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Variation in Rattlesnake Spatial Ecology Among Individuals and Populations

Biologists track animals and study their movements as a way to learn species' spatial use and requirements, as this knowledge is necessary for understanding animal behavior and population ecology as well as for developing wildlife management plans (Chetkiewicz et al. 2006; Durbian et al. 2008; Spencer 2012). Body size, landscape configuration, population density, food

availability, and other variables such as thermal quality of the environment can influence the spatial ecology of many animal species, but the ways in which these factors impact different species vary widely (Gregory et al. 1987; Macartney et al. 1988; Reinert and Zappalorti 1988; Beier and Noss 1998; Chetkiewicz et al. 2006). Given that animal movement can vary across the distribution range of a species (Boyle et al. 2009), it is highly likely that even populations in close geographic proximity might exhibit distinct spatial ecology patterns if their habitats differ (Rohner et al. 1995; Petrie and Kempnaers 1998; Reeve et al. 2009). It therefore seems very important to conduct studies on multiple populations to gain a thorough understanding of a species' ecology across the varying conditions found throughout its distribution range, but very few studies have attempted to simultaneously document variation in spatial ecology among multiple populations, most likely due to the high labor intensity and expense of such studies. Variation in habitat characteristics may have particularly strong effects on the spatial ecology of ambush foraging ectotherms, whose movements and microhabitat selection are likely to be strongly impacted by patterns of prey activity, climate, and other biotic and abiotic factors (Waldron et al. 2006; Hoss et al. 2010). In North America, rattlesnake spatial ecology is commonly studied, but the vast majority of studies are conducted on a single population, and

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TABLE 1. Descriptions of the four field sites in California where spatial ecology of *Crotalus oreganus* was studied from June through October 2017. Temperatures reflect data during the study period from the nearest weather stations.

Population	Lat/Long	Mean daily high temp (°C)	Mean daily low temp (°C)	Habitat
Chimineas Ranch (CR)	35.16580°N 119.8696°W	31.5	18.2	Inland oak woodland and grassland with rocky outcrops
Sedgwick Reserve (SG)	34.69280°N 120.0406°W	31.3	11.8	Inland oak woodland and grassland
Montaña de Oro State Park (MDO)	35.26390°N 120.8632°W	21.1	10.8	Coastal chaparral
Vandenberg Air Force Base (VAFB)	34.74200°N 120.5724°W	23.7	12.8	Coastal chaparral with rocky outcrops

data collection in most snake spatial ecology studies that do span multiple populations typically occurs during separate time periods (e.g., Shine 1987). In addition, investigation of population-level variation in home range size and movement during the non-dispersing active season remains unstudied.

In this study, we simultaneously studied the spatial ecology of four distinct populations of the Pacific Rattlesnake, *Crotalus oreganus*, in California, USA. By studying all four populations simultaneously, we reduce the potential impacts of confounding variables such as interannual climatic variation, differing methodologies, and others, and instead we can associate any interpopulational differences in spatial ecology with site differences in habitat characteristics, weather, prey availability, and adaptive phenotypes of each population. We hypothesized that populations of *C. oreganus* would exhibit variation in home range size and daily movement associated with qualitative habitat characteristics that vary among sites. Specifically, we predicted that snakes from inland populations, where temperatures are higher and more variable, would exhibit larger home range areas and movement distances than snakes from coastal populations where cooler and more consistent temperatures would lead to less frequent and less extreme thermoregulatory movements. The lack of multi-population spatial analysis studies is a gap in research we hope to help fill with this study, and in doing so, evaluate the necessity of analyzing multiple populations of a species over the same period of time.

