio-tracked females throughout their migrations I used dot plots (better suited for small sample sizes than histograms). To determine whether the distribution of mean elevation of migration paths at a study site differed significantly

from a normal distribution I used the Shapiro-Wilk test (Shapiro and Wilk 1965), which is a method for testing normality and can be applied to between 4 and 2000 observations (Stata 2005). I assumed that if the distribution of points on a dot plot for a study site appeared bimodal and the Shapiro-Wilk test determined that the observed distribution deviated significantly from a normal distribution, the distribution was bimodal. Subsequently, I formed two groups within sites based on the discontinuity in the bimodal distribution and examination of the distribution of the migration path relative to the crest of the South Saskatchewan River valley as observed in a GIS. I then calculated the mean elevation of all observed locations of the two groups of females at each site and used two-sample t-tests to determine whether they were significantly different within study sites. To determine how much of the total active season riparian and upland migrants spent in spatially separated habitats I calculated the duration (days) spent by upland migrants in upland habitats and I calculated this value as a percentage of each upland migrants total active season duration.

Movement patterns

The spring migration movements of prairie rattlesnakes radio-tracked in previous studies were often directed, following a relatively straight-line, which maximized displacement from the den of origin relative to the total observed spring migration pathway length (King and Duvall 1990). I considered spring migration movements to have ended at the point of maximum displacement from the den of origin. Although this would seem a reasonable assumption, the movements of some individuals meandered, cycling towards and away from the den repeatedly throughout the active season making

the selection of an end point more complex. To determine whether it was appropriate to designate the point of maximum displacement as the end point of spring migration I used a two sample t-test to compare between sites and within years the date radio-tracked females were observed at their point of maximum displacement from the den of origin. I used a Julian date converter to convert the calendar dates of maximum displacement to numbers permitting me to calculate means and standard errors, and subsequently permitting me to conduct statistical comparisons between sites and within years.

The site fidelity test in the Animal movement extension (Version 2.0, Hooze and Eichenlaub 2000) to ArcView 3.2a used a Monte Carlo simulation procedure developed by Munger (1984) and modified by Danielson and Swihart (1987) and Spencer et al. (1990) to generate random paths for comparison with observed spring migration paths to assess site fidelity or alternatively directedness. Distances between successive recorded locations of an individual's spring migration path were calculated and then randomly chosen without replacement until none remained. Each selected distance was assigned a randomly generated angle over the interval 0° to 360° to calculate the x,y coordinates for a random location. Taken in sequence, these random locations generated a simulated random walk representing a spring migration path. Simulated spring migration paths began at the den site (initial location). Using this procedure, the site fidelity test generated 1000 random movement paths for each individual (user-specified number recommended by Hooze and Eichenlaub 2000). For the purposes of this procedure it was necessary to define the spring migration path by selecting the end point of the spring migration phase of annual movements.

The site fidelity test (Hooge and Eichenlaub 2000) subsequently calculated mean squared distance (MSD (m²)) from the center of activity (Schoener 1981) measuring the spread of habitat use around that central point (i.e., the den site).

$$r^2 = \frac{1}{(n-1)} \sum_{i=1}^{n-1} (x_i - \bar{x})^2 + \frac{1}{(n-1)} \sum_{i=1}^{(n-1)} (y_i - \bar{y})^2, \quad (1)$$

r^2 is the mean squared distance, x and y are Cartesian coordinates, n is the number of observed locations making up the spring migration path, and i denotes the order of the series of observations. Using the mean squared distance (MSD) values resulting from the simulations generated by the site fidelity test I calculated MSD_{diff} (observed MSD – maximum simulated MSD) for each individual, and classified individuals MSD as predicted if MSD_{diff} = negative value (i.e., observed MSD < maximum simulated MSD) or Underpredicted if MSD_{diff} = positive value (i.e., observed MSD > maximum simulated MSD) (Table 2). In other words individuals with observed MSD values that fell within the MSD values of the 1000 simulated random walks were classified as predicted and individuals with observed MSD values greater than all 1000 simulated random walks were classified as underpredicted. This analysis provided a means of determining which individuals engaged in spring migrations that were more directed than would be expected if the bearings of sequential movements were random.

The site fidelity test also calculated a Linearity Index (LI), which is equal to the linear distance between the den site and the point of maximum displacement of an observed or simulated path divided by the total observed or simulated pathway length. Perfectly linear paths yield $LI = 1$ and decreasing values < 1 indicate decreasing linearity.

Appendix II describes all of the variables I measured and analysed to examine variation in elevation, movement, morphometric and reproductive parameters of radio-tracked female rattlesnakes within sites. Movement parameters I calculated included characteristics of movement paths related to scale (i.e., maximum displacement (m)), straightness (i.e., linearity index of observed spring migration path), and total observed pathway length (m). Morphometric and reproductive parameters I measured included initial snout to vent length (cm) and mass (g), growth (i.e., change in snout to vent length (%)), storage (i.e., change in mass (%)), reproductive maturity and the outcome of reproductive activities. I made all comparisons of variation in these variables with respect to habitat use within sites using two-sample t-tests. I also calculated the total duration of movements, the duration of upland habitat use among upland migrants, and the percent of the upland migrants active season spent in the upland habitat (Appendix II).

Mass, length and reproductive status

I measured mass (g) and snout to vent length (cm) for each female during emergence in the spring and upon their return to the den in the fall at the end of the active season (Table 4). I did not obtain measurements for 7 females in the fall (3 at site A; 4 at site B) because they entered the den before being recaptured and did not re-emerge. For my safety I captured snakes using a nylon noose and I inserted their head and neck in a clear plastic tube 28 cm long that best approximated the width of the head. I measured snout to vent length twice using a metre stick upon which I extended the snake's body, and I recorded both measurements and calculated the mean. I recorded mass with a spring scale by weighing the snake in a pre-weighed cloth bag. I recorded two measurements

and calculated the mean. I subtracted the known mass of the implanted radio-transmitter. I calculated the change in length and mass between spring emergence and fall return to the den site (Table 4). I also calculated the proportional increase in length and mass to provide a relative measure of change, potentially avoiding biases that might result from initial differences in size-class.

I palpated rattlesnakes captured at each of the two dens to identify and count developing ova or embryos. As in other studies of reproduction in prairie rattlesnakes (e.g. Kissner et al. 1996), I estimated the size at sexual maturity for females as the shortest snout-to-vent length (SVL) of a female captured with enlarged ova or with embryos. Gravid females were those with developing ova or embryos that I identified by palpation in the fall at the end of the radio-tracking period. The smallest sexually mature female that I identified at site A measured 68.5 cm long and the smallest mature female at site B measured 68.6 cm long (Jørgensen and Nicholson 2007). Using the threshold snout to vent length of 68.5 cm, I divided radio-tracked females into juvenile and adult classes to determine their distribution with respect to riparian and upland habitat use.

Mark-Recapture

Prior to the active season (mid to late April) 2004, I erected drift fences constructed of hardware cloth, using rebar for support, around the perimeters of two hibernacula (den sites A and B; Figure 1). I installed funnel traps (N=3 site A; N=5 site B) constructed of plywood and hardware cloth along the drift fences. I checked traps daily during the spring to capture snakes leaving the hibernaculum (egress) and again in the fall to capture snakes returning to the hibernaculum (ingress). I removed traps

between these times to allow free movement of snakes to and from the den during the active season. I found no snakes or other animals dead in traps.

I captured and implanted rattlesnakes at each of the two hibernacula with a passive integrated transponder (PIT) tag (AVID™) subcutaneously on the right dorsal side approximately 4 cm anterior to the cloaca using a 12-gauge syringe applicator. PIT tags provide a unique ten digit identifier for each marked individual (Appendix III site A; Appendix IV site B). I considered neonates and juvenile rattlesnakes with snout to vent lengths of less than 45 cm too small to mark. During three subsequent mark-recapture sessions (fall 2004 and 2005, spring 2005) I scanned captured snakes to record a PIT tag number, I marked them if necessary, I measured them (snout-vent length and tail length), I sexed them, I palpated them to count food boli or developing ova or embryos, I weighed them, and then I released them.

I used A Jolly-Dickson full model (Population Analyst 5 release C.1; Arnason and Schwarz 2000) to estimate female population size, number of marks in the population, births between capture sessions, survival rate between capture sessions, capture probability, and standard errors (S.E.) associated with each estimate. I assumed constant capture probability because of the high den site fidelity of prairie rattlesnakes observed in both this study ($20/21 = 95\%$) and reviews of previous studies (Gregory 1982, 1984). I recaptured and marked male and female rattlesnakes at dens, but I only considered females in the mark-recapture analysis because I only radio-tracked females. I used an open population estimate, which assumed that individuals may be recruited (births and immigration) or lost from the population (deaths and emigration) during the study. In the open population model I included data from all four mark-recapture sessions to generate

three separate population estimates (one for each recapture session). I used female population estimates to assess the approximate proportion of the total female population that I radio-tracked at den sites A and B in this study.

I computed 95% confidence intervals using the Clopper-Pearson exact test for binomial variables to make inferences regarding the proportion of the female population at each of the two focal den sites that engaged in riparian migrations. In addition I performed a z-test of proportions using proportions of riparian migrants at the two focal den sites to determine whether the proportions were equivalent.

RESULTS

Radio-telemetry

Ten female snakes were tracked in study area A (Figure 2) for an average of 119.8 ± 11.4 days (S.E.; range = 48-158 days), and fourteen females were tracked in study area B (Figure 3) for an average of 128.7 ± 6.2 days (S.E.; range = 75-161 days). Of the twenty one radio-tagged females that completed their annual migration by returning to an overwintering den in the fall (including two whose movement paths were not analysed), only one returned to a den in the fall different than the one from which it emerged in the spring.

Of twenty-four females, five died but movements were tracked for an average of 82.4 ± 13.8 days (S.E.; range = 48-122 days) before dying of factors external to the radio-tracking experiment (predation or human activities; Table 2). One other rattlesnake killed prior to commencing spring migration was not included in calculations of movement

statistics (rattlesnake ID: CC), therefore the total observed number of female mortalities was six.

Habitat use

Based on discontinuity in the dot plot, bimodality was apparent in the distribution of the mean elevations occupied by migrating radio-tracked females throughout the active season at study site B (Figure 4). At site B the distribution of mean elevation of female rattlesnake locations deviated significantly from a Normal distribution (Shapiro-Wilks W test: $N = 14$, $W = 0.805$, $p = 0.006$), which in conjunction with the dot plot suggests bimodally distributed habitat use defined by mean elevation of observed migration paths. Subsequent examination of a Digital Elevation Map, a slope grid and the observed migration paths suggested that among those females composing the group occupying lower mean elevations, their habitat was bounded by the crest of the South Saskatchewan River valley where the slope begins to decline transitioning to the flatter upland habitat. The bimodal distribution resulted in two groups of seven females, one group occupying exclusively low elevation habitats throughout their migrations and the other occupying primarily adjacent uplands or high elevation habitats during their migrations (Figures 5 and 6). The difference in mean elevation of observed locations occupied by seven low elevation migrants (672.5 ± 1.9 m) and seven high elevation migrants (747.5 ± 4.9 m) throughout the active season at site B was statistically significant ($t = -14.229$, d.f. = 12, $p = 0.000$).

The discontinuity in the distribution of elevations occupied by females at study site A was less apparent based on the dot plot (Figure 7). The distribution of mean

elevation appeared either normal or multimodal, but there were two individuals that migrated strictly within the low elevation habitats as defined at site B (Figures 8 and 9). There was not a significant difference between a Normal distribution and the distribution of the mean elevation of locations of migrating radio-tracked females at site A (Shapiro-Wilks test: $N = 10$, $W = 0.885$, $p = 0.15$), although the small number of females migrating strictly within riparian areas at this site ($N = 2$) may have hindered detection of a difference. Partitioning individuals according to the definition of low elevation and high elevation habitats observed at site B, there was a significant difference in the mean elevation of observed locations occupied by the two low elevation migrants (648.6 ± 3.9 m) and eight high elevation migrants (702.2 ± 4.9 m) at site A ($t = -5.157$, d.f. = 8, $p = 0.0009$).

