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Space use and mating activities in the speckled rattlesnake

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SPACE USE AND MATING ACTIVITIES IN THE SPECKLED RATTLESNAKE (*CROTALUS MITCHELLII*)

by

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ABSTRACT

Space use and mating activities in the speckled rattlesnake

(*Crotalus mitchellii*)

by

Xavier Glaudas

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Our understanding of space use variation in response to the temporally varying importance of specific resources is poorly understood in reptiles, because spatial studies are rarely placed into an explicit ecological and behavioral context. I examined how space use differed between the mating and post-mating seasons, and how this variation related to three important resources, mating partners, food, and refuge, in an adult population of the speckled rattlesnake (*Crotalus mitchellii*) in the Mojave Desert of southwestern North America. During the mating season (late April to early June), *C. mitchellii* increased distance traveled per unit time, because wide-ranging behavior likely enhances mating opportunities, and males traveled more than females, because male reproductive success is strongly limited by access to females. At the home range level, *Crotalus mitchellii* did not select specific habitat types (rolling hills, slopes, rock outcrops) during the mating season. At the microhabitat level, snakes did not select specific locations where rodent prey was abundant, possibly because mating activities prevailed over foraging. However, snakes selected microhabitats close to rock refuges, which may partially explain the low predator-induced mortality observed during the mating season. During the post-mating season (early June to mid-October), distance traveled per unit time was reduced, and males moved more than females, suggesting that the sexual difference in movement patterns is not simply a consequence of *C. mitchellii*'s mating system. At the home range level, *C. mitchellii* selected rock outcrops and avoided rolling hills, which positively correlated with the varying abundance of prey and refuges between these macrohabitats. That is, rodents and refuges were more abundant in rock outcrops than in rolling hills. However, at the microhabitat level, *C. mitchellii*'s locations were characterized by low prey availability, because rodents seemingly avoided the areas where snakes occurred. Further, snake locations were also characterized by being close to wood rat (*Neotoma lepida*) nests, and when wood rat nests were not available snakes preferred locations close to rock refuges. These refuges likely provide protection from the high summer temperatures of the Mojave Desert during *C. mitchellii'*s post-mating season, as well as from predators. Yet, predator-induced mortality was high during the post-mating season, suggesting that encounters between *C. mitchellii* and its predators are relatively common at this time of the year. My research indicates that examining patterns of space use in a biologically-relevant temporal framework can reveal significant seasonal variation in the spatial ecology of free-ranging organisms, and effectively demonstrate the behavioral shifts exhibited by organisms in response to seasonally-prevailing activities (e.g., mating and foraging activities).

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CHAPTER 1

SPATIAL ECOLOGY AND MATING ACTIVITIES

Space use virtually affects all the components of an individual's fitness. For instance, the manners in which organisms use the landscape can influence their reproductive success via access to mating partners (Jellen at al., 2007), body condition, growth rate and reproductive output via food intake (Strong and Sherry, 2000; Mägi et al., 2009), and survival via exposure to predators (Panzacchi et al., 2009; Hultgren and Stachowicz, 2010). Because spatial use influences "nearly all of an individual's subsequent choices" (Orians and Wittenberger, 1991: p. S29), examining space use variation in free-ranging organisms in relation to resource use is necessary to better understand the behavioral and evolutionary ecology of animals, and to identify the factors shaping their spatial ecology.

For sexually-reproducing species, mating partners are one key resource, and individuals need to invest time and effort to successfully reproduce (Darwin, 1859, 1871; Trivers, 1972; Andersson, 1994). Investments in mating-related behaviors (which can include mate searching, combat, courtship, copulation, and mate guarding) can profoundly affect the spatial ecology of organisms (Madsen et al., 1993; Kappeler, 1997; Buřič et al., 2009). For instance, the males of many polygamous species exhibit a significant increase in movement behavior during the mating season, presumably because increased movement enhances female encounter rate and reproductive success (Gaulin and FitzGerald, 1988; Kappeler, 1997; Odden and Wegge, 2007). In some species, time and energy allocation to mate acquisition prevails over foraging activities during the breeding season (Madsen and Shine, 2000; Pelletier et al., 2009), and individuals select locations based on the spatiotemporal distribution of mating partners rather than on the spatiotemporal distribution of food resources. These examples demonstrate that space use can vary according to seasonally-prevailing activities such as mating and foraging.

Radiotelemetry is a powerful tool to monitor spatial use and examine how free-ranging animals move around the landscape to use the resources needed for their diverse activities (White and Garrott, 1990). This technique allows researchers to regularly relocate individuals, and has had a profound impact on our understanding of the spatial and behavioral ecology of animals (Millspaugh and Marzluff, 2001). I conducted a radiotelemetry study on an adult population of a secretive, ambush vertebrate predator, the speckled rattlesnake (*Crotalus mitchellii*) in the Mojave Desert of southwestern North America. The objective of my dissertation research was to examine how space use differed between the mating and post-mating seasons in this snake species. More specifically, I investigated temporal variation in movement ecology in *C. mitchellii*, and how movement variation related to mate encounter rate in this rattlesnake (Chapter 2). I also examined seasonal variation in the relative importance of two resources, food and refuges, on the habitat selection process at the landscape (macrohabitat) and local (microhabitat) levels in this rattlesnake (Chapter 3). Finally, I summarize the findings of my dissertation project, and delineated some avenues for future research investigating the causes and consequences of movement variation (Chapter 4). My research is among the most detailed investigations of space use variation in an explicit temporal context of mating versus non-mating seasons in reptiles, and enhances our understanding of the relationship between spatial ecology and the use of resources in free-ranging organisms.

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CHAPTER 2

VAGABOND MALES AND SEDENTARY FEMALES: MOVEMENT ECOLOGY AND MATING SYSTEM OF THE SPECKLED RATTLESNAKE (*CROTALUS MITCHELLII*) [1]

ABSTRACT

I used radiotelemetric data and behavioral observations to examine seasonal (mating vs. post-mating seasons) and sexual variation in movement patterns, and describe characteristics of the mating system of an adult population of speckled rattlesnakes (*Crotalus mitchellii)* in the Mojave Desert of North America. Mating occurs in spring from late April to early June, shortly after emergence from hibernation, when snakes are predictably aggregated around the dens. Males and females traveled further per unit time in the mating season, compared to the post-mating season. Males also traveled longer distances per unit time than females in the mating and post-mating seasons. Additionally, I found a positive (but not statistically significant) relationship between the distances traveled by males and the number of accompanied females, and documented that males with larger home ranges had more potential mating partners. My results suggest that males actively locate females during the mating season, and that the drastic increase in distance traveled by males during the mating season occurs in response to strong male-male competition for access to females, because of the limited availability of sexually receptive females. My study shows that the movement patterns of *C. mitchellii* varies by biologically-relevant seasons, and demonstrates that combining quantitative spatial

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[1] Glaudas, X., and Rodríguez, J.A. Submitted to Oecologia

analyses and behavioral observations in an explicit seasonal context can significantly advance our understanding of organismal mating systems.

Introduction

The spatiotemporal distribution of individuals is fundamentally linked to the fluctuating abundance and distribution of resources important for organismal fitness (MacArthur and Pianka, 1966; Schoener, 1983; Fryxell et al., 2005; Chamaillé-Jammes et al., 2008). Therefore, mobile animals typically move in a deterministic manner to locate the various resources required for survival and reproduction. For sexually-reproducing species, mating partners are one of these key resources, because individuals need to mate to pass on their genes (Darwin, 1859, 1871; Trivers, 1972; Andersson, 1994). Finding mates is a necessary step for successful reproduction, and mate-searching activities can significantly affect the movement ecology of organisms (Madsen et al., 1993; Kappeler, 1997; Schmidt et al., 2009; Buřič et al., 2009). Characterizing the link between space use and mating is therefore essential to better understand the spatial and behavioral ecology of animals (Greene, 1994; Rubenstein and Hobson, 2004). For example, knowledge of the relationship between movement and reproduction has shed light on intrasexual competition and sexually-selected traits (Biedermann, 2002; Kelly et al., 2008), alternative reproductive strategies (Stockley et al., 1994; Shine et al., 2005; Eppley and Jesson, 2008), and ultimately on organismal mating systems (Lambin and Krebs, 1991; Le Galliard et al., 2006; White et al., 2007; Dubey et al., 2009).

The link between space use and mating activity has primarily been studied in mammals, especially rodents. These studies suggest that intraspecific variation (e.g., seasonal, sexual) in movement patterns is strongly affected by the mating system of a species (Ims, 1988; Gaulin and FitzGerald, 1988). In fact, the mating system of some species can be predicted from the spatial use and distribution of individuals over the landscape (Gaulin and FitzGerald, 1988; Komers and Brotherton, 1997). For instance, males of pair-living, monogamous species exhibit little differences in movement patterns between the mating and non-mating seasons, and males and females exhibit similar movement ecology (Gaulin and FitzGerald, 1986, 1988, 1989). In contrast, in polygynous systems, males drastically increase movement during the mating season, which results in significant sexual differences in activity patterns (Gaulin and FitzGerald, 1988; Frank and Heske, 1992; Tew and Macdonald, 1994; Kappeler, 1997; Odden and Wegge, 2007). These seasonal and sexual differences in movement ecology have been linked to the divergent selective pressures operating on individuals of species exhibiting contrasting mating systems. That is, an individual's reproductive success presumably experiences a significant net benefit from increased activity (via accrued access to mating partners) in polygamous, but not in monogamous species. Thus, polygamy is a system that promotes investment in mate-searching activities, at least in non-socially living species.

Like most mammals, snakes are largely polygamous (Rivas and Burghardt, 2005), and studies of their movement ecology have flourished lately (Shine and Bonnet, 2000). Yet most spatial studies only report absolute values of movement parameters, with little consideration for an ecological and/or behavioral context (Waldron et al., 2006), and therefore our understanding of the link between spatial ecology and mating activity in reptiles is relatively poor compared to other groups, such as insects, mammals, and birds (Thornhill and Alcock, 1983, Andersson, 1994). Snakes are particularly well-suited for this kind of study for several reasons. First, most snake species exhibit strong seasonality of mating (Shine, 2003, and references therein), and the mating period can easily be identified, because snakes are largely non-social animals and male-female aggregations are typically a good indicator of mating activity, at least away from den sites. Second, snakes tend to allocate energy to the different components of fitness (e.g., foraging, mating) at specific times of the year (King and Duvall, 1990). For instance, many snake species forgo, or at least decrease, feeding during the mating season, because time and energy allocation to mate acquisition and/or reproduction apparently prevails over feeding activities (Shine, 1980; King, 1986; Madsen and Shine, 2000; Lourdais et al., 2002; Bonnet and Naulleau, 1996; O'Donnell et al., 2004). Consequently, season-specific motivational states allow the relative decoupling of fitness components in snakes, which may cause and/or accentuate diverging patterns of seasonal and sexual behaviors, including movement.

Herein, I relied on radiotelemetry to examine intraspecific variation in movement ecology of a population of a secretive North American viperid snake, the speckled rattlesnake (*Crotalus mitchellii*). I gathered data on male-female interactions and movement patterns of *C. mitchellii* during three consecutive active seasons. My specific objective was to test three hypotheses of sexual and seasonal (mating vs. post-mating seasons) variation in movement patterns, to characterize the mating system of *C. mitchellii*.

Male snakes do not provide parental care to their offspring (Shine, 1988; Greene et al., 2002). As a result, a male's reproductive success is limited by access to females (Darwin, 1871; Kokko and Rankin, 2006). Traits that enhance mate-acquisition should therefore be strongly selected for. One mechanism by which males can maximize access to females is by increasing movement to enhance female encounter rate. Consistent with this idea, males of several snake species exhibit a peak of activity during the mating season (Gibbons and Semlitsch, 1987; Waldron et al., 2006; Jellen et al., 2007; but see Carfagno and Weatherhead, 2008). Consequently, I hypothesized that *C. mitchellii* males exhibit increased movements per unit time in the mating season, compared to the post-mating season (*Hypothesis 1*). The benefits of mating with multiple partners are higher for males than for females (Bateman, 1948; Prosser et al., 2002), because only males can contribute genes to more than one litter at a time. Females also allocate a higher direct energetic investment in the production of eggs and offspring than males (Parker, 1978). For these reasons, selection on mate-searching activities should be male-biased (see Kokko and Wong, 2007 for a theoretical model of sex-biased mate-searching). Consequently, I hypothesized that in *C. mitchellii* mate-searching activities are performed by males, and that they exhibit increased activity, compared to females in the mating season (*Hypothesis 2*). In polygamous systems, the predicted sexual difference in movement ecology during the mating season typically disappears or is strongly decreased during the non-mating season (Trivers, 1972; Gaulin and FitzGerald, 1988, 1989; Frank and Heske, 1992; Kappeler, 1997; Waldron et al., 2006). This lack of sexual difference in the non-mating season has led some authors to propose that the sexual difference in movement patterns during the mating season is not a consequence of sex per se, but rather of the mating system (Trivers, 1972; Gaulin and FitzGerald, 1986). That is, if the sexes intrinsically differ in movement ecology, we expect males and females to exhibit variation in movement patterns during the non-mating season as well. Thus, I hypothesized that sex and season interact with movement, because males would increase movement relative to females in the mating season, but not the post-mating season (*Hypothesis 3*).

Materials and methods

Study site and species

The study site is a ca. 5 km^2 area located in the Eldorado Mountains, Clark County, southern Nevada (35˚44'N, 114˚49'W), in the eastern part of the Mojave Desert. This region is characterized by a dry climate (2006-2009 average annual rainfall [range]: 8.3 cm [5.2-12.5 cm]), with high temperatures in summer (2006-2009 average daily temperatures: 27.1ºC [14.5-36.5ºC]), and relatively cold temperatures (7.1ºC [-7.5-23.7ºC]) in winter (environmental data from Station ID4814, Clark County Regional Flood Control District, Nevada). From June to September, the activity patterns of *C. mitchellii* are highly constrained by environmental temperatures, because midday temperatures approach the critical thermal maximum of desert-dwelling reptiles (ca. 39–42ºC; Brattstrom, 1965), and *C. mitchellii* becomes largely nocturnal. The low winter temperatures also prevent this snake from being active during winter, and *C. mitchellii* hibernates, typically in rock outcrops, from mid-October to late March. I never observed any movements during the hibernation period, although some individuals emerged from their dens during winter rainfall, presumably to drink winter (Glaudas, 2009). Because my intent was to elucidate the movement ecology and mating system of *C. mitchellii*, I only present data for the snake's active season.

The habitat of the study area consists of sparsely vegetated rocky hillsides at an elevation of ca. 1,100 m. Dominant plants include yucca trees (*Yucca* sp.), Brigham tea shrubs (*Ephedra* sp.), buckwheats (*Eriogonum* sp.), catclaw acacias (*Acacia greggii*), creosote bushes (*Larrea tridentata*), and various annual herbaceous plants. The typically high temperatures of the Mojave Desert during *C. mitchellii*'s active season and the reduced vegetation cover seem to preclude snakes from using vegetation as refugia. Instead, snakes rely on crevices, cavities under large rocks, and wood rat (*Neotoma lepida*) nests to escape high temperatures.

Crotalus mitchellii typically aggregated in small numbers (e.g., 2-10) at dens sites for hibernation. Upon emergence from hibernation around late March, snakes traveled a few meters to cavities under rocks, where they remained alone 3-4 weeks with no apparent activity. Although males and females are in close proximity upon emergence from hibernation, I did not monitor indications of active mating-related behaviors at the dens or at the initial refuges used by snakes following emergence. Consequently, I did not use these observations to estimate the duration of the mating season. In mid- to late April, snakes started to be active and male-female interactions became common. These interactions included male-female accompaniment, courtship, and mating. Based on the earliest and latest male-female behavioral interactions, the estimated mating season spanned from 20 April to 6 June. All the mating dates reported elsewhere for *C. mitchellii* fell within the estimated mating season (Brattstrom, 1965; Klauber, 1972; Goldberg, 2000; Gartner and Reiserer, 2003). All movements monitored from 7 June until snakes started hibernation, typically in mid-October, were categorized as post-mating season movements. For the purpose of this study, I consequently use the terms “season/seasonal” to contrast the mating season from the post-mating season. Further, to avoid confusion, the mating season solely refers to the period when males and females engage in sexual intercourse, and excludes the period when females give birth.

Radiotelemetry

From April 2006 to April 2009, I radiotracked 25 *C. mitchellii* (18 males, 7 females). Snakes were opportunistically caught during visits to the field site. I surgically implanted temperature-sensitive radiotransmitters (model SI-2T, 9 g, Holohil Ltd., Ontario, Canada; or model WST2, 5 g, Wildlife Track, Caldwell, ID, USA) in the body cavity of the snakes following established procedures (Reinert and Cundall, 1982; Reinert, 1992). At the time of transmitter implantation, males measured (mean ± SD) 85.3 ± 6.93 cm snout-to-vent length (SVL) and weighed 558.6 ± 144.3 g, and females measured 74.6 ± 2.8 cm SVL and weighed 373.9 ± 53.3 g. The transmitter’s mass was less than 3% of the snake’s body mass in all cases. I released the snakes at their exact capture location 1-3 days following surgery. I used a radio receiver (model WTI-1000, Wildlife Track, Caldwell, ID, USA) and a directional antenna (model F151-3FB, Wildlife Track, Caldwell, ID, USA) to relocate snakes every 2-3 days during the active season, and once per week during the hibernation period. I considered that a snake had moved between successive locations if it traveled a distance ≥ 1m from its previous position. Each time a snake moved, I recorded its geographic coordinates using a sub-meter accuracy GPS unit (model GS20, Leica Geosystems Inc., Torrance, CA, USA). Periods of radiotracking ranged from 15-1073 days per individual (mean ± SD = 407 ± 265 days). In total, my study resulted in 5582 relocations and 1098 movements by snakes.

GIS analysis and movement parameters

Because the field site is mountainous, I generated a 3-dimensional data layer of the study area in a geographic information system (GIS). I used a 20-foot elevation contour map to create a Triangulated Irregular Network (TIN) data layer that enabled me to capture the topography of the field site. Briefly, a TIN is a physical representation of an area that consists of contiguous and non-overlapping triangles with three-dimensional coordinates (x, y, z). Individual triangles are generated using the Delaunay triangulation technique, and each triangle has elevation, slope, and aspect data associated with it (Bolstad, 2005). I imported the geographic coordinates of each snake's relocations onto the TIN map, and used the 3D analyst tool in ArcMap 9.2 (ESRI, Redlands, CA) to estimate the movement parameters of each individual. This technique allowed me to minimize underestimation of a snake's movements by incorporating the topography of the area in the distances traveled by snakes (Greenberg and McClintock, 2008).

My spatial analyses focused on the following parameters: distance traveled between relocations (DBR), distance traveled per known movement (DPM), movement frequency, and directionality. I obtained DBR by calculating the distance between two consecutive locations. Because I relocated all snakes during each visit to the field site, time between relocations is standardized across snakes, and DBR is consequently an estimate of distance traveled per unit time. I calculated DPM by removing from the data set the instances when snakes did not move between successive locations. I obtained the movement frequency data by calculating the number of times that a snake moved during an arbitrarily defined two-week period, out of *n* possibilities (*n* being the number of times I visited the field site, which represents the number of times that I could possibly detect movement). To calculate the directionality of movement, I obtained the bearing of each movement for each snake using the Hawths' Tools software for ArcGIS (Beyer, 2004). I then grouped the bearings by season for each individual and calculated circular variance, a proxy for directionality, using the software Oriana 2.02 (Kovach Computing Services, Anglesey, UK). The circular variance generated is a number between 0 and 1, with smaller values corresponding to an increase in directionality. In addition to the four parameters mentioned above, I calculated the distance between telemetered neighboring snakes, and the distance that snakes ventured away from their respective overwintering dens. This allowed me to investigate the spatial distribution of individuals relative to one another, and to den sites, an important landscape feature to the snakes.

I used the kernel density estimator (KDE) to estimate home range size because this technique includes a utilization distribution function that allows prediction of the probability of finding an animal in a given area within its home range (Millspaugh and Marzluff 2001). I used the methodology recommended to generate KDEs for reptile and amphibian species (Row and Blouin-Demers 2006). I first generated Minimum Convex Polygons (MCPs) that included all of an individual's known locations within the boundary of the smallest polygon possible. I then created 95% KDEs for each individual by manually adjusting *h*, the smoothing parameter, until the MCP and the KDE were of similar size. This technique provides an objective method for selecting *h*, and to generate biologically relevant KDEs for herpetofauna (Row and Blouin-Demers, 2006). All the home ranges were created in the Home Range Tools for ArcGIS (Rodgers et al. 2007).