METHODS

Study species and sites.—*Crotalus oreganus* is a habitat and dietary generalist ranging from southern British Columbia through Baja California, Mexico (Pook et al. 2000), and in coastal California is comprised of either two subspecies (*C. o. oreganus* and *C. o. helleri*, Ashton and de Queiroz 2001) or two species (*C. oreganus* and *C. helleri*, Davis et al. 2016). Our four study sites fall within what has been considered the intergrade zone of the two taxa (Cates et al. 2015), although recent evidence suggests that all of these populations genetically cluster (Holding et al. 2018). For this study, we will refer to them all as *C. oreganus*. Rattlesnakes at the four locations selected for this study do not migrate to mating grounds or communal den sites, and instead search for mates and over-winter near the same home range in which they forage. We only used adult, sexually-mature male snakes in this study to eliminate the effects of sex differences in movement behavior (Gardner-Santana and Beaupre 2009; Putman et al. 2013).

Rattlesnakes were studied from four populations on the central coast of California (Table 1). These included two inland populations: Chimineas Ranch of the Carrizo Plain Ecological Reserve (CR) in San Luis Obispo County and Sedgwick Reserve (SG) in Santa Barbara County; and two coastal populations: Montaña de Oro State Park (MDO) in San Luis Obispo County and Vandenberg Air Force Base (VAFB) in Santa Barbara County. Straight-line distance between each population is 150 km or less. The two inland locations have more variable climates and higher summer daytime temperatures than the coastal locations (National Ocean and Atmospheric Association; Western Regional Climate Center 2017).

Field methodology.—A total of 26 adult, male *C. oreganus* were captured from the four field sites in spring 2017. Following capture, snakes were transported to the laboratory at the California Polytechnic State University (San Luis Obispo, California, USA) where snout-vent length (SVL, cm) and mass (g) were recorded (Table 2). Snakes were surgically implanted with Holohil radio-transmitters (5.2 g, 11 g, and 13.5 g SB-2 and SI-2 models, Holohil Systems Ltd., Carp, Ontario, CA; tags assigned to snakes based on snake mass, with all tags less than 5% of body mass) following the procedures of Lind et al. (2010). Snakes were released within 1-2 days of surgery at the location of capture.

We tracked tagged rattlesnakes 4-5 times per week from June to October 2017, at randomly selected times of day, using a model TR-4K VHF receiver with a RA-14 antenna (Telonics Telemetry-Electronics Consultants, Mesa, Arizona). As *C. oreganus* activity is most restricted by temperature during the summer months (Putman and Clark 2017), daily activity periods vary from site to site based on local climate. We used the iPhone GPS application Bad Elf GPS version 3.3.4 (Bad Elf, LLC, 2010-2017) to record snake location. On rare occasions, GPS coordinates were obtained via triangulation if the snakes were in inaccessible locations. Upon successful location of an individual snake, we recorded a description of its location and cross-referenced it by inputting GPS coordinates into ArcMap v.10.5 (ESRI Inc., Redlands, California, USA). The primary mating period for many populations of *C. oreganus* occurs in the spring after snakes emerge from winter dormancy (Aldridge 2002; Aldridge and Duvall 2002; Lind et al. 2010; Putman et al. 2013). During this time, male snakes tend to exhibit dramatic increases in movement behavior as a result of mate searching. Another mating period occurs during the late summer and fall; however, it is often less significant and results in less dramatic changes in movement behavior. The spring mating period was not included in the study, as a number of the

TABLE 2. Mean morphometric and spatial ecology measurement values and intraspecific coefficients of variation (CV) for each of the four populations of *Crotalus oreganus* on the Central Coast of California. Snakes were tracked from June through October 2017. Means are shown with ± 1 SEM.

