



Vagabond males and sedentary females: spatial ecology and mating system of the speckled rattlesnake (*Crotalus mitchellii*)

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Received 6 September 2010; revised 24 January 2011; accepted for publication 26 January 2011

We used radiotelemetric data and behavioural observations to characterize seasonal (mating versus post-mating seasons) and sexual variation in movement patterns, as well as to examine some of the ecological factors contributing to the evolution of the mating system in a venomous predator from the Mojave Desert of North America, the speckled rattlesnake, *Crotalus mitchellii*. 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 travelled further per unit time in the mating season compared to the post-mating season. Males also travelled longer distances per unit time than females in the mating and post-mating seasons, and males with larger home ranges during the mating season had more potential mating partners. The results obtained suggest that males actively locate females during the mating season, and that the drastic increase in distance travelled by males during the mating season may be caused by strong male–male competition for access to females, probably because of the limited availability of sexually receptive females. Furthermore, males fight for access to females, and males of larger size are more likely to acquire females. Therefore, sexual selection apparently acts on two different male phenotypic traits: investment in mate-searching activities and male body size. The present study demonstrates that combining quantitative spatial analyses and behavioural observations in an explicit temporal context can significantly advance our understanding of the ecology and evolution of organismal mating systems. © 2011 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2011, **103**, 681–695.

ADDITIONAL KEYWORDS: mate-searching activities – Mojave Desert – movement – sex role.

INTRODUCTION

The spatiotemporal distribution of individuals is fundamentally linked to the fluctuating abundance and distribution of resources important for organismal fitness (MacArthur & Pianka, 1966; 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, and factors that enhance mate acquisition, such as mate-searching activities, may be strongly selected for (Darwin, 1859;

Trivers, 1972; Andersson, 1994). Consequently, examining how space use relates to mating can provide valuable insights about the ecological factors shaping the evolution of organismal mating systems (Komers & Brotherton, 1997).

The link between space use and mating activities has been primarily investigated in mammals. These studies suggest that intraspecific variation (e.g. seasonal, sexual) in movement patterns is strongly affected by the mating system of a species (Gaulin & FitzGerald, 1988; Ims, 1988). For example, males of pair-living, monogamous species only exhibit small differences in movement patterns between the mating and non-mating seasons, and males and females have a similar movement ecology (Gaulin & FitzGerald, 1986, 1988, 1989). By contrast, in polygynous systems, males drastically increase movement during

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the mating season, which results in significant sexual differences in activity patterns (Tew & Macdonald, 1994; Odden & Wegge, 2007). These seasonal and sexual differences in spatial ecology have been linked to the divergent selective pressures operating on individuals of species that exhibit contrasting mating systems. That is, a male'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 (Gaulin & FitzGerald, 1986). Thus, polygamy is a system that promotes the evolution of considerable investment in mate-searching activities, at least in nonsocially living species.

Similar to most mammals, snakes are largely polygamous (Rivas & Burghardt, 2005), and studies of their spatial ecology have increased in recent years (Shine & Bonnet, 2000). Yet, most studies only report absolute values of movement parameters, with little consideration of their ecological and/or behavioural context (Waldron, Lanham & Bennett, 2006). Therefore, our understanding of the link between spatial ecology and mating activities in snakes is relatively poor compared to other groups, such as insects, mammals, and birds (Thornhill & Alcock, 1983; Andersson, 1994). Snakes are particularly well-suited for investigations of movement ecology for several reasons. First, most snake species exhibit strong seasonality of mating (Shine, 2003), and the mating period can be identified with relative ease because snakes are largely nonsocial animals and male–female aggregations are typically a good indicator of mating activity, at least away from hibernation (den) sites. Second, snakes tend to preferentially allocate energy to the different components of fitness (e.g. foraging, mating) at specific times of the year (King & Duvall, 1990). For example, several snake species forgo or reduce feeding during the mating season because time and energy allocation to mate acquisition prevails over feeding activities (Bonnet & Naulleau, 1996; Madsen & Shine, 2000; O'Donnell, Shine & Mason, 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 behaviour, including movement. In the present study, we relied on radiotelemetry to quantify variation in movement and the spatial distribution of individuals over the landscape in a population of a North American venomous snake, the speckled rattlesnake, *Crotalus mitchellii*. We combined spatial analyses with behavioural observations of male–female interactions to test two hypotheses of seasonal (mating versus post-mating seasons) and sexual variation in movement patterns in this snake, with the ultimate goal of elucidating some of the ecological factors that

contribute to the evolution of the mating system in *C. mitchellii*.

HYPOTHESIS 1: INTRASEXUAL VARIATION IN MOVEMENT BETWEEN SEASONS

Male snakes do not provide parental care to their offspring (Shine, 1988; Greene *et al.*, 2002). As a result, the reproductive success of a male is limited by access to females (Darwin, 1871; Kokko & 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 & Semlitsch, 1987; Jellen *et al.*, 2007; but see Carfagno & Weatherhead, 2008). Accordingly, we predicted that *C. mitchellii* males increase movement per unit time in the mating season compared to the post-mating season. By contrast, females of most snakes exhibit little difference in activity between the mating and non-mating seasons (Waldron *et al.*, 2006; Carfagno & Weatherhead, 2008), presumably because the fitness benefits acquired from increased movements during the mating season are low or negligible (Gaulin & FitzGerald, 1986). Therefore, we predicted that *C. mitchellii* females do not increase movement per unit time between the mating and post-mating seasons.

HYPOTHESIS 2: SEXUAL VARIATION IN MOVEMENT PATTERNS WITHIN SEASONS

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. Furthermore, females usually invest more energy in the production of eggs and offspring than males (Parker, 1978). For these reasons, selection on mate-searching activities should be male-biased (for a theoretical model of sex-biased mate-searching, see Kokko & Wong, 2007). Consequently, we predicted that mate-searching activities in *C. mitchellii* are mainly performed by males, and thus that males exhibit increased activity levels in the mating season compared to females. Finally, in polygamous systems, the predicted sexual difference in movement ecology during the mating season typically disappears or strongly decreases during the non-mating season (Trivers, 1972; Gaulin & FitzGerald, 1988; Waldron *et al.*, 2006). A lack of sexual difference in movement patterns in the non-mating season would suggest that the sexual difference in movements during the mating season is not a consequence of sex *per se* but rather of

a species' mating system (e.g. a sex-biased investment in mate-searching activities; Gaulin & FitzGerald, 1986). Therefore, if sexes intrinsically differ in movement ecology, we also expect males and females to exhibit variation in movement patterns during the non-mating season, when they are not engaged in mating activities. We examined this idea by testing the prediction that *C. mitchellii* males also have higher activity levels than females in the post-mating season.

MATERIALS AND METHODS

STUDY SITE AND SPECIES

The study site, which consists of sparsely vegetated rocky hillsides at an elevation of approximately 1100 m, is an approximately 6-km² area located in the Eldorado Mountains, Clark County, Nevada (35°44'N, 114°49'W), in the eastern part of the Mojave Desert. This region is characterized by a dry climate [2006–09 mean (range) annual rainfall: 8.3 (5.2–12.5) cm], with high temperatures in summer [2006–09 mean (range) daily temperatures: 27.1 (14.5–36.5) °C], and relatively cold temperatures [7.1 (–7.5–23.7) °C] in winter (environmental data from Station ID4814, Clark County Regional Flood Control District, Nevada). In summer, the activity patterns of *C. mitchellii* are highly constrained by environmental temperature because midday temperatures approach the critical thermal maximum of desert-dwelling reptiles (approximately 39–42 °C; 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 until late March. We never observed any movements during the hibernation period, although some individuals emerged from their dens during winter rainfall, presumably to drink water (Glaudas, 2009). Because the present study aimed to elucidate the spatial ecology and mating system of *C. mitchellii*, we only present data for the snake's active season.