Statistical analyses

I analyzed most of the data using general linear models (ANOVA or ANCOVA). For most movement response variables (DBR, DPM, movement frequency, directionality, home range size), I conducted two separate analyses: one combining the male and female data (which therefore included sex as a class factor), and one with the male data only. I performed two separate analyses because I captured and radiotracked more males (2006: 9; 2007: 12; 2008: 9) than females (2006: 3; 2007: 3; 2008: 5). The relatively low sample size of females per year precluded me from conducting detailed analyses of annual variation in sexual differences (e.g., year × sex, year × sex × season interactions). Consequently, the analysis that includes males and females is best viewed as an average of movement behavior across years for the sexes. On the other hand, the larger male sample size allowed me to examine how male movement varies annually, and how the factors in the models (see below) interact to affect movement.

I included the following factors in the linear model: season (mating vs. post-mating), year (2006, 2007, 2008), sex (in the male-female analysis only), and individual. Season, year and sex were modeled as fixed effects, whereas individual (nested within sex in the male-female analysis) was modeled as a random effect. F-tests of all main effects and interactions were constructed using the mean square of individuals as the error term to avoid pseudoreplication. When necessary, I transformed the movement response variables to meet assumptions of normality and homoscedasticity. The movement parameters of snakes that were radiotracked for multiple years were analyzed together, based on the assumption that snake movements were independent among years. This assumption is reasonable given the significant year-to-year variation in movement patterns within individuals (see Results).

Because the behavior of ectotherms is directly affected by ambient temperature (Huey, 1982; Tewksbury et al., 2008; Huey et al., 2009), I included environmental temperatures as covariates in most analyses. I obtained daily mean (T_{mean}), minimum (T_{min}), and maximum temperatures (T_{max}) from the Nelson Peak weather station (Station ID4814; Clark County Regional Flood Control District, Nevada), located 10 km southwest of the study area. To control for the high correlation among these environmental variables, I used a principal components analysis of all three daily temperature measurements to generate principal component scores (PC1). I then used PC1, which explained 98% of the variance in the three temperature variables, as the environmental covariate in analyses of movement response variables. The eigenvector loadings of T_{mean}, T_{min}, and T_{max} on PC1 were similar and positive (ca. 33 % for each of them). Consequently, an increase in PC1 represents a roughly parallel increase in daily T_{mean}, T_{min}, and T_{max}, and reflects higher environmental temperatures.

In all ANCOVA models of movement variables, I first examined the interactions of the temperature covariate, PC1, with all class factors (season, sex, year). This was necessary to understand the effect of these factors, because the interpretation of these effects using adjusted least squares means is based on the assumption that there is no interaction between class factors and covariates. Consequently, a significant interaction of a class factor with PC1 indicated that the slope of the relationship between temperature and snake movements differs between levels of the factor (e.g., a significant sex × PC1 interaction would indicate that male and female movement behavior was differently affected by environmental temperatures). In other words, tests of the covariate interaction are tests of behavioral differences in snake movement across levels of a factor (e.g., males vs. females, mating vs. non-mating seasons) with respect to temperature. Consequently, when the covariate interacted with a class factor, I performed separate ANCOVAs for each level of the factor. When there was no significant covariate interaction in an ANCOVA, tests of the main effects were based on differences in the least square means (LS means) among levels of a factor after the means were adjusted for the temperature covariate.

Finally, I measured the distance to nearest neighbor for each telemetered individual at weekly intervals. I then calculated the variance-to-mean ratio of the distances to nearest neighbor, an index of dispersion (I), to test whether snakes were spatially aggregated, dispersed or randomly distributed at a given time period (Krebs, 1999). Values of I close to 1 indicate a random distribution, whereas values larger or smaller than 1 indicate that individuals are clumped or dispersed, respectively.

I conducted all statistical analyses using STATISTICA (version 6.0; StatSoft Inc., Tulsa, OK, USA) and SAS (version 9.2; SAS Institute, Cary, NC, USA). Values given are means or adjusted least-square (LS) means ± 1 SE, and all reported *P* values are two-tailed, unless otherwise mentioned. The *P* values for multiple comparisons were adjusted using the Bonferonni method. Significance level for all tests was determined at $\alpha = 0.05$.

Results

Spatial analyses

Individual snakes that were radiotracked for two complete years exhibited significant annual differences in distance traveled between relocations (ca. 2.5 days), specifically during the mating season (Figs. 1A-F). Consequently, I considered that an individual's movements were independent from one year to another.

I present data on distance traveled between relocations by month and by sex for all years combined (Fig. 2). Males exhibited an unimodal activity peak during the mating season, with movement drastically decreasing starting in June, which corresponded to the end of the mating season. The movement pattern of males, as measured by distance traveled between relocations, was very consistent throughout the post-mating season. In contrast, females exhibited a bimodal activity pattern, with increased movement in May-June and then in August, and reduced activity in July. Standard parameters reported in movement studies are presented in Table 1 to facilitate comparisons with other studies. (The values reported in Table 1 are not corrected for the effect of environmental temperatures on movement patterns.)

Distance between relocations (DBR)

Males and females

The environmental covariate, PC1, did not interact with any class factors (PC1 × season: $F_{(1,2498)} = 0.43$, $P = 0.51$; PC1 × sex: $F_{(1,2498)} = 0.49$, P = 0.49; PC1 × year: $F_{(2,2498)} = 0.65$, $P = 0.53$), so I removed these interactions from the model. The ANCOVA revealed that DBR was positively related to environmental temperatures as measured by PC1 ($\beta = 12.51$, $P = 0.004$; Table 2A). Season, sex and year significantly affected DBR

(Table 2A). Snakes increased DBR in the mating season, compared to the post-mating season (LS means ± SE; mating: 53.02 ± 3.34 m; post-mating: 21.02 ± 1.96 m; $P = 0.0004$), and males traveled longer DBR than females (males: 49.41 ± 2.55 m; females: 24.64 ± 3.24 m; $P = 0.01$). Both sexes increased DBR during the mating season relative to the post-mating season (males: mating: 71.8 ± 3.72 m; post-mating: 27.01 ± 2.77 m; n = 1678, t = 4.27, $P < 0.0001$; females: mating: 34.25 ± 5.50 m; post-mating: 15.03 ± 2.92 m; n = 841, t = 2.41, $P = 0.008$). Males exhibited longer DBR than females in the mating (males: 71.80 ± 3.72 m; females: 34.25 ± 5.50 m; n = 579, t = 4.2, $P < 0.0001$) and post-mating season (males: 27.01 ± 2.77 m; females: 15.03 ± 2.92 m; n = 1940, t = 2.05, $P = 0.02$). The sex × season interaction was not significant ($P = 0.1$). Finally, DBR was greater in 2006 (43.99 ± 3.68 m) and 2008 (46.49 ± 2.95 m) compared to 2007 (20.59 ± 3.11 m; pairwise comparisons; 2006-2007: n = 1584, t = 3.72, $P < 0.0001$; 2006-2008: n = 1693, t = -2.32, $P = 1.0$; 2007-2008: n = 1761, t = 3.89, $P < 0.0001$).

Males

I conducted an ANCOVA with year and season as class factors, and PC1 as the covariate. All the terms of the models were highly significant, including the PC1 × year ($F_{(2,1656)} = 6.70$, $P = 0.007$) and PC1 × season ($F_{(1,1656)} = 7.45$, $P = 0.01$) interactions. Therefore, I analyzed the data by year. In 2006 and 2007, PC1 did not affect DBR (2006: ß = -17.81, $F_{(1,555)} = 2.80$, $P = 0.13$; 2007: ß = -4.82, $F_{(1,601)} = 1.73$, $P = 0.21$), and PC1 did not interact with season (2006: $F_{(1,555)} = 0.14$, $P = 0.72$; 2007: $F_{(1,601)} = 0.19$, $P = 0.66$). Further, DBR was higher in the mating season, compared to the post-mating season in 2006 (mating season: 79.09 ± 8.92 m; post-mating season: 39.53 ± 4.02 m;

$F_{(1,555)} = 8.43$, $P = 0.02$) and 2007 (mating season: 38.77 ± 3.41 m; post-mating season: 15.68 ± 3.43 m; $F_{(1,602)} = 4.90$, $P = 0.04$). In 2008, PC1 positively correlated with DBR (ß = 18.5, $F_{(1,498)} = 52.64$, $P = 0.0002$), and the PC1 × season interaction was highly significant ($F_{(1,498)} = 27.18$, $P = 0.001$). This interaction was caused by the stronger positive relationship between PC1 and DBR in the mating season ($F_{(1,113)} = 41.05$, $r^2 = 0.26$; $P < 0.0001$) relative to the post-mating season ($F_{(1,385)} = 19.31$, $r^2 = 0.04$; $P < 0.0001$). Because of the PC1 × season interaction, I could not interpret the seasonal effect in 2008. However, 2008 was the year where the seasonal difference in DBR was the largest.

Distance per movement (DPM)

Males and females

PC1, the environmental covariate, did not interact with any class factors (PC1 × season: $F_{(1,1308)} = 2.19$, $P = 0.15$; PC1 × sex: $F_{(1,1308)} = 0.30$, $P = 0.58$; PC1 × year: $F_{(2,1308)} = 0.09$, $P = 0.91$), so I removed these terms from the model. PC1 marginally affected DPM (ß = 9.6, $P = 0.06$; Table 2B). Sex, season, and year affected DPM (Table 2B). Snakes increased DPM in the mating season, compared to the post-mating season (LS means ± SE; mating: 84.61 ± 5.54 m; post-mating: 46.85 ± 3.66 m; $P = 0.005$), and males traveled longer distances than females (males: 85.44 ± 4.58 m; females: 46.02 ± 5.16 m; $P = 0.007$). Males significantly increased DPM in the mating season, compared to the post-mating season (mating: 112.31 ± 6.28 m; post-mating: 58.57 ± 5.26 m; $n = 898$, $t = 4.03$, $P < 0.0001$), but females did not (mating: 56.9 ± 8.90 m; post-mating: 35.13 ± 5.12 m; $n = 431$, $t = 0.95$, $P = 0.17$). Males traveled longer DPM than females in both the mating (males: 112.31 ± 6.28 m; females: 56.90 ± 8.74 m; $n = 354$, $t = 3.75$,

$P < 0.0001$) and post-mating seasons (males: 58.57 ± 5.26 m; females: 35.13 ± 5.12 m; n = 975, t = 2.36, $P = 0.009$), and the sex × season interaction was not statistically significant ($P = 0.15$). Finally, the year effect was caused by the decreased movement of snakes in 2007 (45.08 ± 5.37 m) compared to 2006 (79.17 ± 6.04 m) and 2008 (72.94 ± 4.94 m; pairwise comparisons; 2006-2007: n = 783, t = 3.76, $P < 0.0001$; 2006-2008: n = 955, t = -2.33, $P = 1.0$; 2007-2008: n = 920, t = 3.9, $P < 0.0001$).

Males

The model indicated that PC1 interacted significantly with season ($F_{(1,876)} = 8.56$, $P = 0.009$) and marginally with year ($F_{(2, 876)} = 2.75$, $P = 0.09$). Because I was primarily interested in seasonal variation in movement patterns, I analyzed the data by year. PC1 did not affect DPM in 2006 (ß = 8.13, $F_{(1,293)} = 0.65$, $P = 0.44$) and 2007 (ß = 1.43, $F_{(1,258)} = 2.15$, $P = 0.17$) but did in 2008 (ß = 9.32, $F_{(1,323)} = 13.75$, $P = 0.007$). The PC1 × season interaction was only significant in 2008 ($F_{(1,323)} = 9.66$, $P = 0.01$). DPM was significantly greater during the mating season in 2007 (mating: 83.90 ± 6.59 m; post-mating: 30.68 ± 7.36 m; $F_{(1,258)} = 9.37$, $P = 0.01$) and marginally larger in 2006 (mating: 115.46 ± 13.74 m; post-mating: 79.05 ± 6.79 m; $F_{(1,293)} = 3.67$, $P = 0.09$). Again, because of the significant PC1 × season interaction in 2008, I could not interpret the seasonal difference in DPM.

Movement frequency

Males and females

Movement frequency was positively related to environmental temperatures (ß = 0.22, $P < 0.0001$; Table 2C), but the covariate did not significantly interact with any class factors (PC1 × season: $F_{(1,778)} = 3.07$, $P = 0.08$; PC1 × sex: $F_{(1,778)} = 0.13$, $P = 0.72$;

PC1 × year: $F_{(2,778)} = 1.42$, $P = 0.26$). Season and year affected movement frequency (Table 2C). That is, movement frequency was higher in the mating season compared to the post-mating season (arcsine-transformed LS mean number of movements per 2 weeks ± SE; mating: 0.91 ± 0.05; post-mating: 0.55 ± 0.02; $P = 0.0006$). Both sexes increased movement frequency during the mating season (males: mating: 0.98 ± 0.05; post-mating: 0.56 ± 0.04; n = 523, t = 4.3, $P < 0.0001$; females: mating: 0.85 ± 0.08; post-mating: 0.54 ± 0.04; n = 260, t = 2.67, $P = 0.004$). The similar frequency of movement of males and females in the mating (n = 161, t = 0.80, $P = 0.21$) and post-mating seasons (n = 622, t = -0.58, $P = 0.72$) resulted in the lack of sexual effect (males: 0.77 ± 0.04; females: 0.69 ± 0.04; $P = 0.47$). Consistent with the other movement variables, frequency of movement was higher in 2006 (0.82 ± 0.05) and 2008 (0.82 ± 0.04) compared to 2007 (0.56 ± 0.04; pairwise comparisons: 2006-2007: n = 488, t = 3.25, $P = 0.0006$; 2006-2008: n = 530, t = -2.33, $P = 1.0$; 2007-2008: n = 548, t = 3.74, $P < 0.0001$).

Males

PC1 significantly interacted with season ($F_{(1,515)} = 5.22$, $P = 0.03$). Consequently, I analyzed the data by year. In 2006 and 2007, PC1 did not affect movement frequency (2006: ß = 0.25, $F_{(1,169)} = 2.35$, $P = 0.16$; 2007: ß = 0.15, $F_{(1,186)} = 0.26$, $P = 0.62$), and the PC1 × season interactions were not significant (2006: $F_{(1,169)} = 1.21$, $P = 0.30$; 2007: $F_{(1,186)} = 2.23$, $P = 0.16$). Males moved more frequently in the mating season in 2006 (mating season: 1.07 ± 0.11; post-mating season: 0.63 ± 0.05; $F_{(1,515)} = 13.15$, $P = 0.006$), but not 2007 (mating season: 0.60 ± 0.08; post-mating season: 0.49 ± 0.07; $F_{(1,186)} = 0.30$, $P = 0.59$). In 2008, movement frequency was affected by PC1 (ß = 0.34, $F_{(1,156)} = 10.06$, $P = 0.01$), PC1 did not interact with season ($F_{(1,156)} = 1.06$, $P = 0.34$), and males moved more frequently in the mating season (mating season: 1.35 ± 0.15; post-mating season: 0.68 ± 0.05; $F_{(1,156)} = 13.31$, $P = 0.01$).

Directionality

Males and females

The number of observations (N obs.) was highly correlated to circular variance (ß = 0.01; $P = 0.005$), and thus I entered this variable as a covariate in the model. N obs. did not interact with any class factors (N obs. × season: $F_{(1,64)} = 2.17$, $P = 0.15$; N obs. × sex: $F_{(1,64)} = 1.99$, $P = 0.17$; N obs. × year: $F_{(2,64)} = 0.35$, $P = 0.71$), and directionality was not affected by year ($F_{(2,64)} = 0.26$, $P = 0.77$). Consequently, I removed these terms from the model.

Sex (mean circular variance ± SE; males: 0.72 ± 0.03; females: 0.68 ± 0.04; $P = 0.52$) and season (mating: 0.68 ± 0.04; post-mating: 0.72 ± 0.04; $P = 0.62$) did not affect directionality (Table 3). However, I detected a sex × season interaction ($P = 0.02$), that was caused by the relatively higher directionality of females compared to males in the mating season. That is, female movement patterns were more directional than males' in the mating season (males: 0.76 ± 0.04; females: 0.60 ± 0.06; n = 33, t = 2.14, $P = 0.02$), whereas the movement patterns of the sexes were similar in the post-mating season (males: 0.67 ± 0.04; females: 0.76 ± 0.06; n = 35, t = 0.88, $P = 0.19$).

Males

The only term that affected directionality was the covariate, number of observations ($F_{(1,35)} = 16.22$, B = 0.007, $P = 0.001$). None of the other terms were significant.

Home range analysis

Males and females

I investigated whether annual home range size varied between the sexes. Snout-to-vent length (SVL) and number of days tracked (N days) were entered as covariates, and I used log-transformed 95% kernels as the dependent variable. The covariates did not significantly interact with sex (SVL × sex: $F_{(1,24)} = 3.10$, $P = 0.1$; N days × sex: $F_{(1,24)} = 0.01$, $P = 0.91$), or SVL ($F_{(1,24)} = 2.33$, $P = 0.14$) and N days ($F_{(1,24)} = 2.76$, $P = 0.11$) did not affect home range size. Consequently, I removed these terms from the analysis. The resulting model indicated that males had larger annual home ranges than females (males: 1.10 ± 0.09 ha; females: 0.66 ± 0.13 ha; $F_{(1,31)} = 7.19$; $P = 0.01$), and that year marginally affected home range size ($F_{(2,31)} = 3.06$, $P = 0.07$).

I investigated whether home range size varied by sex in the mating and post-mating seasons. I used a statistical model which included season, sex, and year as class factors, and N days as a covariate. Year did not affect home range size ($F_{(2,60)} = 1.79$, $P = 0.18$), and the covariate significantly interacted with season ($F_{(1,60)} = 4.41$, $P = 0.05$). Consequently, I removed year from the analysis, and conducted separate analyses for the mating and post-mating seasons. N days did not interact with sex in the mating ($F_{(1,33)} = 2.38$, $P = 0.13$) or post-mating seasons ($F_{(1,30)} = 1.55$, $P = 0.22$), and I therefore excluded this interaction from each model. The analyses showed that N days affected home range size in both seasons (mating season: $ß = 0.03$, $F_{(1,34)} = 7.44$, $P = 0.01$; post-mating season: $ß = 0.01$, $F_{(1,31)} = 13.66$, $P = 0.001$), and that males had larger home ranges than females in both seasons (log-transformed LS mean home range size ± SE;

mating season: males: 0.32 ± 0.17; females: -0.49 ± 0.26, $F_{(1,34)} = 7.65$, $P = 0.01$; post-mating season: males: 0.74 ± 0.17, females: 0.13 ± 0.26; $F_{(1,31)} = 6.1$, $P = 0.02$).

Males

I investigated the consequences of the seasonal difference in movement patterns on home range size. I compared the absolute size of home ranges across seasons to explore whether the seasonal movement differences translated into home ranges of similar or different size, irrespective of the length of the season (i.e., home range size was not adjusted according to the length of the season). Only snakes that were radiotracked for 80% or more of the length of the mating and post-mating seasons were included in this analysis. Home range size of male snakes did not differ between seasons (mating: 0.72 ± 0.13; 0.87 ± 0.11; $F_{(1,27)} = 0.62$, $P = 0.44$).

Spatial distribution

I calculated the variance-to-mean ratio, an index of dispersion, to investigate variation in the spatial distribution of males and females over time. (I combined all years for the male analysis, but I was only able to calculate the index of dispersion for females in 2008, the year during which I radiotracked the largest number of females [n = 5]).
An index of dispersion of ca. 1 indicates a random distribution, whereas values larger than 1 indicate that individuals are clumped (Krebs, 1999). The high values associated with the index of dispersion throughout the active season indicated that males and females were clumped year-round (Fig. 3; all values were statistically different from 1 at $P \leq 0.05$). Males were relatively more clumped during the mating season and at the beginning of the post-mating season than they were during the rest of the active season.

In contrast, I observed no obvious seasonal change in the spatial distribution of females in 2008.

I calculated the distance traveled from the den for each sex. Males were closer to den sites during the mating season and prior to going to hibernation (Fig. 4A), and further from the dens in the middle of the summer. On the other hand, females showed very little variation in distance from the den as a function of time (Fig. 4B).

Seasonal and annual variation in environmental temperatures

Because of the significant interaction between PC1, the temperature covariate, and season in three movement parameters (DBR, DPM, movement frequency) of males, I investigated whether PC1 varied by year and by season. Temperatures were significantly lower in the mating season than in the post-mating season in 2008 (t-tests with unequal variance; mating: -0.21 ± 0.11; post-mating: 0.38 ± 0.06; $t_{(1,65)} = -4.49$, $P < 0.0001$) but not in 2006 (mating: 0.35 ± 0.09; post-mating: 0.24 ± 0.07; $t_{(1,90)} = 0.95$, $P = 0.34$), or 2007 (mating: 0.23 ± 0.09; post-mating: 0.29 ± 0.06; $t_{(1,80)} = -0.48$, $P = 0.62$). The 2008 mating season was significantly cooler than the mating seasons of 2006 and 2007 (one-way ANOVA; $F_{(2,111)} = 8.58$, $P = 0.0003$), but temperatures in the post-mating seasons were similar across the three years ($F_{(2,533)} = 1.06$, $P = 0.34$).