Examining the distribution of the movements of low elevation migrants in a GIS including annual migration paths and slope, the low elevation migrants occupied all elevations within the South Saskatchewan River Valley from the rivers edge through the floodplain, to an apparent boundary at the crest of the valley where the slope declines, transitioning to the upland (Figure 6 site A, Figure 9 site B). Based on this distinction in elevation I termed the habitat occupied by the low elevation migrants the riparian habitat and I termed the females occupying that habitat riparian migrants. I termed the habitat beyond the point where the slope declines and the river valley ends, the upland habitat and all individuals that migrated beyond the riparian habitat occupying primarily the upland habitat throughout the active season were termed upland migrants.

Six upland migrants at site A that survived the entire active season spent an average of 106 ± 7 days (Range = 74 – 122 days) in upland habitats unoccupied by radio-tracked riparian migrants, which amounted to an average of 77 ± 6 % of the upland migrants total active season duration (Range = 125 – 158 days). I calculated this value as a percentage of each upland migrants total active season duration (Appendix IV). Five upland migrants at site B that survived the entire active season spent an average of 75 ± 11 days (Range = 39 – 103 days) in upland habitats unoccupied by radio-tracked riparian migrants, which amounted to an average of 57 ± 7 % of the upland migrants total active season duration (Range = 105 – 149 days). The mean date of arrival in the uplands at site A in 2004 was June 6 (N=2, S.E. = 18 days) and at site B it was June 26 (N = 3, S.E. = 12.5 days). In 2005 the mean date of arrival in the uplands at site A was May 23 (N = 6, S.E. = 5.9 days) and at site B it was June 2 (N = 4, S.E. = 4.3 days).

The mortality rate among radio-tracked female rattlesnakes was 15.4% (2/13) in 2004 and 22.2% (4/18) in 2005. Of the six mortalities, the most frequent source of mortality was predation, which included two individuals consumed by raptors and one individual consumed by a coyote. All three predation events took place in native habitats, two in riparian habitats (1 coyote at site A and 1 raptor at site B) and one in an upland habitat at site A (1 raptor). An agricultural implement, namely a swather, was responsible for the death of two prairie rattlesnakes that were decapitated in upland cultivated fields at site B. At site B all seven upland migrant females encountered and occupied cultivated fields, while only two of eight upland migrants at site A encountered cultivation. Finally, one prairie rattlesnake was struck by a vehicle at a small gravel pit in the upland habitat of site A. Using Fisher's exact test I examined the relationship between habitat

partitioning (riparian vs. upland migrants) and encounters with cultivation by study site and I subsequently tested the relationship between encounters with cultivation and mortality among radio-tracked females. I found that at site A there was no relationship between habitat partitioning (two riparian and eight upland migrants) and encounters with cultivation (Fisher's exact test = 1.0), but there was a significant relationship between habitat partitioning and encounters with cultivation at site B (Fisher's exact test = 0.001). Based on the significant relationship between habitat use and encounters with cultivation at site B, I tested whether encounters with cultivation ($N = 7$) were related to mortality ($2/7$) among radio-tracked females at site B and found that they were not (Fisher's exact test = 1.0).

Movement patterns

The mean date of maximum displacement in 2004 at site A was July 18 ($N = 3$; S.E. = 0 days) and at site B it was July 20 ($N = 8$; S.E. = 5 days). The mean date of maximum displacement in 2005 at site A was July 21 ($N = 7$; S.E. = 10.8 days) and at site B it was July 14 ($N = 6$; S.E. = 9.9). The mean date of maximum displacement between sites in both 2004 ($t = -0.40$, $df = 7$, $p = 0.70$) and 2005 ($t = 0.47$, $df = 11$, $p = 0.65$) were not significantly different. The consistent timing of maximum displacement supported the selection of the point of maximum displacement as the common end point of the spring migration for all radio-tracked female rattlesnakes regardless of migration strategy.

The mean squared distance of 1000 simulated paths generated for comparison with the mean squared distance (MSD) of the observed spring migration path of each

radio-tracked rattlesnake (e.g., Figure 10) identified individuals whose displacement from the den was predicted by the model and those that were underpredicted because their observed value exceeded that of MSD of 1000 simulated paths (Table 3). At site A, the MSD of eight individuals (80%) was not predicted by the model and the MSD of two individuals (20%) was predicted. At site B there were three individuals (21%) whose MSD was not predicted by the model and eleven (79%) whose MSD was predicted by the model. The observed MSD of riparian migrants all fell within the range of simulated MSD generated by assigning random bearings to the observed movement segments making up their spring migration paths. However, the MSD of 1000 simulated paths generated for each individual only encompassed the observed MSD of 4 upland migrants and did not predict the MSD of 11 upland migrants (Table 3).

I used riparian and upland migrant categories as the basis for all subsequent comparisons of variation in measured movement, morphometric, and reproductive traits of radio-tracked female prairie rattlesnakes within and between sites. Within site A the mean maximum displacement of eight upland migrant females (4581 ± 876 m) was significantly greater than that of two riparian migrant females (654 ± 6 m) (d.f. = 7.0, $t = -4.48$, $p = 0.003$; Table 5). The mean maximum displacement of seven upland migrant females (3151 ± 559) at site B was also significantly greater than the maximum displacement of seven riparian migrant females (1268 ± 329) at site B (d.f. = 12, $t = -2.90$, $p = 0.01$; Table 5).

The linearity of observed spring migration paths of two riparian (0.58 ± 0.20) and eight upland migrant females (0.87 ± 0.03) at study site A were not significantly different (d.f. = 1.16, $t = -1.45$, $p = 0.36$), but small sample size and unequal sample variance

contributed to low statistical power, which may have hampered detection of differences. At study site B the linearity of observed spring migration paths of seven upland migrants (0.68 ± 0.05) were significantly straighter than those of seven riparian migrant females (0.45 ± 0.09) (d.f. = 12, $t = -2.26$, $p = 0.04$).

The total observed pathway lengths of annual migrations of two riparian (4474 ± 673 m) and eight upland migrant females (9172 ± 2044 m) at site A were not significantly different (d.f. = 8.7, $t = -2.18$, $p = 0.06$). At site B total observed pathway lengths of seven riparian (5733 ± 1280 m) and seven upland migrant females (8207 ± 1166 m) were not significantly different (d.f. = 12, $t = -1.43$, $p = 0.18$).

Mass, length and reproductive status

The initial mass and snout to vent length of radio-tracked females (Table 4) was compared between riparian and upland migrants within sites. At site A the mean initial mass of two riparian (215 ± 63 g) and eight upland (232 ± 41 g) migrant females did not differ significantly (d.f. = 8, $t = -0.19$, $p = 0.86$). The initial mass of seven riparian migrants (253 ± 27 g) and seven upland migrants (228 ± 32 g) at site B also did not differ significantly (d.f. = 12, $t = 0.60$, $p = 0.56$). The initial snout to vent length of two riparian (76 ± 15 cm) and 8 upland migrants (78 ± 4 cm) at site A did not differ significantly (d.f. = 8, $t = -0.20$, $p = 0.85$). The initial snout to vent length of seven riparian (76 ± 4 cm) and seven upland migrants (77 ± 4 cm) at site B did not differ significantly (d.f. = 12, $t = -0.25$, $p = 0.81$).

Percent changes in mass and snout to vent length of radio-tracked females during the active season were also calculated and compared. Only one riparian migrant female

was recaptured at den site A, precluding statistical comparisons of percent change in mass and snout to vent length between riparian and upland migrant females at site A. At site B the percent change in mass of five riparian migrant females ($22 \pm 13 \%$) was not significantly less than that of five upland migrant females ($57 \pm 12 \%$), although it approached significance (d.f. = 8, $t = -2.0$, $p = 0.08$). The percent change in snout to vent length of five riparian ($6 \pm 4 \%$) and five upland migrant females ($3 \pm 2 \%$) at site B were not significantly different (d.f. = 8, $t = 0.57$, $p = 0.58$).

Using a snout to vent length of 68.5 cm as a threshold (Jørgensen and Nicholson 2007), radio-tracked females were divided into juvenile (< 68.5 cm) and adult (≥ 68.5 cm) size-classes and compared by habitat use. Among riparian migrant females ($N = 9$) two were initially juveniles and seven were adults, while among upland migrant females ($N = 15$) three were initially juveniles and twelve were adults. An assessment of the reproductive status of radio-tracked females at the end of the active season at both sites combined determined that among riparian migrants there were two gravid females and among upland migrants there were two gravid females.

Mark-Recapture

Thirty eight females were marked at den site A; 17 (45%) were recaptured, of which nine were captured twice, five captured three times, and three captured during all four mark-recapture sessions. The estimated capture probability at site A was $66 \pm 11\%$ (S.E.). Of 31 females marked at den site B, 22 (71%) were recaptured and of these, six were captured twice, ten were captured three times and six were captured during all four mark-recapture sessions. Capture probability at site B was $80 \pm 8\%$ (S.E.). The estimated

population parameters are summarized for den sites A and B in Tables 5 and 6 respectively.

At den site A, twelve females were radio-tracked from an estimated minimum female population of 21 ± 3 (S.E.) and a maximum of 35 ± 7 (S.E.) females, estimated during four separate mark-recapture sessions (Table 5). Of the 12 females radio-tracked, two females were lost (one mortality and one signal loss) before sufficient data were obtained to permit classification of these individuals according to the criteria established. The 10 females for which movement patterns could be assigned represented 29-47% of the estimated female population. At site A eight (80%) females were upland migrants; the 95% confidence interval of the proportion of upland migrant females was large (0.44 to 0.98) owing to small sample size.

At den site B, 15 females were radio-tracked. The estimated minimum population was 20 ± 1 (S.E.) and the maximum 25 ± 3 (S.E.) females, estimated during four separate mark-recapture sessions (Table 6). Of the 15 females radio-tracked, one female was not located with sufficient frequency to include in movement analyses. The sample of 14 radio-tracked snakes represented 56 to 71% of the estimated female population. Seven (50%) females at site B were upland migrant females, and due to the small sample size (N=14), the 95% confidence interval of the proportion of upland migrant females was relatively large (0.23 to 0.77).

DISCUSSION

Analyses of the annual migrations of radio-tracked female prairie rattlesnakes revealed habitat partitioning based on the mean elevations occupied by females

throughout their annual migrations at each of the two study sites. Ironically, in some respects this mirrors examples of resource polymorphisms observed among fish species where habitat is often partitioned among morphs based on water depth. The maximum displacement of upland migrant females from the den of origin was significantly greater than that of riparian migrant females at both sites A and B and this emerged as a key trait distinguishing individuals occupying riparian and upland habitats, although there was overlap between groups at site B. Cited examples of radio-telemetry studies of prairie and western rattlesnakes (King 1987; Powell et al. 1998; Parker and Anderson 2007) that observed individuals within the same population engaging in either long or short displacement migrations did not comment on whether these groups occupied differing habitats based on differences in elevation or otherwise.

The activity ranges occupied by riparian migrant females throughout the active season were generally only occupied by upland migrant females during departure from and return to dens. A substantial percentage of the duration of the upland migrants active season was spent in upland habitats unoccupied by riparian migrants at both site A ($77 \pm 6\%$) and site B ($57 \pm 7\%$), supporting the notion of both spatial and temporal habitat partitioning between riparian and upland migrants at each study site. Mating activities of riparian and upland migrants also took place in spatially segregated activity ranges because upland activity dates of upland migrants encompassed the known mating period of prairie rattlesnakes.

As capital breeders, body fat reserves are critical to reproduction in female rattlesnakes (Aldridge, 1979; Galligan and Dunson, 1979; Blem 1982; Diller and Wallace 1984; Macartney and Gregory 1988; Charland and Gregory 1989; Brown 1991). It is

believed that in a given year female vipers do not initiate vitellogenesis (i.e., follicle development) until they have accumulated sufficient energy stores to reach a high body condition threshold (Naulleau and Bonnet 1996). With the exception of a lone riparian migrant female at site A that changed very little (Appendix IV, ID: BB), both riparian and upland migrant females secured prey, increasing their mass by an average of 22.1% to 57.0% and their length by an average of 3.1% to 5.5%. The difference in increase in mass of upland and riparian migrants at site B approached significance, with upland migrants generally increasing their mass to a greater extent. I speculate that this difference could be the result of increased primary productivity in irrigated fields which made up the majority of the cultivation in site B uplands. In turn irrigated fields might support a greater abundance of prey, but this hypothesis was not tested. Habitat partitioning and migration patterns observed among female prairie rattlesnakes could not be attributed to differential migration or ontogenetic differences (Snorrason et al. 1994) sometimes associated with resource polymorphisms, because initial mass and length did not differ and both riparian and upland migrants included both reproductively immature (juvenile) and reproductively mature (adult) females. Partial migration as defined by Dingle and Drake (2007) does not apply because this case defies the condition that a portion of the population remains either in its breeding or its non-breeding area while the remainder moves away. With respect to reproductive outcomes of annual movements I found that both females engaging in riparian and upland migrations encountered males, mated, and became gravid during the active season when radio-tracking occurred. Therefore in terms of size-class, reproductive maturity and reproductive outcomes, individuals occupying each of the habitats did not differ within sites.