Crotalus mitchellii hibernated singly or, more commonly, in small numbers (e.g. 2–10) at den sites in rock outcrops. Upon emergence from hibernation, snakes travelled a few metres to cavities under rocks, where they remained alone for 3–4 weeks, with little or no apparent activity. 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. On the basis of these behaviours, the estimated mating season for *C. mitchellii* spanned from 20 April to 6 June, and all the mating dates previously reported for this species fall within

our estimated mating season (Brattstrom, 1965; Klauber, 1972; Goldberg, 2000; Gartner & Reiserer, 2003). Therefore, *C. mitchellii* only breeds in spring, a rare phenomenon in North American pitvipers (Aldridge & Duvall, 2002). 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 the present study, we use the terms 'season' and 'seasonal' to contrast the mating season from the post-mating season. To avoid confusion, 'mating season' refers exclusively to the period when males and females engage in copulation, and excludes the period when females give birth (i.e. summer).

RADIOTELEMETRY

From April 2006 to April 2009, we radiotracked 25 *C. mitchellii* (18 males, seven females). Snakes were opportunistically caught during visits to the field site. We surgically implanted temperature-sensitive radiotransmitters (model SI-2T, 9 g; Holohil Ltd) in the body cavity of the snakes in accordance with established procedures (Reinert & Cundall, 1982; Reinert, 1992). At the time of transmitter implantation, males measured (mean \pm SD) 85.3 \pm 6.9 cm snout–vent length (SVL) and weighed 558.6 \pm 144.3 g, whereas females measured 74.6 \pm 2.8 cm SVL and weighed 373.9 \pm 53.3 g. The transmitter's mass was less than 3% of the body mass of the snake in all cases. We released the snakes at their exact capture location 1–3 days after surgery. We used a radio receiver (model WTI-1000; Wildlife Track) and a directional antenna (model F151-3FB; Wildlife Track) to relocate snakes every 2–3 days during the active season, and once per week during the hibernation period. We considered that a snake had moved between successive locations if it travelled a distance \geq 1 m from its previous position. Each time that a snake moved, we recorded its geographic coordinates using a sub-meter accuracy GPS unit (model GS20; Leica Geosystems Inc.). Periods of radiotracking ranged from 15–773 days per individual (mean \pm SD = 407 \pm 265 days). In total, the present study resulted in 5582 relocations and 1098 movements by snakes.

GEOGRAPHIC INFORMATION SYSTEM ANALYSIS AND MOVEMENT PARAMETERS

Because the field site is mountainous, we generated a three-dimensional (3D) data layer of the study area in a Geographic Information System. We used a 20-foot elevation contour map to create a Triangulated Irregular Network (TIN; Bolstad, 2005) data layer that enabled us to capture the topography of the field

site. We imported the geographic coordinates of each snake's relocations onto the TIN map, and used the 3D analyst tool in ARCMAP, version 9.2 (ESRI) to estimate the movement parameters of each individual. This technique allowed us to incorporate the topography of the area when calculating the distances travelled by snakes, and thus to minimize the underestimation of an individual's movements (Greenberg & McClintock, 2008).

Our spatial analyses focused on the following parameters: distance travelled between relocations (DBR), distance travelled per known movement (DPM), minimum movement frequency, and directionality. We obtained DBR by calculating the distance between two consecutive locations. Because we 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 travelled per unit time. We calculated DPM by removing from the data set the instances when snakes did not move between successive relocations. We obtained a minimum estimate of movement frequency data by calculating the number of times that a snake moved during an arbitrarily defined 2-week period, out of N possibilities (where N is the number of times that we visited the field site, which represents the number of times that we could possibly detect movement). To calculate the directionality of movement, we obtained the bearing of each movement for each snake using the Hawth's Tools software for ARCGIS (Beyer, 2004). We grouped the bearings by season for each individual and calculated circular variance, a proxy for directionality, using the software ORIANA, version 2.02 (Kovach Computing Services). The circular variance generated is a number between 0 and 1, with smaller values corresponding to an increase in directionality.

We 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 (Millsbaugh & Marzluff, 2001). We used the methodology recommended to generate KDEs for reptile and amphibian species (Row & Blouin-Demers, 2006). We first generated minimum convex polygons (MCPs) that included all of an individual's known locations within the boundary of the smallest polygon possible. We then created 95% KDEs for each individual by manually adjusting h , the smoothing parameter, until the KDE and the MCP were of similar size. This technique provides an objective method for selecting h , and for generating biologically relevant KDEs for herpetofauna (Row & Blouin-Demers, 2006). All the home ranges were created in the Home Range Tools for ARCGIS (Rodgers *et al.*, 2007).

STATISTICAL ANALYSIS

We analyzed most of our data using general linear models [analysis of variance (ANOVA) or analysis of covariance (ANCOVA)]. The factors included in the linear models were: season (mating versus post-mating), year (2006, 2007, 2008), sex, and individual. Season, year, and sex were modelled as fixed effects. Individual (nested within sex and year) was modelled as a random effect, and F -tests of all main effects and interactions were constructed using the mean square of individuals as the error term. Therefore, we included multiple movement data from each individual in our analyses, although the values from the same individual were averaged in the model to avoid pseudoreplication. When necessary, the movement response variables were transformed to meet assumptions of normality and homoscedasticity. For season and sex (which were the variables of primary interest in our study), we also independently calculated effect size (i.e. Cohen's d), which measures the strength of the relationship between these variables and movement data. Effect sizes are considered small when $d = 0.2$, medium when $d = 0.5$, and large when $d \geq 0.8$ (Cohen, 1988).

Because the behaviour of ectotherms is directly affected by ambient temperature (Huey, 1982; Huey *et al.*, 2009), we included environmental temperature as a covariate in most analyses. We obtained daily mean, minimum, and maximum temperatures from the Nelson Peak weather station (Station ID4814; Clark County Regional Flood Control District, Nevada), located 10 km south-west of the study area. To control for the high correlation among these environmental variables, we performed a principal component analysis of the three daily temperature measurements to generate principal component scores (PC_{Te}). We then used PC_{Te} , which explained 98% of the variance in the three temperature variables, as the environmental covariate in analyses of movement. In all ANCOVA models of movement, we first examined the interactions of PC_{Te} with all class factors (season, sex, year) because the interpretation of these effects using adjusted least squared means is based on the assumption that there is no interaction between class factors and covariates. PC_{Te} did not interact significantly with any class factors. Consequently, we do not report these nonsignificant interactions in the Results.

Finally, we measured the distance to the nearest neighbor for each individual snake at weekly intervals. We then calculated the variance-to-mean ratio of the distances to the nearest neighbour, 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

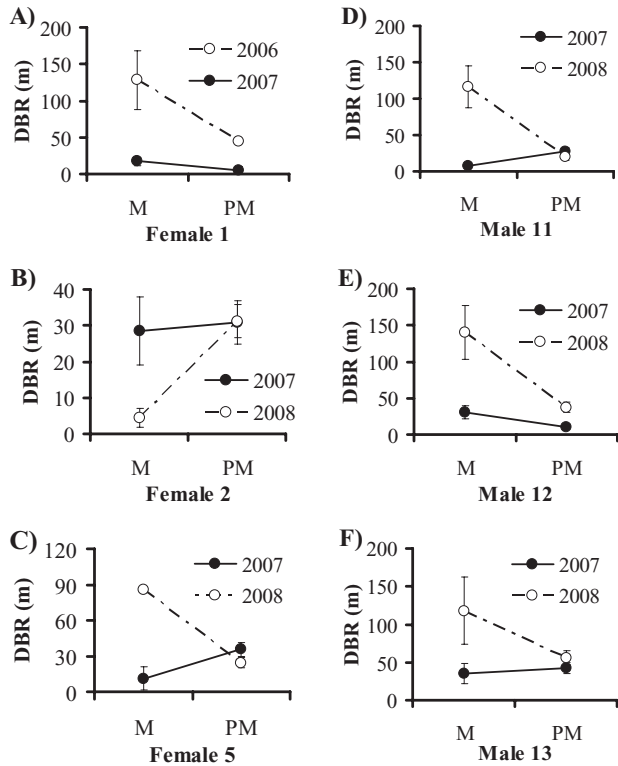


Figure 1. Interannual variation in distance travelled between relocations (approximately 2.5 days) in three female (A, B, C) and three male (D, E, F) *Crotalus mitchellii* that were radiotracked for a full 2 years in the eastern Mojave Desert of southern Nevada, USA. (The remaining 19 snakes were radiotracked for less than 2 years.) ‘M’ and ‘PM’ refer to the mating season and post-mating season, respectively. (In some cases, the SEs associated with the means were very small and are not visible on the figures.)

or smaller than 1 indicate that individuals are clumped or dispersed, respectively. Our objective was not to calculate an absolute estimate of the spatial distribution of *C. mitchellii*, which would require radiotracking the entire or most of the adult population in the study area. Rather, we used the index of dispersion to estimate the spatial distribution of the radiotracked individuals relative to one another, to investigate whether this parameter varied seasonally.

