TEXAS J. OF SCI. 77(1): ARTICLE 1 2025

HABITAT USE, HOME RANGE SIZE, AND MOVEMENT RATES IN TWO SYMPATRIC PITVIPERS (CROTALINAE) IN FAR WEST TEXAS

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Abstract.–Niche partitioning, or differential resource use, is a possible explanation for the coexistence of multiple species that would otherwise be in competition. In this study, we examined two sympatric desert snakes, the eastern black-tailed rattlesnake (*Crotalus ornatus*) and western diamondback rattlesnake (*Crotalus atrox*) on Indio Mountain Research Station (IMRS) in Hudspeth County, Texas, for evidence of partitioning along the spatial dimension of the niche. We tracked the movements of the two species using radiotelemetry and analyzed macrohabitat and microhabitat data using a combination of multinomial logit models and chi-square tests. Evidence of niche partitioning along the spatial dimension of the niche exists between the two species, with *C. ornatus* showing a higher affinity for southwest facing, rocky slopes and *C. atrox* showing a relatively diverse use of all habitats with a slight preference for northeastern slopes. Our results largely compare to previous studies at both IMRS and throughout the range of each species.

Keywords: *Crotalus,* spatial ecology, niche partitioning

Niche partitioning, or differential resource use, can exist between species to avoid competitive exclusion (MacArthur & Levins 1967). Species engage in niche partitioning along a variety of axes including, but not limited to, the spatial, temporal, thermal, and dietary axes (Pianka 1986; McDonald 2002; Lara et al. 2009; Goiran et al. 2020). In reptiles and amphibians, partitioning along the spatial axis is common in lizards via the selection of different microhabitats (Pianka 1986). Snakes have generally been regarded to partition primarily along the dietary axis (Luiselli 2006) although partitioning along the spatial axis

DOI 10.32011/txjsci_77_1_Article1

has been reported in some species, particularly those in extreme environments such as montane and desert environments (Pough 1966; Beck 1995).

Sympatric desert snakes inhabit resource-poor environments, which may increase selective pressure for partitioning resources. In the absence of dietary niche partitioning, snake species that have similar diets are likely to be in greater competition for food resources than those with differing diets (Himes 2003). Partitioning along spatial or temporal niche dimensions can allow the coexistence of closely related sympatric snake species with similar diets (Luiselli 2006), such as *Crotalus ornatus* (eastern black-tailed rattlesnake) and *Crotalus atrox* (western diamondback rattlesnake).

The spatial ecology of pitvipers is a rich field containing many studies, particularly of North American species. Historically, studies have analyzed the effects of body size, sex, and more recently, season (Whitaker & Shine 2003; Roth 2005; Blouin-Demers et al. 2007; Glaudas & Rodríguez-Robles 2011). Modern studies have begun investigating the effects of anthropogenic disturbances such as the influence of roads (Tipton et al. 2023) and man-made refugia (DeSantis et al. 2019). Despite the vast literature on the topic, data are either limited or non-existent for many species and few studies evaluate differences in space use interspecifically (Pough 1966; Beck 1995; Waldron et al. 2006).

Adult *C. atrox* average 91 to 122 cm in total length and are ambush foragers that predate lizards, birds, frogs and toads, and a variety of small mammals (Werler & Dixon 2000). *Crotalus atrox* ranges from the Mexican states of Sinaloa and San Luis Potosí, north to southeastern California and Arizona and east across New Mexico and Texas to Arkansas and Oklahoma (Ernst 1992). *Crotalus atrox* is a habitat generalist that primarily inhabits dry or semi-arid lowland areas of brush covered plains, dry washes, rocky outcrops, and desert foothills below 1500 m elevation (Degenhardt et al. 1996), which aligns with previous reported information in far west Texas (DeSantis et al. 2019).

Adult *C. ornatus* average 76 to 107 cm in total length and are ambush foragers that primarily prey on lizards, birds, and small mammals (Werler & Dixon 2000). *Crotalus ornatus* ranges from the Mexican states of Chihuahua and Coahuila, north to south-central Texas and northwest into south-central New Mexico (Anderson & Greenbaum 2012). *Crotalus ornatus* is a habitat generalist, usually occurring in a wide variety of semi-montane habitats such as rock ledges and high-altitude pine-oak and boreal forests, but are most commonly found in rocky areas of mountain foothills (Degenhardt et al. 1996). In far west Texas, they are reported to prefer rocky slope and arroyo habitat (Emerson et al. 2022).

