

# Does Size Matter? Factors Influencing the Spatial Ecology of Northern Pacific Rattlesnakes (*Crotalus oreganus oreganus*) in Central California

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**The spatial ecology of animals is influenced by a combination of factors. Spatial ecology parameters are commonly calculated for rattlesnakes of the genus *Crotalus*, but they are highly variable within and among populations and species. Rattlesnake movements can be influenced by sex, body size, season, and abiotic factors, but the relative importance of each still remains unknown. We quantified aspects of the spatial ecology of a population of Northern Pacific Rattlesnake (*Crotalus oreganus oreganus*) in the southern part of its range in order to determine the factors that influence its spatial ecology. We found that males had larger home range sizes than females for the entire 14-month study. However, sex differences in movements were present during the spring mating season but not the summer post-mating season, suggesting that male mate searching causes males to have larger overall home ranges than females. We also found that body size was not related to home range size, but this effect was sensitive to the inclusion of two outlier males. Our seasonal analyses revealed that outside the mating season, male body size was negatively related to mean daily movement, while female body size was positively related to mean daily movement. In the spring, larger males made their first long distance movement earlier than smaller males, suggesting that body size may influence the timing of mate searching activity. Our study shows that sex and season, which are influenced by the mating system, are important factors that determine the spatial ecology of *C. o. oreganus*.**

THE spatial ecology of rattlesnakes is influenced by a combination of interacting factors. Individuals within a population require resources such as prey, mates, and suitable habitat (Burt, 1943; Schoener, 1968; Gittleman and Harvey, 1982; Borger et al., 2006), but how individuals locate these resources can be influenced by sex, season, and body size (Harestad and Bunnell, 1979; Attuquayefio et al., 1986; Rocha, 1999). Spatial ecology data have been published for several rattlesnake species within the genus *Crotalus* (Macartney et al., 1988; Secor, 1994; Waldron et al., 2006a; Jørgensen et al., 2008; Glaudas and Rodríguez-Robles, 2011), but, surprisingly, the relative importance of sex, size, and abiotic factors in determining the spatial ecology of these animals remains unclear. Among populations, no clear patterns may exist because of different selection pressures (due to habitat, climatic, and species community differences). Also, the limitations in tracking a large number of individuals for long periods of time often creates large inter-individual variability in movements within populations, hindering our ability to generalize. Understanding the factors that affect spatial ecology among and within populations can provide insight into how rattlesnakes maximize their individual fitness and the constraints that may limit their ability to do so.

Male rattlesnakes often have home range sizes equal to or greater than females (Waldron et al., 2006a; Brown et al., 2008; Cardwell, 2008; Anderson, 2010), and sex differences in home range size are usually attributed to the crotaline mating system (Duvall et al., 1993; Waldron et al., 2006b; McGowan and Madison, 2008). In many populations, male rattlesnakes actively search for widely spaced, sedentary females during the late summer mating season (Duvall and Schuett, 1997). On the other hand, in populations that overwinter at communal hibernacula and mate upon spring emergence, males do not need to search widely because

females are clumped at the hibernacula (Glaudas and Rodríguez-Robles, 2011). In yet other populations, mating occurs in both the spring and the late summer (Secor, 1994; Taylor and DeNardo, 2005a; Lind et al., 2010), and therefore the distribution of females in either season could potentially influence male movements.

Body size may also affect rattlesnake spatial ecology. Large individuals are often older and more experienced than smaller, younger snakes, and their experience moving about the landscape could affect future movements (Clark, 1974; Secor, 1994). However, some studies have found that body size alone has no effect on the home range sizes of rattlesnake species (Macartney et al., 1988; Secor, 1994; Goode et al., 2008). Most rattlesnake species exhibit male-biased sexual size dimorphism (Klauber, 1972; Shine, 1978; Taylor and DeNardo, 2005b); thus, it is important to attempt to separate the effects of sex and body size. It is logical that sex would affect spatial ecology if males search for sedentary females during the mating season, but sex differences in body size may confound this interpretation when studies do not acknowledge them.