Field site (N)	Mass (g)		SVL (cm)		100% MCP (ha)		95% MCP (ha)		50% MCP (ha)		95% KDE (ha)		50% KDE (ha)		Daily movement (m)	
	Mean	CV	Mean	CV	Mean	CV	Mean	CV	Mean	CV	Mean	CV	Mean	CV	Mean	CV
CR (5)	524.00 \pm 32.34	85.94 \pm 3.20	12.10 \pm 5.18	95.70%	10.56 \pm 3.96	83.76%	2.39 \pm 1.31	122.74%	8.73 \pm 3.04	77.97%	1.11 \pm 0.44	88.65%	18.84 \pm 2.75	32.60%		
SG (8)	643.00 \pm 68.63	94.10 \pm 4.44	16.42 \pm 2.25	38.69%	10.48 \pm 1.82	49.22%	1.53 \pm 0.25	46.98%	8.71 \pm 1.46	47.38%	0.92 \pm 0.16	49.87%	39.02 \pm 5.02	36.36%		
MDO (6)	387.00 \pm 57.79	72.08 \pm 3.32	5.26 \pm 0.70	32.51%	3.87 \pm 0.37	23.30%	0.84 \pm 0.20	57.15%	3.16 \pm 0.39	30.37%	0.26 \pm 0.08	76.41%	28.88 \pm 2.94	24.91%		
VAFB (7)	344.00 \pm 28.90	70.40 \pm 2.83	8.79 \pm 2.42	73.02%	8.27 \pm 2.53	81.05%	1.55 \pm 0.44	74.81%	6.05 \pm 1.79	78.36%	0.86 \pm 0.53	161.78%	27.09 \pm 3.99	38.98%		

study snakes were captured opportunistically in the post-mating season. Instead, our study took place in the summer and early fall in an attempt to encompass normal seasonal movements, driven by hunting and thermoregulation rather than mate-searching, common to all four populations.

Data analysis.—We calculated home range areas (in ha) as minimum convex polygons (MCP) and kernel density estimates (KDE), which are both common estimates used in snake studies (Hayne 1949; Worton 1989; Moore and Gillingham 2006; Darden and Dabelsteen 2007). For 100%, 95% and 50% MCP calculations, we used the R-packages “sp” (v.1.4-2; Pebesma et al. 2020) and “adehabitatHR” (v.0.4.18; Calenge 2020), and for KDE, we used the ArcMap 10.5 (ESRI Inc., Redlands, California, USA) default setting for determining KDE bandwidth, which utilizes the methods outlined in Silverman (1986). Although Row and Blouin-Demers (2006) demonstrated that KDE may not be appropriate for most reptiles due to inconsistencies involved with selecting the appropriate smoothing factor, we chose to calculate KDE in addition to MCP to facilitate comparisons with other snake studies (Reinert and Zappalorti 1988; Secor 1994; Parker and Anderson 2007; Putman et al. 2013). In the Discussion, we focus mainly on our MCP results and caution over-interpretation of KDE results. ArcMap 10.5 was also used to estimate daily movement by generating a polyline connecting each tracked GPS point in chronological order, then divided the resulting total length of the polyline by the total number of days between the first and final tracking event to generate a mean daily movement estimate.

We used a Levene’s test to test for unequal variance among the means of each population for each of the six spatial ecology parameters: 100% MCP, 95% MCP, 50% MCP, 95% KDE, 50% KDE, and mean daily movement. To meet statistical assumptions of normality, we log-transformed the mean daily movement data. We ran separate two-way ANOVAs to analyze MCPs, KDEs, and daily movement values among field sites. Snake snout-vent length (SVL) and the interaction between SVL and field site were also included in each model, and a partial F-test was used to test the significance of each covariate.

RESULTS

Minimum Convex Polygon (MCP) home ranges.—Neither 100% MCP (Fig. 1a; $F_{7,18} = 1.55$, $p = 0.21$), 95% MCP (Fig. 1b; $F_{7,18} = 1.06$, $p = 0.43$), nor 50% MCP (Fig. 1c; $F_{7,18} = 1.25$, $p = 0.33$) varied significantly among sites, though there is a slight trend for larger MCPs in the two inland populations. The biggest interpopulation differences were between SG (inland) and MDO (coastal), with the mean 100% MCP of SG snakes being more than three times larger than that of MDO snakes. However, intrapopulation coefficients of variation (CV) for 100% MCP were often far higher (Table 2) than the interpopulation CV (100% MCP = 45%; 95% MCP = 38%; 50% MCP = 40%), so differences among populations were not statistically significant. SVL was not a significant predictor of MCP size across the four populations (100% MCP, $F_{4,18} = 0.52$, $p = 0.72$; 95% MCP, $F_{4,18} = 0.65$, $p = 0.63$; 50% MCP, $F_{4,18} = 1.37$, $p = 0.28$).