Based on similarities in body size, foraging mode, prey base, and phylogenetic relationship (members of the same clade but different groups), we assessed habitat use of sympatric *C. ornatus* and *C. atrox* in the Chihuahuan Desert of far west Texas to determine if they differ along any spatial dimensions of the niche. We also assessed home range and movement rates as metrics of space use. Due to the more general use of habitat by *C. atrox* and preference for rocky habitat by *C. ornatus* as previously documented in the literature, we predict that the two species will partition along the spatial dimension of the niche.

MATERIALS & METHODS

Indio Mountain Research Station (IMRS; centered on 30° 45' N, 105° 00' W; WGS 84; ca. 1200 m elev.) covers approximately 15,000 ha of Chihuahuan Desert habitat located approximately 40 km southwest of Van Horn, Hudspeth County, Texas (Worthington et al. 2020). The vegetation of IMRS is typical Chihuahuan Desert scrubland (creosotebush-lechuguilla-ocotillo-yucca associations) and tobosa/ black grama desert grassland, although habitat associations vary with elevation and slope. In the steeper, rockier regions, vegetation associations are typically ocotillo and cactus. In the adjacent bajada sections, yucca, creosotebush, and grasses numerically dominate. Prior to 1986, IMRS was used primarily for livestock grazing and mining (Worthington et al. 2020).

We located snakes opportunistically, by searching suitable habitat on foot throughout IMRS. Search areas consisted of different plant communities, substrates, and slope orientations that are known to occur at IMRS and recorded by previous studies (Mata-Silva et al. 2018; Worthington et al. 2020; Emerson et al. 2022). We implanted snakes with radio transmitters (Model SI-2T, Holohil Systems, Ltd.) following standard procedures (Reinert & Cundall 1982; Hardy & Greene 1999b, 2000). Transmitter mass was less than 5% of snake body mass. Snakes were released at the original site of capture within 24–48 hours post-surgery.

We monitored snake activities between September 2003 and November 2005 for both species. On average, snake locations were recorded 12 days per month between 0700 and 2300 h. Relocations occurred evenly throughout the month, and we relocated snakes once per relocation event. We measured snakes at the exact spot we relocated them. Field personnel made an effort to not disturb the snake, maximizing the observation distance and minimizing time in proximity to the snake. We also recorded date, time, GPS location, macrohabitat, and microhabitat at each individual relocation. Macrohabitat was classified as one of four major habitat types: (1) "Rocky Slope," sloped areas covered with rocks of at least cobble sized bedrock (>50 mm in diameter); (2) "Arroyo," areas that contain ephemeral watercourses such as those for landscape drainage purposes, including arroyo bed and banks; (3) "Alluvial Flat/Bajada," flat areas that are upland and immediately adjacent to aforementioned arroyos; (4) "Disturbed," areas such as roads, man-made earthen stock tanks, and man-made structures (i.e., buildings, mine dumps). Microhabitat data included shelter type (under shrubs, in rock crevices, in burrows), sun exposure (the percentage of snake body that had sun, 0–100%), cardinal direction (N, S, E, W, or combination; recorded with a compass), and general slope aspect (flat or slope).

We used GPS locations to calculate home range for each snake as minimum convex polygons (MCP) and 95% weighted autocorrelated kernel densities (AKDE) using R software packages adehabitatHR and ctmm (Calenge 2006; Calabrese et al. 2016). We used ArcGIS software (version 10.5) to determine minimum straight-line distance travelled (MSL), and daily distance moved (DDM) for each as the sum of MSL divided by the number of days tracked for each individual. We also calculated movement frequency for each individual as the number of movements divided by the number of days tracked. We used T-tests for two sample means to compare average home ranges, daily distances moved, and movement frequencies between the two species. We tested the normality of each metric using Shapiro-Wilk tests in addition to F-tests to ensure equal variances. When data did not meet the assumption of normality, we either log transformed it or used a Mann-Whitney U test. We log transformed data for daily distance moved and conducted a Mann-Whitney U test for movement frequency, all other data was normally distributed. We considered only individuals with a minimum of 30 location points for home range analysis.