Seasonality and variation in abiotic conditions could also affect movements and home range sizes in rattlesnake populations. Rattlesnakes exhibit seasonal behaviors that are associated with the use of different habitats (Klauber, 1972). The annual behavioral patterns of rattlesnakes can be divided into the inactive “winter” season, when snakes exhibit decreased movements while overwintering in hibernacula, and the active season when snakes move to different microhabitats to reproduce and forage. Areas utilized during the active season may differ due to annual differences in precipitation or temperature. For example, Twin-spotted Rattlesnakes (*Crotalus pricei*) move longer distances to vegetated areas during dry, hot years than during other years when snakes generally remain on open rocky hillsides

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(Prival et al., 2002). Differences in latitude or elevation may produce different movement patterns among populations of the same species, and within a single population, movements can fluctuate seasonally or year-to-year.

We examined the factors that affect movements and home ranges in *Crotalus oreganus oreganus*, a subspecies of the Western Rattlesnake complex that spans from central California to southern British Columbia (Ashton and de Queiroz, 2001). The spatial ecologies of related rattlesnake populations (*C. viridis* spp. and *C. oreganus* spp.) have been studied, and sex differences were not found in those studies that tested for them (King and Duvall, 1990; Graves and Duvall, 1993; Reed and Douglas, 2002; Parker and Anderson, 2007). However, most of these previously studied populations were at high elevations, experience extreme seasonal weather with cold winters (producing a greatly reduced active season), and den communally. In contrast, populations of *C. o. oreganus* along the central coast of California occur at lower elevations, experience mild Mediterranean climate, and generally do not den communally (Fitch, 1949; Lind et al., 2010). *Crotalus o. oreganus* exhibits a bimodal pattern of reproduction with mating occurring in the spring and late summer/early fall (Lind et al., 2010), while many other rattlesnake populations exhibit different reproductive phenologies (King and Duvall, 1990; Ashton, 2003). We examined the effect of sex, body size, and season on spatial parameters in a population of *C. o. oreganus* at the southernmost part of the subspecies' range to better understand its spatial ecology and to provide data for comparative analyses with other rattlesnake populations. Based on the mating system of our study population (Lind et al., 2010), we hypothesized that because males must search for receptive females during the mating season, sex and season would have the strongest effects on home range size and movement distances.

## MATERIALS AND METHODS

**Field methodology.**—We studied a population of *C. o. oreganus* on the Chimineas Ranch unit of the Carrizo Plain Ecological Reserve in San Luis Obispo County, California. The study area is approximately 800 hectares and is characterized by grazed plains and hills interspersed with oak and juniper woodland with prominent rock outcrops. Adult *C. o. oreganus* were collected in fall 2006 and spring 2007. A total of 20 snakes were captured (9 male and 11 female). After capture, snakes were transported to the laboratory at the California Polytechnic State University in San Luis Obispo where they were anesthetized with inhaled isoflurane gas. Mass ( $\pm 1.0$  g) and snout–vent length (SVL,  $\pm 0.5$  cm) were measured while snakes were anesthetized using a digital scale and measuring tape. Each snake was injected with a passive integrated transponder (PIT) tag (AVID Identification Systems, Inc., Norco, CA) and given a unique three-color rattle code for visual identification in the field. The rattle code was made by injecting acrylic paint into the three proximal rattle segments. Radio-transmitters (SI-2T 11–13 g transmitters, Holohil, Carp, Ontario, Canada) were implanted into the coelomic cavity (Reinert and Cundall, 1982). After surgery, the snakes were kept in the laboratory for 2–3 days for observation, then released at the original sites of capture.

From April–August 2007 and March–May 2008, snakes were tracked an average of 5.1 times per month (range 3–8). From September 2007–February 2008, snakes were tracked

1–2 times per month. Although this intermittent sampling may make our home range and movement estimates conservative, all snakes were tracked the same number of times, allowing us to make comparisons between individuals without adjusting for relocation effort. Each time a snake was found, we used a Garmin Legend global positioning system (GPS) unit to record its location (accuracy ca. 6 m). Also, since these snakes were used in a separate study on reproduction and hormones (Lind et al., 2010), blood samples were taken from each individual once per month. Over the course of the study, one female went missing and two females went into burrows and activity ceased thereafter. We therefore collected data on a total of 17 snakes (nine male, eight female). Possibly because the study was conducted during a period of drought, none of the females reproduced during the time they were tracked.