We conducted all statistical analyses using STATISTICA, version 6.0 (StatSoft Inc.) and SAS, version 9.2 (SAS Institute). Values given are means or adjusted least-square (LS) means ± 1 SE, and all reported *P*-values are two-tailed. All *P*-values reported for pairwise comparisons are adjusted using Tukey’s honestly significant difference method. Significance level for all tests was determined at $\alpha = 0.05$.

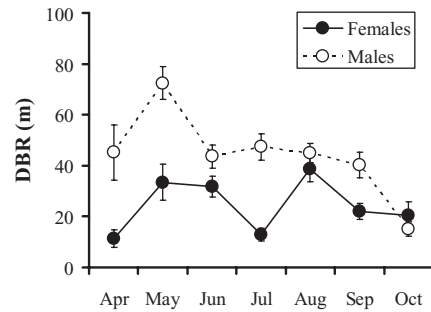


Figure 2. Distance travelled between relocations (m; approximately 2.5 days) per month for male and female *Crotalus mitchellii* for all years combined (2006–08). The values are not adjusted for the effect of environmental temperature on movement.

RESULTS

SPATIAL ANALYSIS

The six individual snakes that we radiotracked for two complete consecutive years (2006–07 and 2007–08) exhibited significant annual differences in distance travelled between relocations (approximately every 2.5 days), specifically during the mating season (Fig. 1). Consequently, we considered that movements of individual snakes were independent between years. Data on distance travelled between relocations by month and by sex for all years combined (2006–08) are illustrated in Figure 2, and standard parameters reported in movement studies (average distance travelled per day, minimum distance per movement, home range size) are presented in Table 1. (We calculated the average distance travelled per day by dividing the total distance travelled by a snake by the number of days that the snake was radiotracked for.)

DBR

The ANCOVA revealed that DBR was positively related to environmental temperature, as measured by PC_{Te} ($\beta = 12.5$, $P < 0.0001$; Table 2). Season, sex, and year significantly affected DBR (Table 2). Snakes had greater DBR in the mating season compared to the post-mating season (LS means \pm SE; mating: 58.8 ± 3.4 m; post-mating: 24.7 ± 2 m; $P < 0.0001$; Cohen’s $d = 0.78$), and males travelled longer DBR than females (males: 53.8 ± 2.5 m; females: 29.7 ± 3.1 m; $P < 0.0001$; Cohen’s $d = 1.1$). Both sexes increased DBR during the mating season, relative to the post-mating season (males: mating: 77.7 ± 3.7 m; post-mating: 29.8 ± 2.8 m; $P < 0.0001$; females: mating: 39.9 ± 5.4 m; post-mating: 19.5 ± 2.8 m; $P = 0.007$). Males exhibited longer DBR than females in the mating ($P < 0.0001$) and post-mating seasons ($P = 0.01$). DBR was greater in 2006 (50.2 ± 3.2 m) and 2008 (48.3 ± 3.2 m) compared to 2007

Table 1. Movement parameters of *Crotalus mitchellii* during a 3-year period (2006–08) in the eastern Mojave Desert of southern Nevada, USA

Movement	Mating (range)	Post-mating (range)	Overall (range)
Average distance travelled per day (m)			
All individuals ($N = 40$)	26.2 ± 19.4 (2.1–63.4)	13.7 ± 9.1 (0.3–33.9)	16.1 ± 9.1 (3.0–38.2)
Males ($N = 29$)	30.2 ± 19.2 (2.3–63.4)	15.2 ± 9.9 (0.3–33.9)	18.0 ± 9.2 (3.1–38.2)
Females ($N = 11$)	16.8 ± 17.4 (2.1–53.9)	10.6 ± 6.0 (1.9–22.1)	11.2 ± 6.9 (3.0–26.1)
Minimum distance per movement (m)			
All individuals ($N = 40$)	101.0 ± 57.0 (8.7–221.9)	58.3 ± 32.4 (4.3–145.3)	70.0 ± 31.7 (17.4–155.1)
Males ($N = 29$)	115.9 ± 54.5 (12.0–221.9)	63.0 ± 36.3 (4.3–145.3)	77.6 ± 32.5 (26.4–155.1)
Females ($N = 11$)	66.3 ± 48.3 (8.7–157.6)	47.8 ± 18.4 (20.6–80.7)	50.0 ± 18.8 (17.4–78.4)
Home range size (ha)			
All individuals	7.2 ± 9.0 (24) (0.07–29.5)	9.4 ± 8.9 (25) (0.06–30.5)	15.0 ± 14.8 (25) (0.9–60.3)
Males	9.7 ± 9.4 (15) (0.07–29.5)	12.3 ± 10.1 (15) (0.8–30.5)	19.0 ± 15.8 (16) (0.9–60.3)
Females	3.0 ± 7.1 (9) (0.1–22.05)	5.1 ± 4.7 (10) (0.06–16.5)	8.0 ± 10.3 (9) (1.05–34.7)

The movement parameters gathered on an individual snake over several years were considered independent (see Results). Numbers in parenthesis represent the 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. Because, for the home range analysis, the number of radiotracked snakes varied according to season, sample size is reported in parenthesis next to the season-specific values. Values represent the mean \pm SD.

(26.7 ± 3.1 m; pairwise comparisons; 2006–07: $P < 0.0001$; 2006–08: $P = 0.88$; 2007–08: $P < 0.0001$).

and 2008 (73 ± 4.6 m; pairwise comparisons; 2006–07: $P < 0.0001$; 2006–08: $P = 0.25$; 2007–08: $P = 0.002$).

DPM

PC_{Tb} affected DPM ($\beta = 9.6$, $P = 0.04$; Table 2). Sex, season, and year affected DPM (Table 2). Snakes had higher DPM in the mating season compared to the post-mating season (LS means \pm SE; mating: 89.8 ± 5.4 m; post-mating: 47.8 ± 3.4 m; $P = 0.003$; Cohen's $d = 0.7$), and males travelled longer distances than females overall (males: 86.2 ± 3.7 m; females: 51.5 ± 5 m; $P < 0.0001$; Cohen's $d = 1.3$). Males significantly increased DPM in the mating season compared to the post-mating season (mating: 116.8 ± 5.9 m; post-mating: 55.5 ± 4.6 m; $P < 0.0001$), as did females (mating: 62.8 ± 8.6 m; post-mating: 40.1 ± 5 m; $P = 0.02$). Males travelled longer DPM than females in the mating season ($P < 0.0001$) but not in the post-mating season ($P = 0.09$). The year effect on DPM was caused by the decreased movement of snakes in 2007 (49.9 ± 5.5 m) compared to 2006 (83.4 ± 5 m)