The limited significance of differences in the linearity of spring migration paths between riparian and upland migrants within sites suggests that linearity may not be a key trait distinguishing these groups. However the results of comparisons of the maximum mean squared distance (MSD) of 1000 simulated migration paths generated by the site fidelity model and the MSD of observed migration paths does suggest that random bearings assigned to observed movement segments accounted for the spring migrations of riparian migrants but generally could not account for the spring migrations of upland migrants.

The high degree of linearity of observed spring migration paths of upland migrant females at site B within an upland landscape highly modified by cultivation, resulted in all of them traversing or occupying cultivated fields. This included observation of an individual encountering and traversing a recently tilled field devoid of vegetation or any cover, over a stretch of at least 800 m during the day. Cultivation exposed this snake to a situation in which it lacked cover, potentially increasing its risk of predation, which might contribute to differential predation risk between riparian and upland migrants. Maintaining a highly linear spring migration path as many upland migrants did, particularly when encountering landscapes highly altered by human activities (e.g., cultivation), might limit opportunities for encounters with suitable habitat, while also potentially limiting the ability of an individual to access escape cover to avoid predation.

I cannot be certain that the untracked female population of focal dens consisted predominantly of individuals exhibiting one habitat preference or the other based on the sample of radio-tracked females and calculated confidence intervals. There could be several explanations for observed habitat partitioning, none of which can be ruled out by

this study. I believe that one interesting question is whether factors influencing habitat use and movement strategies are inherent to the individual (i.e., genotype) or a result of external factors and phenotypic plasticity (e.g., competition, prey availability, habitat loss or fragmentation, mortality risk) that may contribute to variation in individual spring migration patterns and ultimately to variation in proportions of riparian and upland migrants among populations. I am currently engaged in a collaborative effort to analyse approximately 250 genetic samples collected during this study, which may reveal whether genetic differences are correlated with habitat use at each site. Although it is not known whether the sample of individuals engaging in differential habitat use will be sufficiently large to test for genetic differences, it is a reasonable hypothesis considering that examples of both morphological and behavioural polymorphisms have been shown to have a heritable genetic basis (Dingle 1996).

It seems unlikely that upland migrant females migrated in response to the deterioration of their current local resource conditions in riparian habitats, because the habitat they initially occupied but left, sustained the riparian migrant females that remained within this habitat in closer proximity to the den. Other studies have demonstrated that most radio-tracked rattlesnakes habitually use specific sites (for shelter, mating, foraging) within their activity range in consecutive years (*C. o. lutosus*, C. Peterson, pers. comm. as cited in Parker and Anderson 2007; *C. o. concolor*, Parker and Anderson 2007). Fixed habitat preference across years would potentially facilitate repeated use of specific sites.

Long and short displacement migration patterns have been observed in three previous radio-telemetry studies, one study of *Crotalus v. viridis* in Wyoming (King

1987) another in Alberta (Powell et al. 1998) and a study of *Crotalus oreganus concolor* in Wyoming (Parker and Anderson 2007). Although I can only speculate on whether the distinct movement patterns observed by Parker and Anderson's (2007) represent an expression of behavioural polymorphism within populations, it appears that when significant differences in net displacement occur among prairie rattlesnakes with access to spatially separated heterogeneous habitats it can result in differential habitat use within populations, which can likely be considered resource polymorphism in this instance (*sensu* Skulason and Smith 1995).

If habitat use is fixed, the occurrence of riparian migrant females might increase the likelihood that prairie rattlesnake populations would persist if high levels of human activity (e.g., cultivation agriculture and high-traffic routes) remain in uplands. The size of habitat fragments necessary to limit the exposure of riparian migrant females to direct threats of mortality (e.g., agricultural implements, vehicular traffic) would presumably be relatively smaller than among upland migrants because of their significantly shorter mean displacement from the den. I speculate that historically riparian migrant females would have been rare at den sites supporting hundreds or thousands of rattlesnakes because prey sources near the den would be depleted quickly as individuals dispersed, necessitating greater displacement of occupants. Similarly, Gregory and Stewart (1975) hypothesized that long distance migrations of red-sided gartersnakes (*T. s. parietalis*) from communal dens supporting tens of thousands of snakes in Manitoba might be caused by the partitioning of necessary resources among all the snakes at a communal den, which they felt would require a very large area. If numbers of rattlesnakes occupying dens are relatively low, as found in this study (e.g., den sites A and B) and there are fewer active

dens (Kissner and Nicholson 2003), a relatively small area surrounding a den (e.g., 1-3 km radius) might be capable of supporting populations consisting primarily of riparian migrant females assuming a sufficient carrying capacity.

Development of riparian areas could result in the destruction of dens and the extinction of populations, with little opportunity for escape and re-colonization due to high den site fidelity observed among radio-tracked females. During this study of twenty one females radio-tracked returning to a den, the only observed example of relocation to a different over-winter den was undertaken by a riparian migrant female, suggesting that destruction of dens is a concern for both riparian and upland migrants.

Shorter displacement from the den among riparian migrant females could contribute to higher levels of inbreeding. Significantly greater maximum displacement of upland migrant females from dens and riparian areas into adjacent uplands creates the potential for encounters with males from more distant dens, potentially increasing the likelihood that mates are unrelated.

This study identified the occurrence of what would likely be considered a resource polymorphism among female prairie rattlesnakes, a remarkable phenomenon that appears to be more widespread than once thought (reviewed by Skulason and Smith 1995). The small sample of radio-tracked rattlesnakes, divided between two study sites and two distinct habitats failed to provide significant insight into mortality risks associated with their active ranges. Increased knowledge of their distribution during the active season provides a foundation for further investigation of the costs and benefits of changing land uses within the species range in Alberta, but the results raise as many questions as they answer. Several studies of prairie rattlesnakes in southeastern Alberta have collected

valuable information regarding the ecology, population biology, and genetics of prairie rattlesnakes and their interaction with human land uses and activities. Collaboration amongst the researchers that have gathered these data may be the most logical and important next step that can be taken in assessing the conservation status of the species and subsequently developing management actions to ensure effective conservation of the species. Alberta Sustainable Resource Development might consider acting as a facilitator of such a collaboration since the resulting information would presumably be of value to wildlife managers and land use planners.

CHAPTER THREE: KEY FINDINGS, MANAGEMENT RECOMMENDATIONS, AND FUTURE RESEARCH

INTRODUCTION

Previous studies of radio-tagged prairie rattlesnakes in Alberta occupying relatively intact native prairie landscapes reported long distance directed movements (Didiuk 1999).

Based on earlier radio-telemetry studies in Wyoming this movement pattern was presumed to be typical of northern populations of communally denning prairie rattlesnakes (King and Duvall 1990). There are isolated examples of radio-tracked prairie and western rattlesnakes moving relatively short distances following multidirectional paths within migratory populations (King 1987; Powell et al. 1998; Parker and Anderson 2007). I used radio-telemetry to assess whether two or more discrete habitat use patterns exist among female prairie rattlesnakes in Alberta. This study is important for wildlife managers in Alberta because it provides greater insight into the distribution of prairie rattlesnakes during the active season, offering a greater understanding of encounters with varying landscapes and human activities.

KEY FINDINGS

- Bimodal distribution of mean elevation of observed locations making up the annual migration paths of radio-tracked female prairie rattlesnakes permitted classification of individuals into one of two groups. Individuals assigned to these groups were termed either riparian or upland migrant females.
- The maximum displacement of riparian and upland migrants from dens within sites was significantly different at den sites A and B.

- Upland migrant females were characterized by annual maximum displacement of between 1.22 and 9.94 km from the den. All upland migrant females occupied upland sites during the majority of foraging and mating activities.
- Riparian migrant females were characterized by annual maximum displacement of less than 2.64 km from the den resulting in activity ranges within riparian habitats occurring between the rivers edge and the point at which the slope of the river valley begins to decline transitioning to the relatively flatter upland habitats.
- Foraging ranges of riparian and upland migrants rarely overlapped.
- Cultivated fields served as foraging and mating habitat but agricultural activities also contributed to mortality of radio-tracked upland migrant female prairie rattlesnakes, although encounters with cultivation did not significantly increase probability of mortality of radio-tracked females.
- Female prairie rattlesnakes demonstrated extremely high den site fidelity, with only one instance of switching ($1/21 = 5\%$) over-winter dens observed among twenty one females radio-tracked returning to dens.
- My data suggests that female prairie rattlesnakes rarely disperse across the South Saskatchewan River ($1/27 = 3.7\%$) but when they do, they can successfully navigate back to the den to overwinter.
- At one study site differential habitat use among migrants did contribute to differing probability of exposure to cultivation and I speculate that a larger sample would reveal differences in mortality risk associated with differential habitat use and encounters with human activities and human modified landscapes.

MANAGEMENT RECOMMENDATIONS

Land use planning

Protected Areas / Critical habitat

An important aspect of rattlesnake conservation that will have to be addressed by wildlife managers should prairie rattlesnakes be designated a federally listed wildlife species is the identification of critical habitat. Critical habitat as defined by Canada's *Species at Risk Act (SARA)* is "the habitat that is necessary for the survival or recovery of a listed wildlife species and that is identified as the species' critical habitat in the recovery strategy or in an action plan for the species". Over-wintering dens and natal den sites are clearly necessary habitat and their protection has recently been addressed by wildlife managers in Alberta based on analysis of the activities of gravid females in southeastern Alberta (Jørgensen and Nicholson 2007). My finding that only 1/21 (5%) female prairie rattlesnakes returned to a different over-winter den reinforces the importance of protecting known den sites.

The problem of identifying critical habitat becomes more complex when examining the question of critical foraging and migration habitat. My research has supplemented data on habitat use centered on den sites. Only one of the radio-tracked females migrated across the South Saskatchewan River and therefore the radius of critical habitat need only extend from the river or the den on one side of the river. Based on the movement patterns observed among riparian migrant females the critical habitat that appears to encompass all movements would be the approximate crest of the river valley where the slope begins to decline transitioning to the upland habitat. However, it is more difficult to delineate

critical habitat encompassing most upland migrant females' movements, since the mean was approximately 3.9 km, but migration distances of upland migrants are highly variable. Some radio-tracked females in this study migrated up to 9.9 km from dens, while another study observed a female migrating 25 km from a den (Didiuk 1999). The need for protection of a critical radius around dens rather than specific habitat features within the annual activity ranges of upland migrants will potentially simplify delineation of critical habitat but will encompass large areas and offer unique challenges for designation and enforcement under the *SARA* or provincial wildlife legislation.

If protection of critical habitat becomes necessary wildlife managers will have to decide whether to buffer known den sites or alternatively riparian corridors (Figure 11) known to support rattlesnake over-winter dens. If prairie rattlesnakes are legally designated a species at risk, protection of their foraging habitat could provide a habitat umbrella to numerous prairie species relying on riparian corridors. It seems relatively unlikely that large buffers (e.g., 10 km's) would be designated critical habitat for prairie rattlesnakes. However, identification of the necessary radius of buffers could be used as an opportunity to contribute to a plan to protect the riparian corridors of Alberta's Grassland natural region when considered in conjunction with the ecological services they provide and their significant value to a broader suite of endemic species, particularly those at risk. Upland arrival and departure dates observed in this study (Appendix IV) may provide a basis for the timing of any restrictions on human activities in upland habitats thought to be detrimental to prairie rattlesnakes.

RECOMMENDATIONS FOR FUTURE RESEARCH

Statistical analyses currently being undertaken may establish whether genetics of radio-tracked females (e.g., relatedness) is correlated with differential habitat use.

Population genetic analyses of genetic samples collected from all captured rattlesnakes at the two focal dens and two adjacent dens may also reveal genetic correlates of differential habitat use.