**Spatial ecology parameters.**—We analyzed data collected from a period in which all 17 snakes were tracked (24 March 2007 to 4 May 2008) in order to directly compare the home range sizes of males and females in the same time period. Spatial data were analyzed using ArcView 3.3 software (ESRI Inc., Redlands, California, USA) with the Animal Movement Analysis extension (Hooge and Eichenlaub, 1997) and the Home Range extension (Rodgers and Carr, 1998). We calculated home range areas (ha) using the 100% and 95% minimum convex polygon (MCP) and the 95% and 50% fixed kernel (FK) density estimates using the optimal smoothing factor with least squared cross-validation (LSCV; Dugan et al., 2008; Goode et al., 2008; Smith et al., 2010). The 95% MCP is a home range measure that removes outlier relocation points that are outside the distribution of other movements. Unlike MCP, fixed kernel accounts for area usage by creating volume contours around each relocation point based on the likelihood of animal presence. The 95% FK estimate is a measure of home range size comparable to the 95% MCP, and the 50% FK is a measure of core activity area (Worton, 1989). Because rattlesnakes can cluster around a single activity area (e.g., when overwintering), MCP is argued to be a more appropriate method for calculating home range size than kernel density estimates (Row and Blouin-Demers, 2006). We included the overwintering period when calculating home range size, but these points did not significantly increase home range estimates produced with the kernel method (ANOVA; males:  $F_{2,24} = 0.97$ ,  $P = 0.39$ ; females:  $F_{2,21} = 0.49$ ,  $P = 0.62$ ). We report both FK and MCP estimates since each is an informative way of representing home range size, and so that our data can be compared to studies that use one or the other.

We also calculated mean daily movements (m/day) of each snake from April–August 2007 and March–May 2008, when most snakes were tracked at least once per week. Measurements of mean daily movements were calculated by determining the distance moved between consecutive locations (m), dividing by the number of days, and averaging the estimates (Dugan et al., 2008). We used the mean daily movement calculations to examine seasonal effects on spatial ecology.

**Data analysis.**—We examined how body size (SVL) and sex affected the home range sizes of *C. o. oreganus* (see Table 1 for raw data). We did not examine the effect of body condition because this factor varies seasonally. Since our

**Table 1.** Raw Data Used in This Spatial Ecology Study of *Crotalus o. oregonus* in Central California. Three home range estimates (100% MCP, 95% MCP, 95% FK) and one estimate of core area usage (50% FK) were used to test for the effects of sex and body size. MCP = minimum convex polygon, FK = fixed kernel.

ID	Sex	SVL (cm)	Mass (g)	100% MCP (ha)	95% MCP (ha)	95% FK (ha)	50% FK (ha)
C01	M	101.5	836	5.84	5.83	5.89	0.73
C03	M	96.5	1091	9.82	4.48	7.06	0.70
C04	M	88.0	561	7.25	4.98	5.79	0.59
C05	M	112.0	1284	2.79	2.58	3.49	0.52
C06	M	108.0	1122	1.13	0.44	0.62	0.06
C07	M	96.0	1192	5.72	5.72	9.36	0.99
C08	M	96.0	1205	5.18	4.95	5.23	0.43
C10	M	110.5	1335	6.50	3.42	9.06	1.50
C11	M	79.5	466	1.62	1.48	1.83	0.22
C12	F	76.5	304	0.12	0.11	0.22	0.04
C14	F	86.0	527	2.00	1.89	2.07	0.21
C15	F	75.5	373	0.15	0.08	0.16	0.02
C16	F	79.0	367	2.00	1.98	1.40	0.23
C17	F	70.0	318	0.29	0.22	0.44	0.05
C18	F	84.0	550	0.48	0.41	0.49	0.08
C19	F	82.5	444	2.73	0.84	0.90	0.14
C20	F	82.5	424	1.03	0.30	0.39	0.08

study animals were initially captured at different times of year and our SVL and mass measurements were recorded at time of capture, this factor may not be consistent with the time periods over which the snakes were tracked. Instead, SVL was used as a measure of size because it does not change appreciably in adult rattlesnakes. All statistical analyses were conducted using SYSTAT 12 (Systat Software Inc., Chicago, IL). In order to satisfy the assumptions of normality and homoscedasticity, we square root transformed all home range estimates. Because SVL was positively correlated with all home range estimates within the general population, we conducted an analysis of covariance (ANCOVA) on each of the estimates with sex as the factor and SVL as the covariate. In all cases, assumptions of ANCOVA were met (i.e., no significant sex by SVL interaction). Although we had little overlap of SVL between the sexes, we still felt that ANCOVA was an appropriate test because of the large amount of shared variation between body size and sex.