Minimum movement frequency

Movement frequency was positively related to environmental temperature ($\beta = 0.2$, $P < 0.0001$; Table 2). Season and year affected movement frequency (Table 2). Movement frequency was higher in the mating season than in the post-mating season (arcsine-transformed LS mean number of movements per 2 weeks \pm SE; mating: 0.9 ± 0.05 ; post-mating: 0.6 ± 0.03 ; $P < 0.0001$; Cohen's $d = 0.82$). Both sexes increased movement frequency during the mating season (males: mating: 1 ± 0.05 ; post-mating: 0.6 ± 0.03 ; $P < 0.0001$; females: mating: 0.8 ± 0.08 ; post-mating: 0.5 ± 0.04 ; $P = 0.001$). The similar frequency of movement between males and females in the mating ($P = 0.1$) and post-mating seasons ($P = 0.32$) resulted in a lack of sexual effect (males: 0.8 ± 0.03 ; females: 0.7 ± 0.04 ; $P = 0.11$; Cohen's $d = 0.5$). Consistent with the other movement vari-

Table 2. Analysis of covariance of distance travelled between relocations (DBR, m; approximately every 2.5 days), distance travelled per movement (DPM, m), and arcsine-transformed movement frequency (during a 2-week period) of *Crotalus mitchellii* in the eastern Mojave Desert of southern Nevada, USA

Source	d.f.	MS	<i>F</i>	<i>P</i>
DBR (error d.f. = 39; number of observations = 2472)				
PC _{Te}	1	359677	21.2	< 0.0001
Season	1	372793	21.9	< 0.0001
Sex	1	188962	11.1	0.002
Year	2	229100	6.74	0.003
Season × Sex	1	65297	3.8	0.06
DPM (error d.f. = 39; number of observations = 1313)				
PC _{Te}	1	96990	4.6	0.04
Season	1	272982	13	0.0009
Sex	1	232751	11	0.002
Year	2	103325	4.9	0.01
Season × Sex	1	69481	3.31	0.08
Movement frequency (error d.f. = 39; number of observations = 774)				
PC _{Te}	1	34.3	66	< 0.0001
Season	1	12.71	24.41	< 0.0001
Sex	1	1.38	2.66	0.11
Year	2	6	5.8	0.006
Season × Sex	1	0.3	0.6	0.44

We used a principal component value of environmental temperatures (PC_{Te}) 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 (MS) of variation among individual snakes as the error term to avoid pseudoreplication.

ables, frequency of movement was higher in 2006 (0.8 ± 0.04) and 2008 (0.8 ± 0.03) compared to 2007 (0.6 ± 0.04 ; pairwise comparisons: 2006–07: $P = 0.005$; 2006–08: $P = 0.28$; 2007–08: $P < 0.0001$).

Directionality

The number of relocations (i.e. the number of vectors per individual) was positively correlated to circular variance ($\beta = 0.01$; $P = 0.005$), and thus we entered this variable as a covariate in the model. Because directionality was not affected by year ($F_{2,64} = 0.2$, $P = 0.77$), we removed this factor from the model. Sex (mean circular variance \pm SE: males: 0.7 ± 0.03 ; females: 0.6 ± 0.04 ; $F_{1,64} = 0.4$, $P = 0.52$) and season (mating season: 0.6 ± 0.04 ; post-mating season: 0.7 ± 0.04 ; $F_{1,64} = 0.2$, $P = 0.62$) did not affect directionality. However, we detected a sex \times season interaction ($F_{1,64} = 5.8$, $P = 0.02$) because female movement patterns were more directional than males' in the mating season (males: 0.7 ± 0.04 ; females: 0.6 ± 0.06 ; $t = 2.1$, $N = 33$, $P = 0.02$) but not in the post-mating season (males: 0.6 ± 0.04 ; females: 0.7 ± 0.06 ; $t = 0.8$, $N = 35$, $P = 0.19$).

Home ranges

We investigated whether annual home range size (95% kernels) varied between the sexes. Body size (SVL;

$F_{1,24} = 2.3$, $P = 0.14$) and number of radiotracking days ($N_{\text{radiotracking d}}$; $F_{1,24} = 2.7$, $P = 0.11$) did not affect home range size, and we therefore excluded these variables from the analysis. The ANOVA indicated that males had larger annual home ranges than females (males: 1.1 ± 0.09 ha; females: 0.6 ± 0.1 ha; $F_{1,31} = 7.1$; $P = 0.01$), and that year marginally affected home range size ($F_{2,31} = 3.0$, $P = 0.07$). We also investigated whether home range size varied by sex in the mating and post-mating seasons. Because the covariate ($N_{\text{radiotracking d}}$) significantly interacted with season ($F_{1,60} = 4.4$, $P = 0.05$), we conducted separate analyses for the mating and post-mating seasons. The analyses showed that $N_{\text{radiotracking d}}$ affected home range size in both seasons (mating season: $\beta = 0.03$, $F_{1,34} = 7.4$, $P = 0.01$; post-mating season: $\beta = 0.01$, $F_{1,31} = 13.6$, $P = 0.001$), and that males had larger home ranges than females in both seasons (log-transformed LS mean home range size \pm SE; mating season: males: 0.3 ± 0.1 ; females: -0.4 ± 0.2 , $F_{1,34} = 7.6$, $P = 0.01$; post-mating season: males: 0.7 ± 0.1 , females: 0.1 ± 0.2 ; $F_{1,31} = 6.1$, $P = 0.02$). The home ranges of males did not differ in size between seasons (mating season: 0.7 ± 0.1 ; post-mating season: 0.8 ± 0.1 ; $F_{1,27} = 0.6$, $P = 0.44$), despite the fact that the post-mating season is much longer (approximately 5 months) than the mating season (approximately 1.5 months).

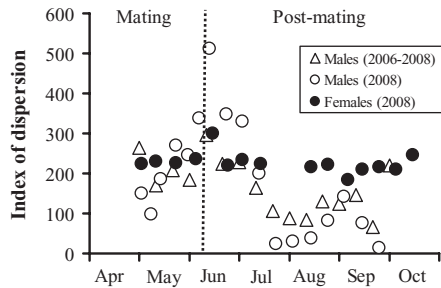


Figure 3. Index of dispersion of male (2006–08 combined and 2008 only) and female (2008 only) *Crotalus mitchellii* as a function of time of the year. Values greater than 1 indicate that the snakes exhibit a clumped distribution. The dashed line separates the mating season from the post-mating season.

Spatial distribution

We calculated the spatial distribution of males and females over time using the index of dispersion, I . For males, we conducted two analyses, one combining all years of the study (2006–08), and one for 2008 only. We performed an analysis of male spatial distribution for 2008 to specifically compare the distribution of males and females during the same year, because we could only calculate I for females in 2008 (the year during which we radiotracked the largest number of females, $N = 5$). Overall, males and females were clumped year-round (all values were statistically different from 1 at $P \leq 0.05$; Fig. 3). 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, and this pattern was similar when analyzing all years combined (2006–08) or 2008 only. By contrast, we observed no seasonal change in the spatial distribution of females.

MOVEMENT PARAMETERS, BODY SIZE, AND MATE ACQUISITION

We investigated how the total distance travelled by males within the mating season correlated with the number of known accompanied females. Using the residual scores of the linear regression of distance travelled on number of days monitored as the predictor variable, we found no statistically significant relationship between distance travelled by males and number of known accompanied females ($r^2 = 0.1$, $F_{1,21} = 2.2$, $P = 0.15$). However, the only two males that we observed with more than one female within a single mating season were those that travelled the longest distances. We found a significant positive relationship between male body size (SVL) and the number of known females that males

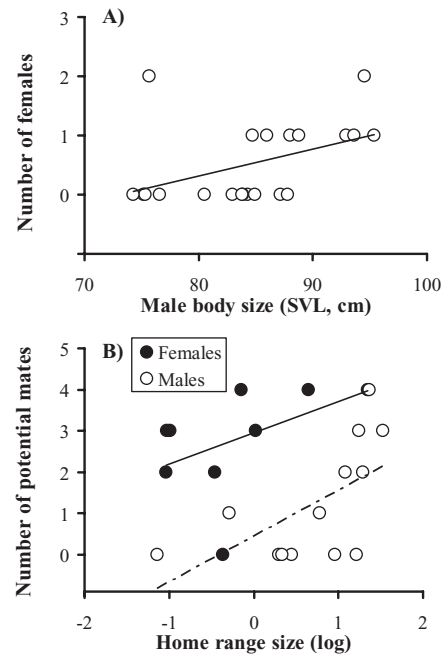


Figure 4. The relationship between (A) body size (snout-vent length, cm) of *Crotalus mitchellii* males and the number of accompanied females ($r^2 = 0.19$, $F_{1,19} = 4.6$; $P = 0.04$), and between (B) the number of potential mates for male and female *Crotalus mitchellii* and (log-transformed) home range size. 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.

were found with ($r^2 = 0.2$, $F_{1,19} = 4.6$, $P = 0.04$; Fig. 4A).