Kernel Density Estimates (KDE) of home ranges.—Similar to MCP, there was no significant difference in 95% KDE size among study sites (Fig. 1e; $F_{7,18} = 1.66$, $p = 0.18$), but snakes from inland sites (CR and SG) tended to have larger mean 95% KDE home range areas than the two coastal locations. The inter-population CV for 95% KDE was 40%, and intra-population CVs were higher for three of the four sites (Table 2). SVL was not a significant predictor of 95% KDE ($F_{4,18} = 1.23$, $p = 0.33$). The two inland populations also

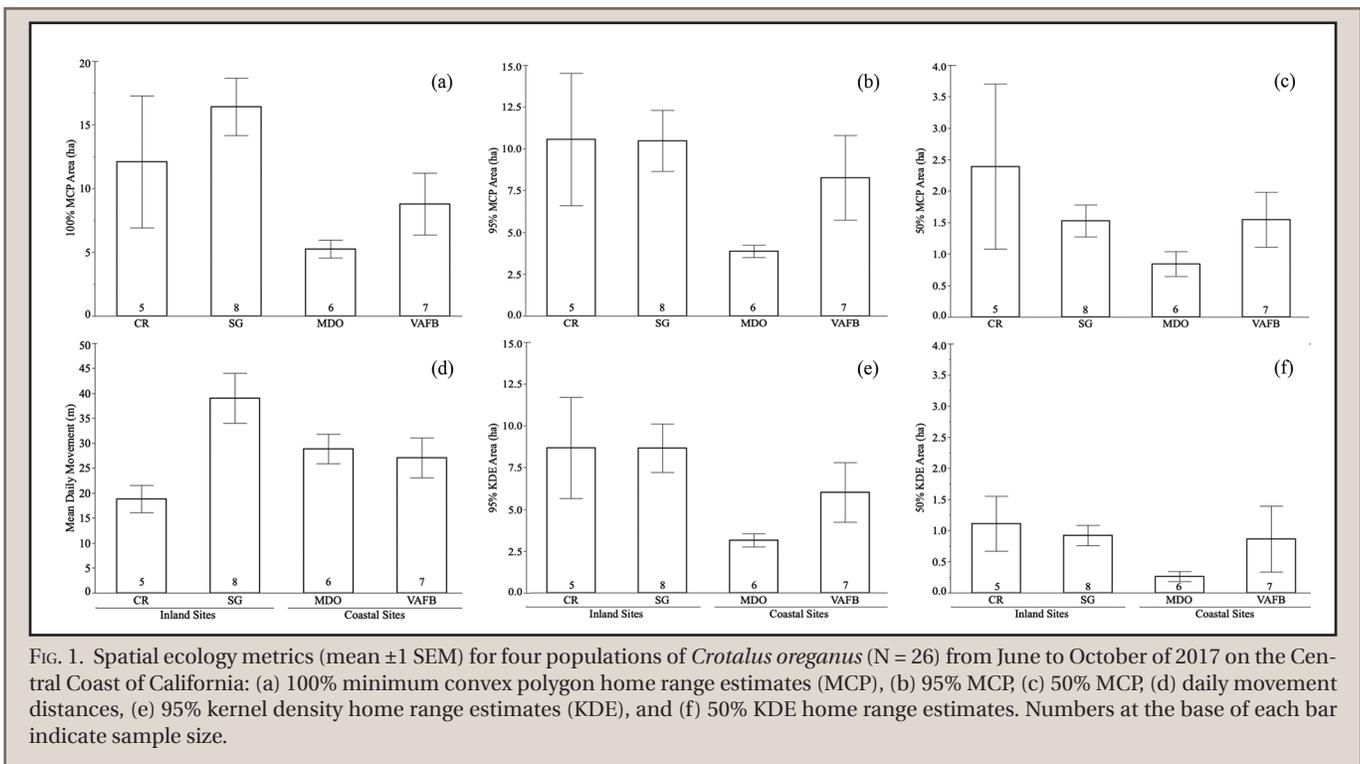


FIG. 1. Spatial ecology metrics (mean \pm 1 SEM) for four populations of *Crotalus oregonus* ($N = 26$) from June to October of 2017 on the Central Coast of California: (a) 100% minimum convex polygon home range estimates (MCP), (b) 95% MCP, (c) 50% MCP, (d) daily movement distances, (e) 95% kernel density home range estimates (KDE), and (f) 50% KDE home range estimates. Numbers at the base of each bar indicate sample size.