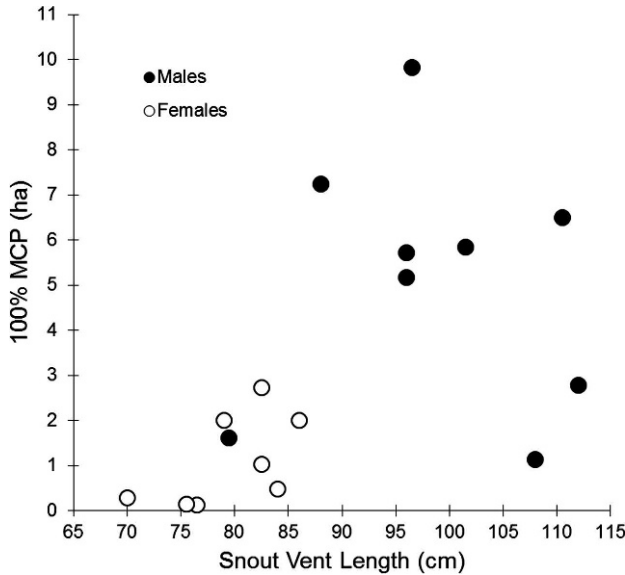
To examine seasonal effects on movement distances, we compared mean daily movements made by males and females in the spring 2007 mating season to the summer 2007 post-mating season. We did not include the late summer/early fall mating season in our analyses because snakes were tracked infrequently during this time and because drought conditions caused a decrease in surface activity, which likely led to a decrease in observed mating activity in the late summer (Lind et al., 2010). We identified the mating season as April–May, and the post-mating season as June–July. Although the spring mating season may start earlier than April (Lind et al., 2010), we only included the months in which the snakes were tracked at least once per week. We log-transformed (base 10) mean daily movements to satisfy assumptions of normality and homoscedasticity, and we reduced the number of snakes examined to satisfy our criterion of a once per week GPS fix. Thus, eight males and five females were used in the analyses. We analyzed data using two-way analysis of variance (ANOVA) with sex and season as fixed factors. Because we found a significant interaction between sex and season ( $F_{1,24} = 6.00, P = 0.02$ ), we examined sex differences using separate one-factor

ANOVAs on mean daily movement in the mating season and post-mating season. We also used paired t-tests to examine seasonal differences in mean daily movement within each sex, and we used linear regression to test for relationships between SVL and mean daily movement within each season. Finally, we tested the effect of male body size on the timing of mate searching, or the first long distance movement made (>100 m) away from the overwintering site. Since snakes were not tracked daily, we could not determine the exact date movements were made. However, we could estimate the week when movements occurred because snakes were tracked at least once every six days. Thus, using linear regression, we examined the relationship between male SVL and the week in which their first long distance movement was made in spring 2008.

After analyzing ANCOVA results, we found two male snakes (snakes C05 and C06) that had high leverage suggesting that they were extreme outliers (Cook's Distances for snake C05, 100% MCP: 1.04, 95% MCP: 0.72, 95% FK: 1.12, 50% FK: 1.23; for snake C06, 100% MCP: 0.45, 95% MCP: 0.56, 95% FK: 0.67, 50% FK: 0.88). We removed the data from these snakes to examine whether the model was sensitive to the effects of two animals. Snake C05 exhibited atypical male behavior in the summer of 2007 by remaining in the same locality for over one month. Snake C06, on the other hand, did not appear behaviorally or physically abnormal and is thus a statistical, not a true, outlier. Because of this, we based our conclusions on the full model, but we report both analyses (the full and reduced models) as a means of demonstrating the individual variability in spatial ecology parameters exhibited by crotaline snakes, and the potential for such variability to drive results in studies with similar sample sizes.

## RESULTS

**Home range estimates.**—Body size was not significantly related to any of the home range estimates in the full model ( $n = 17$ ; all  $P > 0.05$ ) even though the sample population displayed extreme sexual size dimorphism ( $t =$



**Fig. 1.** Relationship between body size (SVL) and a home range estimate (100% minimum convex polygon) for nine male and eight female *Crotalus o. oreganus*. Males had significantly larger body sizes and home range sizes than females.