I believe that quantifying the magnitude of both the positive and negative effects of cultivation should be a high priority for wildlife managers. Cultivation was the second most frequent cause of mortality among radio-tracked females, despite the fact that encounters with cultivation did not significantly increase the probability of mortality within my sample of radio-tracked females. A comprehensive mark-recapture program conducted in spring and fall over at least two years could be initiated to compare survivorship using a network of drift fences and funnel traps erected in uplands adjacent to the South Saskatchewan River at a series of paired agricultural and native prairie sites. I suggest trapping individuals during spring migration as they encounter cultivated and native upland habitats, trapping at the same sites in the fall and calculating the relative proportion of individuals that return in the fall in each landscape type. From these results researchers may be able to derive reasonable estimates of survivorship relative to the presence or absence of cultivation. If such a study yielded reliable data on survivorship of prairie rattlesnakes in these two contrasting habitats it could provide guidance on whether expansion of cultivated areas adjacent to the South Saskatchewan River would be beneficial or pose risks to the persistence of prairie rattlesnake populations.

To build on the findings of differential habitat use in this study, I recommend further exploration of potential diet specialization associated with riparian and upland habitat use. The study might incorporate the observed locations and migration paths of female prairie rattlesnakes radio-tracked in this study for selection of small mammal trapping sites. An experiment could be designed to examine whether the composition and availability of small mammal prey populations differ in riparian and upland habitats occupied by prairie rattlesnakes. Trapping effort could be designed to target varying vegetation types and conditions including native dry mixed-grass, sage brush dominant, tame pasture, dry-land and irrigated cultivation, according to their availability. Such a study might offer insight into whether riparian and upland habitats provide access to differing resources and whether human land uses and activities contribute to varying costs and benefits associated with prey availability.

In the discussion I speculated that historically riparian migrant females would have been rare at den sites supporting hundreds or thousands of rattlesnakes because prey sources near the den would be depleted quickly as individuals emerged and left the den, necessitating greater displacement of occupants to reduce competition. A mark-recapture study at a den site in Alberta involved marking approximately 400 rattlesnakes and resulted in a population estimate of 700 to 1900 rattlesnakes occupying the den (M. Proctor Pers. Comm.). The existence of this den presents an opportunity to examine whether the density of snakes at a den site influences habitat use and maximum displacement of rattlesnakes occupying the den. It would also provide an excellent opportunity to examine the distribution and availability of prey in relation to proximity to

the den site and temporal changes that might occur throughout the active season as a result of varying rattlesnake density and prey depletion.

Based on three years of mark-recapture data, Jørgensen and Nicholson (2007) analysed the mean number of ova carried by gravid females ($N = 57$) at two den sites and the reproductive frequency of females ($N = 6$). Data gathered during other mark-recapture studies in Alberta (e.g. Powell et al. 1998; Didiuk 1999; Proctor and Hoffmann unpubl. data) should be used to further analyse mean reproductive output and reproductive rates of female prairie rattlesnakes in Alberta to determine the range of population growth rates expected of prairie rattlesnake populations in the province. In conjunction with estimates of mortality rates associated with traffic on roads, cultivation, or other mortality risks, population growth rates could be used to explore activities that would result in population declines in areas deemed a priority for prairie rattlesnake conservation.

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Table 1. Radio-tracked movements (mean \pm 1 SE) of Prairie Rattlesnakes (*Crotalus v. viridis*) and Western Rattlesnakes (*Crotalus oreganus* subspecies) compiled from Jørgensen et al. (2008).

Reference and species	Study site	N and sex of radio-tagged snakes	N and sex of snakes analysed	Radio-tracking period (days)	Maximum displacement from den (km)	Total observed pathway length (km)
Duvall et al., 1985; King, 1987 <i>C. v. viridis</i>	Wyoming USA	61: unspecified	9 m 3 ngf, 1 gf	*54.7 \pm 13.3 (N = 3) NR	*5.13 \pm 1.39 (L) (N = 3) NR	5.64 \pm 1.57 (N = 3) NR
King and Duvall, 1990 <i>C. v. viridis</i>	Wyoming USA	61: unspecified	16 m 7 ngf	65.1 \pm 9.4 88.3 \pm 14.5	2.57 \pm 0.66 (C) (N = 15) 2.03 \pm 1.10 (C) (N = 6)	3.51 \pm 1.02 2.76 \pm 1.36
Powell et al., 1998 <i>C. v. viridis</i>	Alberta Canada	8: 5 m, 3 ngf	2 m 1 ngf	66.6 (N = 8) 66.6 (N = 8)	4-12 (L) 0.300 (L)	NR <1.00
Didiuk, 1999 <i>C. v. viridis</i>	Alberta Canada	20: 12 m, 3 gf, 5 ngf	3 m 2 ngf	NR NR	*15.1 \pm 1.9 (L) *20.0 \pm 4.7 (L)	*32.2 \pm 8.3 (N = 2) *43.8 \pm 8.9
Ashton, 2003 <i>C. o. concolor</i>	Wyoming USA	9 (8 m, 1 ngf)	8 m	*48.8 \pm 7.4	NR	*0.26 \pm 0.12
Parker and Anderson, 2007 <i>C. o. concolor</i>	Wyoming USA	50 (33 m, 17 f)	21 m 4 f	166 \pm 17.1 195 \pm 55.7	0.78 \pm 0.09 0.68 \pm 0.14 (N = 3)	2.12 \pm 0.24 1.96 \pm 0.15 (C) (N = 3)
Jenkins and Peterson, 2005 <i>C. o. lutosus</i>	Idaho USA	30 (12 m, 18 ngf)	12 m 18 ngf	*66.5 \pm 5.6 *62.3 \pm 5.1	*1.30 \pm 0.14 (L) *1.43 \pm 0.19 (L)	*5.42 \pm 1.22 *2.40 \pm 0.37

m = male; ngf = non-gravid female; gf = gravid female; NR = not reported; N/A = not applicable; * = calculated based on raw data in the source document; C = Cumulative distance; L = linear distance

Table 2. Observed mortality of radio-tracked female prairie rattlesnakes, *Crotalus v. viridis*.

Site	Snake ID	Niche	Cause	Date	Mortality site description	Distance from den (m)	Distance from river (m)
A	CC	Unknown	Predator - Coyote	May 16 2005	Native prairie	127	749
A	P	Upland	Human - Vehicle	June 21 2005	Gravel pit	5608	6296
A	U	Upland	Predator - Raptor	June 21 2005	Native prairie	3639	4194
B	Q	Upland	Human - Ag. implement	July 7 2005	Cultivated field	2170	2164
B	F	Riparian	Predator - Raptor	Aug. 8 2004	Native prairie	273	76
B	J	Upland	Human - Ag. implement	Sept. 1 2004	Cultivated field	1885	1186

Table 3. Habitat, elevation, displacement, linearity, and total observed pathway length of radio-tracked female prairie rattlesnakes, *Crotalus v. viridis*. The observed mean squared distance of spring migrations was either predicted by the site fidelity model or underpredicted if random bearings assigned to migration path segments did not account for the mean squared distance of spring migrations. Note: * = Mortalities

ID	Site	Year	Habitat use	Obs. mean squared distance	Mean elevation (m)	Maximum displacement (m)	Observed linearity index	Total obs. pathway length (m)
B	A	2005	Riparian	Predicted	645	659	0.78	5147
N	A	2004	Riparian	Predicted	653	648	0.39	3801
R	A	2005	Upland	Underpred.	691	2640	0.75	6956
Z	A	2005	Upland	Underpred.	692	2450	0.89	5280
L	A	2004	Upland	Underpred.	693	3037	0.89	7200
U	A	2005	Upland	Underpred.	697	3639	0.97	3767
K	A	2005	Upland	Underpred.	699	3869	0.74	9314
A	A	2005	Upland	Underpred.	699	5102	0.93	10856
P*	A	2005	Upland	Underpred.	719	5969	0.83	7585
A	A	2004	Upland	Underpred.	729	9938	0.95	22416
M	B	2004	Riparian	Predicted	666	2641	0.38	11541
F*	B	2004	Riparian	Predicted	670	466	0.76	1598
D	B	2004	Riparian	Predicted	670	1357	0.74	5625
B	B	2004	Riparian	Predicted	671	2239	0.49	8415
S	B	2005	Riparian	Predicted	674	1076	0.33	5890
G	B	2004	Riparian	Predicted	676	598	0.3	2812
V	B	2005	Riparian	Predicted	681	499	0.17	4248

O	B	2005	Upland	Predicted	735	1218	0.53	5745
H	B	2004	Upland	Predicted	735	1810	0.48	6080
T	B	2005	Upland	Predicted	738	2857	0.62	8997
X	B	2005	Upland	Underpred.	741	5686	0.83	14044
Q	B	2005	Upland	Predicted	758	3141	0.71	6282
J*	B	2004	Upland	Underpred.	763	3163	0.79	6140
E	B	2004	Upland	Underpred.	763	4181	0.8	10164

Table 4. Reproductive maturity, initial snout to vent length, initial mass, and active season growth of radio-tracked female prairie rattlesnakes, *Crotalus v. viridis*.

ID	Site	Year	Niche	Reproductive Maturity	Initial SVL (cm)	Change in SVL (cm)	Initial mass (g)	Change in mass (g)
N	A	2004	Riparian	Juvenile	61.1	unknown	152	unknown
L	A	2004	Upland	Juvenile	66.6	9.0	205	40
P*	A	2005	Upland	Juvenile	67.9	unknown	139	unknown
Z	A	2005	Upland	Adult	73.8	1.5	175	2
R	A	2005	Upland	Adult	74.3	1.3	195	53
AA	A	2005	Upland	Adult	76.8	1.0	183	62
U*	A	2005	Upland	Adult	78.6	unknown	180	unknown
K	A	2005	Upland	Adult	84.5	-1.0	274	43
BB	A	2005	Riparian	Adult	90.2	-3.5	278	12
A	A	2004	Upland	Adult	98.5	2.7	505	180
G	B	2004	Riparian	Juvenile	56.1	10.8	145	13
J*	B	2004	Upland	Juvenile	62.3	3.5	130	45
F*	B	2004	Riparian	Adult	69.7	unknown	200	unknown
H	B	2004	Upland	Adult	70.1	unknown	235	unknown
D	B	2004	Riparian	Adult	72.4	4.4	220	3
B	B	2004	Riparian	Adult	74.8	unknown	335	unknown
O	B	2005	Upland	Adult	75.1	-1.6	166	76
X	B	2005	Upland	Adult	78.9	5.0	262	194
Q*	B	2005	Upland	Adult	79.7	unknown	174	unknown
V	B	2005	Riparian	Adult	83.2	-0.1	265	56
T	B	2005	Upland	Adult	84.6	-1.3	251	89
S	B	2005	Riparian	Adult	87	-0.6	259	188
M	B	2004	Riparian	Adult	88.4	2.6	346	24
E	B	2004	Upland	Adult	90.3	6.5	382	363

Note: * Mortalities

Table 5. Population parameters for female prairie rattlesnakes, *Crotalus v. viridis*, at den site A estimated from four mark-recapture sessions in 2004 and 2005.

Mark-recapture session	Population size (S.E.)	Estimated marks in population (S.E.)	Estimated births between capture sessions (S.E.)	Estimated survival rate between capture sessions (S.E.)	Estimated capture probability (S.E.)
Spring 04	0	0	0	0.72 (0.14)	0.66 (0.11)
Fall 04	21.38 (3.33)	10.78 (1.06)	1.13 (3.00)	0.95 (0.15)	0.66 (0.11)
Spring 05	21.38 (3.35)	16.84 (2.48)	18.51 (4.36)	0.76 (0.21)	0.66 (0.11)
Fall 05	34.84 (7.32)	15.15 (3.81)	0	0	0.66 (0.11)

Table 6. Population parameters for female prairie rattlesnakes, *Crotalus v. viridis*, at den site B estimated from four mark-recapture sessions in 2004 and 2005.