tended to have larger mean 50% KDE home range values than the coastal populations, but differences among the populations were not statistically significant (Fig. 1f; $F_{7,18} = 2.05$, $p = 0.10$). Similar to 95% KDE, the intra-population CVs were all higher for 50% KDE than the inter-population CV of 46% (Table 2). SVL was not a significant predictor of 50% KDE home range size, but larger males tended to have larger 50% KDE ($F_{4,18} = 2.62$, $p = 0.07$).

Daily movement.—We observed a non-significant trend for differences in log-transformed mean daily movement among the four populations (Fig. 1d; $F_{7,18} = 2.17$, $p = 0.09$), with values for the two coastal locations MDO and VAFB intermediate between the means of SG and CR. The inter-population CV for mean daily movement was 29%, and intra-population CVs were similar (Table 2). SVL did not significantly affect daily movement ($F_{4,18} = 0.78$, $p = 0.56$). The SVL \times site interactions were not significant for any of the spatial metrics evaluated.

DISCUSSION

Overall, our study demonstrates that while examining home range metrics among populations does not always yield statistically significant differences, it can elucidate intrapopulation trends among individuals as well as highlight many of the challenges of undertaking such studies. Analyzing inter-population variation in spatial ecology parameters is difficult because intra-population variation is often extremely high. High variation in the behavior of individuals, which is a common phenomenon in field studies involving snakes (Macartney et al. 1988; Whitaker and Shine 2003; Parker and Anderson 2007; Putman et al. 2013), combined with relatively low sample size can make potential biologically significant differences fail tests of statistical significance, especially when degrees of freedom are taken by including additional variables in the model. Maintaining SVL in the models even though it was not a significant predictor of spatial ecology variables was appropriate because our goal was to model the

differences in spatial ecology among populations while controlling for body size, a variable that is known to impact rattlesnake spatial ecology (e.g., Putman et al. 2013). In our discussion of our results below, we explore qualitative patterns in the context of variation within and among populations.

The total home range of a snake (100% MCP) was characterized by high inter- and intra-population variation, and so mean population MCPs were not significantly different despite displaying up to a 3-fold difference in size between populations. Of the four sites, the mean MCP area for snakes from the inland SG site was largest while the mean from the coastal site MDO was smallest, and the two other sites were intermediate. The variation in home range size likely reflects many factors, including, but not limited to, topography, prey availability, weather, and human interactions. For example, one potential explanation for the small home ranges at the coastal MDO site is that it is a popular state park, and our study snakes occupy an area frequented by hundreds of hikers and joggers every day. Human activity at MDO could discourage snakes from moving throughout their habitat, reducing their MCPs (Parent and Weatherhead 2000). Other factors that could explain variation in spatial ecology include the spatial distribution of water sources (Valenzuela and MacDonald 2002), the amount of vegetative cover (Tufto et al. 1996), prey densities (Herfindal et al. 2005), and idiosyncratic variation among snakes within each site (e.g., Parker and Anderson 2007). Notably, despite these qualitative trends, MCP home ranges did not differ significantly among populations, suggesting that even major differences in climate experienced by rattlesnakes do not translate into different macro-patterns of habitat use.