−4.765,  $P < 0.0001$ ; Fig. 1). Males had larger home range sizes than females (100% MCP, 95% MCP, and 95% FK), but no sex difference in the core activity area estimate of 50% FK was detected ( $P = 0.084$ ; Table 2). For the reduced model ( $n = 15$ ) in which we removed data associated with two male snakes, ANCOVA results showed that both body size and sex were significantly related to all estimates except for 95% MCP, for which the effect of body size was not significant ( $P = 0.09$ ; Table 2).

**Movement distances.**—In the 2007 spring mating season, male rattlesnakes had higher mean daily movements than females ( $F_{1,11} = 18.91$ ,  $P = 0.001$ ), but this difference disappeared in the summer post-mating season ( $F_{1,11} = 0.04$ ,  $P = 0.85$ ; Fig. 2). Males showed a significant difference in mean daily movement between the two seasons ( $t = 6.70$ ,  $P < 0.001$ ), but females did not ( $t = 1.15$ ,  $P = 0.32$ ; Fig. 2). Linear regression analyses revealed a positive relationship between SVL and mean daily movements for females ( $F_{1,3} = 10.75$ ,  $R^2 = 0.78$ ,  $P = 0.05$ ) and a negative relationship for males ( $F_{1,6} = 6.93$ ,  $R^2 = 0.54$ ,  $P = 0.04$ ) in the summer post-mating season, but these relationships were not apparent for either sex in the spring mating season (females:  $F_{1,3} = 3.18$ ,  $R^2 = 0.52$ ,  $P = 0.17$ ; males:  $F_{1,6} = 0.619$ ,  $R^2 = 0.09$ ,  $P = 0.46$ ).

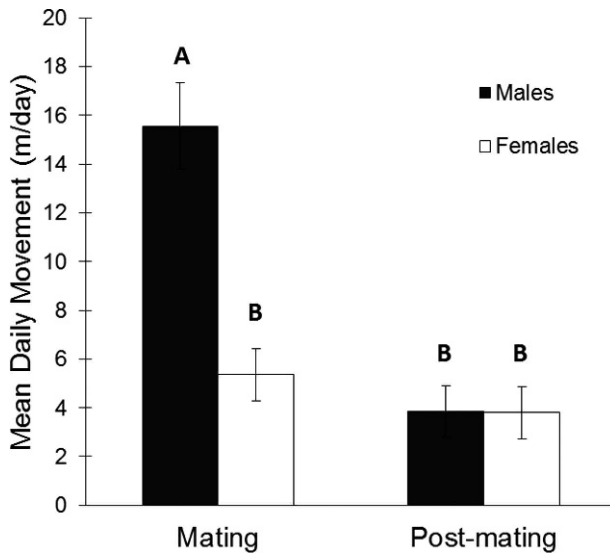
We found a negative relationship between male SVL and the week in which the first spring long distance movement was made ( $F_{1,7} = 34.27$ ,  $R^2 = 0.83$ ,  $P = 0.001$ ; Fig. 3), suggesting that larger males start to search for receptive females earlier in the spring than smaller males.

**DISCUSSION**

The spatial ecology of *C. o. oreganus* is greatly influenced by sex and season, but body size also appears to contribute at finer scales. We found that in a population at the southern edge of the subspecies' range, males had larger home range sizes than females for all estimates except for 50% FK. Our study is the first to report a sex difference in spatial parameters for this species (Reed and Douglas, 2002; Parker

**Table 2.** Average Home Range Estimates of Male and Female *Crotalus o. oreganus* in Central California. ANCOVA results for the reduced model revealed an effect of body size that was not present in the full model. MCP = minimum convex polygon, FK = fixed kernel.