We assessed whether sex and home range size affected the number of known potential mates during the mating season. (We only included snakes that were radiotracked for at least 80% of the mating season in this analysis.) We performed a linear regression of 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: $r^2 = 0.6$, $F_{1,12} = 16.5$, $P = 0.001$; Fig. 4B). We found no such statistical relationship for females ($r^2 = 0.2$, $F_{1,7} = 1.5$, $P = 0.25$; Fig. 4B). The intercept of the latter two regression lines was significantly different from the origin for females ($F_{1,7} = 29.4$, $P = 0.0009$) but not for males ($F_{1,12} = 2.7$, $P = 0.12$; Fig. 4B). 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 ($F_{3,18} = 17.2$, $P = 0.0006$; Fig. 4B).

BEHAVIOURAL INTERACTIONS

Most male–female interactions occurred in spring, from 20 April to 6 June (male–female accompaniment: $N = 16$; courting behaviour: $N = 4$; mating behaviour: $N = 1$). On two occasions in Autumn 2006 (25 September, 6 October), we 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, these interactions did not necessarily reflect sexual activity.

We 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 copulating with Female 2 (71.7 cm SVL, 313.5 g) when she was being courted by a smaller male (Male 18, 76.5 cm SVL, 330 g). In general, males appeared to compete for access to the few sexually receptive females. For example, on 26 April 2007 we caught Male 13 (88 cm SVL, 551 g) moving around the refuge of Female 5 (77.8 cm SVL, 444 g). On 29 April 2007, Female 5 had not moved, and we found the large Male 15 coiled at the entrance of her refuge. On 1 May 2007, Female 5 still had not moved, and another large male, Male 16 (92.9 cm SVL, 649.3 g) was coiled at the entrance of her refuge. In summary, we found three different males at the entrance of the refuge of Female 5 over three consecutive visits to our field site, although she only spent time (17 days) under a boulder with Male 15, the largest male. One instance of male–male combat was observed on our study area, on 28 April 2007 (R. McKeever, pers. comm.).

DISCUSSION

We 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 activities. Below, we first summarize and discuss how space use varies intrasexually between seasons and intersexually within seasons in *C. mitchellii*. We then discuss our findings in a comparative framework to better understand the ecological factors contributing to the evolution of the mating system of *C. mitchellii*.

HYPOTHESIS 1: INTRASEXUAL VARIATION IN MOVEMENT BETWEEN SEASONS

The present study demonstrates that the spatial ecology of *C. mitchellii* varies by biologically-relevant seasons. Both sexes exhibited higher activity in the mating season compared to the post-mating season. Accordingly, our prediction that males increase movement per unit time in the mating season compared to the post-mating season was supported. However, we did not predict that females would also increase

movement in the mating season. We discuss the intra-sexual variation in movement between seasons for males and females separately.

Males

Males increased 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 (approximately 1.5 months) is considerably shorter than the post-mating season (approximately 5 months). Additionally, we documented that males with larger home ranges had a significantly higher number of potential mating partners. 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 & Oring, 1977; Duvall, Schuett & Arnold, 1993; Arnold & Duvall, 1994). Males increase their fitness by mating with multiple females, which allows them to produce more offspring. 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 & Macdonald, 1994), and snakes (Madsen *et al.*, 1993; Brown & Weatherhead, 1999; Weatherhead *et al.*, 2002), supports the hypothesis that increased movement by males enhances their reproductive success. The data obtained in the present study 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, we detail the evidence that corroborates this hypothesis.

For the 3-year period (2006–08) of the present study we have direct evidence (i.e. observation of female with her offspring) of only one female reproductive event. Therefore, female *C. mitchellii* produce offspring infrequently, a conclusion supported by the low frequency of vitellogenic or pregnant *C. mitchellii* females found in museum collections (X. Gludas, unpubl. data). Although the reproductive frequency observed in this study is low, females of most rattlesnake species reproduce at most biennially (Aldridge & Duvall, 2002; Gludas, Goldberg & Hamilton, 2009), and triennial or longer cycles are well-documented (Gibbons, 1972; Martin, 2002; Jenkins, 2007). The infrequent reproduction of female *C. mitchellii* results in a highly male-biased operational sex ratio, which promotes male–male competition for access to females (Emlen & Oring, 1977; Madsen & Shine, 1993). This prediction is supported by our behavioural observations because we often observed multiple males in the vicinity of a single

female, and because male–male combat occurs in our study population. (We only observed 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, but also they need to fight off rival males. In conclusion, because reproductively active females are a limiting resource, increased movement by *C. mitchellii* males and associated behaviours, such as intrasexual contests, possibly enhance male fitness by increasing female encounter rate and acquisition.

Females

Females increased distance travelled per movement and movement frequency in the mating season, which resulted in an increase in distance travelled per unit time. The increase in female movement may be 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 (approximately 5 months) during which they did not feed. Second, in most animals, including *C. mitchellii*, mate-searching activities are typically performed by males (see Hypothesis 2 below), which reduces the investment needed by females to find mates (Hammerstein & Parker, 1987; Kokko & Wong, 2007). Third, female *C. mitchellii* reproduce infrequently, which implies that many females may not exhibit sexually-driven behaviour in a given year.

Nevertheless, at least seven of nine females radiotracked throughout the mating season (including three individuals radiotracked for two mating seasons) were accompanied by males for extended periods of time (mean \pm SD: 10 ± 4.3 days; X. Glaudas, unpubl. data), suggesting that mating may have occurred. Interestingly, six of these seven females apparently 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 after the mating event. Alternatively, females may benefit from mating in years when they do not

reproduce because female rattlesnakes can store sperm for extended periods of time (Schuett, 1992). This behaviour may promote sperm competition (multiple paternities are common in snakes; Uller & Olsson, 2008), and/or provide a larger pool of sires if females can cryptically choose sperm. Thus, reproductive behaviour may be partly responsible for the increased movement of females during the mating season (see below).

HYPOTHESIS 2: SEXUAL VARIATION IN MOVEMENT PATTERNS WITHIN SEASONS

Male *C. mitchellii* exhibited increased DBR and DPM relative to females in the mating season, although movement frequency was similar between the sexes. Overall, these observations were consistent with our prediction that, compared to females, males increase movements during the mating season. Furthermore, we predicted that if males and females fundamentally differ in spatial ecology, the sexes should also exhibit variation in movement patterns during the non-mating season, when they are not engaged in reproductive activities. Indeed, the sexual differences in spatial ecology observed in the mating season persisted throughout the post-mating season. This finding suggests that the sexual difference in movement patterns is not only a result of the mating system, but also that sex *per se* also affects the spatial ecology of *C. mitchellii*. Below, we discuss the sexual difference in movement for the mating and post-mating seasons separately.

Mating season

Male *C. mitchellii* travelled 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. Coupled with our field observations, this finding indicates that males actively locate females, a conclusion further supported by the sexual difference in the intercept of the regression lines of number of potential mates versus home range size (Fig. 4B). That is, 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 & Alcock, 1983; Jellen *et al.*, 2007; Odden & Wegge, 2007). This ubiquitous pattern is well-supported by theoretical models for

systems in which sperm competition occurs (Kokko & Wong, 2007), a condition that likely exists in our system. Multiple matings and paternities may be the rule rather than the exception in snakes (Uller & Olsson, 2008). Although there is no direct evidence that this is the case in *C. mitchellii*, the typical mate-guarding behaviour exhibited by males (X. Glaudas, pers. observ.) indicates the potential for sperm competition and multiple paternities in this species.