Mark-recapture session	Population size (S.E.)	Estimated marks in population (S.E.)	Estimated births between capture sessions (S.E.)	Estimated survival rate between capture sessions (S.E.)	Estimated capture probability (S.E.)
Spring 04	0	0	0	0.88 (0.08)	0.80 (0.08)
Fall 04	19.73 (1.02)	18.48 (0.80)	4.78 (1.31)	0.93 (0.10)	0.80 (0.08)
Spring 05	23.22 (1.94)	18.20 (1.32)	5.41 (1.64)	0.85 (0.14)	0.80 (0.08)
Fall 05	25.10 (3.46)	18.82 (2.82)	0	0	0.80 (0.08)

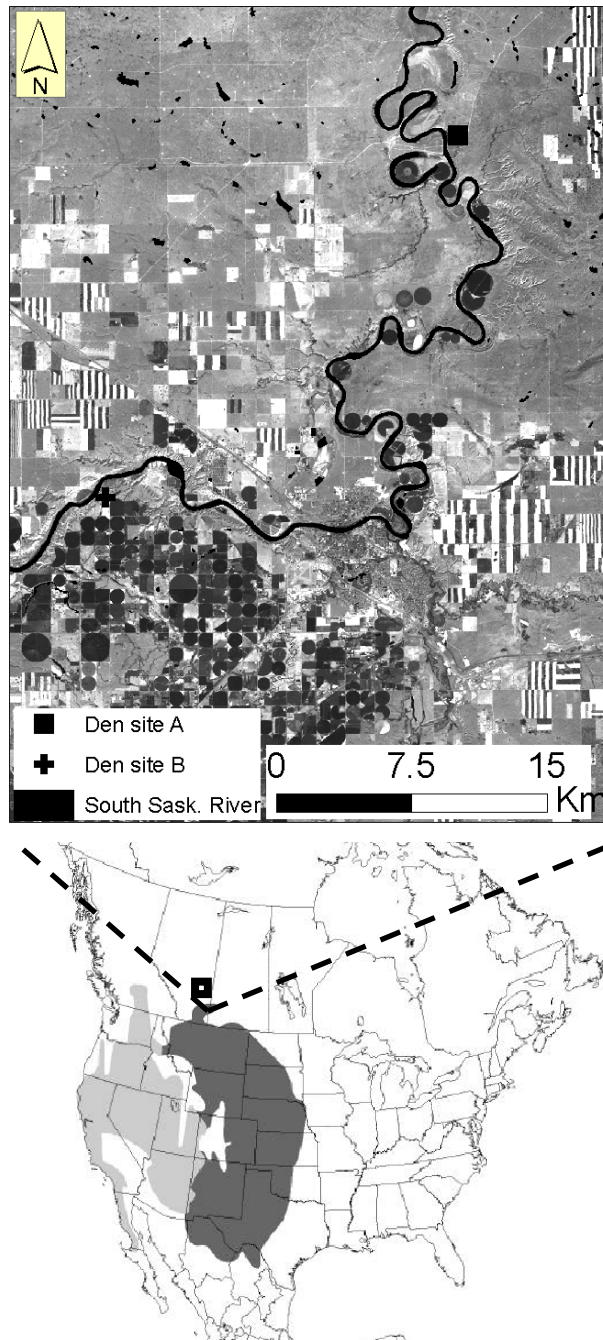


Figure 1. The range of the prairie rattlesnake (Watson and Russell 1997), *Crotalus v. viridis* (dark gray) in North America including the location of the study area (black box) in Alberta and the relative location of den sites A and B within the enlarged study area. The two den sites are approximately 28 km apart. Visible extent of the satellite image UTM NAD 83 (Left: 503813, Right: 536766, Top: 5572254, Bottom: 5526987).

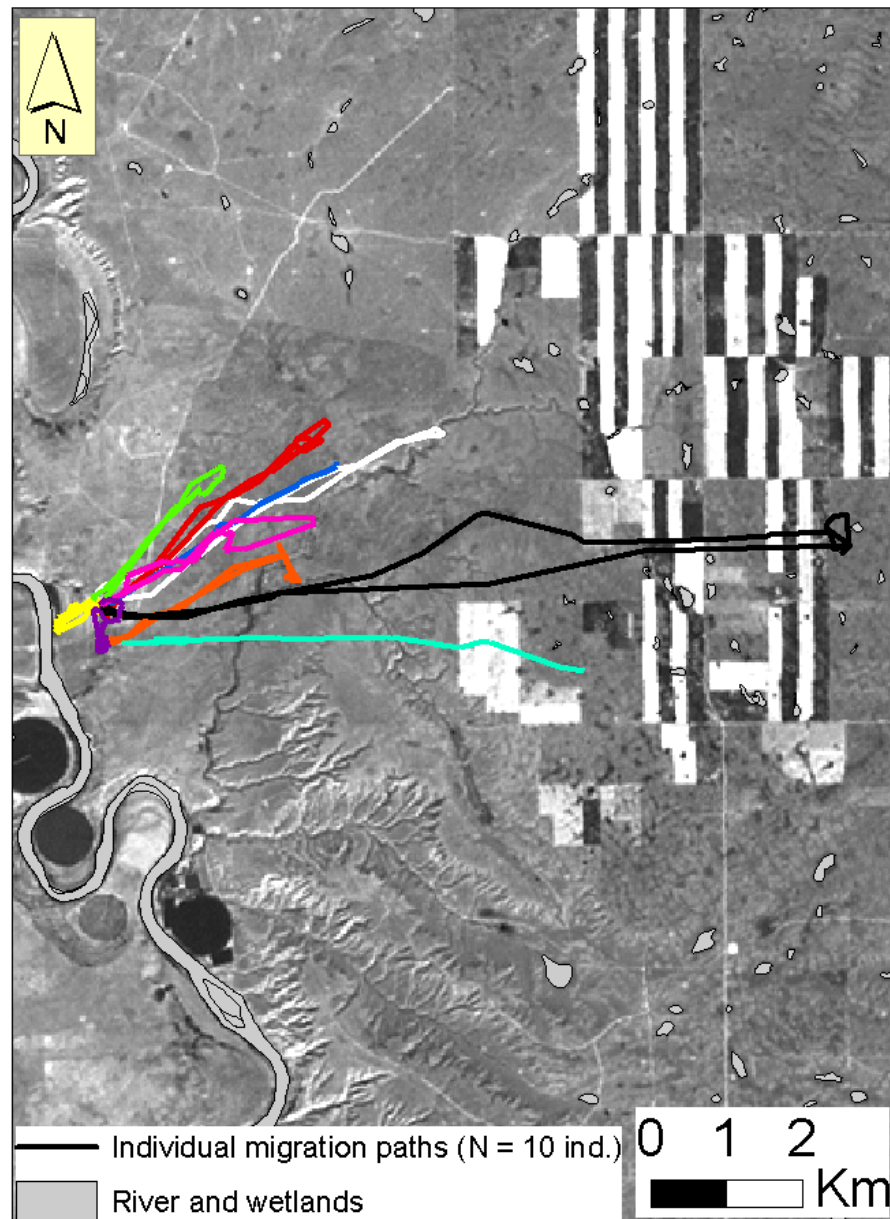


Figure 2. Annual observed movement paths of 10 female prairie rattlesnakes, *Crotalus v. viridis*, radio-tracked at study site A. Each individual's movement path is identified by a distinct colour. Site A consists primarily of native prairie. Dark and light rectangular and circular patterns in the satellite image are areas of cultivation. Visible extent of figure UTM NAD 83 (Left: 527623, Right: 538979, Top: 5572912, Bottom: 5557311).

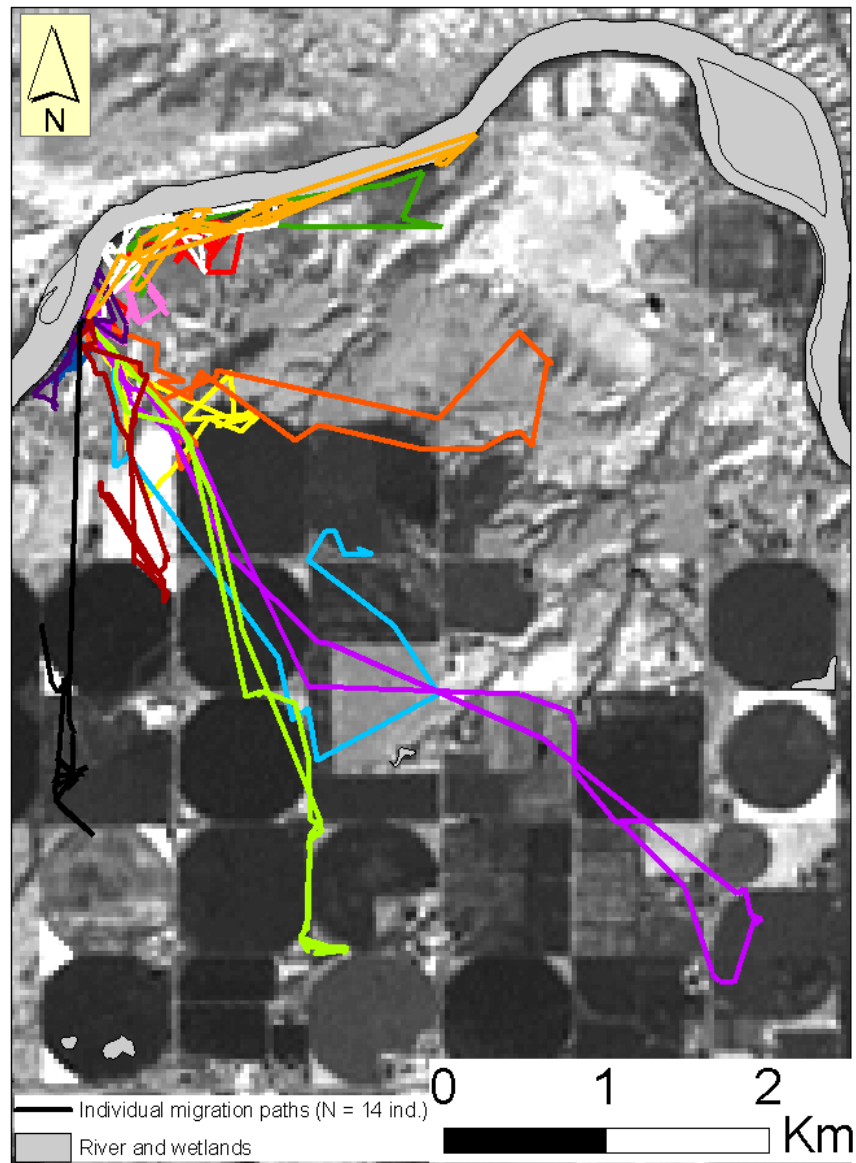


Figure 3. Annual observed movement paths of 14 female prairie rattlesnakes, *Crotalus v. viridis*, radio-tracked at study site B. Each individual's movement path is identified by a distinct colour. Site B consists primarily of pivot irrigated cultivation. Dark circular patterns in the satellite image are areas of cultivation and pivot irrigation. Visible extent of figure UTM NAD 83 (Left: 527623, Right: 538979, Top: 5572912, Bottom: 5557311).

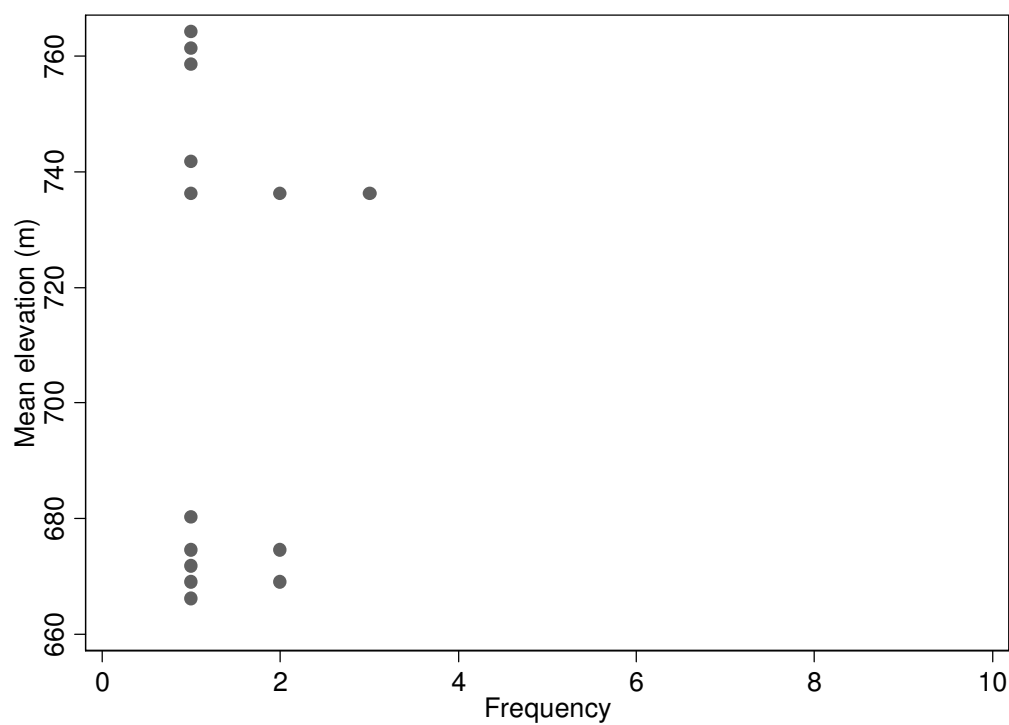


Figure 4. Dot plot of the frequency distribution of the mean elevation of observed locations of individual radio-tracked female prairie rattlesnakes, *Crotalus v. viridis*, throughout their annual migration at site B.