Dependent variable	Full model ( $n = 17$ )						Reduced model ( $n = 15$ )						
	Male			Female			Male			Female			
	Mean±SE	Mean±SE	P	df	F	P	Mean±SE	Mean±SE	df	F	P		
100% MCP (ha)	5.09±0.94	1.10±0.36	0.039	1,14	5.20	0.039	6.00±0.93	1.10±0.36	1,12	5.34	0.039	5.78	0.033
95% MCP (ha)	3.76±0.64	0.73±0.28	0.020	1,14	6.96	0.020	4.41±0.58	0.73±0.28	1,12	8.55	0.013	3.44	0.088
95% FK (ha)	5.37±1.00	0.76±0.24	0.020	1,14	6.90	0.020	6.32±0.97	0.76±0.24	1,12	13.27	0.003	13.01	0.004
50% FK (ha)	0.64±0.14	0.10±0.03	0.084	1,14	3.46	0.084	0.74±0.16	0.10±0.03	1,12	5.93	0.031	21.46	0.001

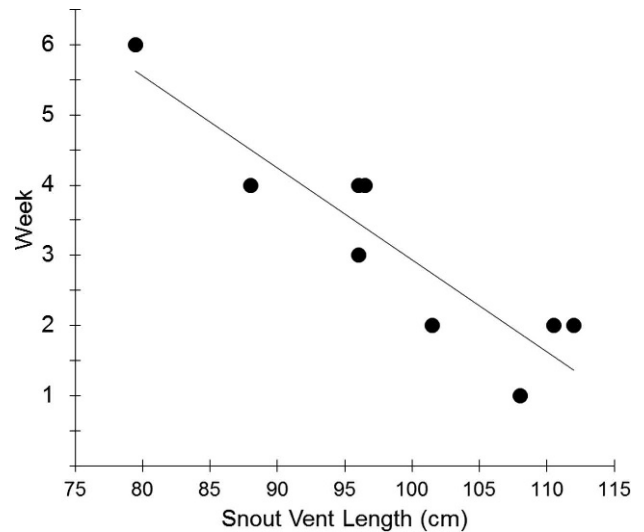


**Fig. 2.** A sex difference in mean daily movements ( $\pm 1$  SEM) of *Crotalus o. oregonus* was observed in the spring mating season but not in the summer post-mating season. Males also greatly reduced their movements in the post-mating season while females did not. Letters over the bars indicate statistical significance.

and Anderson, 2007). However, our results are consistent with most rattlesnake spatial ecology studies, which show that males tend to have larger home range sizes and movement distances than females (Waldron et al., 2006a; Brown et al., 2008; Cardwell, 2008; Goode et al., 2008; Glaudas and Rodríguez-Robles, 2011).

We found that season can influence rattlesnake movements, but its effects are greater on males than females. Female movements remained relatively constant regardless of season, while males greatly increased their movements during the spring mating season compared to the summer post-mating season. Thus, the sex differences in spatial ecology for the entire tracking period appear to result from male mate searching, which occurs only a few months out of the year. Also, we found no sex difference in 50% FK estimates probably because these are less affected by occasional, lengthy movements like those that occur when males search for females during the mating season(s). We were unable to incorporate data from the late summer/early fall mating season into our analyses, but in other rattlesnake species that mate bimodally such as the Sidewinder (*C. cerastes*), males move longer distances than females during both mating seasons (Secor, 1994). Nonetheless, female distributions at the start of each mating season could differ, affecting the male movements of our population. Future studies on *C. o. oregonus* and other rattlesnakes that mate bimodally should examine how both mating seasons influence movement patterns. In general, our results support our hypothesis that sex and season affect rattlesnake spatial ecology, with seasonal sex differences likely producing the observed annual sex differences in home range size.

We examined the effects of body size on spatial ecology in *C. o. oregonus* because of the extreme sexual size dimorphism present in our population, and because it has been shown to affect the spatial ecology of other snake species. For instance, Cottonmouth (*Akistrodon piscivorus*) home range size is affected by both sex and body size (Roth, 2005), and among rattlesnakes, body size correlates with spatial parameters in the Eastern Diamond-backed Rattlesnake (*C.*



**Fig. 3.** Relationship between body size (SVL) of male *Crotalus o. oregonus* and the week of the first long distance spring movement ( $>100$  m). Week one, when the first male movement occurred, starts on 23 March 2008. Week 6, when the final movement occurred, ends on 4 May 2008. Larger males began moving earlier than smaller males.