However, sex role theory predicts that females may invest time and/or energy in mate-searching if the associated costs are low (Kokko & Wong, 2007). This is likely the case in our system because males appears readily available during the mating season, and thus the costs of finding mates for females are probably low. As previously noted, 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 & Alcock, 1983: 65). Females may invest in mating effort not necessarily by actively looking for males but, instead, by increasing the odds that they are detected by males. For example, 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; Schwenk, 1994). 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 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 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. The latter idea is supported by computer-based simulations of optimal search strategies. When an individual is located within a resource-rich patch (in our case, a den site where females are aggregated), the random directionality of movement increases resource detection by decreasing the likelihood that searchers (i.e. males) exit the patch (Duvall *et al.*, 1997; Benhamou, 2007).

Post-mating season

DBR was significantly higher in males than in females. As a result, males had larger home ranges than females during the post-mating season, and

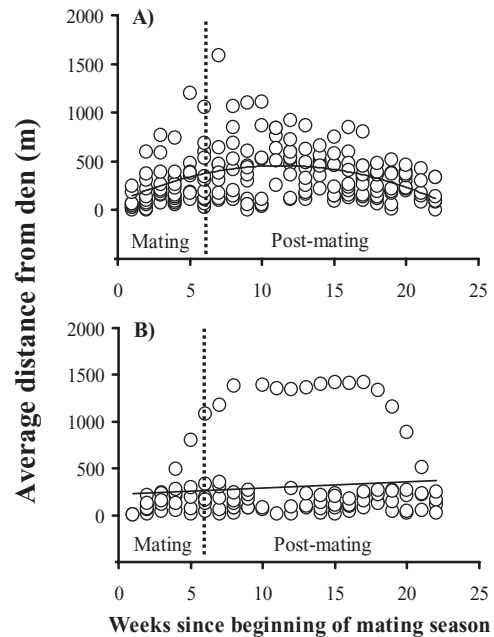


Figure 5. The average distance from the den for (A) male and (B) female *Crotalus mitchellii* as a function of time of the year. Each datum represents the weekly average for each individual. Trend lines are included for clarity only and are not regression lines. The point of reference of the x-axis, 1, is our estimated first week of the mating period (20–27 April), and each consecutive number is a subsequent week, in chronological order. The vertical dashed lines separate the mating season from the post-mating season.

females stayed relatively close to hibernacula, whereas males ventured much farther away from the dens (Fig. 5). The factor(s) responsible for this sexual difference remain unknown, although they may be related to predation pressure. During the course of the present study, seven (six males, one female) of the 25 snakes we radiotracked were eaten by predators. This translated into a higher, although not statistically different, average annual mortality rate as a result of predation for males (21.8%) than for females (8.4%; $\chi^2 = 0.75$, d.f. = 1, $P = 0.38$). Unexpectedly, and in contrast to other snake studies (Aldridge & Brown, 1995; Bonnet, Naulleau & Shine, 1999), all these predation events occurred during the non-mating season. Consequently, the decreased movement of *C. mitchellii* females may be a mechanism to reduce predation because evidence suggests that site fidelity and reduced activity decrease predator-induced mortality (Yoder, Marschall & Swanson, 2004; Sperry & Weatherhead, 2009). However, this hypothesis does not explain why males have larger home ranges than females in the post-mating season, unless males trade-off predation risk for increased foraging opportunities.

ECOLOGICAL IMPLICATIONS FOR THE
EVOLUTION OF MATING SYSTEMS

Strong male–male competition is a component of many snake mating systems. For example, in a summer-breeding species, the prairie rattlesnake (*Crotalus viridis*), males travel long distances to locate reproductive females, which are scattered over the landscape, because snakes have already left the den sites when the mating season starts (Duvall & Schuett, 1997). In this mating system, named ‘prolonged mate-searching polygyny,’ males engage in scramble competition to locate potential mates (i.e. the first male that locates a female has a mating advantage). Because competing *C. viridis* males rarely encounter each other, male–male combat is absent or reduced, and mate-locating abilities are apparently 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-defence polygyny strategy, in which males physically fight for access to females. Similarly, the mating system of *C. mitchellii* is intermediate between these two strategies because males move extensively in search of females and male–male combat occurs.

One critical aspect of the mating system of *C. mitchellii* that differs from those described above is that females are clumped during the mating season (Fig. 3). Similar to many snakes from temperate regions (Gregory, 1982), *C. mitchellii* aggregates in rock outcrops to overwinter (X. Glaudas, unpubl. data). Upon emerging from hibernation in spring, snakes are clustered in space, a characteristic that has strong implications for their mating system, because *C. mitchellii* is one of only two rattlesnakes (of more than 30 currently recognized species; Campbell & Lamar, 2004) known to only mate in spring (Aldridge & Duvall, 2002). (The red diamond rattlesnake, *Crotalus ruber*, is the other species known to exclusively mate in spring; Dugan, Figueroa & Hayes, 2008.) Theoretical models and empirical data support the contention that a clumped and predictable spatiotemporal distribution of females promotes male–male encounters, and therefore intensifies interference competition (i.e. aggressive physical interactions; Emlen & Oring, 1977; Clutton-Brock, 1989). Our observations are consistent with this hypothesis because male–male interactions in

C. mitchellii are apparently common, and males fight to gain access to females.

Why do *C. mitchellii* males engage in prolonged mate-searching activities given that females are aggregated, and that males are in the vicinity of females at the start of the mating season? Our 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 those females. Therefore, males likely invest considerable time and effort visiting den sites to locate potential mates. For smaller males, the challenge is even harder because locating females does not guarantee reproduction in that larger males typically defeat smaller ones during male–male combats for access to females (Madsen *et al.*, 1993; Greene, 1997; Schuett, 1997). Overall, the mating system of *C. mitchellii* appears more similar to the distantly-related European adder (*Vipera berus*) than to other rattlesnake species. Similar to *C. mitchellii*, *V. berus* mates only in spring, and females are 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 fight for access to females. The similar mating system of these two distantly-related viperid snakes suggests that mating phenology may affect organismal mating systems via the spatiotemporal distribution of potential mates, which can possibly lead to convergent evolution of mating systems.

CONCLUSIONS

The present study shows that time of the year (mating versus post-mating season) and sex affect the movement ecology of *C. mitchellii*. Males actively locate females, which are clumped around den sites during the mating season. The low reproductive rate of females, combined with their clumped distribution, increase male–male competition for access to females, and sexual selection seemingly acts on two male phenotypic traits: investment in mate-searching activities (which increase female encounter rate) and male body size (because larger males are more likely to acquire and defend a female partner against other males). The findings of the present study demonstrate that combining quantitative spatial analyses and behavioural observations in an explicit temporal context can provide valuable insights about the ecological factors shaping the evolution of organismal mating systems.

ACKNOWLEDGEMENTS

We thank D. B. Thompson, R. N. Reed, M. M. Elenich, and T. C. Piechota for their help throughout

the various stages of this study, V. Sarukhanov, J. S. Sutton, M. E. Moon, and W. G. Masters for assisting with surgical procedures, and A. M. Ambos, R. W. Bryson Jr, M. E. Eckstut, B. T. Hamilton, A. L. Heindl, T. Jezkova, S. D. Jones, J. M. García, A. Martinson, R. W. McKeever, S. A. Neiswenter, G. P. Robinson, R. N. Reed, G. Sauthier, C. M. Vaughn, M. M. Webber, P. E. Weintraub, and A. B. Williams for field assistance. This project was completed as a part of X. Glaudas' dissertation research at the University of Nevada, Las Vegas (UNLV), and conducted under IACUC permit R701-0306-207. Specimens were collected under scientific research permits S29820 and NV-052-UA-06-010 issued by the Nevada Department of Wildlife and the Bureau of Land Management, respectively. This research was partly funded by a grant from the National Science Foundation (EPS-0447416) to J.A.R.R., and by the President's Graduate Fellowship, the Hermsen Fellowship, Graduate Research Training Assistantships, Summer Session Scholarships, and Graduate and Professional Student Association Grants to X.G.