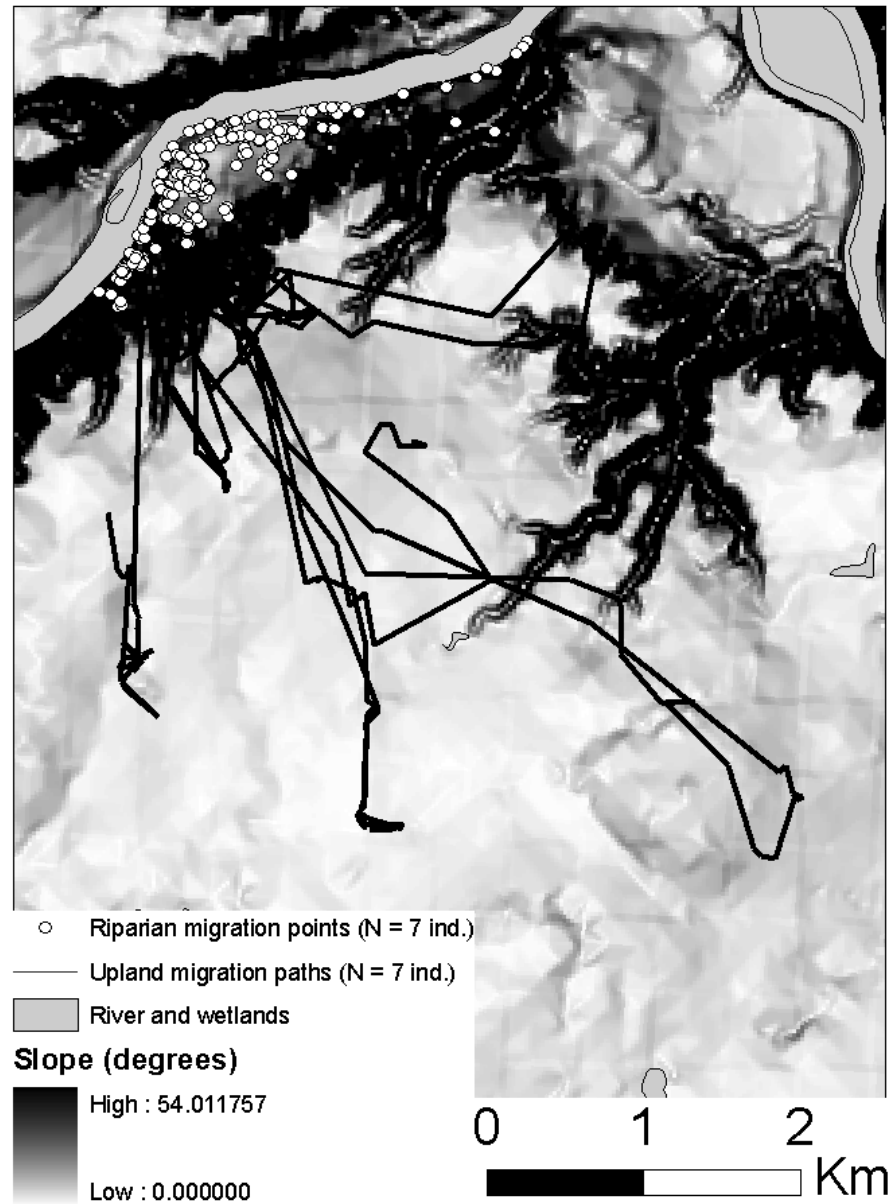


Figure 5. Annual movement paths of seven upland (paths) and seven riparian (points) radio-tracked female prairie rattlesnakes, *Crotalus v. viridis*, at study site B. Paths and points were used for ease of visualization. See Figure 9 for riparian migrant paths. Visible extent of figure, UTM NAD 83 (Left: 507970, Right: 513511, Top: 5546783, Bottom: 5539192).

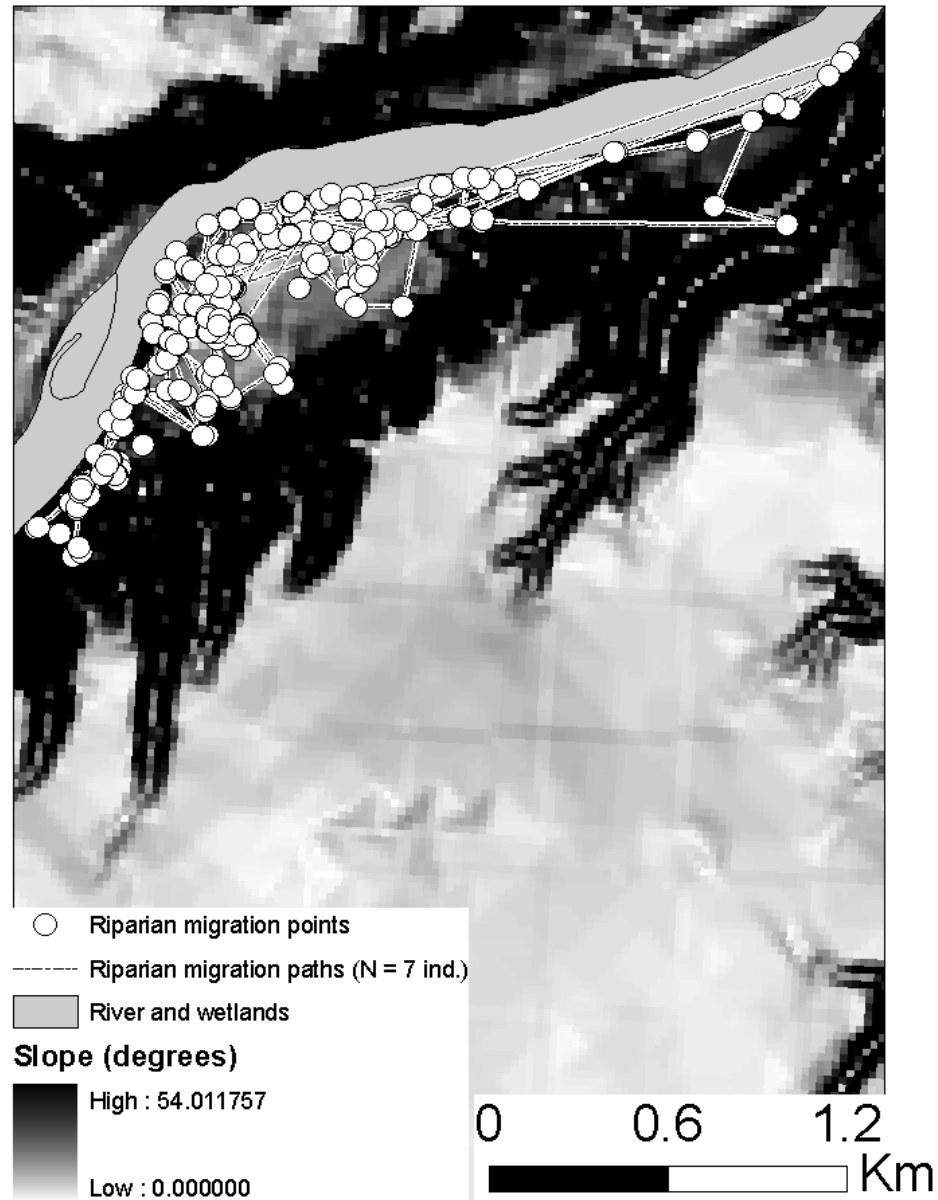


Figure 6. Annual migrations of seven riparian radio-tracked female prairie rattlesnakes, *Crotalus v. viridis*, at study site B. Riparian migrants occupy the area from the South Saskatchewan River to the crest of the river valley. Visible extent of figure, UTM NAD 83 (Left: 508434, Right: 511353, Top: 5546723, Bottom: 5542712).

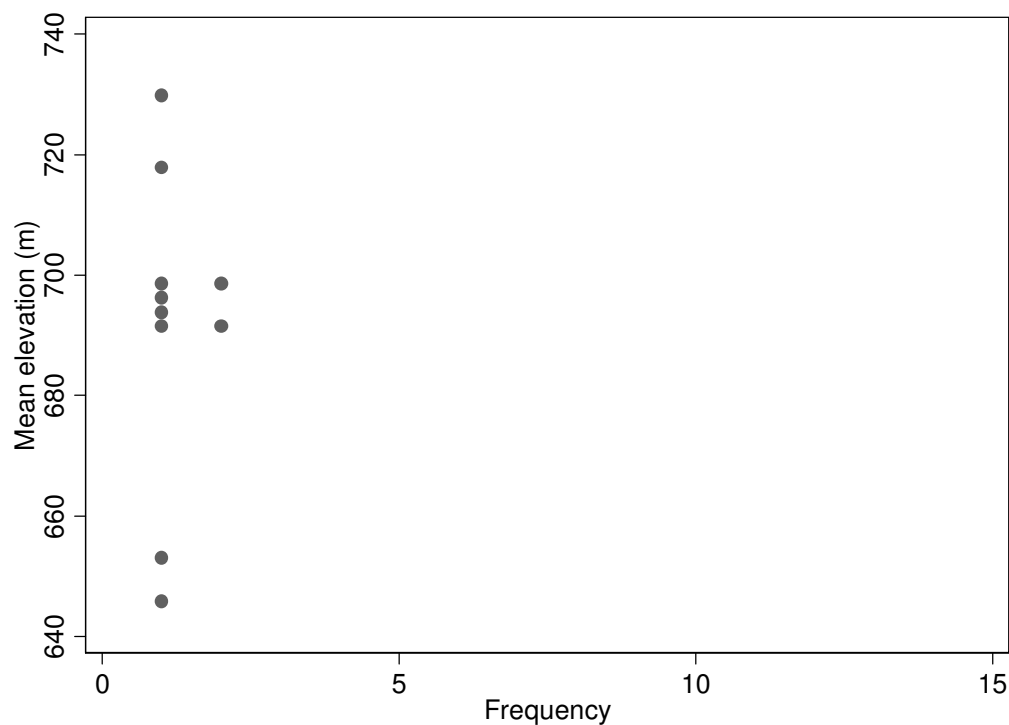


Figure 7. Dot plot of the frequency distribution of the mean elevation of observed locations of radio-tracked female prairie rattlesnakes, *Crotalus v. viridis*, throughout their annual migrations at site A.