Body size, body condition, movement parameters and mate acquisition

I used the residuals of the regression of log-transformed body mass on log-transformed body size (SVL) to calculate a body condition index for each individual snake (Bonnet and Naulleau, 1994, 1996). Snakes exhibited variation in body condition (mean ± SD; males: 0.01 ± 0.07; females: -0.01 ± 0.04), but I found no significant relationship between the body condition of snakes at the start of the active season and the distance traveled per day within that active season. This was the case for males (active season: $r^2 = 0.02$, $F_{(1,24)} = 0.66$, $P = 0.42$, $y = 17.79 + 22.15x$; mating season: $r^2 = 0.005$, $F_{(1,20)} = 0.66$, $P = 0.94$, $y = 30.02 + 5.2x$; post-mating season: $r^2 = 0.05$, $F_{(1,21)} = 1.27$, $P = 0.27$, $y = 14.55 + 32.5x$), and females (active season: $r^2 = 0.02$, $F_{(1,8)} = 0.21$, $P = 0.65$, $y = 10.69 + 27.84x$; mating season: $r^2 = 0.0005$, $F_{(1,8)} = 0.004$, $P = 0.94$, $y = 12.73 – 8.3x$; post-mating season: $r^2 = 0.04$, $F_{(1,8)} = 0.36$, $P = 0.56$, $y = 10.31 + 31.12x$).

I investigated how the absolute distance traveled by males within the mating season correlated with the number of known accompanied females. Using the residual scores of the regression of distance traveled on number of days monitored as the predictor variable, I found a positive but non-significant trend between distance traveled by males and number of known accompanied females ($r^2 = 0.09$, $F_{(1,21)} = 2.2$, $P = 0.15$). The only two males that I observed with more than one female within a single mating season were those that traveled the longest distances of all males tracked. I also estimated how male size (SVL) related to the number of known accompanied females. I found a significant positive relationship between SVL and the number of known females that males were found with ($r^2 = 0.19$, $F_{(1,19)} = 4.6$, $P = 0.04$, $y = -3.35 + 0.04x$; Fig. 5).

Finally, I assessed whether sex and home range size affected the number of known potential mates during the mating season. (I only included snakes that were radiotracked for 80% ore more of the mating season in this analysis.) I regressed the number of known potential mates on home range size for each sex separately. Males with larger home ranges overlapped with the home ranges of more potential mates (linear regression: $r^2 = 0.60$, $F_{(1,12)} = 16.52$, $P = 0.001$, $y = 0.03 + 0.1x$; Fig. 6). I found no such statistical relationship for females ($r^2 = 0.18$, $F_{(1,7)} = 1.56$, $P = 0.25$, $y = 2.5 + 0.07x$; Fig. 6). The intercept of the latter two regression lines was significantly different from the origin in females ($F_{(1,7)} = 29.46$, $P = 0.0009$) but not in males ($F_{(1,12)} = 2.7$, $P = 0.12$; Fig. 6). Finally, an ANCOVA showed that, after controlling for home range size, females had more potential mates in their territories, compared to the number of females in male territories ($F_{(3,18)} = 17.20$, $P = 0.0006$).

Behavioral interactions

Most male-female interactions occurred in spring, from 20 April to 6 June (male-female accompaniment: n = 16; courting: n = 4; mating: n = 1). On two occasions in fall 2006 (25 September, 6 October), I found a male close to a female's refuge. However, both of these observations were made close to den sites, when snakes were about to enter hibernation. Consequently, I do not believe that these interactions reflected sexual activity.

I witnessed mating only once on 12 May 2008. Male 15 (94.5 cm SVL, 765.2 g), the largest male monitored over the course of this study, was mating with Female 2 (71.7 cm SVL, 313.5 g) while she was being courted by a smaller male (Male 18, 76.5 cm SVL, 330 g). Although Male 18 seemed to be focusing on the female, he sometimes aligned his body with the larger male (Male 15), presumably to challenge him. I did not observe any obvious response of Male 15 toward Male 18.

Overall, males appeared to compete for access to females. The following example illustrates this behavior: On 6 April 2007, I caught Female 5 (77.8 cm SVL, 444 g) for transmitter implantation, and released her three days later. On 26 April 2007, I caught Male 13 (88 cm SVL, 551 g), wandering around her refuge. On 29 April 2007, Female 5 had not moved, and I found the large Male 15 coiled at the entrance of her refuge. On the next visit to the site, I relocated Female 5, which again had not moved, and found another large male, Male 16 (92.9 cm SVL, 649.3 g) coiled at the entrance of her refuge. In the end, Female 5 spent 17 days under a boulder with Male 15, the largest male. In summary, I found three different males at the entrance of one female's refuge over three consecutive visits to the field site, and the male that I subsequently found her with was the largest one of the three.

Because I caught all the males mentioned in the example above for transmitter implantation, I could not monitor the interactions among them. Yet, a couple of anecdotal male-male interactions are relevant to better understand *C. mitchellii*'s mating system. After Male 15 successfully mated with Female 2 on 12 May 2008, Male 15 made extensive movements (ca. 824 m), until he was found with another female, Female 5, on 21 May 2008 (Females 2 and 5 were actually in close proximity [ca. 130 m]). Male 15 stayed with Female 5 until 2 June 2008, after which he visited Female 2 again. Female 2 had been accompanied by a smaller male, Male 6 (75.7 cm SVL, 377 g), since 30 May 2008, when it was joined by Male 15 on 2 June 2008. Between 30 May 2008 and 4 June 2008, Male 6 moved a distance of ca. 1.1 km in a highly directional fashion. The extensive distance covered by Male 6 may have been in response to the potential encounter with Male 15. Finally, one instance of male-male combat was observed on the study area on 28 April 2007 (Robert McKeever, pers. comm.), and male-male combat has been reported in this species (Klauber, 1972).

Discussion

In this study, I investigated variation in movement patterns in a vertebrate predator, with emphasis on seasonal and sexual effects, to characterize the link between space use and mating activity. Below, I first summarize and discuss how space use varies intrasexually between seasons and intersexually within seasons in *Crotalus mitchellii.* I then discuss my findings in a comparative framework to better understand organismal mating systems.

Hypothesis 1: Intrasexual variation in movement between seasons

My study demonstrates that the movement ecology of *C. mitchellii* varies by biologically-relevant seasons. Both sexes increased activity in the mating season compared to the post-mating season. Accordingly, my prediction that males increase movement per unit time in the mating season compared to the post-mating season was supported. However, I did not predict that females would also increase movement in the mating season. Below I discuss the intrasexual variation in movement between seasons for males and females separately.

Males

Males increased distance traveled per unit time (DBR) by increasing distance per movement and movement frequency. The strong increase in movement during the mating period resulted in home ranges of similar size between seasons, despite the fact that the mating season (ca. 1.5 months) is considerably shorter than the post-mating season (ca. 5 months). Additionally, I found a positive (but non-significant) trend between distance traveled by males and the number of females located, and documented that larger home ranges contained significantly more females. Sexual selection theory predicts that in species where males do not invest in parental care, such as snakes (Shine, 1988), the reproductive success of males is limited by access to females (Emlen and Oring, 1977; Duvall et al., 1993; Arnold and Duvall, 1994). Males increase their fitness by producing more offspring, and therefore by mating with multiple females. Traits that enhance the ability of males to successfully reproduce with multiple females should consequently be selected for. Empirical evidence from various taxa, including shrews (Stockley et al., 1994), rodents (Tew and Macdonald, 1994; Lane et al., 2009; Spritzer et a., 2005), and snakes (Madsen et al., 1993, Duvall and Schuett, 1997; Brown and Weatherhead, 1999; Weatherhead et al., 2002), supports the hypothesis that increased movement by males enhances their reproductive success. My data suggest that the increased movement by *C. mitchellii* males in the mating season may be a sexually-selected trait that evolved in response to selection for increased reproductive success. Below I detail the evidence supporting this hypothesis.

Female *C. mitchellii* reproduce infrequently. Over a three-year period, I have direct (i.e., observation of female with her offspring, n = 1) or indirect evidence (i.e., significant change in female's mass, n = 3) for four female reproductive events. The minimal estimate of female reproductive frequency during this study is thus 33% (4 females reproduced out of 12 female "snake years", i.e., the total number of female active seasons). This number suggests that females reproduce on average once every three years, a conclusion supported by the very low frequency of vitellogenic or pregnant *C. mitchellii* females found in museum collections (Glaudas, unpublished data). This low estimate is not surprising because, due to their prolonged reproductive cycle, females of most rattlesnake species reproduce at best biennially (Aldridge and Duvall, 2002;

Glaudas et al., 2009), and triennial or longer cycles are well-documented (Gibbons, 1972; Martin, 2002; Jenkins, 2007). The infrequent reproduction of females results in a highly male-biased operational sex ratio, which promotes male-male competition for access to females (Emlen and Oring, 1977; Madsen and Shine, 1993a). This prediction is supported by my behavioral observations, because I observed multiple males in the vicinity of a single female, and male-male combat in my study population. (I have evidence for only one instance of male-male combat. However, the male-biased sexual size dimorphism of *C. mitchellii*, which presumably evolved in response to intrasexual selection for access to females, and observations of male-male combat elsewhere, suggests that male-male combat is common in this species [Klauber, 1972; Shine, 1978; Greene, 1992].) Therefore, not only do males have to successfully locate a female, they also need to physically defend their mate(s) against potential rivals. In conclusion, because reproductively active females are a limiting resource, increased movement by males and associated behaviors, such as intrasexual contests and mate guarding, likely enhance male fitness by increasing female encounter rate.

Females

Females did not increase distance per movement but increased movement frequency, which resulted in an increase in distance traveled per unit time in the mating season. The increase in female movement is likely driven, at least in part, by factors other than mating activity. There are at least three reasons for this hypothesis. First, in most animal species the reproductive success of females is more limited by food than by mating partners (Trivers, 1972; Ostfeld, 1986). Therefore, *C. mitchellii* females may increase movement in the mating season to increase foraging efficiency, specifically after a long period of hibernation during which they did not feed for ca. 5 months. Second, in most animal systems, including *C. mitchellii*, mate-searching activities are typically performed by males (see Intersexual variation in movement within seasons, below), which reduces the investment needed by females to find mates (Hammerstein and Parker, 1987; Kokko and Wong, 2007). Third, female *C. mitchellii* reproduce infrequently, which implies that many females may not exhibit sexually-driven behaviors in a given year.

Nevertheless, at least seven of nine females radiotracked throughout the mating season were accompanied by males for extended periods of time (mean ± SD: 10 ± 4.3 days; Glaudas, unpublished data), suggesting that mating may have occurred. Interestingly, at least 3 of these 7 females did not produce offspring that active season, a pattern also reported for the water snake (*Nerodia sipedon*; Prosser et al., 2002). One possible explanation for this observation is that females did not have the energetic resources (i.e., stored body fat) to start or complete their follicular cycle following the mating event. Alternatively, females may benefit from mating in years when they do not reproduce, because female rattlesnakes store sperm for extended periods of time (Schuett, 1992). This behavior may promote sperm competition (multiple paternities are common in snakes; Uller and Olsson, 2008, and references therein), and/or provide a larger pool of sires if females can cryptically choose sperm (although undocumented in snakes). In conclusion, although the increased movement by females during the mating season may not be as driven by mating activity compared to males, I can not reject the hypothesis that female increased activity during the mating season is partly related to mating factors (see below).

Hypotheses 2 and 3: Intersexual variation in movement within seasons

Male *C. mitchellii* exhibited increased distance between relocations (DBR) and distance per move (DPM) relative to females in both the mating and post-mating seasons, but movement frequency was similar between the sexes. This observation was consistent with the hypothesis that males exhibit increased movement compared to females during the mating season. In contrast, the prediction that sex and season interact, because males increase movement relative to females only in the mating season, was rejected. The lack of interaction was caused by the similar increase in movement patterns of males and females in the mating season, compared to the post-mating season. This finding suggests that the sexual difference in movement patterns is not solely due to the mating system, but that sex *per se* also affects the spatial ecology of *C. mitchellii.* Below I discuss the sexual difference in movement for the mating and post-mating seasons separately.

Mating season

Male *C. mitchellii* traveled longer DBR than females. The difference was caused by the greater DPM of males relative to females, because both sexes increased and did not differ in movement frequency during the mating season. The increased DBR in males translated into significantly larger male home ranges, compared to those of females. These results, coupled with my field observations, indicate that males actively locate females. This idea is supported by the sexual difference in the intercept of the regression lines of number of potential mates versus home range size (Fig. 6). A small home range size (e.g., 0.01 ha) likely translates into no mating opportunities for males, but not for females (i.e., the regression line goes through the origin only for males). A higher investment by males relative to females in mate-searching activities is widespread in animal systems, including insects, mammals, and non-avian reptiles (Thornhill and Alcock, 1983; Gaulin and FitzGerald, 1988; Frank and Heske, 1992; Tew and Macdonald, 1994; Duvall and Schuett, 1997; Jellen et al., 2007; Kokko and Wong, 2007; Odden and Wegge, 2007). This ubiquitous pattern is well-supported by theoretical models for systems in which sperm competition occurs and females are not sperm-limited (Kokko and Wong, 2007). These two conditions likely exist in *C. mitchellii*'s system. Multiple matings and paternities may be the rule rather than the exception in snakes (Uller and Olsson, 2008). Although there is no direct evidence that this is the case in *C. mitchellii*, the typical mate-guarding behavior exhibited by males indicates the potential for multiple paternities. Further, because of the male-biased operational sex ratio males are not a limited resource for females.

Nevertheless, sex role theory predicts that females may invest time and/or energy in mate-searching if the associated costs are low (Kokko and Wong, 2007). This is the case in this system, because males are readily available during the mating season, and thus the costs of finding mates for females are likely low. As mentioned above, the increased movement frequency of females may partly represent an investment in mating effort (i.e., "the component of reproductive effort expended in attempts to acquire mates", Thornhill and Alcock, 1983, p. 65). Females may invest in mating effort not necessarily by actively looking for males, but by increasing the odds that they are detected by males. For instance, sexually receptive female snakes lay a pheromone trail as they move around the landscape, and males rely on their highly developed chemosensory abilities to locate females (Mason, 1992, 1993; Schwenk, 1994, 1995; Fornasiero et al., 2007). Accordingly, increased movement by females could be a mechanism that enhances mate acquisition. The sexual difference in relative directionality in the mating season (females exhibit relatively straighter movement patterns than males) could in fact reflect alternative, but complementary sex-specific strategies to enhance mate acquisition. Most males and females are predictably and spatially aggregated around den sites during the mating season (see mating system, below). Consequently, the straighter movements of females around the dens may increase their range of detection by males. On the other hand, males may be more likely to detect a female's chemical trail by randomly shifting direction in the vicinity of the den sites. This latter idea is supported by computer-based simulations of optimal searching strategies, which show that when resources (in this case females) are spatially clumped, the random directionality of movement of an individual within a resource-rich patch is more efficient at locating resources than straight-line movements (Benhamou, 2007).

Post-mating season

Distance traveled per unit time and DPM were significantly higher in males than in females. As a result, males had larger home ranges than females. Females stayed relatively close to the dens throughout the active season, while males ventured farther away from the dens. Several factors can explain this sexual difference in movement patterns during the post-mating season. First, in mammals, including humans, the spatial memory of females is known to be less developed than that of males (Astur et al., 1998; Barkley and Jacobs, 2007, and references therein). This difference has been proximally linked to the female's smaller relative size of the hippocampus (i.e., the part of the brain where spatial information is stored and processed; Jacobs et al., 1990, Nadel, 1991), and ultimately to the strong sexual selection operating on males for locating females in polygynous systems (Gaulin and Fitzgerald, 1986, 1989). Consequently, the decreased activity patterns of females compared to males may be related to their reduced spatial cognition aptitude. That is, females may cope with lower spatial abilities by reducing activity. However, there is little evidence of sexual differences in spatial cognition, and/or the size of the pallium (the presumed reptilian homologue of the hippocampus of higher vertebrates; Rodríguez et al., 2002) in reptiles. Studies specifically design to address this hypothesis will be informative.

Second, the sexual difference in home range size may be related to differences in feeding ecology and/or life history strategy. Male and female *C. mitchellii* do not differ in the types of prey they feed on (i.e., the proportion of mammalian vs. reptilian prey; Glaudas, unpublished data). However, males grow larger than females, and increased movement by males may simply be caused by the greater food resources required to sustain larger-sized animals (McNab, 1963). Another explanation for the larger home range of males is that females may adopt a more sedentary lifestyle compared to males in an effort to save energy for reproduction. Sedentariness has been linked to superior body condition (i.e., increased fat reserves) in some vertebrate species, including humans (Marti et al., 2004; Hay et al., 2008), but available data suggest that female snakes with better body condition have larger home ranges (Webb and Shine, 1997; Roth II and Greene, 2006). However, the causal relationship between these two variables is unclear. That is, does increased movement cause (e.g., through increased foraging efficiency) or is the result of superior body condition (e.g., the snakes have more energy reserves)? Relevant data are surprisingly scarce in the literature, and studies linking mobility to foraging efficiency and body condition variation are required to answer this question. At any rate, the hypothesis that female *C. mitchellii* decrease activity to increase the energy allocated to reproduction requires that reduced activity in females does not translate into a net energetic loss caused by the possible decreased foraging opportunities.

Finally, the sexual difference in activity may be related to predation pressure. During the course of this study, 7 (6 males, 1 female) of the 25 snakes I radiotracked were eaten by predators. This translated into a higher average annual mortality rate due to predation in males (21.8%) than in females (8.4%). Surprisingly, and in contrast to other snake studies (Aldridge and Brown, 1995; Bonnet et al., 1999; Whitaker and Shine, 2000; Sperry and Weatherhead, 2009), all these predation events occurred during the non-mating season. Consequently, the decreased movement of females may be a mechanism to reduce predation, because evidence suggests that site fidelity and reduced activity decrease predator-induced mortality (Clarke et al., 1993; Yoder et al., 2004; Sperry and Weatherhead, 2009). Yet this hypothesis does not explain why males have larger home ranges, unless males trade-off predation risk for increased foraging opportunities. All these explanations are not mutually exclusive, and conceivably a combination of factors contributes to the sexual difference in home range size during the post-mating season.

Mating system

Strong male-male competition is a component of many snake mating systems. For instance, male prairie rattlesnakes (*Crotalus viridis)* in Wyoming travel long distances to locate the few and scattered reproductive females during the summer mating season (Duvall and Schuett, 1997). This mating system was named "prolonged mate-searching polygyny", because males engage in scramble competition to locate potential mates. Because competing *C. viridis* males rarely encounter each other, male-male combat is absent or reduced, and mate-locating abilities are seemingly under strong sexual selection, a perspective that led to the hypothesis that the prolonged mate-searching polygyny strategy evolved in response to the dispersed and unpredictable distribution of females over the landscape. Male massasaugas (*Sistrurus catenatus)* also cover extensive distances to locate wide-ranging reproductive females during the summer breeding season (Jellen et al., 2007). However, male-male combat is common in massasaugas, and their mating system is intermediate between the prolonged mate-searching polygyny and female-defense polygyny strategy, in which males physically fight for access to females. Likewise, *C. mitchellii*'s mating system is intermediate between these two strategies, because males move extensively in search of females and male-male combat occurs.

One critical aspect of *C. mitchellii*'s mating system that differs from those described above is that females are clumped and predictably distributed during the mating season (Fig. 3). Theoretical models and empirical data support the idea that a clumped and predictable spatiotemporal distribution of females promotes male-male encounters, and therefore intensifies interference competition (Emlen and Oring, 1977; Clutton-Brock, 1989). Like many snakes from temperate regions (Gregory, 1982), *C. mitchellii* aggregates in rock outcrops to overwinter (Glaudas, unpublished data). Upon emerging from hibernation in spring, snakes are predictably clustered in space, which has strong implications for their mating system, because *C. mitchellii* is one of the very few species of rattlesnakes known to mate only in spring (Aldridge and Duvall, 2002). My observations are consistent with the hypothesis that the predictably clumped distribution of snakes promotes intrasexual competition, because male-male interactions in

C. mitchellii are seemingly common, and males fight to gain access to females. Further, this observation suggests that the close proximity of females in early spring may allow male rattlesnakes to monopolize females: Male 15, the largest male that I monitored, apparently reproduced with two females during the mating season of 2008 (direct observation of copulation with Female 2 and of behaviors highly suggestive of mating with Female 5), and seemingly kept competitors away from his two mating partners by regularly visiting the two females.