While the 100% MCP is a polygon that encompasses the entire activity range as well as potentially unused space within that polygon, the 95% and 50% MCP values remove forays to the edges of the home range, and KDE values produce probability distributions for home range and core range, respectively. The MCP and KDE values observed in our study are comparable

to those of a previous study on *C. oreganus* at our CR field site (Putman et al. 2013), but are smaller than those reported from studies on other *Crotalus* species (Reinert and Zappalorti 1988; Secor 1994; Parker and Anderson 2007), likely due to the absence of seasonal migration at our field sites and the restriction of our study period to summer activity without spring mating forays. The 95% and 50% KDE values were also smaller than 95% and 50% MCP values, respectively, for all field sites. The high intra-population CV for KDEs again precluded detection of any differences among populations, for reasons similar to that described above for MCP. However, we did observe a non-significant trend for the two inland rattlesnake populations to have larger core range sizes than the two coastal populations. As with MCP, this may represent the effects of factors including topography, food availability, climate, presence of humans, and more.

Another way to examine spatial ecology is to quantify the daily distance moved within an activity range, which can reflect snakes moving from refugia to hunting locations, searching for mates (although our study was outside of the main mating season), selecting thermally favorable microhabitats, and other behaviors. Daily movement was calculated with straight line distances between tracking locations. Since normal animal movement patterns are nonlinear, the actual distance travelled by individuals was higher than the numbers reported in this study. While we had predicted that we would observe differences between inland and coastal populations, significant differences were not observed between any of the four field sites. Qualitatively, SG snakes traveled almost twice the distance of CR snakes on a given day, despite the fact that these two inland sites are separated by only 55 km and have similar climates. This may reflect the topography of the two sites, where snakes at CR utilize clusters of rocky outcrops for refugia while SG snakes tend to regularly move among ground squirrel burrows in open fields. The rocks at CR clearly provide favorable conditions (e.g., high thermal quality, access to mates and prey, cover from predators; Ashton 2003; Whitaker and Shine 2003; Gomez 2007), and snakes tended to move about within rocky outcrops and only occasionally travel between them, resulting in low daily movement distances. Importantly, the habitat and climate of SG and CR are otherwise similar, as is the body size of SG and CR snakes. Although the differences observed between these two groups were not statistically significant, this highlights the fact that populations in habitats with similar climates and other characteristics may actually exhibit variation in spatial ecology patterns. We suspect that increasing the sample sizes of snakes tracked between these two sites would yield detectably significant differences in habitat use and daily movement values.

Body size (i.e., SVL) is an important covariate to consider in all analyses of the spatial ecology of snakes because it can encompass many factors that may affect movement and habitat use, including age (larger snakes are often older, and may have more experience in utilizing an annual core range; small, juvenile snakes may disperse and/or explore areas suitable for establishing activity range; Clark 1974; Secor 1994), body condition (a snake's body condition may impact hunting behavior; Wasko and Sasa 2012); and dominance (large male snakes often win fights for access to females; Shine 1978; Ashton 2003). In some species, large male snakes have larger home ranges and/or movement distances than small snakes (Whitaker and Shine 2003), other studies have failed to document body size effects on spatial ecology (Miller et al. 2012; Delisle et al. 2019), and another study on *C. oreganus* at CR found that small males actually had larger home ranges outside the spring mating period (Putman et al. 2013). Snake

length and mass are highly correlated (Feldman and Meiri 2012), and studies vary in terms of which variable they examine for effects on spatial parameters. We incorporated SVL into this study as a covariate rather than body mass as snake growth, in terms of length, increases only in very small increments once adulthood is reached, and body mass can fluctuate dramatically based on a variety of factors such as hydration and time since the last meal. Nonetheless, we found no evidence for a relationship between SVL and any spatial ecology parameters in this study of *C. oreganus*.

In summary, we have shown that spatial parameters including 100% MCP, 95% KDE/MCP, 50% KDE/MCP, and mean daily movement are more variable at the intrapopulation level rather than across rattlesnake populations, such that seemingly large differences between populations are not always significant. Ambush predators, like rattlesnakes, select their daily microhabitats from complex habitat mosaics influenced by weather, solar radiation, wind speed, mate availability, camouflage from predators and prey, and more; variation in these factors leads to complex patterns in spatial ecology. Predicting the home range size or movement distance of any given individual is not possible, but for large-scale applications we may be able to extrapolate results from a study on a single population to produce generalizations about a given species.

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