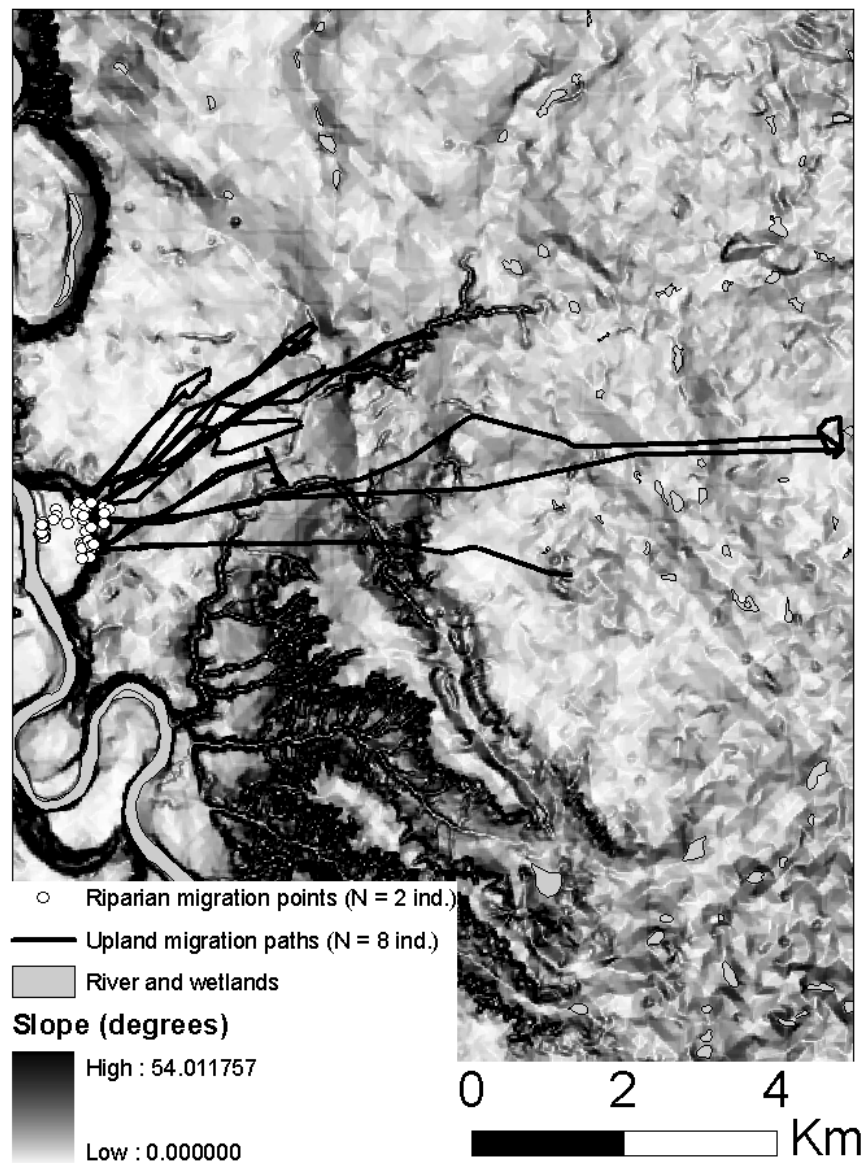


Figure 8. Annual migrations of eight upland (paths) and two riparian (points) radio-tracked female prairie rattlesnakes, *Crotalus v. viridis*, at study site A. Paths and points were used for ease of visualization. See Figure 7 for riparian migrant paths. Visible extent of figure, UTM NAD 83 (Left: 527721, Right: 538730, Top: 5571620 Bottom: 5556497).

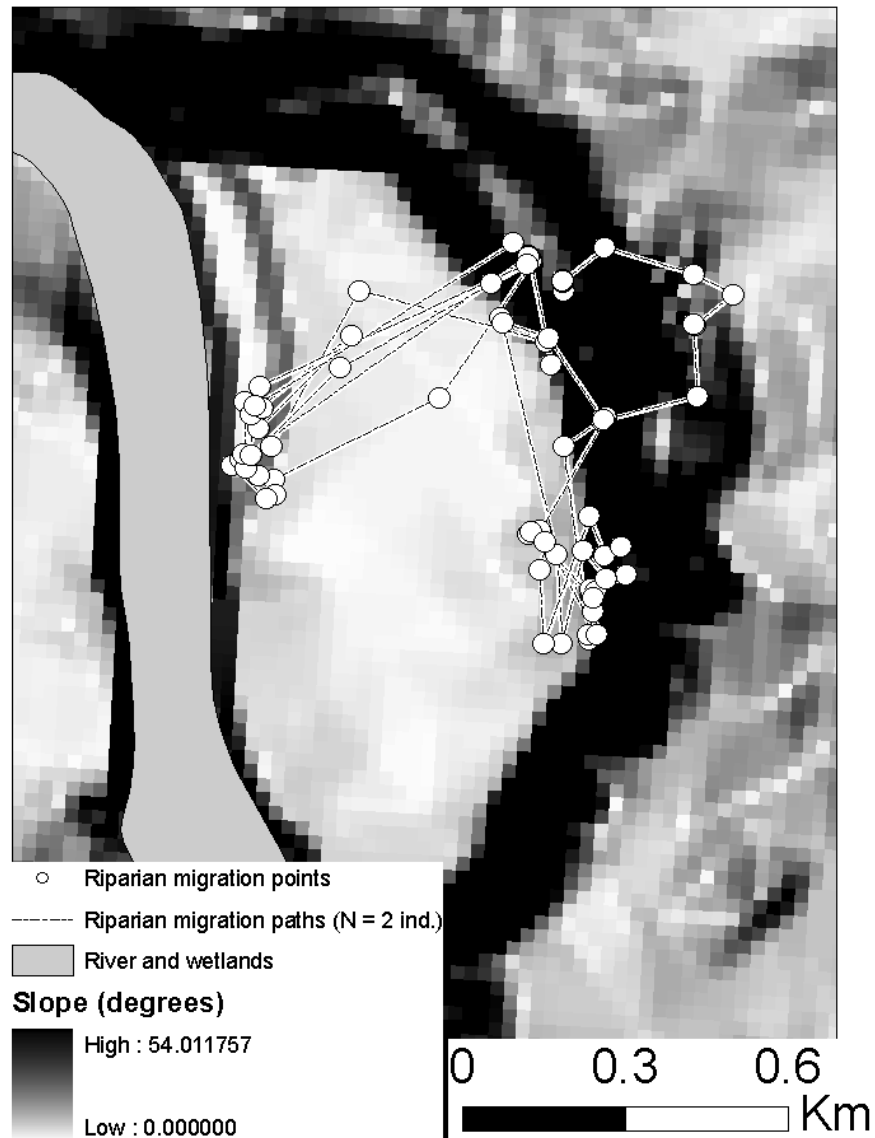


Figure 9. Annual migrations of two riparian radio-tracked female prairie rattlesnakes, *Crotalus v. viridis*, at study site A. Riparian migrants occupy the area from the South Saskatchewan River to the crest of the river valley. Visible extent of figure, UTM NAD 83 (Left: 527667, Right: 529183, Top: 5565604, Bottom: 5563521).

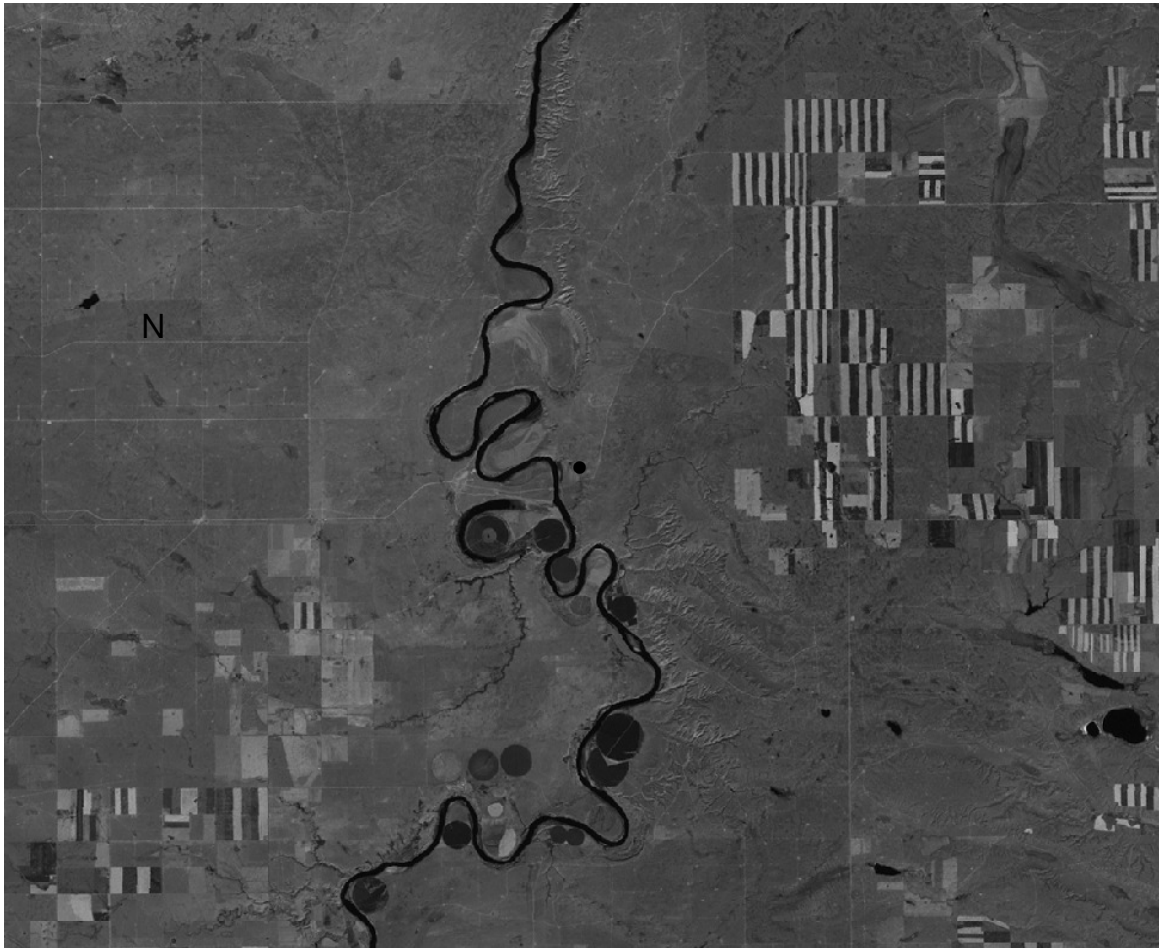


Figure 10. An example of one thousand random walk spring migration paths (white) generated using all observed path segment lengths (rattlesnake ID: A) each assigned random bearings in walks beginning at the den site (central black point) (Site fidelity test, Animal Movement extension, ArcView 3.2; Hooze and Eichenlaub 2000). Compare these random walks (white) to the observed spring migration path of rattlesnake A (red) which resulted in greater mean squared distance than all randomly generated walks. The black outer circle represents a ten km radius from the den site of origin.

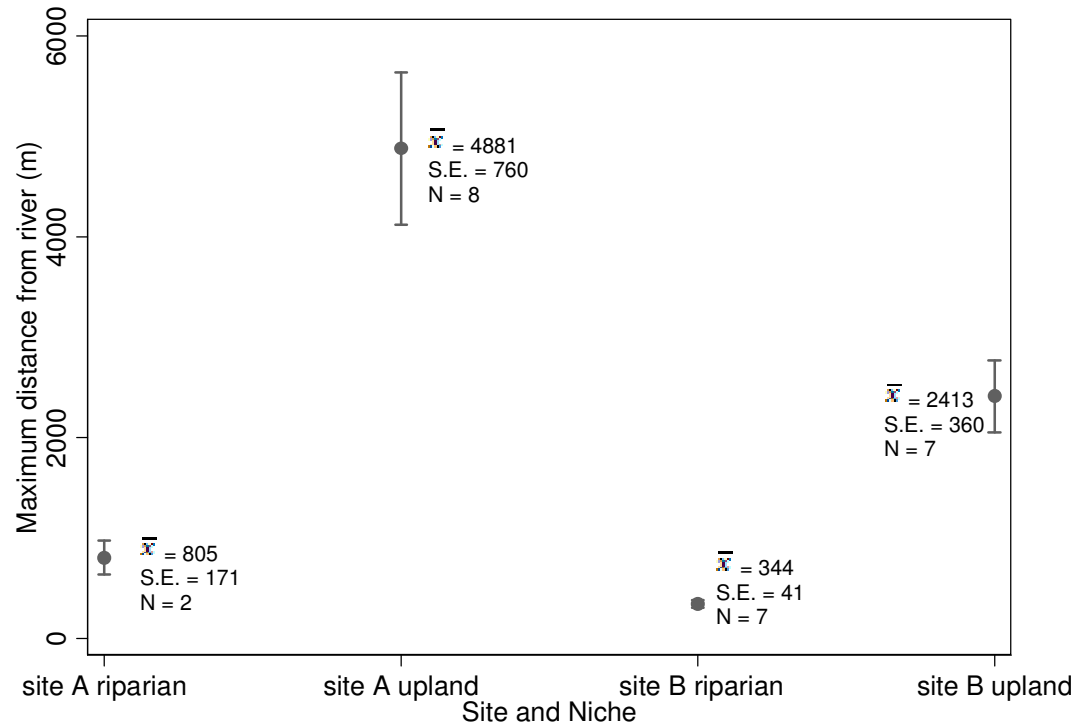


Figure 11. Maximum distance of riparian and upland migrant radio-tracked female prairie rattlesnakes, *Crotalus v. viridis*, from the South Saskatchewan River, by site (mean and standard error). Maximum distance from the South Saskatchewan River was determined by measuring the shortest distance from the point of maximum displacement to the South Saskatchewan River.