REFERENCES

- Aldridge RD, Brown WS. 1995.** Male reproductive cycle, age at maturity and cost of reproduction in the timber rattlesnake (*Crotalus horridus*). *Journal of Herpetology* **29**: 399–407.
- Aldridge RD, Duvall D. 2002.** Evolution of the mating season in the pitvipers of North America. *Herpetological Monograph* **16**: 1–25.
- Andersson M. 1994.** *Sexual selection*. Princeton, NJ: Princeton University Press.
- Arnold SJ, Duvall D. 1994.** Animal mating systems: a synthesis based on selection theory. *American Naturalist* **143**: 317–348.
- Bateman AJ. 1948.** Intrasexual selection in *Drosophila*. *Heredity* **2**: 349–368.
- Benhamou S. 2007.** How many animals really do the Lévy walks? *Ecology* **88**: 1962–1969.
- Beyer HL. 2004.** *Hawth's analysis tools for ArcGIS*. Available at: <http://www.spatial ecology.com/htools>
- Bolstad P. 2005.** *GIS fundamentals: a first text on geographic information systems*. White Bear Lake, MN: Eider Press.
- Bonnet X, Naulleau G. 1996.** Are body reserves important for reproduction in male dark green snakes (Colubridae: *Coluber viridiflavus*)? *Herpetologica* **52**: 137–146.
- Bonnet X, Naulleau G, Shine R. 1999.** The dangers of leaving home: dispersal and mortality in snakes. *Biological Conservation* **89**: 39–50.
- Brattstrom BH. 1965.** Body temperatures of reptiles. *American Midland Naturalist* **73**: 376–422.
- Brown GP, Weatherhead PJ. 1999.** Female distribution affects mate searching and sexual selection in male northern water snakes (*Nerodia sipedon*). *Behavioral Ecology and Sociobiology* **47**: 9–16.
- Campbell JA, Lamar WW. 2004.** *The venomous reptiles of the Western Hemisphere*, Vol. 2. Ithaca, NY: Cornell University Press.
- Carfagno GL, Weatherhead PJ. 2008.** Energetics and space use: intraspecific and interspecific comparisons of movements and home ranges of two colubrid snakes. *Journal of Animal Ecology* **77**: 416–424.
- Chamaillé-Jammes S, Fritz H, Valeix M, Murindagomo F, Clobert J. 2008.** Resource variability, aggregation and density dependence in an open context: the local regulation of an African elephant population. *Journal of Animal Ecology* **77**: 135–144.
- Clutton-Brock TH. 1989.** Mammalian mating systems. *Proceedings of the Royal Society of London Series B, Biological Sciences* **236**: 339–372.
- Cohen J. 1988.** *Statistical power analysis for the behavioral sciences*. Hillsdale, NJ: Lawrence Earlbaum Associates.
- Darwin CR. 1859.** *On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life*. London: John Murray.
- Darwin CR. 1871.** *The descent of man and selection in relation to sex*. London: John Murray.
- Dugan EA, Figueroa A, Hayes WK. 2008.** Home range size, movements, and mating phenology of sympatric red diamond (*Crotalus ruber*) and southern Pacific (*C. oreganus helleri*) rattlesnakes in southern California. In: Hayes WK, Beaman KR, Cardwell MD, Bush SP, eds. *Biology of the rattlesnakes*. Loma Linda, CA: Loma Linda University Press, 353–364.
- Duvall D, Schuett GW. 1997.** Straight-line movement and competitive mate searching in prairie rattlesnakes, *Crotalus viridis viridis*. *Animal Behaviour* **54**: 329–334.
- Duvall D, Schuett GW, Arnold SJ. 1993.** Ecology and evolution of snake mating systems. In: Seigel RA, Collins JT, eds. *Snakes: ecology and behavior*. Caldwell, ID: Blackburn Press, 165–200.
- Duvall D, Chiszar D, Mintzer RA, Roster NO. 1997.** Experimental simulation in behavioral ecology: a multimedia approach with the spatial searching simulation RattleSnake[®]. *Experimental Biology Online* **2**: 16.
- Emlen ST, Oring LW. 1977.** Ecology, sexual selection, and the evolution of mating systems. *Science* **197**: 215–223.
- Gartner GEA, Reiserer R. 2003.** *Crotalus mitchellii*. Mating. *Herpetological Review* **34**: 65.
- Gaulin SJC, FitzGerald RW. 1986.** Sex differences in spatial ability: an evolutionary hypothesis and test. *American Naturalist* **127**: 74–88.
- Gaulin SJC, FitzGerald RW. 1988.** Home range size as a predictor of mating systems in *Microtus*. *Journal of Mammalogy* **69**: 311–319.
- Gaulin SJC, FitzGerald RW. 1989.** Sexual selection for spatial-learning ability. *Animal Behaviour* **37**: 322–331.
- Gibbons JW. 1972.** Reproduction, growth, and sexual dimorphism in the canebrake rattlesnake (*Crotalus horridus atricaudatus*). *Copeia* **1972**: 222–226.
- Gibbons JW, Semlitsch RD. 1987.** Activity patterns. In: Seigel RA, Collins JT, Novak SS, eds. *Snakes: ecology and evolutionary biology*. New York, NY: McGraw-Hill, 396–421.