So why do males engage in prolonged mate-searching activities given that females are predictably aggregated, and that males are in the vicinity of females at the start of the mating season? My data suggest that the increased movement of males may occur in response to the low availability of reproductive females, and the resulting strong competition for access to these females. Therefore, males invest considerable time and effort visiting known den sites to locate potential mates. For smaller males, the challenge is seemingly even harder, because locating females does not guarantee reproduction, for larger males typically win combats (Shine, 1978; Madsen and Shine, 1993b; Madsen et al., 1993; Greene, 1997; Schuett, 1997). Overall, the mating system of *C. mitchellii* is more similar to the distantly-related European adder (*Vipera berus*) than to other rattlesnake species. Like *C. mitchellii*, *V. berus* mates only in spring, and females are predictably clumped at the start of the breeding season because snakes aggregate at den sites for hibernation (Madsen et al., 1993). Males increase movement during the short breeding season, and males fight for access to females. The similar mating system of these two distantly-related viperid snakes suggests that mating phenology can affect organismal mating systems via the spatiotemporal distribution of potential mates, and that it can possibly lead to the convergent evolution of mating systems.

In conclusion, my study shows that the movement patterns of a vertebrate predator vary by biologically-relevant seasons. I combined quantitative spatial analyses and behavioral observations in an explicit seasonal framework to characterize aspects of the mating system of a reptile species. My research demonstrates that studying the link between spatial ecology and mating activity can significantly advance our understanding of organismal mating systems.

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Table 1. Movement parameters of *Crotalus mitchellii* during a 3-year period (2006-2008) in the eastern Mojave Desert of southern Nevada, USA. The movement parameters gathered on an individual snake over several years were considered independent. Numbers in parenthesis represents sample size. For home range size, only snakes that were radiotracked for at least 80% of a given season (mating, post-mating, overall) were included in the analysis. Values represent means ± SD.

MOVEMENT/SEASON	**Mating [range]**	**Post-mating [range]**	**Overall [range]**
Distance per day (m)			
All individuals (n = 41)	26.23 ± 19.45	13.79 ± 9.14	16.18 ± 9.16
	[2.11-63.43]	[0.38-33.95]	[3.01-38.29]
Males (n = 30)	30.24 ± 19.24	15.20 ± 9.98	18.02 ± 9.29
	[2.34-63.43]	[0.38-33.95]	[3.19-38.29]
Females (n = 11)	16.87 ± 17.45	10.60 ± 6.07	11.27 ± 6.95
	[2.11-53.93]	[1.93-22.15]	[3.01-26.15]
Distance per move (m)			
All individuals (n = 41)	101.08 ± 57.01	58.39 ± 32.45	70.08 ± 31.73
	[8.72-221.99]	[4.37-145.32]	[17.40-155.12]
Males (n = 30)	115.96 ± 54.56	63.06 ± 36.34	77.61 ± 32.50
	[12.09-221.99]	[4.37-145.32]	[26.47-155.12]

Table 1. Continued

Females (n = 11)	66.38 ± 48.34	47.86 ± 18.43	50.01 ± 18.86
	[8.72-157.65]	[20.60-80.77]	[17.40-78.46]
Number of movements per day			
All individuals (n = 41)	0.24 ± 0.1	0.22 ± 0.06	0.22 ± 0.06
	[0.04-0.5]	[0.08-0.32]	[0.11-0.34]
Males (n = 30)	0.25 ± 0.1	0.22 ± 0.06	0.22 ± 0.06
	[0.09-0.5]	[0.09-0.31]	[0.11-0.34]
Females (n = 11)	0.22 ± 0.09	0.21 ± 0.07	0.21 ± 0.06
	[0.04-0.34]	[0.08-0.32]	[0.11-0.33]
Home range size (ha)			
All individuals (n = 25)	7.22 ± 9.07	9.48 ± 8.98	15.13 ± 14.85
	[0.07-29.52]	[0.06-30.57]	[0.91-60.36]
Males (n = 16)	9.78 ± 9.46	12.34 ± 10.10	19 ± 15.88
	[0.07-29.52]	[0.81-30.57]	[0.91-60.36]
Females (n = 9)	3 ± 7.18	5.18 ± 4.70	8 ± 10.38
	[0.11-22.05]	[0.06-16.59]	[1.05-34.78]

Table 2. ANCOVAs of distance between relocations (DBR, m; ca. every 2.5 days); distance per move (DPM, m); and arcsine-transformed movement frequency (during a 2-week period) of *Crotalus mitchellii* in the eastern Mojave Desert of southern Nevada, USA. I used a principal component value of environmental temperatures (PC1) as a covariate in all analyses. The F-tests of main effects of season (mating, post-mating), sex (male, female), year (2006, 2007, 2008), and their interactions were tested using the mean square (M.S.) of variation among individual snakes as the error term.

Source	D.F	M.S.	F Value	*P*
DBR (individual snakes D.F. = 24; total error D.F. = 2498)				
PC1	1	354368.2	17.8	0.0004
Season	1	341946.5	17.1	0.0004
Sex	1	158837.4	7.9	0.01
Year	2	114854.2	5.7	0.009
Season × sex	1	59581.2	3.0	0.10
DPM (individual snakes D.F. = 24, total error D.F. = 1308)				
PC1	1	89166.1	3.75	0.06
Season	1	229517.62	9.66	0.005
Sex	1	213698.7	9	0.007
Year	2	94334.67	3.97	0.03
Season × sex	1	51309.17	2.16	0.15

Table 2. Continued

Movement frequency (individual snakes D.F. = 24, total error D.F. = 778)				
PC1	1	35.74	43.57	< 0.0001
Season	1	13.21	16.11	0.0006
Sex	1	0.43	0.53	0.4744
Year	2	3.71	4.53	0.0225
Season × sex	1	0.29	0.36	0.5556

Table 3. ANCOVA of circular variance in directionality of *Crotalus mitchellii*. I used number of observations (N obs.) as the covariate. The F-tests of main effects of season (mating and non-mating), sex (male, female), and their interactions were tested using the mean square (M.S.) of variation among snakes as the error term (individual snakes D.F. = 21, total error D.F. = 64). Because I did not find a year effect (*P* = 0.77), I did not include this factor in this analysis.

Source	D.F	M.S.	F Value	*P*
N obs.	1	0.59	14.63	0.0011
Sex	1	0.01	0.42	0.5248
Season	1	0.01	0.25	0.6253
Season × sex	1	0.24	5.86	0.0256

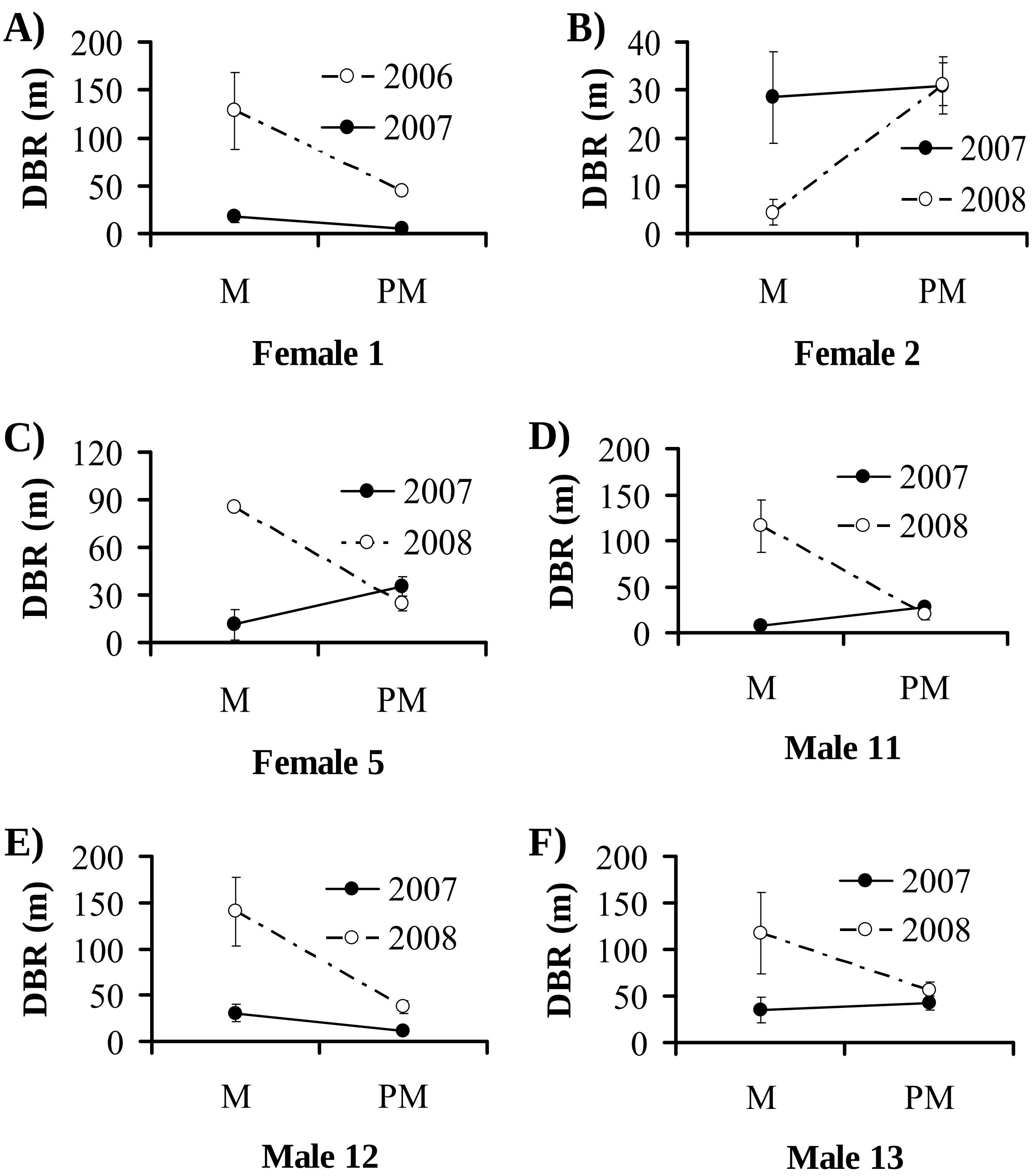

A)
DBR (m)
200
150
100
50
0
2006
2007
M
PM
Female 1
B)
DBR (m)
40
30
20
10
0
2007
2008
M
PM
Female 2
C)
DBR (m)
120
90
60
30
0
2007
2008
M
PM
Female 5
D)
DBR (m)
200
150
100
50
0
2007
2008
M
PM
Male 11
E)
DBR (m)
200
150
100
50
0
2007
2008
M
PM
Male 12
F)
DBR (m)
200
150
100
50
0
2007
2008
M
PM
Male 13

Figure 1 – Interannual variation in distance traveled between relocations (ca. 2.5 days) in three female (A-C) and three male (D-F) *Crotalus mitchellii* individuals that were radiotracked for two full years in the eastern Mojave Desert of southern Nevada, USA (the remaining 19 snakes were radiotracked for one full year and only part of another year). M and PM refer to the mating season and post-mating season, respectively. (In some cases the standard errors associated with the means were very small and are not visible on the figures.)

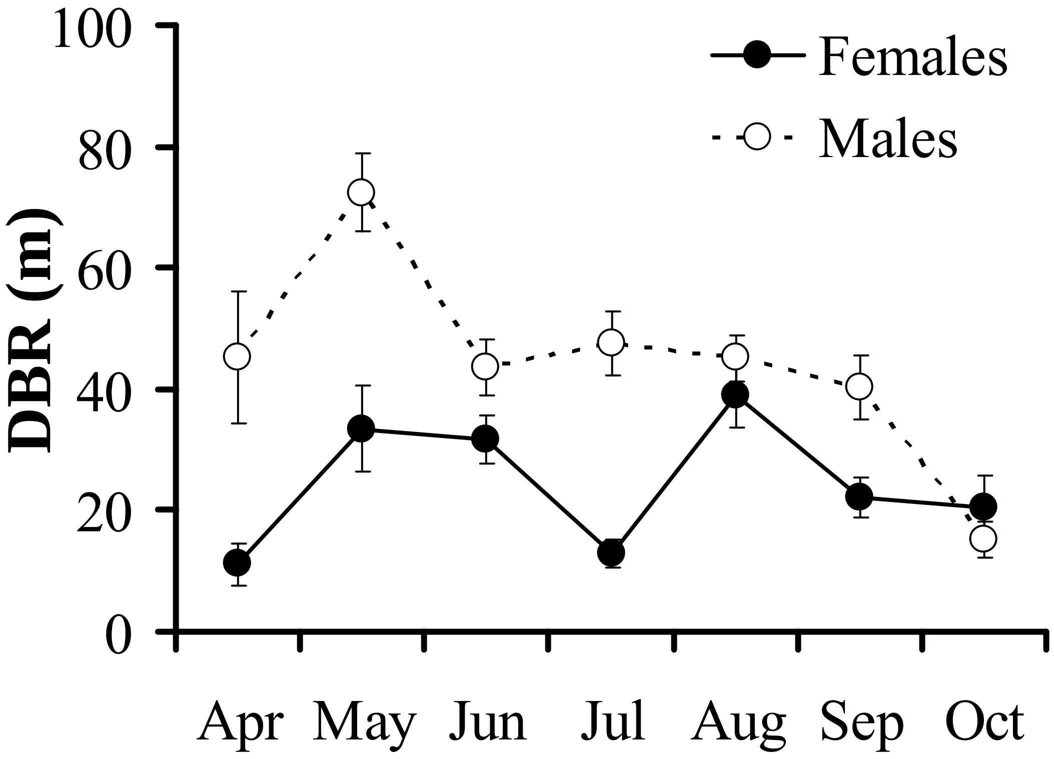


Figure 2 – Distance traveled between relocations (m; ca. 2.5 days) per month for male and female *Crotalus mitchellii* for all years combined (2006-2008). The values are not adjusted for the effect of environmental temperatures on movement.

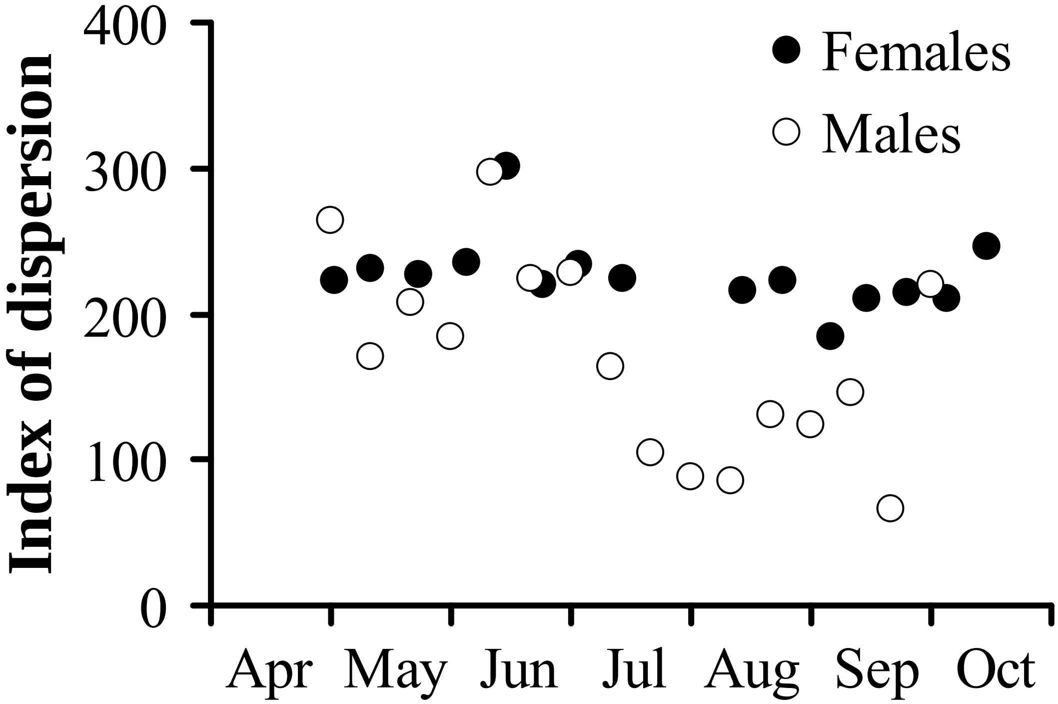
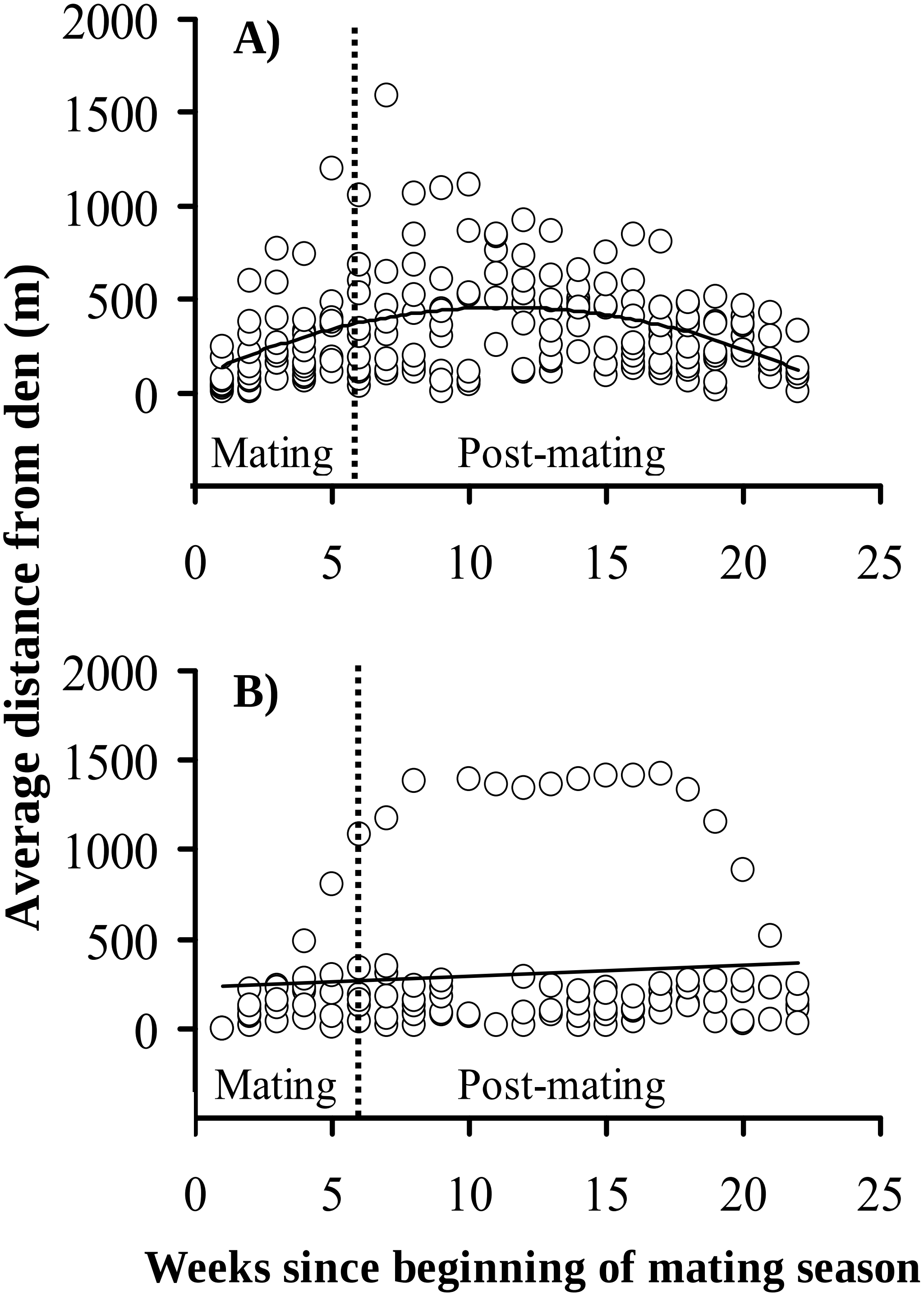


Figure 3 – Index of dispersion of male and female *Crotalus mitchellii* as a function of time of the year. The index was generated using the variance-to-mean ratio. Values greater than 1 indicate that the snakes exhibit a clumped distribution. The data indicate that males and females were aggregated year-round, and that males were relatively more clumped during the mating period and at the beginning of the post-mating season.



A)
B)
2000
1500
1000
500
0
Mating
Post-mating
0
5
10
15
20
25
Average distance from den (m)
Weeks since beginning of mating season

Figure 4 – The average distance from the den of (A) male and (B) female *Crotalus mitchellii* as a function of time of the year. Each datum represents the weekly average for each individual. Trend lines are included on the figures for graphical purposes only, and are not regression lines. The point of reference of the x-axis, 1, is the estimated first week of the mating period (20 - 27 April), and each consecutive number is a subsequent week, in chronological order. The dashed line indicates the mating season, and the continuous line indicates the post-mating season.