APPENDIX I – Surgical procedure (developed by D.V.M Douglas Whiteside of the Calgary Zoo Animal Health Centre)

Prior to surgery, transmitter antennae were coated with silicone and once cured were sterilized with ethylene oxide. Anesthesia was induced with intravenous propofol (6-7 mg/kg) injected into the ventral coccygeal (tail) vein. Anesthesia was maintained with gas on a non-rebreathing Bain circuit using isoflurane (2-3%) and nitrous oxide (500 mL/min) with an oxygen flow rate of 1 L/min. Anesthesia was monitored using a combination of an ultrasonic doppler with a 9.6 MHz probe that was positioned over the heart and visual observations by an animal health technologist. Pre-operatively trimethoprim-sulfa (30 mg/kg) was administered by intramuscular injection for antibacterial prophylaxis. Meloxicam (0.1 mg/kg subcutaneously) and butorphanol (1 mg/kg intramuscularly) or hydromorphone (0.05 mg/kg intramuscularly) were administered for analgesia. To surgically implant the transmitter a 2 cm long oblique incision (parallel to the underlying ribs) was made between the scales on the lateral body wall that ended two to three rows dorsal to the junction of lateral scales and ventral scutes. The site of the incision was approximately 60% of the total body length to ensure the transmitter would be placed past the level of the liver and stomach. The coelomic cavity was entered between a pair of ribs, and the transmitter body was placed intracoelmically on the left side. The antenna base was sutured to the cranial rib with 3-0 polydioxanone (PDS II™). The antenna was then fed caudally into the coelomic cavity using a fenestrated endoscopic grasping forcep. Closure was done in two layers, with the peritoneum and musculature closed, followed by skin closure, with 3-0 poliglecaprone (Monocryl™) in a horizontal mattress pattern. The surgical incision was sealed with surgical tissue glue followed by application of a moisture vapour permeable spray

dressings (Op-site™). The snakes received intracoelomic crystalloid fluids (0.45% Sodium chloride in Plasmalyte 7.4®) post-operatively at a dosage of 50 mL/kg to ensure hydration.

APPENDIX II – Prairie rattlesnake, *Crotalus v. viridis*, morphometric and movement variable definitions

Variables	Description
1. Measures of morphometry	
Initial mass (grams)	Initial mass measured in spring
Final mass (grams)	Final mass measured in fall
Change in mass (grams)	Annual change in mass (final_mass - initial_mass)
Change in mass (%)	Proportional annual change in mass ((final_mass - initial_mass)/initial_mass)
Initial snout to vent length (cm)	Initial snout to vent length measured in spring
Final snout to vent length (cm)	Final snout to vent length measured in fall
Change in snout vent length (cm)	Annual change in snout to vent length (final_svl - initial_svl)
Change in snout vent length (%)	Proportional annual change in snout to vent length ((final_svl - initial_svl)/initial_svl)
2. Measures of duration	
Total duration of active season	Number of days between departure and return to den or until death
Total duration of upland activity (upland migrants only)	Julian date of departure from upland habitat – Julian date of arrival in upland habitat
Percent of active season spent in upland habitat (upland migrants only)	(Total duration of upland activity/Total duration of active season) * 100
3. Measures of distance	
Observed spring migration pathway length (m)	Observed spring migration pathway length to the point of maximum displacement from the den of origin
Total observed pathway length (m)	Total observed pathway length over the entire active season or until death
Maximum displacement (m)	Maximum displacement from the den over the entire active season or until death
4. Measures of straightness	
Linearity index of observed spring migration path	Maximum displacement / observed spring migration pathway length
5. Measures of elevation	
Mean elevation (m)	Mean elevation of all points composing the movement path

APPENDIX III – Classification of radio-tracked female prairie rattlesnakes, *Crotalus v. viridis*, spring migration paths as predicted or underpredicted using the observed mean squared distance (MSD) and the maximum simulated MSD drawn from 1000 random walks generated for each individual (site fidelity test, Animal Movement Analysis Extension, Hooze and Eichenlaub 2000).

Site	Tracking Year	Snake ID (N= 24)	Observed MSD (m ²)	Max. simulated MSD (m ²)	Obs. MSD – Max. simulated MSD (m ²)	MSD
A	2004	A	7993724.5	7381701	612023.5	Underpredicted
A	2004	L	713714.5	570202.8	143511.7	Underpredicted
A	2004	N	80690.2	170813.9	-90123.7	Predicted
A	2005	AA	3368718	2589822	778896	Underpredicted
A	2005	BB	102827.2	121689.8	-18862.6	Predicted
A	2005	K	1945927.3	1633277	312650.3	Underpredicted
A	2005	P*	4406507	3732720	673787	Underpredicted
A	2005	R	1337277.9	1261795	75482.9	Underpredicted
A	2005	U*	1460632.6	1001090	459542.6	Underpredicted
A	2005	Z	828535.7	654371.4	174164.3	Underpredicted
B	2004	B	526828.9	1228320	-701491.1	Predicted
B	2004	D	104019.9	145936.5	-41916.6	Predicted
B	2004	E	1823122.5	1388834	434288.5	Underpredicted
B	2004	F*	29197.2	30994.7	-1797.5	Predicted
B	2004	G	77950	252409.4	-174459.5	Predicted
B	2004	H	321009.5	699294	-378284.5	Predicted
B	2004	J*	1395551.4	1266055	129496.4	Underpredicted
B	2004	M	255918.9	1241498	-985579.1	Predicted
B	2005	O	254118.8	529843.4	-275724.6	Predicted
B	2005	Q*	1442009.5	1585031	-143021.5	Predicted
B	2005	S	166384.8	399522.6	-233137.8	Predicted
B	2005	T	901372.1	1442555	-541182.9	Predicted
B	2005	V	29634.9	471088.5	-441453.6	Predicted
B	2005	X	4595129.5	3800723	794406.5	Underpredicted

Note: * Mortalities

APPENDIX IV – Timing and duration of upland migrant activities in upland habitats. The percent of the active season spent in upland habitat was not calculated for mortalities because it does not accurately reflect the percent of time these migrants would have spent in upland habitats had they survived.

ID	Site	Upland arrival date	Date of maximum displacement	Upland departure date	Total duration of upland activity (days)	Total duration of active season (days)	Percent of active season in upland habitat
A	A	25-Jun-04	18-Jul-04	07-Sep-04	74	141	52
AA	A	30-May-05	7-Aug-05	06-Sep-05	99	136	73
E	B	2-Jun-04	16-Jul-04	13-Sep-04	103	145	71
H	B	12-Jul-04	7-Aug-04	20-Aug-04	39	105	37
J*	B	6-Jul-04	6-Aug-04	01-Sep-04	57	122	NA
K	A	18-May-05	11-Aug-05	06-Sep-05	111	143	78
L	A	20-May-04	18-Jul-04	12-Sep-04	115	132	87
O	B	15-Jun-05	5-Jul-05	23-Aug-05	69	125	55
P*	A	14-May-05	21-Jun-05	21-Jun-05	38	48	NA
Q*	B	31-May-05	19-Jun-05	07-Jul-05	37	75	NA
R	A	18-May-05	28-Jul-05	17-Sep-05	122	125	98
T	B	2-Jun-05	1-Jul-05	15-Aug-05	74	149	50
U*	A	14-May-05	21-Jun-05	21-Jun-05	38	61	NA
X	B	26-May-05	3-Jul-05	22-Aug-05	88	123	72
Z	A	20-Jun-05	31-Aug-05	14-Oct-05	116	158	73

Note: * Mortalities

APPENDIX V – Mark-recapture history of 38 female prairie rattlesnakes, *Crotalus v. viridis*, captured at den site A during four mark-recapture sessions in 2004 and 2005 (PIT = Passive Integrated Transponder; 0 = uncaptured, 1 = marked-recaptured).

PIT #	Transmitter	Reproductive maturity	Spring 2004	Fall 2004	Spring 2005	Fall 2005	# of captures
113115243A	NO	ADULT	0	0	1	1	2
133534517A	YES	ADULT	1	1	1	0	3
133564270A	YES	ADULT	1	1	1	1	4
133566347A	YES	ADULT	1	0	1	1	3
133612726A	YES	ADULT	1	1	1	1	4
133623645A	NO	JUVENILE	0	0	0	1	1
133638227A	YES	ADULT	1	1	1	1	4
133715592A	YES	ADULT	0	0	1	1	2
133738337A	NO	JUVENILE	0	0	0	1	1
133739113A	NO	JUVENILE	0	1	1	0	2
133746793A	NO	ADULT	0	0	0	1	1
133839361A	NO	ADULT	0	1	0	1	2
133936615A	NO	JUVENILE	0	1	1	0	2
133938483A	YES	JUVENILE	1	0	0	0	1
133955270A	YES	ADULT	1	1	1	0	3
134427680A	YES	JUVENILE	0	0	1	0	1
134428551A	NO	ADULT	0	1	0	1	2
134433270A	NO	JUVENILE	1	1	1	0	3
134444545A	YES	ADULT	0	1	1	0	2
134464115A	NO	JUVENILE	0	0	0	1	1
134467312A	NO	ADULT	1	0	0	0	1
134474683A	NO	ADULT	1	0	0	0	1
134639625A	NO	JUVENILE	0	0	0	1	1
134674612A	NO	ADULT	0	1	0	0	1
134724563A	NO	ADULT	0	0	0	1	1
134909090A	YES	ADULT	1	0	0	1	2
135109616A	NO	ADULT	0	1	0	0	1
135115566A	NO	ADULT	0	0	0	1	1
135115663A	NO	ADULT	1	0	0	0	1
135118114A	NO	ADULT	0	0	0	1	1
135121392A	NO	ADULT	1	1	0	0	2
135121634A	NO	JUVENILE	0	0	0	1	1
135121752A	NO	ADULT	0	0	0	1	1
135127340A	NO	JUVENILE	0	0	0	1	1
135135521A	NO	JUVENILE	0	0	0	1	1
135136256A	NO	ADULT	1	0	0	0	1
135144586A	YES	JUVENILE	1	1	0	1	3
135948665A	NO	ADULT	0	0	0	1	1
			Sum = 15	Sum = 15	Sum = 13	Sum = 23	Mean = 1.7

APPENDIX VI – Mark-recapture history of 31 female prairie rattlesnakes, *Crotalus v. viridis*, captured at den site B during four mark-recapture sessions in 2004 and 2005 (PIT = Passive Integrated Transponder; 0 = uncaptured, 1 = marked-recaptured).

PIT #	Transmitter	Reproductive maturity	Spring 2004	Fall 2004	Spring 2005	Fall 2005	# of captures
133545583A	NO	JUVENILE	0	0	0	1	1
133549326A	YES	ADULT	1	1	1	1	4
133553326A	NO	ADULT	1	0	0	0	1
133554225A	YES	ADULT	1	0	1	1	3
133556217A	NO	ADULT	0	0	0	1	1
133569096A	NO	JUVENILE	0	0	1	0	1
133579392A	YES	JUVENILE	1	1	1	0	3
133609165A	NO	JUVENILE	0	1	1	1	3
133619613A	YES	ADULT	1	1	1	0	3
133639352A	YES	ADULT	0	0	1	1	2
133644355A	NO	ADULT	1	1	1	0	3
133651360A	YES	JUVENILE	1	0	0	0	1
133718245A	NO	ADULT	0	0	1	1	2
133726171A	YES	ADULT	1	1	1	1	4
133729596A	YES	ADULT	1	1	1	1	4
133737113A	YES	ADULT	1	1	1	0	3
133931663A	NO	ADULT	0	0	0	1	1
133937460A	NO	ADULT	1	1	0	0	2
133961464A	YES	JUVENILE	1	0	0	0	1
133968486A	YES	ADULT	1	0	1	1	3
134512567A	YES	ADULT	1	1	1	1	4
134619121A	NO	ADULT	1	1	0	0	2
134619657A	NO	ADULT	1	0	1	1	3
134671550A	YES	ADULT	1	1	0	1	3
135109156A	NO	ADULT	1	1	1	1	4
135128551A	NO	ADULT	0	0	1	1	2
135132557A	YES	ADULT	1	0	0	1	2
135135252A	NO	JUVENILE	1	1	1	0	3
135139666A	YES	ADULT	1	1	1	1	4
135964723A	NO	ADULT	0	0	0	1	1
136169626A	NO	ADULT	0	0	0	1	1
			Sum = 21	Sum = 15	Sum = 19	Sum = 20	Mean = 2.4