- Glaudas X. 2009.** Rain harvesting in the southwestern speckled rattlesnake (*Crotalus mitchellii pyrrhus*). *Southwestern Naturalist* **54**: 518–521.
- Glaudas X, Goldberg SR, Hamilton BT. 2009.** Timing of reproduction of a cold desert viperid snake from North America, the Great Basin rattlesnake (*Crotalus lutotus*). *Journal of Arid Environments* **73**: 719–725.
- Goldberg SR. 2000.** Reproduction in the speckled rattlesnake, *Crotalus mitchellii* (Serpentes: Viperidae). *Bulletin of the Southern California Academy of Sciences* **99**: 101–104.
- Greenberg DB, McClintock WJ. 2008.** Remember the third dimension: terrain modeling improves estimates of snake home range. *Copeia* **2008**: 801–806.
- Greene HW. 1992.** The ecological and behavioral context for pitviper evolution. In: Campbell JA, Brodie ED Jr, eds. *Biology of the pitvipers*. Tyler, TX: Selva, 107–118.
- Greene HW. 1997.** *Snakes: the evolution of mystery in nature*. Berkeley, CA: University of California Press.
- Greene HW, May PG, Hardy Sr. DL, Sciturrro JL, Farrell TM. 2002.** Parental behavior by vipers. In: Schuett GW, Höggren M, Douglas ME, Greene HW, eds. *Biology of the vipers*. Eagle Mountain, UT: Eagle Mountain Publishing, 179–206.
- Gregory PT. 1982.** Reptilian hibernation. In: Gans C, Pough FH, eds. *Biology of the Reptilia*, Vol. 13. *Physiological ecology*. London: Academic Press, 53–154.
- Hammerstein G, Parker GA. 1987.** Sexual selection: games between the sexes. In: Bradbury JW, Andersson MB, eds. *Sexual selection: testing the alternatives*. Chichester: Wiley, 119–142.
- Huey RB. 1982.** Temperature, physiology, and the ecology of reptiles. In: Gans C, Pough FH, eds. *Biology of the Reptilia*, Vol. 12. *Physiology*. London: Academic Press, 25–91.
- Huey RB, Deutsch CA, Tewksbury JJ, Vitt LJ, Hertz PE, Álvarez Pérez HJ, Garland Jr. T. 2009.** Why tropical forest lizards are vulnerable to climate warming? *Proceedings of the Royal Society of London Series B, Biological Sciences* **276**: 1–10.
- Ims RA. 1988.** Spatial clumping of sexually receptive females induces space sharing among male voles. *Nature* **335**: 541–543.
- Jellen BC, Shepard DB, Dreslik MJ, Phillips CA. 2007.** Male movement and body size affect mate acquisition in the eastern massasauga. *Journal of Herpetology* **41**: 451–457.
- Jenkins CL. 2007.** Ecology and conservation of rattlesnakes in a sagebrush steppe ecosystems: landscape disturbance, small mammal communities, and Great Basin rattlesnake reproduction. PhD Thesis, Idaho State University, Pocatello.
- King MB, Duvall D. 1990.** Prairie rattlesnake seasonal migrations: episodes of movement, vernal foraging and sex differences. *Animal Behaviour* **39**: 924–935.
- Klauber LM. 1972.** *Rattlesnakes: their habits, life histories, and influence on mankind*. Berkeley, CA: University of California Press.
- Kokko H, Rankin DJ. 2006.** Lonely hearts or sex in the city? Density-dependent effects in mating systems. *Philosophical Transactions of the Royal Society of London Series B* **361**: 319–334.
- Kokko H, Wong BBM. 2007.** What determines sex roles in mate searching? *Evolution* **61**: 1162–1175.
- Komers PE, Brotherton PNM. 1997.** Female space use is the best predictor of monogamy in mammals. *Proceedings of the Royal Society of London Series B, Biological Sciences* **264**: 1261–1270.
- Krebs CJ. 1999.** *Ecological methodology*. Menlo Park, CA: Benjamin/Cummings.
- MacArthur RH, Pianka ER. 1966.** On optimal use of a patchy environment. *American Naturalist* **100**: 603–609.
- Madsen T, Shine R. 1993.** Temporal variability in sexual selection acting on reproductive tactics and body size in male snakes. *American Naturalist* **141**: 167–171.
- Madsen T, Shine R. 2000.** Energy vs. risk: costs of reproduction in free-ranging pythons in tropical Australia. *Austral Ecology* **25**: 670–675.
- Madsen T, Shine R, Loman J, Håkansson T. 1993.** Determinants of mating success in male adders, *Vipera berus*. *Animal Behaviour* **45**: 491–499.
- Martin WH. 2002.** Life history constraints on the timber rattlesnake (*Crotalus horridus*) at its climatic limits. In: Schuett GW, Höggren M, Douglas ME, Greene HW, eds. *Biology of the vipers*. Eagle Mountain, UT: Eagle Mountain Publishing, 285–306.
- Mason RT. 1992.** Reptilian pheromones. In: Gans C, Crews D, eds. *Biology of the Reptilia*, Vol. 18. *Hormones, brain and behavior*. Chicago, IL: University of Chicago Press, 144–228.
- Millsbaugh JJ, Marzluff JM. 2001.** *Radio tracking and animal populations*. San Diego, CA: Academic Press.
- O'Donnell RP, Shine R, Mason RT. 2004.** Seasonal anorexia in the male red-sided garter snake, *Thamnophis sirtalis parietalis*. *Behavioral Ecology and Sociobiology* **56**: 413–419.
- Odden M, Wegge P. 2007.** Predicting spacing behavior and mating systems of solitary cervids: a study of hog deer and Indian muntjac. *Zoology* **110**: 261–270.
- Ostfeld RS. 1986.** Territoriality and mating systems of California voles. *Journal of Animal Ecology* **55**: 691–706.
- Parker GA. 1978.** Searching for mates. In: Krebs JR, Davies NB, eds. *Behavioural ecology: an evolutionary approach*. London: Blackwell Press, 214–244.
- Prosser MR, Weatherhead PJ, Lisle Gibbs H, Brown GP. 2002.** Genetic analysis of the mating system and opportunity for sexual selection in northern water snakes (*Nerodia sipedon*). *Behavioral Ecology* **43**: 800–807.
- Reinert HK. 1992.** Radiotelemetric field studies of pitvipers: data acquisition and analysis. In: Schuett GW, Höggren M, Douglas ME, Greene HW, eds. *Biology of the vipers*. Eagle Mountain, UT: Eagle Mountain Publishing, 185–198.
- Reinert HK, Cundall D. 1982.** An improved surgical implantation method for radio-tracking snakes. *Copeia* **1982**: 702–705.
- Rivas JA, Burghardt GM. 2005.** Snake mating systems, behavior, and evolution: the revisionary implications of recent findings. *Journal of Comparative Psychology* **119**: 447–454.
- Rodgers AR, Carr AP, Beyer HL, Smith L, Kie JG. 2007.**

- HRT: home range tools for ArcGIS v1.1*. Thunder Bay: Ontario Ministry of Natural Resources, Centre for Northern Forest Ecosystem Research.
- Row JR, Blouin-Demers G. 2006.** Kernels are not accurate estimators of home-range size for herpetofauna. *Copeia* **2006**: 797–802.
- Schuett GW. 1992.** Is long-term sperm storage an important component of the reproductive biology of temperate pitvipers? In: Campbell JA, Brodie ED Jr, eds. *Biology of the pitvipers*. Tyler, TX: Selva, 169–184.
- Schuett GW. 1997.** Body size and agonistic experience affect dominance and mating success in male copperheads. *Animal Behaviour* **54**: 213–224.
- Schwenk K. 1994.** Why snakes have forked tongues. *Science* **263**: 1573–1577.
- Shine R. 1978.** Sexual size dimorphism and male combat in snakes. *Oecologia* **33**: 269–277.
- Shine R. 1988.** Parental care in reptiles. In: Gans C, Huey RB, eds. *Biology of the Reptilia*, Vol. 16. *Ecology B, Defense and life history*. New York, NY: Alan R. Liss Inc., 275–330.
- Shine R. 2003.** Reproductive strategies in snakes. *Proceedings of the Royal Society of London Series B. Biological Sciences* **270**: 995–104.
- Shine R, Bonnet X. 2000.** Snakes: a new ‘model organism’ in ecological research? *Trends in Ecology and Evolution* **15**: 221–222.
- Sperry JH, Weatherhead PJ. 2009.** Sex differences in behavior associated with sex-biased mortality in an oviparous snake species. *Oikos* **118**: 627–633.
- Stockley P, Searle JB, Macdonald DW, Jones CS. 1994.** Alternative reproductive tactics in male common shrews: relationships between mate-searching behaviour, sperm production, and reproductive success as revealed by DNA fingerprinting. *Behavioral Ecology and Sociobiology* **34**: 71–78.
- Tew TE, Macdonald DW. 1994.** Dynamics of space use and male vigour amongst wood mice, *Apodemus sylvaticus*, in the cereal ecosystem. *Behavioral Ecology and Sociobiology* **34**: 337–345.
- Thornhill R, Alcock J. 1983.** *The evolution of insect mating systems*. Cambridge, MA: Harvard University Press.
- Trivers RL. 1972.** Parental investment and sexual selection. In: Campbell B, ed. *Sexual selection and the descent of man, 1871–1971*. Chicago, IL: Aldine, 136–179.
- Uller T, Olsson M. 2008.** Multiple paternity in reptiles: patterns and processes. *Molecular Ecology* **17**: 2566–2580.
- Waldron JL, Lanham JD, Bennett SH. 2006.** Using behaviorally-based seasons to investigate canebrake rattlesnake (*Crotalus horridus*) movement patterns and habitat selection. *Herpetologica* **62**: 389–398.
- Weatherhead PJ, Prosser MR, Gibbs HL, Brown GP. 2002.** Male reproductive success and sexual selection in northern water snakes determined by microsatellite DNA analysis. *Behavioral Ecology* **13**: 808–815.
- Yoder JM, Marschall EA, Swanson DA. 2004.** The cost of dispersal: predation as a function of movement and site familiarity in ruffed grouse. *Behavioral Ecology* **15**: 469–476.