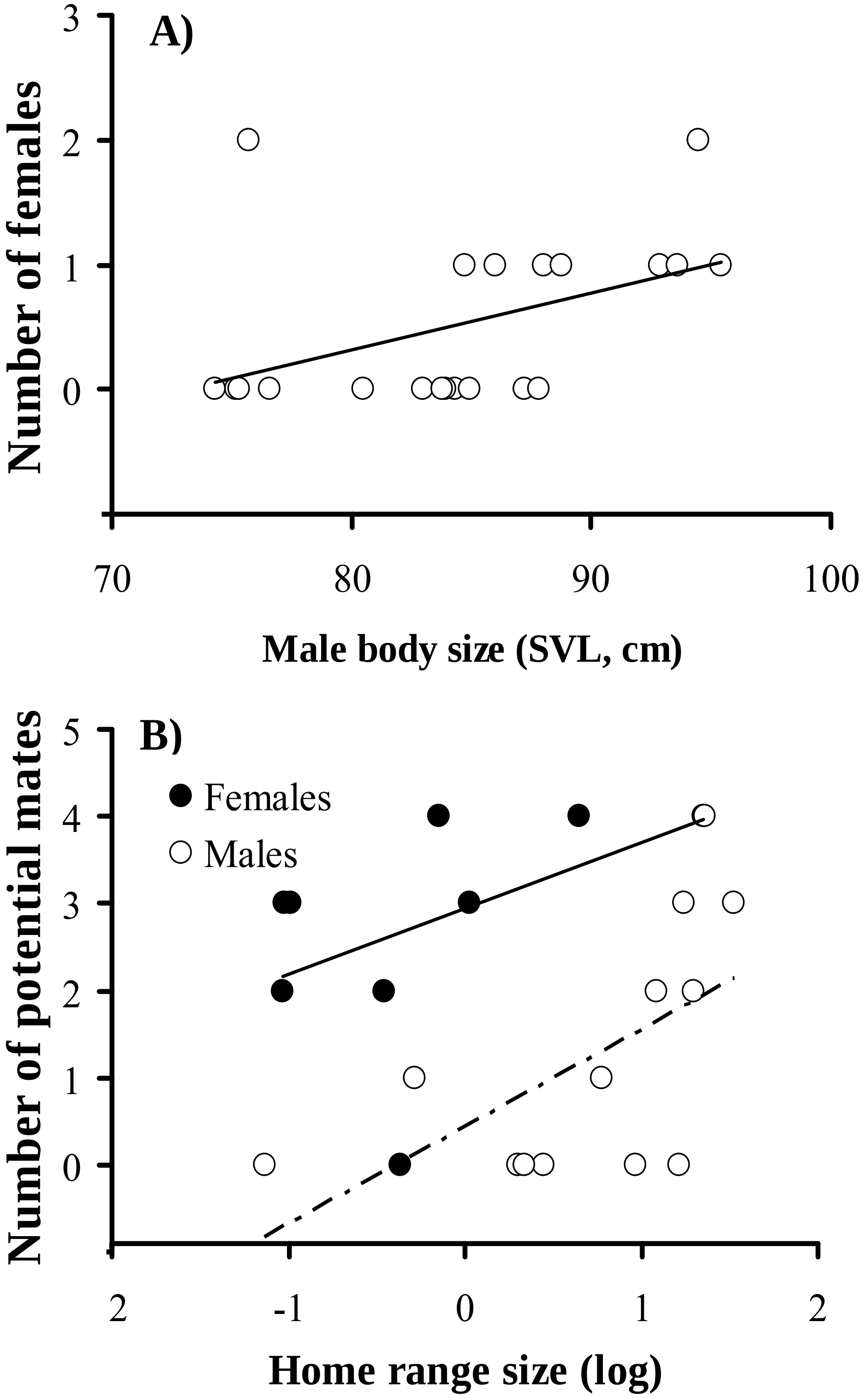

A)
Number of females
3
2
1
0
70
80
90
100
Male body size (SVL, cm)
B)
Number of potential mates
5
4
3
2
1
0
● Females
○ Males
2
-1
0
1
2
Home range size (log)

Figure 5 – The relationship between (A) body size (snout-to-vent length, cm) of male *Crotalus mitchellii* and the number of accompanied females, and (B) the number of potential mates for male and female *Crotalus mitchellii*, as a function of (log-transformed) home range size. For (B), the relationship is significant for males (continuous regression line; $F_{(1,12)} = 16.52$, $r^2 = 0.60$, $P = 0.001$) but not for females (dashed regression line; $F_{(1,7)} = 1.56$, $r^2 = 0.18$, $P = 0.25$). The data were log-transformed for graphical presentation only. Note the contrasting intercepts for the sexes.

CHAPTER 3

TEMPORAL VARIATION IN RESOURCE SELECTION IN A SECRETIVE, AMBUSH PREDATOR (*CROTALUS MITCHELLII,* SERPENTES)[2]

ABSTRACT

An individual's fitness is fundamentally linked to access to several critical resources that vary in space and time. Accordingly, a multivariate resource-based approach to study habitat choice is required to identify the determinants of this important decision-making process in free-ranging animals. I investigated the significance of prey and refuge availability on macro and microhabitat selection in an explicit temporal framework (mating [late April to early June] vs. post-mating seasons [early June to mid-October]) in an adult population of speckled rattlesnakes (*Crotalus mitchellii*) from the Mojave Desert of southwestern North America. At the macrohabitat level, *C. mitchellii* selected and avoided habitats during the post-mating season only. The preference of rock outcrops and the avoidance of rolling hills by *C. mitchellii* at this time of the year positively correlated with the varying availability of rodent prey and refuges between these two macrohabitats, because rodents and refuges were significantly more common in rock outcrops. At the microhabitat level, during the mating season (late April to early June) prey availability did not differ between snake and random locations, and snakes selected areas close to rock refuges. This suggests that mating activities may prevail over foraging at this time of the year, and that snakes selected relatively safe areas when they did not travel. During the post-mating season, prey was more common at random than at snake locations, likely

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[2] Glaudas, X., and Rodríguez, J.A. To be submitted

because rodents avoided the areas where the snakes occurred. Further, snake locations were positively associated with the presence of wood rat (*Neotoma lepida*) nests, an important environmental feature for *C. mitchellii*, and were closer to rock refuges when wood rat nests were not available. These two types of refuges are important to *C. mitchellii,* because they likely provide protection from predators and the extreme environmental temperatures of the Mojave Desert during the post-mating season. The results of this study demonstrate that the preference of *C. mitchellii* for macrohabitats with relatively high prey availability did not translate into access to food at the microhabitat level, and that refuges are an important determinant of macro and microhabitat selection in a secretive ambush predator.

Introduction

Habitat selection is one of the most important factors affecting organismal fitness (Bearhop et al., 2004; Norris et al., 2004; Gunnarsson et al., 2005), because the potential for an individual's growth, survival, and reproduction is fundamentally linked to access to several critical resources (e.g., food, water, mates, refuges) that vary in space and time (MacArthur and Pianka, 1966; Schoener, 1983; Fryxell et al., 2005). Accordingly, animals need to balance the costs and benefits of settling in a specific place with the various resources required to survive and successfully reproduce (Pitt, 1999). Because the complexity of habitat selection may be underestimated when only one of several critical factors is considered (Huston, 2002), a multivariate resource-based approach to study habitat choice is required to identify the determinants of this important decision-making process in free-ranging animals.

The availability of food and refuges is regarded as two key resources affecting habitat selection. The significance of food resources on habitat selection is long-established (Charnov, 1976), because food acquisition directly affects all the components of fitness (growth, survival, reproduction). Refuges are also important, because they reduce predation risk (Lima and Dill, 1990; Sinclair and Arcese, 1995; Spencer and Thompson, 2003), and allow animals living in climatically extreme environments to escape otherwise costly and/or lethal abiotic conditions (Huey et al., 1989; Ockenfels and Brooks, 1994; Potter et al., 2009). The combined importance of food and refuges on habitat choice is effectively demonstrated by the food for safety trade-off often found in a variety of organisms. For instance, many prey species prefer safer habitats with less food when predation risk positively covaries in space with food availability (Wirsing et al., 2007; Mukherjee et al., 2009; Godvik et al., 2009). However, when predation risk is homogeneous and food abundance varies among habitats, individuals are predicted to select the habitat where food is most abundant (Lima and Dill, 1990), everything else being equal.

The significance of food and refuges on habitat choice can vary temporally, because some activities may prevail over others at certain times of the year. For example, during the breeding season, adult individuals typically engage in mating activities in an attempt to reproduce. Mating activities, which can include mate-searching, male-male combat, mate-guarding, courtship, and copulation, require a considerable investment by individuals (Andersson, 1994). These behaviors may interfere with feeding and safety (Holand et al., 2006; Plath et al., 2007), because organisms need to allocate time and effort to successfully reproduce. Consequently, due to the potential trade-offs between mating activities and food and safety, we expect individuals to exhibit variation in the use of resources, such as food and refuges, between the mating and non-mating seasons.

Snakes provide an excellent model system to study how factors such as the availability of food and refuges affect habitat selection, and how these factors vary seasonally. First, because of their well-developed chemosensory perception (Ford and Burghardt, 1993; Schwenk, 1994, 1995), snakes can assess the distribution of prey based on the presence of chemical cues, and experiments demonstrate that these reptiles presumably maximize feeding opportunities by selecting ambush sites where prey scent is the strongest (Duvall et al., 1990; Roth et al., 1999; Theodoratus and Chiszar, 2000; Clark, 2004). Second, predation-induced mortality can be high in snakes (Madsen and Shine, 1993; Sperry and Weatherhead, 2008), and the activity patterns of reptiles, specifically desert species, can be highly constrained by environmental temperatures (Cowles and Bogert, 1944; Huey et al., 1989; Beaupre, 1995), which suggest that refuges are an important resource for snakes. Third, snakes presumably allocate energy to the various components of fitness (e.g., foraging, mating) at specific times of the year (King and Duvall, 1990), which allows researchers to formulate predictions of seasonal variation in resource selection. Finally, some snakes are ambush foragers that can spend a considerable amount of time (e.g., hours, days) at the same place (Reinert et al., 1984; Greene, 1992, 1997; Clark, 2006). This foraging strategy facilitates identifying the exact locations that snakes select, and quantifying the factors predicting habitat selection. Ironically, few studies have examined how ambush site selection in snakes relates to prey availability in the field (Shine and Sun, 2002). Consequently, our knowledge of foraging behavior in these secretive vertebrate predators is largely based on laboratory studies, and our understanding of this behavior in nature is limited.

In this study, I investigated habitat selection in an adult population of speckled rattlesnakes (*Crotalus mitchellii*) from the Mojave Desert of southwestern North America. I examined habitat selection at two spatial scales, the landscape (=macrohabitat) and local (=microhabitat) levels, because patterns of habitat selection can be scale-dependent (Wheatley and Johnson, 2009). My objectives were (1) to monitor *C. mitchellii'*s macrohabitat selection, and examine how this process relates to the spatial distribution of prey and refuges across the landscape, (2) to quantify the microhabitat preferences of *C. mitchellii*, with emphasis on prey and refuge availability, to test specific hypotheses of seasonal (mating vs. post-mating) variation in *C. mitchellii*'s resource use (see below), and (3) to examine whether detection of *C. mitchellii's* resource use varied according to the scale considered, namely the macro and microhabitat levels.

Mating activities may conflict with feeding and safety in several ways (Holand et al., 2006; Plath et al., 2007). First, a variety of organisms foregoes, or at least decreases, feeding during the mating season, because time and energy allocation to mate acquisition prevails over foraging activities (Madsen and Shine, 2000; Bonnet and Naulleau, 1996; Plath et al., 2007; Pelletier et al., 2009). Consequently, I hypothesized that during the mating season snakes do not select sites with high prey availability, because they are involved in mating activities *(Hypothesis 1).* Second, mating activities may conflict with safety, because individuals engage in conspicuous behavior during the breeding season (Reaney, 2007; Hoefler et al., 2008). For instance, many species, including mammals, lizards, and *C. mitchellii* (San José and Lovari, 1998; Stark et al., 2005; White et al., 2007), range widely during the mating season to find potential mates. Wide-ranging behavior may cause individuals to venture away from their refuges, and increase their vulnerability to predators (Sperry and Weatherhead, 2009). Empirical evidence in snakes supports this contention, because predator-induced mortality is typically higher during the mating season than in the non-mating season (Aldridge and Brown, 1995; Bonnet et al., 1999; Sperry and Weatherhead, 2009). Because of this potential trade-off between mate acquisition and safety, I hypothesized that, during the mating season, snake locations are not characterized by being close to refuges *(Hypothesis 2).* During the non-breeding season, individuals are not engaged in mating activities, and therefore mate acquisition does not conflict with feeding and safety. Individuals can allocate more time and effort to feeding, and make-up for the lost foraging opportunities caused by mating activities. Evidence suggests that some snake species use the non-mating period to restore their body condition (Bonnet and Naulleau, 1996; Madsen and Shine, 1993; Madsen and Shine, 2000). Therefore, I hypothesized that, during the non-mating season, snake locations are characterized by higher prey availability *(Hypothesis 3)*. Finally, refuges are an important resource for *C. mitchellii*, because these structures allow snakes to decrease their exposure to predators, and to the potentially lethally high summer temperatures of the Mojave Desert, that are typical of *C. mitchellii*'s non-mating season (June-September). Further, the refuges used by *C. mitchellii* are also commonly used by their rodent prey (Deacon et al., 1964; Johnson and Armstrong, 1987; pers. obs.), which renders a food for safety trade-off improbable. Consequently, I hypothesized that the foraging locations selected by snakes during the non-mating season are close to refuges *(Hypothesis 4).*

Materials and methods

Study site and species

The study site is a ca. 5 km^2 area located in the Eldorado Mountains, Clark County, southern Nevada (35˚44'N, 114˚49'W), in the eastern part of the Mojave Desert. This region is characterized by an extremely arid climate (2006-2009 average annual rainfall [range]: 8.3 cm [5.2-12.5 cm]), with high temperatures in summer (2006-2009 average daily temperatures: 27.1ºC [14.5-36.5ºC]), and relatively cool temperatures in winter (7.1ºC [-7.5-23.7ºC]; environmental data from Station ID4814, Clark County Regional Flood Control District, Nevada). The study area consists of a sparsely vegetated rocky desert at an elevation of ca. 1,100 m. Dominant plants include yucca trees (*Yucca* sp.), Brigham tea shrubs (*Ephedra* sp.), buckwheats (*Eriogonum* sp.), catclaw acacias (*Acacia greggii*), creosote bushes (*Larrea tridentata*), and various annual herbaceous plants. Four macrohabitat types are found on the study site: rolling hills, washes, slopes, and rock outcrops (Fig. 1). The rolling hills consist of sparsely vegetated and gently sloping ridges. Yucca trees (*Yucca* sp.) are common in this habitat, and wood rat (*Neotoma lepida*) nests are sometimes found at the base of the yuccas. The substrate of this habitat mostly consists of gravel, and rocks that could provide refuge to snakes are rare. Thus, snakes typically shelter in wood rat nests in this habitat type. The rolling hills are dissected by a few washes that are typically dry most of the year (e.g., flowing water is sometimes found in winter), and vegetation is relatively more common than in the rolling hills. The slope habitat consists of steep and long versants, and is characterized by a relatively high shrub cover, compared to other habitats. These slopes lead to rock outcrops, which typically occur at the highest elevation on the study site. Rocks and boulders of various sizes dominate this habitat type, and rock refuges (e.g., crevices, cavities under rocks) are readily available.

Crotalus mitchellii is a medium-sized rattlesnake that typically thrives in the rocky habitats of the Mojave Desert, where it mostly feeds on rodents, and occasionally lizards (Glaudas and Rodríguez-Robles, unpublished data). This snake is usually active from April to October. During the summer, the activity patterns of *C. mitchellii* are constrained by environmental temperatures, because midday temperatures approach the critical thermal maximum (ca. 39–42ºC; Brattstrom, 1965) of many reptiles, including desert-dwelling species. Consequently, *C. mitchellii* is rarely found on the surface during the day in summer. The low winter temperatures also prevent this snake from being active during this time of the year, and *C. mitchellii* hibernates, typically in crevices, from mid-October to late March. The movement patterns of *Crotalus mitchellii* vary seasonally. Adult snakes of both sexes display increased activity during the mating season (late April to early June), which occurs shortly after emergence from hibernation, compared to the post-mating season (early June to mid-October). Therefore, I conducted analyses of habitat selection for the entire active season (mid-April to mid-October), as well as for the mating (mid-April to early June) and post-mating seasons (early June to mid-October) separately to investigate seasonal variation in habitat selection.

Radiotelemetry

From April 2006 to April 2009, I radiotracked 25 *C. mitchellii* (18 males, 7 non-gravid females). Snakes were opportunistically caught during visits to the field site. I surgically implanted temperature-sensitive radiotransmitters (model SI-2T, 9 g, Holohil Ltd., Ontario, Canada; or model WST2, 5 g, Wildlife Track, Caldwell, ID, USA) in the body cavity of the snakes following established procedures (Reinert and Cundall, 1982; Reinert, 1992). At the time of transmitter implantation, males measured (mean ± SD) 85.3 ± 6.93 cm snout-to-vent length (SVL) and weighed 558.6 ± 144.3 g; females measured 74.6 ± 2.8 cm SVL and weighed 373.9 ± 53.3 g. The transmitter's mass was less than 3% of the snake's body mass in all cases. I released the snakes at their exact capture location 1-3 days following surgery. I used a radio receiver (model WTI-1000, Wildlife Track, Caldwell, ID, USA) and a directional antenna (model F151-3FB, Wildlife Track, Caldwell, ID, USA) to relocate snakes every 2-3 days during the active season, and once per week during the hibernation period. Each time a snake moved, I recorded its geographic coordinates using a sub-meter accuracy GPS unit (model GS20, Leica Geosystems Inc., Torrance, CA, USA), as well as the macrohabitat type where the snake was found. Periods of radiotracking ranged from 15-1073 days per individual (mean ± SD = 407 ± 265 days). In total, my study resulted in 5582 relocations and 1098 movements by snakes.

Macrohabitat selection

Using a geographic-information system (GIS; ArcGIS 9.2), I generated a detailed macrohabitat data layer using a 1 m resolution aerial photography of the study area. This data layer included the four main macrohabitat types found in the study area: rolling hills, washes, slopes, and rock outcrops (Fig. 1). I checked the accuracy of the map by comparing the macrohabitat predicted by the map at particular locations to the actual macrohabitat in the field. The map was 85% (417/492 points) accurate.

Some snakes were radiotracked during multiple active seasons. Because the home range of snakes that were radiotracked for two complete active seasons overlapped between years (e.g., site fidelity between years; mean ± SD: 52 ± 8.6%, n = 6), I randomly picked one year for each snake, so that each individual snake was only included once in the analysis. Only snakes that were radiotracked for the entire focal season (entire active season, mating, post-mating) were included in the macrohabitat analysis, resulting in 13 males and 7 females.

I used the kernel density estimator (KDE) to estimate home range size, because this technique includes a utilization distribution function that allows prediction of the probability of finding an animal in a given area within its home range (Millspaugh and Marzluff 2001). I used the methodology recommended to generate KDEs for reptile and amphibian species (Row and Blouin-Demers 2006). I first generated Minimum Convex Polygons (MCPs) that included all of an individual's known locations within the boundary of the smallest polygon possible. I then created 95% KDEs for each individual by manually adjusting *h*, the smoothing parameter, until the MCP and the KDE were of similar size. I calculated 50% KDEs by plotting the 50% contour line within the 95% KDEs. (95% KDEs provide an estimate of the overall size of a home range, whereas 50% KDEs identify the core area used by snakes within the overall home range.) This technique provides an objective method for selecting the smoothing parameter *h*, and generates biologically relevant KDEs for herpetofauna (Row and Blouin-Demers, 2006). All the home ranges were created in the Home Range Tools (Rodgers et al. 2007) for ArcGIS.

Using the macrohabitat layer (Fig. 1), I determined the proportion of each macrohabitat type within the home range of each snake. For each snake home range, I generated 10 random home ranges of similar size in the data layer to determine the availability of macrohabitats on the study site. For example, if a snake had a home range of 10 ha, I generated 10 random home ranges of 10 ha. For simplicity, I created circular home ranges to circumvent the problem associated with home range orientation.

I determined the location of the random home ranges by generating random points within the macrohabitat data layer that included all of the snake locations. I used the randomly generated point locations as the center of the circular home ranges, and calculated the proportion of habitat types in the randomly generated home ranges, and compared it to the snake home ranges.