*adamanteus*), the Aruba Island Rattlesnake (*C. unicolor*), and the South American Rattlesnake (*C. durissus*; Reinert et al., 2008; Tozetti et al., 2009; Hoss et al., 2010). For our population of *C. o. oregonus*, we did not find an effect of body size on spatial ecology when all snakes were included in analyses. However, we found a latent effect of body size after removing two male snakes that had large Cook's distance values. Our reduced model revealed significant effects of both body size and sex on home range size, implying that body size may have some role in influencing rattlesnake spatial ecology. Even though our reduced model had sample sizes equal to or greater than many studies that analyze rattlesnake spatial data (Timmerman, 1995; Nowak et al., 2002; Brown et al., 2008; Smith et al., 2008; Hoss et al., 2010), it is clear that when possible studies should examine larger samples of mature snakes of all sizes and reproductive conditions in order to more accurately ascertain the effect of body size on spatial parameters. However, the expense and time needed to continually track large numbers of individuals for long periods of time will likely continue to limit sample sizes in radiotelemetric studies. Given these limitations, we feel the best solution is to examine the effect of inter-individual variability on overall conclusions, as we have done here.

Body size also affected rattlesnake spatial ecology at finer temporal scales than the entire 14-month tracking period, and its effects differed between the sexes. Seasonal analyses revealed relationships between body size and mean daily movements only in summer, when male activity is greatly reduced. During this time of year, larger females moved more than smaller females, and conversely, larger males moved less than smaller males. Other studies have found sex differences in the relationship between body size and spatial ecology in snakes. For example, body size can have a significant effect on home range size for females only (Webb and Shine, 1997; Roth and Greene, 2006) or for males only (Whitaker and Shine, 2003). In *C. o. oregonus*, the opposing relationships in movement distances and body size between the sexes could be the result of sex differences in foraging behaviors, or could result from a conservation of energy

expenditure by large males that have depleted energy reserves after the mating season. Additional empirical data would be required to further evaluate these hypotheses.

We furthermore found a significant, negative relationship between male body size and the week in which the first long distance movement occurred in the spring. Body size, which is a sexually selected trait, probably contributes to reproductive success in males (Shine, 1978, 1994). Large males may be more successful at mating than smaller males, not only because of their competitive advantage in male–male combat (Schuett, 1997), but also because they start to search for receptive females sooner. This effect of size could be due to the experience of larger, older individuals and their greater familiarity with the landscape compared to younger, smaller individuals. Future studies should examine fine-scale movement patterns during particular seasons, and other aspects such as the timing of movements, as they appear to differ among individuals and could be important factors in determining spatial ecology.

The home range sizes that were produced from our analyses are small compared with those reported from other *Crotalus* spp. (Reinert and Zappalorti, 1988; Secor, 1994; Parker and Anderson, 2007), but the magnitude of home range size probably varies year to year due to environmental factors. For terrestrial organisms, precipitation is likely to affect inter-annual variation in home range sizes in populations because it is directly linked to primary production. We believe that a drought during which our study took place led to reduced home range sizes. After this drought, male rattlesnakes in the same population exhibited home range sizes almost three times larger calculated during a study period of just three months (Holding et al., 2012). Other studies have revealed similar trends. Cardwell (2008) found that during a drought year, Mohave Rattlesnakes (*C. scutulatus*) dramatically reduce their movements, and Goode et al. (2008) found a positive relationship between movements and precipitation in male Tiger Rattlesnakes (*C. tigris*). However, Prival et al. (2002) found that *C. pricei* moved more and exhibited larger home range sizes during a dry year than a wet year. Rattlesnake populations may differ in response to climatic events due to differences in habitat structure and usage; thus, understanding how abiotic factors affect movement patterns can further shed light on how animals interact with their environment and how spatial use may change as a result of future climate change.

Our study shows that many factors can affect spatial ecology and should be considered by snake researchers. It is apparent that the mating system and reproductive behaviors are important factors that determine the significance of sex and season on rattlesnake spatial ecology. However, what determines the importance of body size and the reasoning why body size affects spatial ecology are less clear. Additionally, we have only a limited understanding of what factors are responsible for the observed inter-individual variation within the sexes. We conducted analyses with and without two outlier males that exhibited atypical behavior by not moving long distances during the mating season. Analyses without these males were substantially different. If making long distance movements increases male reproductive success, as has been suggested in the literature (Duvall and Schuett, 1997; Cardwell, 2008), why did these males not exhibit such behavior? In order to fully understand the factors that determine snake spatial ecology and reproductive success, we need to examine how variation at all levels

of organization, including differences in genetics, circulating hormones, and personalities (individual behavioral types), influences snake movements and home ranges.

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