Microhabitat selection

To examine microhabitat selection in *C. mitchellii*, I quantified prey availability and the structural characteristics (see below) at a subset of snake locations where snakes were found coiled on the surface or in a refuge, a behavior that indicated that the snake had selected a site, and at random locations. I generated the random locations using the snake locations as a point of reference. From each snake location, I walked a randomly generated distance (from 30-100 m) in a randomly generated direction (north, east, south, west). Each snake location where I recorded microhabitat characteristics was paired to a random location within the same macrohabitat type. I quantified microhabitat characteristics at snake locations (sometimes using the same individual snake) at 3-week intervals to ensure that these locations were relatively independent.

Prey availability

I quantified prey rodent availability at the snake and random locations throughout the active season using baited Sherman live-traps (Bock et al., 2002; Reed and Douglas, 2002). Sherman traps allow researchers to capture small mammals without injuring them. I placed 8 rodent traps equidistant from each other in a 2 m radius circle around 86 snake and 86 random locations, resulting in 1376 trap nights. I opened traps in the early evening (1800-2100h), when rodents typically started to become active. I checked and closed the traps early the following mornings (0400-0700h) to prevent rodent mortality (0%). At the snake locations, I found the snakes at the same sites in the morning 84% (72/86) of the time. The estimate of prey availability was not affected by the presence or absence of the snake the following morning (mean ± SE; presence: 0.05 ± 0.02; absence: 0.05 ± 0.01; $F_{(1,84)} = 0.002$, $P = 0.96$), and consequently I combined all the snake locations to estimate prey availability at the snake-selected sites. After identifying the rodents to species level, I released them unharmed at their place of capture. To eliminate the effect of environmental conditions (e.g., temperature, cloud cover, lunar cycle) on rodent activity, I trapped at a paired snake and random locations on the same night. The number of rodents caught at a location provided an estimate of prey availability.

Structural characteristics (including refuge availability)

I recorded the following structural characteristics at most of the snake (75/86, 87%) and random (74/86, 86%) locations where I trapped rodents. (I did not quantify the structural characteristics at all the locations where I trapped rodents, because some of the flags I used to mark the areas where I trapped disappeared, and I was sometimes unable to find the exact trapping locations.) I recorded the number of shrubs and visually estimated the percentage cover of shrub, gravel and small rocks (≤ 10 cm in either width, length, and height), medium and large rocks (10 cm > x < 50 cm), and boulders (≥ 50 cm) in a 2 m radius area around each location. I used a circular cardboard representing 1% of the 2 m radius area as a calibrating device to quantify the percentage cover of the aforementioned structural variables. *Crotalus mitchellii* almost exclusively use cavities under rocks, crevices, and wood rat nests as retreat sites. Consequently, to quantify refuge availability at the snake and random locations, I recorded absence/presence of a wood rat nest at each location, and measured the distance of the location to the closest potential rock refuge (i.e., a rock or crevice that a snake could use as a refuge) within a 10 m radius of the location using a metric tape. When a rock refuge was not available in the 10 m radius area, I scored this variable as "10 m +".

Statistical analyses

Logistic regressions have become increasingly popular to analyze use-availability data in habitat selection studies (Keating and Cherry, 2004), because this technique allows to model the probability occurrence of an event based on the factors inserted in the analysis. The predictive power of logistic regressions is effectively demonstrated by the odds ratio, which estimates how a change in one unit of an independent variable affects the probability of occurrence of an event, in this case the occurrence of a snake at a particular location. (The change in one unit of an independent variable increases or decreases the probability of occurrence of an event if the estimate is positive or negative, respectively.) Further, researchers can specify the use of a controlled variable in the logistic regression. This statistical approach, called the case-controlled logistic regression, allows one to compare the use-availability data within a specified controlled variable, which is in essence similar to a paired t-test. Herein, I used case-controlled logistic regressions to model *C. mitchellii*'s habitat preferences by comparing the recorded variables at snake (use) and random (availability) home ranges at the macrohabitat level, and snake (use) and random (availability) locations at the microhabitat level, in a controlled variable design. Below I provide the detailed descriptions of the logistic regression analyses used to examine macro and microhabitat selection in *C. mitchellii*.

Macrohabitat selection

I used case-controlled logistic regressions to examine macrohabitat selection. I implemented the case control method because home range size varied for individual snakes. I used individuals as the case control, and thus each snake home range was compared to a specific set of 10 random home ranges of the same size. Initial analyses of macrohabitat selection indicated that the least common habitat on the study area, washes, were not preferred or avoided by snakes. I therefore excluded washes from the macrohabitat analysis to ensure that the habitat proportions were relatively independent from one another (i.e., adding the proportion of macrohabitat types within a home range will not add to 1). I entered "snake vs. random home ranges" as the dependent variable, and the proportion of habitat types ("rolling hills", "slopes", "rock outcrops") as the independent variables. I conducted macrohabitat selection analyses for the entire active season, and for the mating and post-mating seasons separately.

I used parametric (ANOVA, MANOVA) and non-parametric tests (Kruskal-Wallis ANOVA, chi-square test, Fisher's exact test) to examine variation in prey availability and structural characteristics among macrohabitat types.

Microhabitat selection

I analyzed prey availability and structural characteristics data separately using case-controlled regressions. I conducted separate analyses for two reasons. First, I did not quantify the structural characteristics at all the locations where I trapped rodents (see above). Consequently, separate analyses allowed me to increase the sample size for the prey availability data. Second, when I combined the prey availability and structural characteristics of the locations in a logistic regression using the paired snake and random locations as the case control, the error associated with "absence/presence of a wood rat nest" variable was very high, and the models became questionable. (The results of the separate analyses were overall very similar to those combining all variables, apart from the problem sometimes associated with the large error of the "absence/presence of a wood rat nest" variable in the latter.)

I used the paired snake and random locations as the case control in the prey availability analysis. This statistical design allowed me to control for macrohabitat type (because the paired locations were in the same habitat) and for temporal variation in rodent activity (because I trapped rodents at paired locations on the same night). In this analysis, I entered "snake vs. random location" as the dependent variable, and "number of rodents caught" as the independent variable.

For the structural characteristics analysis, I combined two of the recorded microhabitat independent variables into principal component values to facilitate the interpretation of the models. First, I merged the percentage cover of gravel and small rocks, medium and large rocks, and boulders into a single variable, "rock size", which explained 41% of the variance in the data. Smaller values indicated that the substrate was dominated by rocks of small size (e.g., gravel), and larger values represented an increase toward larger rocks and boulders. Second, I combined the percentage of shrub cover and the number of shrubs into a single variable, “shrubiness”. This variable explained 74.5% of the variance in the data, with increasing values indicating bushier habitats. I used macrohabitat type as the case control to account for structural differences among macrohabitats. I entered “snake vs. random location” as the dependent variable, and “distance to rock refuge (m)”, “absence/presence of a wood rat nest”, “rock size” and “shrubiness”, as independent variables. I also included the “distance to rock refuge × absence/presence of wood rat nest” interaction in all analyses of structural characteristics, because these two structures are important refuges for snakes. For instance, the presence of a wood rat nest at a snake location could decrease the odds that a snake was close to a rock refuge. When this interaction was not significant, I removed it from the model.

I conducted prey availability and structural characteristics analyses for the entire active season, and for the mating and post-mating seasons separately. I also modeled the structural characteristics predicting prey rodent occurrence using microhabitat analyses similar to these used for the snake analyses (see Results below for details).

Finally, I examined whether males and females differed in their macro and microhabitat preferences, to ensure that combining males and females in the analyses was appropriate. I conducted all analyses using the statistical programs STATISTICA (version 6.0; StatSoft Inc., Tulsa, OK, USA) and SAS (version 9.2; SAS Institute, Cary, NC, USA). Values given are means ± 1 SE unless otherwise mentioned, and all reported P values are two-tailed. The P values reported for multiple comparisons are adjusted using the post-hoc Bonferonni method. Significance level for all tests was determined at $\alpha = 0.05$.

Results

Snake macrohabitat selection

Entire active season

I examined whether snakes selected macrohabitats during the active season. Using the overall home range of snakes (95% KDEs), the model demonstrated that *C. mitchellii* selected specific macrohabitats (Wald statistic; $\chi^2 = 19.13$, df = 3, $P = 0.0003$; Table 1). Snakes used rock outcrops significantly more than randomly expected, whereas rolling hills and slopes were used according to their availability. On the other hand, I found no evidence of macrohabitat selection in *C. mitchellii* when I used the snake's core activity areas (50% KDEs). Sex did not affect the proportion of macrohabitat types in the 95% and 50% KDEs of snakes (Table 2).

Mating season

I investigated whether snakes preferred certain macrohabitats during the mating season. *Crotalus mitchellii* did not select macrohabitats during the mating season for the 95% and 50% KDEs (Table 1). The proportion of rock outcrops in the home ranges of females was higher than in males' for the 95% and 50% KDEs (Table 2). However, sex-specific analysis of macrohabitat selection indicated that males and females did not select habitat at the landscape level, because both sexes used all macrohabitats in proportion to their availabilities.

Post-mating season

I explored whether snakes selected macrohabitats during the post-mating season. The models revealed a significant association between snakes and macrohabitat types for the 95% and 50% KDEs (95% KDEs: $\chi^2 = 13.55$, df = 3, $P = 0.003$; 50% KDEs: $\chi^2 = 17.95$, df = 3, $P = 0.0004$; Table 1). The proportion of rock outcrop habitat in the 95% KDEs of snakes was higher than randomly expected, whereas the core activity area (50% KDEs) of snake home ranges was negatively associated with the rolling hills habitat. Sex did not affect the proportion of macrohabitat types in the 95% and 50% KDEs of snakes (Table 2).

Differences in prey availability and structural characteristics among macrohabitats

At the study site, I caught 90 rodents (trap success: 6.54% [90/1376]) representing four species: canyon mouse (*Peromyscus crinitus*, n = 68), long tailed pocket mouse (*Chaetodipus formosus*, n = 18), Merriam's kangaroo rat (*Dipodomys merriami*, n = 3), and desert wood rat (*Neotoma lepida*, n = 1). Examination of museum specimens revealed that rodents composed 65% (50/77 prey items) of the diet of adult *C. mitchellii*, and that the four genera caught in this study accounted for 48% (37/77) of the total prey items consumed by speckled rattlesnakes (Glaudas and Rodríguez-Robles, unpublished data). Therefore, the abundance of the four rodent species at the study site is an adequate proxy of the prey available to *C. mitchellii*.

I tested whether prey availability varied among rolling hills, slopes, and rock outcrops at the random locations, to assess whether the macrohabitat selected by snakes was associated with prey availability. Rodent prey, as measured by rodent trap success, was equally available among macrohabitats (Kruskal-Wallis ANOVA; $F_{(2,82)} = 4.61$, $P = 0.09$;

Fig. 2A). I compared prey availability between the preferred rock outcrops and avoided rolling hills, during the post-mating season, to investigate whether selection and avoidance of macrohabitats correlated with variation in prey availability between these macrohabitats. Rodents were significantly more common in rock outcrops than in rolling hills (ANOVA; $F_{(1, 47)} = 3.79$, $P = 0.05$). This difference in prey availability between rock outcrops and rolling hills was primarily caused by the preference of *Peromyscus crinitus* (i.e., the most common rodent on the study area, and the most frequent prey of *C. mitchellii;* Glaudas and Rodríguez-Robles, unpublished data) for rock outcrops, because the capture frequency of *Peromyscus* was significantly higher in rock outcrops than in rolling hills (rock outcrops: 57% [20/35 locations]; rolling hills: 7% [1/13]; Fisher's exact test: $P = 0.001$).

I examined whether macrohabitat types (rolling hills, slopes, rock outcrops) differed in structural characteristics, to correlate macrohabitat selection in *C. mitchellii* to variation in refuge availability across the landscape. I only used the random locations in this analysis, because including the snake locations could bias the estimate of macrohabitat structural characteristics, if the snakes exhibited macrohabitat-specific preferences for structural features. Further, I did not include data from the wash macrohabitat, because *C. mitchellii* rarely used this habitat, and consequently wash locations were under-represented in the data set. The analysis revealed that "distance to rock refuge", "shrubiness", and "rock size" varied significantly among macrohabitats (MANOVA; Wilks' λ, $F_{(6,132)} = 14.09$, $P < 0.0001$; Table 3; the directions of these differences are presented in Figure 2B-D). I also tested for a difference in the availability of wood rat nests among macrohabitat types at the random locations. The analysis demonstrated that wood rat nests were equally common across macrohabitats (proportion of locations with a wood rat nest: rolling hills: 0% [0/15]; slopes: 5.56% [2/36]; rock outcrops: 15% [3/20]; $\chi^2 = 3.81$, df = 2, $P = 0.14$). Because wood rat nests were uncommon at random locations, the low sample size in most cells of this analysis may have precluded detection of a statistical pattern (Zar, 1984).

Snake microhabitat selection

Entire active season

I examined whether snake and random locations differed in prey availability during the snake's active season. The significantly negative estimate associated with the variable "number of rodents caught" indicated that rodents were significantly less common at snake than at random locations (Table 4). The odds ratio showed that the probability of snake occurrence decreased by a factor of 0.61 for each rodent caught at a location. Sex-specific analysis revealed that rodents were marginally more common at random locations compared to male locations (estimate ± SE: -0.47 ± 0.26, n = 108, $\chi^2 = 3.32$, df = 1, $P = 0.07$) but not to female locations (-0.49 ± 0.45, n = 64, $\chi^2 = 1.55$, df = 1, $P = 0.28$).

I investigated whether snakes selected structural characteristics at the microhabitat level (Table 5). The regression model was statistically significant (Wald statistic; $\chi^2 = 30.88$, df = 5, $P < 0.0001$), because snakes preferred areas close to rock refuges and with a wood rat nest. The odds ratio indicated that each meter further away from a rock refuge decreased the probability of a snake's occurrence by a factor of 0.39, and that presence of a wood rat nest at a given location increased the probability of a snake's occurrence by a factor of 4.3. The significant interaction between "distance to rock refuge

× absence/presence of a wood rat nest” showed that rock refuges were specifically selected by snakes when a wood rat nest was absent. “Rock size” and “shrubiness” were not significantly associated with a snake’s occurrence. A similar analysis with sex as a factor revealed that sex did not significantly affect the model (female: 0.35 ± 0.49, $\chi^2 = 0.49$, df = 1, $P = 0.48$).

Mating season

I tested the hypothesis that prey availability does not differ between snake and random locations during the mating season (Hypothesis 1). The analysis supported this idea, because rodent prey was equally available at snake and random locations (Table 4). The results were similar when I conducted sex-specific analysis (estimate ± SE; males: 0.25 + 0.50, n = 28, $\chi^2 = 0.2$, df = 1, $P = 0.61$; females: 0.4 ± 0.91, n = 18, $\chi^2 = 0.19$, df = 1, $P = 0.65$).

I assessed whether the structural characteristics of the microhabitats differed at snake and random locations, and tested the hypothesis that snake locations are not in proximity to refuges during the mating season (Hypothesis 2). Although the regression model was not statistically significant ($\chi^2 = 7.77$, df = 4, $P = 0.1$), the factor “distance to rock refuge” was negatively associated with a snake’s occurrence, because *C. mitchellii* preferred locations close to rock refuges (Table 5). Therefore, the results do not support the hypothesis that snakes do not select locations close to refuges during the mating season. The odds ratio indicated that for each meter further away from a rock refuge, the probability of snake occurrence at a location decreased by a factor of 0.23. The variables “absence/presence of a wood rat nest”, “rock size”, and “shrubiness” were not significantly associated with snake occurrence. A similar analysis with sex as a factor revealed that sex did not significantly affect the model (female: 1.56 ± 1.11, χ^2 = 1.96, df = 1, *P* = 0.16).

Post-mating season

I tested the hypothesis that snakes select locations with higher prey availability during the post-mating season (Hypothesis 3; Table 4). I rejected this hypothesis because rodents were more common at random than at snake locations. The odds ratio showed that the probability of finding a snake at a given location decreased by a factor of 0.45 for each rodent captured at a location. Sex-specific analyses revealed that rodents were significantly more common at random locations compared to male locations (estimate ± SE ;-0.77 + 0.34, n = 80, χ^2= 4.91, df = 1, *P* = 0.02), but not female locations (-0.81 ± 0.56, n = 46, χ^2 = 2.07, df = 1, *P* = 0.15). However, the trend was negative and the estimate very similar in both sexes.

I investigated whether snakes selected structural characteristics at the microhabitat level, and tested the hypothesis that snakes select locations close to refuges during the post-mating season (Hypothesis 4). The analysis supported this hypothesis (χ^2 = 22.86, df = 5, p = 0.0004), because snake locations were characterized by the presence of a wood rat nest (Table 5). The probability of a snake's occurrence at a location increased by a factor of 5.69 when a wood rat nest was present. Further, I detected a significant interaction between "distance to rock refuge × absence/presence of a wood rat nest", indicating that snakes were closer to rock refuges when a wood rat nest was absent (Table 5). A similar analysis with sex as a factor revealed that sex did not significantly affect the model (estimate ± SE; female: 0.17 ± 0.62; χ^2 = 0.08, df = 1, *P* = 0.77).

Temporal variation in prey availability and prey microhabitat selection

I examined whether prey availability varied temporally (=monthly) at the snake and random locations separately. I conducted separate analyses because prey availability differed between snake and random locations, and to investigate whether temporal trends of rodent availability differed between the snake and random locations. Because the sample size for July was low (n = 5), I removed this month from the analyses. There was no monthly variation in rodent availability at the snake locations (one-way ANOVA; $F_{(3,74)} = 0.39$, $P = 0.75$; Fig. 3). In contrast, rodent availability varied monthly at the random locations ($F_{(3,74)} = 3.41$, $P = 0.02$; Fig. 3). This statistical difference was caused by the significantly higher availability of rodents in June compared to other months (least square difference *post hoc* tests; June > May: $P = 0.005$; June > August: $P = 0.04$; June > September: $P = 0.01$). In addition, I explored whether prey availability temporally differed between the snake and random locations. I used a factorial ANOVA with month (May, June, August, September), location (snake vs. random), and their interaction as factors. The analysis confirmed that rodent availability was lower at snake locations than at random locations ($F_{(1,156)} = 4.12$, $P = 0.04$), and that it varied by month ($F_{(3,156)} = 2.87$, $P = 0.03$), with a peak in June (June > May, September; $P = 0.01$). The "month × location" interaction ($F_{(3,156)} = 0.55$, $P = 0.65$) was not significant, but the statistical power of this test was low (0.16), suggesting that the probability to detect a significant effect of the "month × location" interaction, when this interaction is real, was small.

I modeled microhabitat selection by rodent prey to investigate whether the structural characteristics at locations where I trapped rodents affected the probability of catching rodents. I used the locations where I caught a least one rodent ("rodent presence") vs. the locations where I did not ("rodent absence") as the dependent variable in the logistic regression. I used macrohabitat as the case control to account for the potential variation in rodent structural microhabitat preferences among macrohabitats. I included all the structural variables ("distance to rock refuge", "absence/presence of a wood rat nest", "rock size", "shrubiness") used in the snake analyses, and added two categorical variables: "season" (snake mating and post-mating seasons), and "absence/presence of a snake" (i.e., random and snake locations, respectively). The statistically significant model ($\chi^2 = 17.15$, df = 7, $P = 0.01$; Table 6) revealed that rodents preferred locations with high vegetation cover (i.e., "shrubiness") and, consistent with the snake analysis, that rodents were less common at snake than at random locations.

Finally, I assessed whether rodent prey exhibited a shift in microhabitat preferences in relation to the presence or absence of a snake, by examining the structural characteristics predicting rodent occurrence at the snake and random locations separately. I used the locations where I caught a least one rodent ("rodent presence") vs. the locations where I did not ("rodent absence") as the dependent variable in the logistic regressions. I also included "season" (snake mating and post-mating seasons) as a categorical variable in these analyses to examine whether prey availability fluctuated seasonally. At the snake locations, none of the factors significantly predicted rodent occurrence (Table 6). At the random locations, rodents preferred microhabitats with high shrub cover, were less abundant during the snake mating season (Table 6), but surprisingly were not positively associated with the presence of a wood rat nest, which are structures made by rodents. These nests were highly uncommon at random locations

(6.8% [5/73] of locations), which possibly precluded detection of an effect of the variable "absence/presence of a wood rat nest" in the random location analysis. I used a χ^2 analysis to examine if the probability of catching a rodent when a wood rat nest was present differed between snake and random locations during the post-mating season. The analysis showed that the frequency capture of rodents around wood rat nests was higher at random (100% [4/4]) than at the snake locations (26.6% [8/30]; Fisher's exact test: $P = 0.01$).

Discussion

I investigated seasonal variation in habitat selection at the landscape (macrohabitat) and local (microhabitat) levels in an ambush vertebrate predator, and studied the significance of two critical resources, food and refuges, on this decision-making process. Below, I discuss, first, how the availability of prey and refuges related to *C. mitchellii*'s macrohabitat selection, and then, the differential use of prey and refuges by *C. mitchellii* in the mating and the post-mating seasons at the microhabitat level. Finally, I examine whether the perception of *C. mitchellii's* habitat selection relative to the availability of food and refuges differed between the macro and microhabitat scales.

Macrohabitat selection

I examined macrohabitat selection in *C. mitchellii*, and assessed the relationship between macrohabitat choice and prey and refuge availability across the landscape. During the entire active season, *C. mitchellii* preferred rock outcrops in their overall home range (95% KDEs). This pattern was due to the propensity of snakes to preferentially use rock outcrops during the post-mating season, because I found no evidence of macrohabitat selection during the mating season. The lack of habitat selection in the mating season is possibly related to mate-searching activities, because snakes range widely at this time of the year, which may cause them to use habitats according to their relative availability. Because males actively locate females, the male-biased investment in mate-searching activities may explain the lower proportion of rock outcrops in the home ranges of males, compared to females. That is, the mating season of *C. mitchellii* starts shortly after spring emergence from hibernation, and snakes typically overwinter in or close to rock outcrops. Females remain in the vicinity of these dens during the mating season, and males typically visit multiple dens to find sexually receptive females. Therefore, males may travel through habitats other than rock outcrops (e.g., rolling hills, slopes) more frequently than females when searching for mates.

In contrast to the mating season*, C. mitchellii* selected specific macrohabitats during the post-mating season. Snakes preferred rock outcrops in their overall home ranges (95% KDEs) and avoided rolling hills in their core area (50% KDEs) of activity. The preference of rock outcrops and avoidance of rolling hills correlated with the varying availability of prey between these two macrohabitats, because rodent prey was significantly more abundant in rock outcrops than in rolling hills. This result is consistent with the prediction that food is an important factor affecting the macrohabitat selection process in a variety of species (Madsen and Shine, 1996; Bost et al., 2009; Skomal et al., 2009). Further, refuge availability differed between the preferred rock outcrops and avoided rolling hills. Rock outcrops were characterized by a significantly higher availability of rock refuges compared to rolling hills, and wood rat nests were on average (but not significantly) more common in the former habitat. This suggests that the availability of refuges also accounts for *C. mitchelii*'s preference of rock outcrops and avoidance of rolling hills. In conclusion, the selection and avoidance of macrohabitats positively correlated with the distribution of prey and refuges across the landscape.

Microhabitat selection

Hypothesis 1: Snakes do not select prey-rich sites during the mating season

I hypothesized that snakes do not select prey-rich sites during the mating season, because mating activities may conflict with foraging. Indeed, prey availability did not differ between snake and random locations, which indicate that *C. mitchellii* may trade off foraging for mating. Evidence for trade offs between feeding and mate acquisition is widespread across taxa, because many organisms reduce or do not feed during the breeding season to increase time allocation to mating activities (Madsen and Shine, 2000; Plath et al., 2007; Pelletier et al., 2009). *Crotalus mitchellii* ranges widely during the mating season, because increased activity enhances mate-encounter rates during this short breeding season (i.e., ca. 5-6 weeks). Consequently, the lack of selection of prey-rich sites by *C. mitchellii* may be caused by a conflict between mating and foraging activities, with mate acquisition prevailing over foraging.

The reduction or lack of feeding during the mating season is especially pronounced in males, which typically invest the most in mating activities (Kokko and Wong, 2007). For instance, male harbor seals (*Phoca vitulina*) decrease the frequency of their offshore foraging trips to patrol the shallow waters near breeding colonies. This behavioral shift by the seals results in loss of body mass, but presumably increases female encounter rate (Coltman et al., 1997). Likewise, in primates, mate guarding imposes an energetic cost on males, because males need to prevent competitors access to their female(s), and time allocated to foraging bouts is reduced (Alberts et al., 1997). Although the feeding for mating trade-off is particularly prominent in males, females may also reduce feeding during the mating season. For example, in some fishes and ungulates, female sexual harassment by males during the breeding season interferes with the female's feeding behavior, and results in reduced food intake by females (Plath et al., 2007; Holand et al., 2006). In *C. mitchellii*, the investment in mate-searching activities is male-biased, and consequently we may expect females to forage more than males during the mating season. Yet, analyses revealed that rodents were equally abundant at random locations and at male and female locations. This result demonstrates that despite the sexual difference in mate-searching behavior in *C. mitchellii*, the locations selected by males and females did not differ in prey availability.

The similar prey availability at snake and random locations, however, does not necessarily indicate that snakes trade off foraging for mating activities. At least three scenarios may account for the comparable prey availability at snake and random locations. First, snakes may not select locations where food is the most abundant, because there is plenty of food available at any given location for snakes to feed. This explanation seems unlikely because the primary productivity of the Mojave Desert is low (Rundel and Gibson, 1996) due to the scarcity of rain, and rodent abundance is often linked to habitat primary productivity (Lima et al., 1999; Báez et al., 2006). At the study site, mean rodent trap success was 8% during the mating season, and I caught on average 0.5 rodents at snake and random locations, suggesting that rodents are not particularly abundant. Second, *C. mitchellii* may trade off food for safety. For instance, microhabitats that contain more prey may attract a higher number and diversity of predators (Neil, 1990;

Huang and Sih, 1991), which may feed on the prey species as well as on other predatory species (intraguild predation). Although I can not evaluate this hypothesis, some of the predators that feed on the rodents that occur at the study site are also known predators of the speckled rattlesnake (e.g., great horned owls [*Bubo virginianus*], bobcats [*Lynx rufus*], coyotes [*Canis latrans*], ring-tailed cats [*Bassariscus astutus*]). Therefore, *C. mitchellii* may avoid locations where prey is more abundant to decrease its exposure to predators. Third, snakes may select locations with higher prey density, but rodents decrease their activity or leave the sites after the snakes arrive. Alternatively, snakes consume the rodents at those sites, which could result in an apparent lower prey availability at the snake locations (see Hypothesis 3, below). At this time, the reason(s) for the similar prey availability at random and snake locations remain(s) unclear.

Hypothesis 2: Snake locations are not close to refuges during the mating season

I hypothesized that snake locations are not close to refuges during the mating season, because snakes venture away from their retreat sites to find mating partners. My findings did not support this hypothesis, because snake locations were closer to rock refuges, compared to random locations. The observation that *C. mitchellii* did not select locations with wood rat nests suggests that snakes preferred to use rocks and crevices instead of wood rat nests as a refuge during the mating season. Mating activity is known to affect predation risk, because some organisms exhibit risk-prone behaviors to acquire mates (Reaney, 2007). For example, the courtship behavior of the wolf spider *Pardosa milvina* has a survival cost, because displaying individuals are more likely to be eaten by predators than non-courting individuals (Hoefler et al., 2008). In many snakes, including venomous species, the extensive movements of individuals searching for mates increase detectability by predators and mortality (Aldridge and Brown, 1995; Bonnet et al., 1999; Sperry and Weatherhead, 2009). *Crotalus mitchellii* increases movement per unit time during the mating season, which could expose it to predators. Still, I only recorded one predation event on a snake during the mating season in three years of study (mating season survival rate; 2006: 100% [12/12]; 2007: 94% [15/16]; 2008: 100% [12/12]). This finding suggests that mating activities did not have a significant mortality cost, and that *C. mitchellii* may not experience a trade-off between mate acquisition and safety.

I quantified refuge availability at snake locations where I found snakes coiled on the surface or in a refuge, but not when they were moving. Consequently, the low predator-induced mortality of *C. mitchellii* during the mating season could be attributable to the fact that snakes selected locations close to refuges when they were not traveling. Yet snakes are likely more detectable by predators when they move around the landscape, and *C. mitchellii* travels widely during the mating season. The low predator-induced snake mortality at a time when snakes move extensively in search of mates suggests that rattlesnakes and their predators may not often interact during the mating season. Specifically, *C. mitchellii* is mainly diurnal during the mating season, because environmental temperatures allow them to be on the surface during daytime. Because the snake's main predators are typically nocturnal (e.g., great horned owls, bobcats, coyotes, ring-tailed cats; Reid, 2006), the contrasting diel activity of rattlesnakes and their predators in the mating season could account for the low rattlesnake mortality due to predation at this time of the year.

Regardless of the factor(s) responsible for the low predation on *C. mitchellii* during the mating season, this pattern has implications for the evolution of mating phenology in this snake, because *C. mitchellii* is one of only two rattlesnakes (of more than 30 species) known to exclusively mate in spring (Aldridge and Duvall, 2002; Glaudas, unpublished data). Other rattlesnake species reproduce in the summer or in both spring and late summer or fall. It has been proposed that ecological factors, such as predation risk, may explain the diversity in mating phenology observed in rattlesnakes (Aldridge and Duvall, 2002). That is, the evolution of mating phenology may have occurred in response to species-specific predation risk, and thus favor the season(s) when it is safer for snakes to engage in mate-searching activities. My observations partially support this hypothesis because predation on *C. mitchellii* is lower during the mating season compared to the post-mating season (see Hypothesis 4, below), despite a strong increase in distance traveled per unit time during the former.

Hypothesis 3: Snakes select prey-rich sites during the post-mating season

I hypothesized that during the post-mating season snakes select locations with higher prey availability, because individuals are not engaged in mating activities, and therefore can allocate more time and effort to foraging. Unexpectedly, rodents were less common at snake than at random locations. Several explanations can account for this pattern. (1) Snakes actively select areas where prey is less available. This explanation is counterintuitive, because it suggests that food resources are unimportant for *C. mitchellii*. This presumed avoidance behavior of prey-rich locations by *C. mitchellii* could be explained by a strong food for safety trade-off. That is, snakes may prefer areas with lower prey abundance, because locations where rodents are more available may also attract other predatory species, which could feed on *C. mitchellii*. This explanation seems unlikely, because predator-induced mortality was high during the post-mating season (see

Hypothesis 4, below), suggesting that *C. mitchellii*'s microhabitat selection in relation to predation risk was not particularly efficient. (2) *Crotalus mitchellii* and its rodent prey exhibit contrasting patterns of microhabitat selection. During the post-mating season, snakes preferred sites with wood rat nests, and rodents selected areas with high vegetation cover. However, I did not find any evidence that the snakes and the rodents actively avoided each other's preferred microhabitats. Further, the rodents caught at trap locations constitute a significant portion of *C. mitchellii*'s diet (Glaudas, unpublished data), which indicates that interactions between *C. mitchellii* and these mammals are relatively common. Consequently, the putative contrasting patterns of microhabitat selection by predator and prey are unlikely. (3) *Crotalus mitchellii* consume most of the rodents at the snake locations, resulting in significantly fewer rodent captures at these sites, compared to the random locations. This explanation requires snakes to consistently remove a portion of the rodent population at their selected locations to cause a statistical difference at the snake and random locations. Although there is little doubt that snakes were sometimes successful at capturing rodents, the systematic capture of rodents by snakes is improbable. This idea is supported by the typical low prey capture success of vipers (Shine et al., 2002; Clark, 2006), the group of snakes to which rattlesnakes belong, and by the lack of body condition improvement of *C. mitchellii*, which suggests that snakes did not feed often during this study (Glaudas, unpublished data). (4) Rodents avoid areas with snakes or reduce activity at snake locations, decreasing prey availability in these areas. Although I can not directly test the hypothesis that rodents avoided the snake locations, evidence suggests that this is the most likely scenario. Prey abundance was consistently low at snake locations, and the temporal variation in rodent availability at random locations contrasted with the lack of variation at snake locations (Fig. 2). Further, wood rat nests, an actively selected microhabitat feature by *C. mitchellii*, are structures made by rodents, and are seemingly an important resource for many rodent species (Vestal, 1938; Stones and Hayward, 1968; pers. obs.). A χ^2 analysis revealed that the odds of catching a rodent when a wood rat nest was present at a location were much higher at random locations than at snake locations, indicating that wood rat nests were more commonly used by rodents when snakes were absent. This finding suggests that the rodents adjusted their behavior in response to the presence of a snake, to presumably decrease predation risk (Lima and Dill, 1990). Further, avoidance of snakes by desert rodents has been demonstrated in the laboratory. The deer mouse (*Peromyscus maniculatus*), a close relative of the canyon mouse (*Peromyscus crinitus*; i.e., a modal prey species of *C. mitchellii,* and by far the most commonly captured species at the study site), avoided captures by Great Basin rattlesnakes (*Crotalus lutosus*) 75% of the time in a confined environment (Pierce et al., 1992). Collectively, active avoidance of *C. mitchellii* by rodent prey is the most likely explanation for the decreased prey availability at the snake locations.

In ambush predators, such as *C. mitchellii*, food intake is likely correlated with prey abundance (Huey and Pianka, 1981), and field and laboratory experiments have demonstrated that these “sit-and-wait” predators presumably maximize feeding opportunities by selecting ambush sites where prey is most available (Duvall et al., 1990; Roth et al., 1999; Theodoratus and Chiszar, 2000; Clark, 2004). The behavior of prey in response to the presence of ambush predators is not well-known. My study demonstrates that prey availability is low at snake locations, seemingly because rodents avoid sites where snakes occur. As a result, *C. mitchellii*'s prey-encounter rate is probably low*,* and *C. mitchellii* may be food-limited. I estimated that females in this population reproduced on average once every three years. This observation provides further support for the idea that the lower availability of prey at snake compared to random locations was not due to the snakes depleting food resources at their selected sites, because one would expect females of this medium-size rattlesnake species to reproduce more frequently if snakes often fed. A food supplementation study on rattlesnakes in the field effectively demonstrates that some rattlesnakes are food-limited. Free-ranging female western diamond-backed rattlesnakes (*Crotalus atrox*) that were supplementally-fed significantly increased their reproductive frequency (Taylor et al., 2005). The hypothesis that rodents avoided locations where *C. mitchellii* occurred, thereby decreasing the snake's prey-encounter rate, may explain why some rattlesnakes are food-limited, and therefore why females of some rattlesnake species, including *C. mitchellii*, reproduce infrequently.

Hypothesis 4: Snakes select locations close to refuges during the post-mating season

I hypothesized that during the post-mating season snakes selected locations close to refuges to reduce exposure to predators and to the potentially lethally high summer temperatures characteristic of the Mojave Desert. The results supported this hypothesis, because presence of a wood rat nest was a significant predictor of *C. mitchellii*'s occurrence. Further, rock refuges were an important resource to *C. mitchellii* when wood rat nests were absent. Wood rat nests and rock refuges are important to *C. mitchellii*, because they likely provide protection from predators. Over a three year period (2006-2008), the mean annual predator-induced mortality rate at the study site was 17% (standard deviation: 6.2%), suggesting that predation is a strong selective pressure acting on *C. mitchellii*. Eighty five percent (6/7) of the predation events witnessed in this study occurred during the post-mating season, when snakes are close to wood rat nests or rock refuges, and when distance traveled per unit time is decreased. Encounters between rattlesnakes and their predators may be common during the post-mating season, because predators may be particularly abundant at this time of the year, or because rattlesnakes and predators are both active at night at this time of the year. The temporal difference in predation risk study could also reflect seasonal prey choice by predators. For instance*,* *C. mitchellii* is highly venomous, and predators may feed on this potentially dangerous prey when safer prey is uncommon. Alternatively, the use of refuges may not be driven by predation risk, but rather by the hot diurnal environmental temperatures of the Mojave Desert. The shade daytime temperatures in the Mojave Desert approach the critical thermal maximum of many desert reptiles, including *C. mitchellii* (Brattstrom, 1965), and thus rattlesnakes likely use wood rat nests and rock refuges as thermal refugia. Therefore, selecting an ambush site close to these refuges could allow snakes to quickly retreat to a thermal refuge in the morning, when temperatures start to increase.

The scale-dependency of habitat selection

The habitat selection process is hierarchical, because animals select habitats at multiple spatial scales (Johnson, 1980; Levin, 1992). Animals choose a home range at the landscape level (macrohabitat selection), and then select specific foraging sites (microhabitat selection) within their home range. Because the selection process occurs at multiple scales, researchers have extensively studied the scale-dependency of resource selection. The question most often asked is: how do specific resources correlate with habitat selection at multiple spatial scales? The answer to this question is species-specific, because studies have revealed that patterns of resource selection may or may not be affected by scale (Ward and Saltz, 1994; Mysterud et al., 1999; Fortin et al., 2003). My study shows that the relationship between prey availability and habitat selection in *C. mitchellii* was affected by the spatial scale considered. At the macrohabitat (the home range) level, rodent prey was significantly more available in the preferred rock outcrops, compared to the avoided rolling hills. In contrast, at the microhabitat level (locations within the home range), snake-locations were characterized by lower prey availability. Consequently, the relatively higher availability of prey in *C. mitchellii*'s preferred macrohabitat did not translate into high prey availability at the microhabitats selected by snakes, seemingly because the rodents avoided the sites where the snakes occurred. In contrast to prey availability, refuge availability was a consistent predictor of habitat selection across scales, because refuges were more available in the preferred rock outcrops, compared to the avoided rolling hills, and because the microhabitats selected by snakes were close to refuges. Therefore, my study demonstrates that in predator-prey systems, detection of habitat selection in relation to mobile prey can be scale-dependent.

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Table 1. Logistic regressions (with individual snakes as the case control) of macrohabitat selection by *Crotalus mitchellii* (13 males, 7 females) in the Eldorado Mountains (southern Nevada) for the entire active season (mid-April to mid-October), the mating season (mid-April to early June), and the post-mating season (early June to mid-October). Degree of freedom is 1 for all tests. Asterisks indicate statistically significant differences between the availability of a specific habitat and the use of that habitat by *C. mitchellii*.

Season	Habitat types	Estimate ± SE (odds, 95% confidence intervals)	χ^2	*P*
Entire active season				
95% KDEs	Slopes	0.0003 ± 0.02 (1.0003, 0.98-1.02)	0.003	0.98
	Rolling hills	-0.01 ± 0.02 (0.99, 0.97-1.01)	0.29	0.58
	Rock outcrops	0.05 ± 0.02 (1.05, 1.03-1.07)	3.88	0.04*

Table 1. Continued

50% KDEs	Slopes	0.005 ± 0.01 (1.005, 0.99-1.01)	0.1	0.75
	Rolling hills	-0.01 ± 0.01 (0.99, 0.98-1)	0.32	0.56
	Rock outcrops	0.02 ± 0.01 (1.02, 1.01-1.03)	2.57	0.1
Mating season				
95% KDEs	Slopes	0.004 ± 0.01 (1.004, 0.99-1.15)	0.1	0.74
	Rolling hills	-0.02 ± 0.01 (0.98, 0.97-0.99)	1.85	0.17
	Rock outcrops	0.01 ± 0.01 (1.01, 1-1.02)	0.57	0.44
50% KDEs	Slopes	0.01 ± 0.01 (1.01, 1-1.02)	0.59	0.44
	Rolling hills	-0.01 ± 0.01 (0.99, 0.98-1)	0.44	0.50
	Rock outcrops	0.02 ± 0.01 (1.02, 1.01-1.03)	2.57	0.10

Table 1. Continued

Post-mating season				
95% KDEs	Slopes	-0.0001 ± 0.01 (0.99, 0.98-1)	0.0001	0.99
	Rolling hills	-0.007 ± 0.01 (0.993, 0.98-1)	0.17	0.67
	Rock outcrops	0.04 ± 0.02 (1.04, 1.02-1.06)	3.54	0.05*
50% KDEs	Slopes	-0.01 ± 0.01 (0.99, 0.98-1)	1.1	0.28
	Rolling hills	-0.02 ± 0.01 (0.98, 0.97-0.99)	4.06	0.04*
	Rock outcrops	0.01 ± 0.01 (1.01, 1-1.02)	1.05	0.30

Table 2. The effect of sex on the proportions of habitat types in the home ranges of *Crotalus mitchellii* (13 males, 7 females) in the Eldorado Mountains (southern Nevada) for the entire active season (mid-April to mid-October), the mating season (mid-April to early June), and the post-mating season (early June to mid-October). All analyses were conducted using Kruskal-Wallis ANOVAs, and degree of freedom is 1 for all tests. Asterisks indicate statistically significant differences between males and females.

Season	Variables	χ^2	*P*
Entire active season			
95% KDEs	Slopes	1.34	0.24
	Rolling hills	0.001	0.96
	Rock outcrops	0.03	0.84
50% KDEs	Slopes	0.001	0.96
	Rolling hills	0.86	0.35
	Rock outcrops	2.57	0.1
Mating season			
95% KDEs	Slopes	0.29	0.59
	Rolling hills	0.29	0.58
	Rock outcrop	3.70	0.05*

Table 2. Continued

50% KDEs	Slopes	0.06	0.79
	Rolling hills	0.09	0.76
	Rock outcrops	4.43	0.03*
Post-mating season			
95% KDEs	Slopes	0.10	0.75
	Rolling hills	0.04	0.84
	Rock outcrops	0.001	0.96
50% KDEs	Slopes	0.01	0.90
	Rolling hills	1.40	0.23
	Rock outcrops	0.00	1.0

Table 3. Microhabitat differences among macrohabitat types (rolling hills, rock outcrops, slopes; MANOVA, Wilks' lambda, $F_{(6,132)} = 14.09$, $P < 0.0001$) in the Eldorado Mountains (southern Nevada). Asterisks indicate statistically significant differences in microhabitat characteristics among macrohabitat types.

Variable	df	MS	F-value	*P*
Dist to rock refuge (log-transformed)	2	3.32	7.18	0.001*
Shrubiness	2	5.50	8.37	0.0006*
Rock size	2	13.86	27.89	0.0001*

Table 4. Logistic regressions (with paired snake and random locations as the case control) of the availability of rodent prey in the Eldorado Mountains (southern Nevada) at *Crotalus mitchellii*'s locations for the entire active season (mid-April to mid-October), the mating season (mid-April to early June), and the post-mating season (early June to mid-October). Degrees of freedom (df) is 1 for all tests. Asterisks indicate statistically significant differences in microhabitat characteristics between the snake and random locations.

Parameters	Estimate ± SE (odds, 95% confidence intervals)	χ^2	*P*
Entire active season (86 random locations, 86 snake locations)			
Number of rodents	-0.48 ± 0.22 (0.61, 0.49-0.77)	4.47	0.03*
Mating season (23 random locations, 23 snake locations)			
Number of rodents	0.28 ± 0.44 (1.32, 0.85-2.05)	0.42	0.51
Post-mating season (63 random locations, 63 snake locations)			
Number of rodents	-0.78 ± 0.29 (0.45, 0.34-0.61)	6.94	0.008*

Table 5. Logistic regressions (with macrohabitat type as the case control) of the structural characteristics at *Crotalus mitchellii*'s locations in the Eldorado Mountains (southern Nevada) for the entire active season (mid-April to mid-October), the mating season (mid-April to early June), and the post-mating season (early June to mid-October). Degree of freedom (df) is 1 for all tests. Asterisks indicate statistically significant differences in microhabitat characteristics between the snake and random locations.

Parameters	Estimate ± SE (odds, 95% confidence intervals)	χ^2	*P*
Entire active season (75 snake locations, 74 random locations)			
Distance to rock refuge (m)	-0.93 ± 0.27 (0.39, 0.30-0.51)	11.43	0.001*
Wood rat nest (present)	1.46 ± 0.61 (4.30, 2.33-7.92)	5.59	0.01*
Distance to rock refuge × wood rat nest (absent)	-0.93 ± 0.31 (0.39, 0.28-0.53)	8.67	0.003*
Rock size	0.10 ± 0.31 (1.1, 0.81-1.5)	0.13	0.71
Shrubiness	0.01 ± 0.26 (1.01, 0.77-1.30)	0.004	0.94

Table 5. Continued

Mating season (21 snake locations, 20 random locations)			
Distance to rock refuge (m)	-1.43 ± 0.67 (0.23, 0.12-0.46)	4.48	0.03*
Wood rat nest (present)	1.86 ± 1.34 (16.42, 1.68-24.53)	1.92	0.16
Rock size	-1.07 ± 0.78 (0.34, 0.15-0.74)	1.88	0.17
Shrubiness	-0.02 ± 0.68 (0.98, 0.49-1.93)	0.001	0.97
Post-mating season (54 snake locations, 54 random locations)			
Distance to rock refuge (m)	-0.09 ± 0.23 (0.91, 0.72-1.15)	0.15	0.69
Wood rat nest (present)	1.74 ± 0.74 (5.69, 2.71-11.94)	5.51	0.02*
Distance to rock refuge × wood rat nest (absent)	-0.76 ± 0.32 (0.46, 0.33-0.64)	5.64	0.01*
Rock size	0.37 ± 0.33 (1.44, 1.04-2.01)	1.24	0.26
Shrubiness	0.24 ± 0.29 (1.27, 0.95-1.69)	0.69	0.40

Table 6. Logistic regressions (with macrohabitat type as the case control) of the microhabitat characteristics at locations where I caught rodent(s), for the snake and random locations, the snake locations, and the random locations. Degree of freedom (df) is 1 for all tests. Asterisks indicate statistically significant differences in microhabitat characteristics between the locations where I caught rodents and those where I did not.

Parameters	Estimate ± SE (odds, 95% confidence intervals)	χ^2	*P*
Snake and random locations (71 random locations, 71 snake locations)			
Distance to rock refuge (m)	0.07 ± 0.09 (1.07, 0.98-1.17)	0.59	0.44
Wood rat nest (present)	-0.49 ± 0.50 (0.61, 0.37-1.01)	0.95	0.32
Shrubiness	0.60 ± 0.23 (1.82, 1.44-2.29)	6.82	0.009*
Rock size	0.44 ± 0.26 (1.55, 1.19-2.01)	2.86	0.09
Season (mating)	-0.18 ± 0.42 (0.83, 0.54-1.27)	0.18	0.66
Snake (present)	-1.41 ± 0.46 (0.24, 0.15-0.38)	9.2	0.002*

Table 6. Continued

Snake locations (71 snake locations)			
Distance to rock refuge (m)	0.09 ± 0.14 (1.09, 0.95-1.25)	0.40	0.52
Wood rat nest (present)	0.38 ± 0.63 (1.46, 0.78-2.74)	0.38	0.53
Shrubiness	0.53 ± 0.33 (1.69, 1.22-2.36)	2.58	0.10
Rock size	0.71 ± 0.39 (2.03, 1.37-3)	3.26	0.07
Season (mating)	1.03 ± 0.62 (2.80, 1.50-5.20)	2.74	0.09
Random locations (71 random locations)			
Distance to rock refuge (m)	0.19 ± 0.13 (1.21, 1.06-1.37)	2.20	0.13
Wood rat nest (present)	1.02 ± 1.35 (2.77, 0.72-10.69)	0.57	0.44
Shrubiness	0.83 ± 0.37 (2.29, 1.58-3.32)	4.97	0.02*
Rock size	0.37 ± 0.45 (1.44, 0.92-2.27)	0.67	0.40

Table 6. Continued

Season (mating)	-1.30 ± 0.65 (0.27, 0.14-0.52)	4.04	0.04*

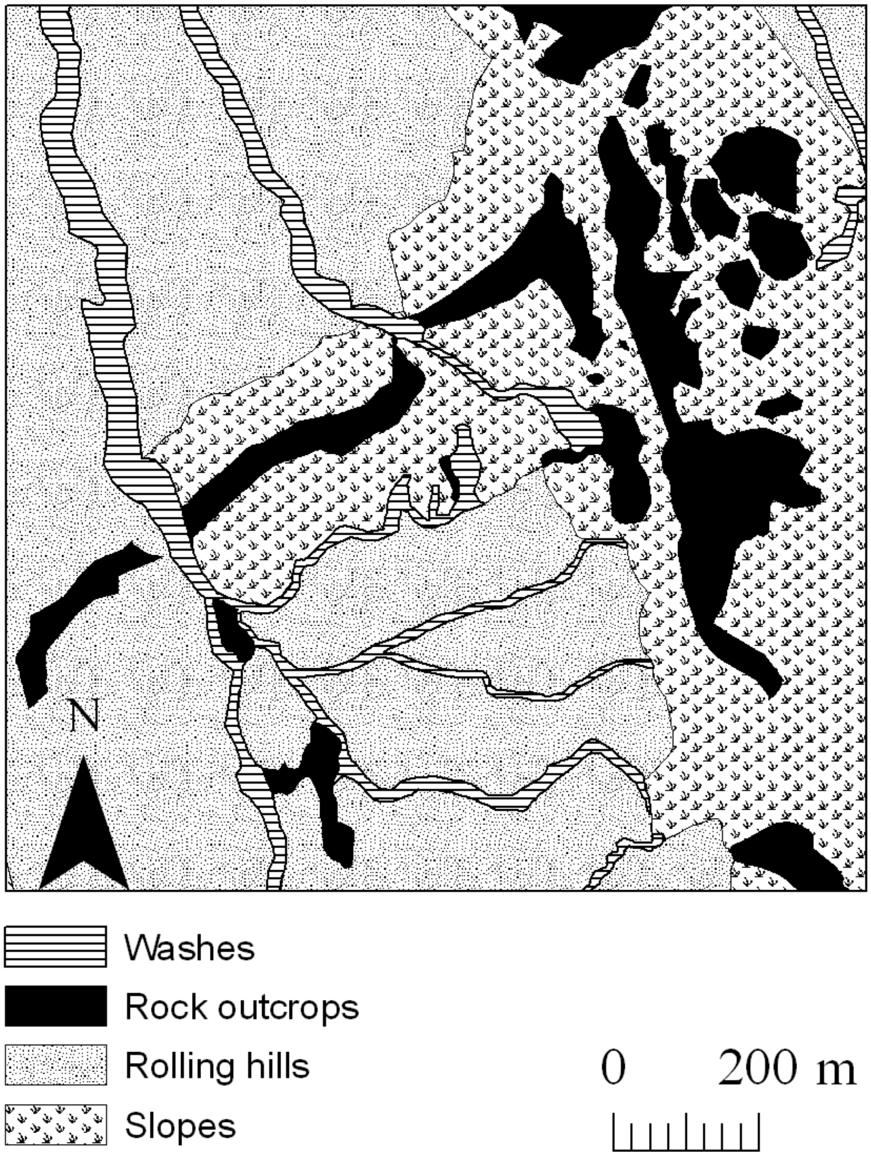

Figure 1 – Macrohabitat GIS data layer of the study site, located in the Eldorado Mountains, Clark County, southern Nevada (35˚44’N, 114˚49’W), in the eastern part of the Mojave Desert.

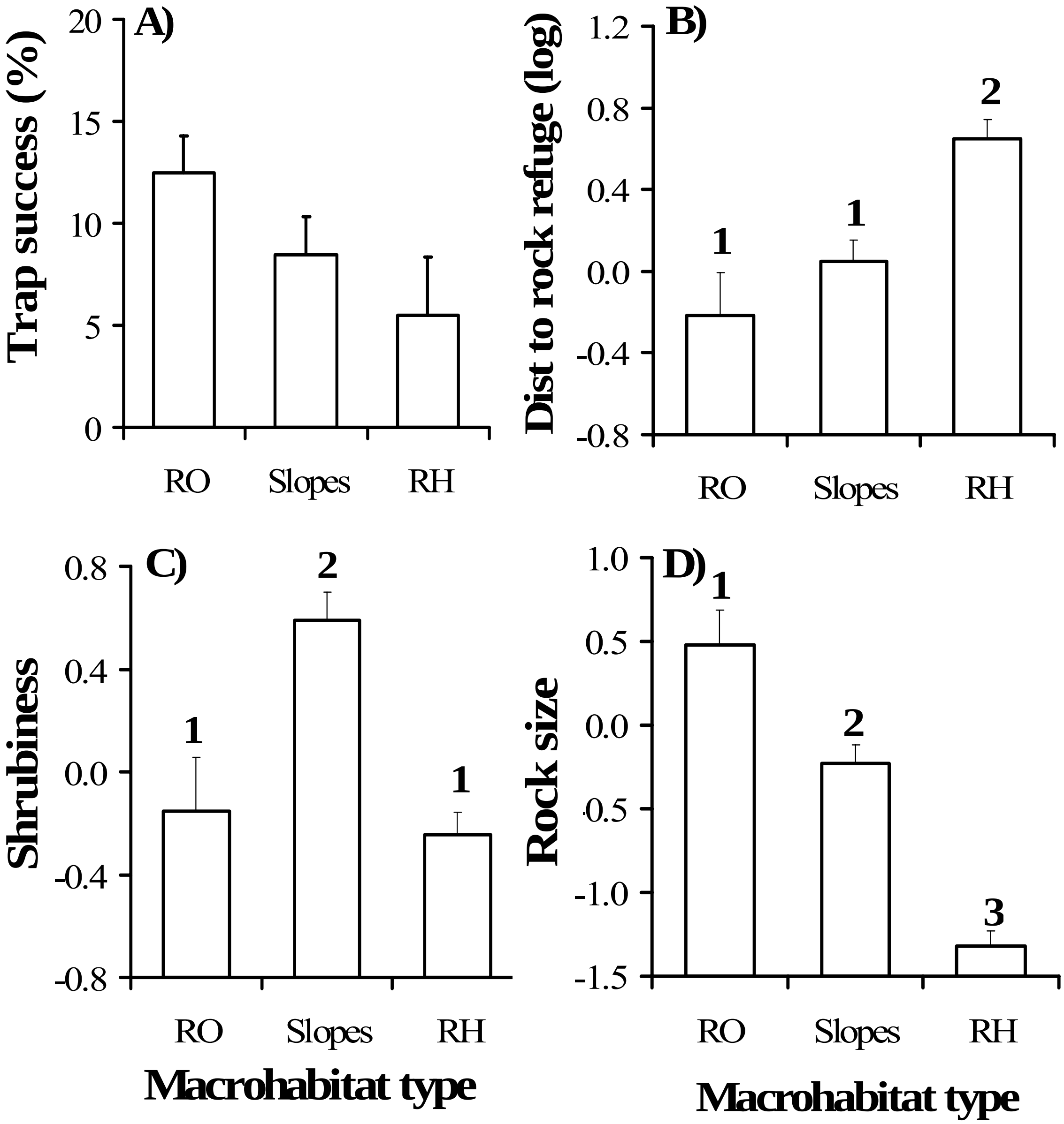

Figure 2 – Microhabitat characteristics of the three major macrohabitat types (rolling hills, slopes, rock outcrops) found in the Eldorado Mountains (southern Nevada) at the random locations: A) location rodent trap success (%); B) distance to rock refuge (m; log-

transformed data); C) shrubiness; and D) rock size. RO and RH refer to rock outcrops and rolling hills, respectively. In C) and D), larger values represent an increase in shrub cover and rock size, respectively. Sample sizes are 20 (rock outcrops), 36 (slopes), and 15 (rolling hills). The *P* values reported for multiple comparisons are adjusted using the Bonferonni-Dunn method, and the group means with the same number above the bars are not statistically different at $P \leq 0.05$.

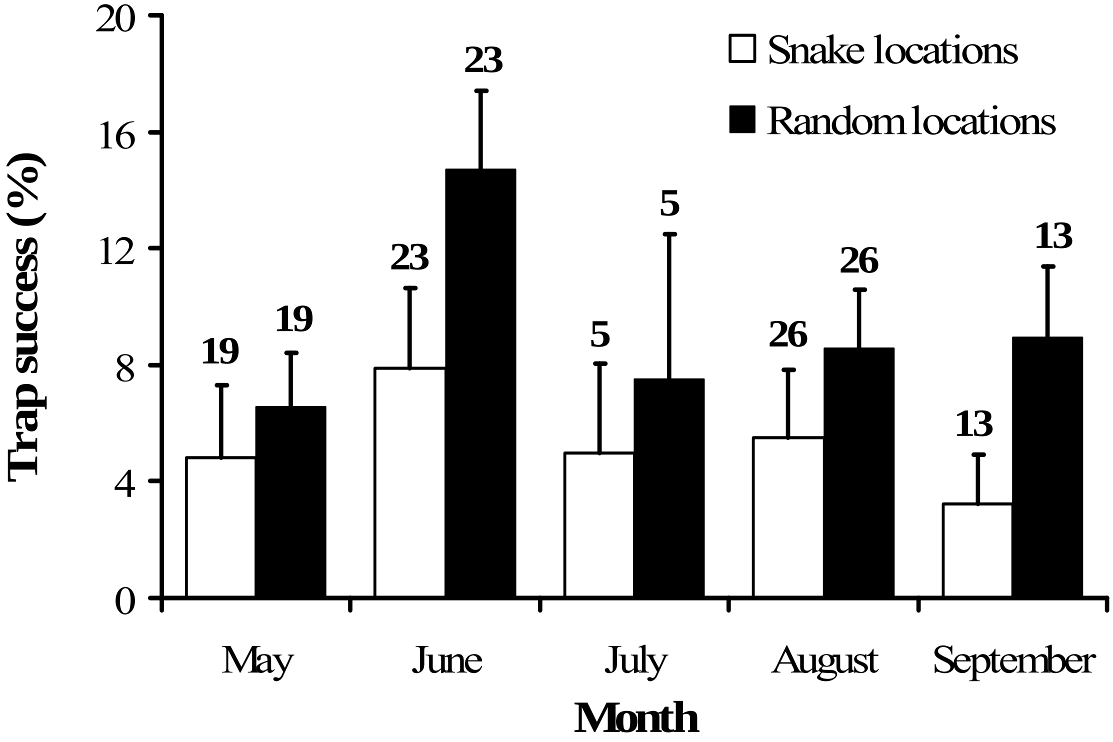

Figure 3 – Temporal variation in rodent prey abundance (*Chaetodipus formosus* [*n* = 18], *Dipodomys merriami* [*n* = 3], *Neotoma lepida* [*n* = 1], *Peromyscus crinitus* [*n* = 68]) in the Eldorado Mountains of the Mojave Desert, southern Nevada. The number of traps that successfully caught a rodent at a given location were used to estimate rodent abundance at snake and random locations. Numbers above bars indicate sample size.

CHAPTER 4

SPACE USE AND SEX: A RATTLESNAKE'S PERSPECTIVE

I investigated temporal variation in the spatial ecology of an ambush vertebrate predator, the speckled rattlesnake (*Crotalus mitchellii*). I specifically examined how space use differed between the mating (late April to early June) and post-mating seasons (early June to mid-October), and how this variation related to some important resources, such as mating partners, food, and refuges.

My findings effectively demonstrates the behavioral shifts exhibited by organisms in response to seasonally-prevailing activities (mating and foraging), because most of the parameters I estimated varied between the mating and post-mating seasons. First, *C. mitchellii* increased distance traveled per unit time in the mating season compared to the post-mating season, presumably because wide-ranging behavior during the mating season enhances reproductive success. Second, the lack of selection of habitat types during the mating season (Rock outcrops, slopes, rolling hills) contrasted with the snake's preference for rock outcrops and avoidance of rolling hills during the post-mating season. The rattlesnake's preference and avoidance of rock outcrops and rolling hills, respectively, positively correlated with the varying abundance of rodents and refuges between these macrohabitats, because rodent prey and refuges were more abundant in rock outcrops than in rolling hills. This contrasting pattern of macrohabitat selection between seasons suggests that food resources are relatively more important to *C. mitchellii* during the post-mating season, a time at which snakes can allocate more time and effort to foraging compared to the mating season. Finally, the characteristics of the specific locations (microhabitats) selected by snakes also differed by seasons. During the mating season, snakes did not select prey-rich sites, but preferred locations close to rock refuges, which may partly explain the low predator-induced mortality at this time of the year. During the post-mating season, snake locations were characterized by low prey abundance, seemingly because rodents avoided the snake locations, which suggests that food intake in *C. mitchellii* is probably low and that this rattlesnake may be food-limited. Further, snake locations were characterized by being close to wood rat (*Neotoma lepida*) nests, and by being close to rocks, specifically when wood rat nests were not available. The common use of these refuges during the post-mating season by *C. mitchellii* may allow snakes to avoid predators and the high daytime summer temperatures of the Mojave Desert.

The differences in *C. mitchellii*'s spatial ecology between the mating and the post-mating seasons that I reported herein illustrate the need to examine patterns of space use in a biologically-relevant temporal framework, because some of these patterns may have gone unnoticed if only the entire active season had been considered. Therefore, testing hypotheses of spatial ecology in an explicit temporal context may be necessary to gain a more detailed understanding of the spatial ecology of free-ranging organisms.

My study reported significant variation in the spatial ecology of a rattlesnake. The descriptive nature of my dissertation project did not allow me to identify the exact determinants of space use variation in *C. mitchellii*. Consequently, an experimental approach to study spatial ecology is required to elucidate the causes and consequences of space use variation in *C. mitchellii* (and other systems). For example, a study manipulating access to food by supplementally feeding a portion of a radiotracked population could investigate how variation in food access affects investments in mating activities, and ultimately the number of offspring produced using DNA fingerprinting analysis. Linking the effect of food resources on movement variation, and ultimately on reproductive success in a natural system could lead to important discoveries regarding the ecology and evolution of space use in free-ranging organisms, and I am hopeful to address some of these questions in my future studies.

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Dissertation Title: Space Use and Mating Activities in the Speckled Rattlesnake (*Crotalus mitchellii)*

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