We analyzed habitat use with multinomial logit models fit with maximum likelihood estimation. We included two predictor variables: (1) species and (2) season (spring = Mar–May; summer = Jun–Oct; winter = Nov–Feb). Snake ID was used as a random factor. We employed a model comparison approach using AIC and a forward stepwise selection process following Mata-Silva et al. (2018) and Emerson et al. (2022) for model selection. We analyzed microhabitat using a variety of methods as these data were highly varied. First, for sun exposure, we used a Poisson GLM as these data most closely matched a Poisson distribution and comprised solely of integers. To test for overdispersion in our model, we conducted a dispersion test. For all other microhabitat variables (shelter type and slope aspect), we generally compared results with chi-square (X^2) tests as these data contained many factors (5 and 8 respectively). We performed all statistical analyses with R software (version 4.3.0) and an alpha of 0.05.

RESULTS

We radiotracked four adult male *C. ornatus* and five adult male *C. atrox* during the study. Average tracking duration was 10 months for *C. ornatus* and 23 months for *C. atrox*. Relocations ranged from 12 to 73 and averaged (± SE) 42.5 ± 5.54 relocations. We used only three *C. ornatus* for home range analysis, as one did not meet the required minimum 30 location points.

There was no significant difference in DDM between *C. ornatus* (42.6 ± 30.3 m/day) and *C. atrox* (16.5 ± 4.96 m/day) (T-test; $T = 0.1603$, $df = 7$, $P = 0.8771$). There was also no significant difference in movement frequency between *C. ornatus* (0.806 ± 0.130) and *C. atrox* (0.877 ± 0.034) (Mann-Whitney U Test; $W = 10$, $P = 1$). There was no significant difference in average MCP home range between *C. ornatus* (13.94 ± 4.37 ha) and *C. atrox* (37.4 ± 8.67 ha) (T-test; $T = 1.9563$, $df = 6$, $P = 0.0982$). There was no significant difference in 95% AKDE home range between *C. ornatus* (47.8 ± 17.4 ha) and *C. atrox* (67.2 ± 14.8 ha) (T-test; $T = 0.8260$, $df = 6$, $P = 0.4404$).

Habitat use differed significantly between *C. ornatus* and *C. atrox* (Table 1), with *C. ornatus* utilizing rocky slopes more often than expected, while *C. atrox* utilized all other habitats more often than expected (Table 2). We also found a significant effect of season, with rocky slopes avoided during summer and preferred during winter (Table 1). Microhabitat use as sun exposure was not significantly different between species (Poisson GLM; $Z = 1.323$, $P = 0.186$). All other microhabitat variables were significantly different between species. *Crotalus ornatus* was most frequently observed in crevices with *C. atrox* most frequently observed in shrubs ($X^2 = 38.79$, $df = 5$, $P < 0.001$; Table 3). Slope use was also significantly different between species ($X^2 = 23.84$, $df = 8$, $P = 0.002$). Since slope face also included flat, we compared the occurrence of the two species between slopes (N, S, E, W, or combination) and flat, with *C. ornatus* more frequently located on slopes and *C. atrox* on flats ($X^2 = 7.097$, $df = 1$, $P = 0.008$; Table 4). In order to examine slope without flat we evaluated the direct-

Table 1. Results of the best-fitting multinomial logit model showing species and season were the best predictor of habitat selected by *Crotalus atrox* and *C. ornatus* at IMRS. The model was a random slopes and intercepts model, controlling for snake ID, with an AIC = 752.56. The reference level was arroyo.

		Predictors			
		(Intercept)	Species (*C. ornatus*)	Season (Summer)	Season (Winter)
Bajada	Odds ratio	0.44	0.26	0.85	0.60
	SE	0.23	0.24	0.32	0.53
	Cl	0.16–1.21	0.04–1.60	0.41–1.77	0.10–3.46
	Z	-1.60	-1.45	-0.44	-0.58
	P	0.109	0.146	0.663	0.565
Disturbed	Odds ratio	0.07	0.65	1.97	2.60
	SE	0.06	0.79	1.11	2.56
	Cl	0.01–0.34	0.06–7.13	0.65–5.95	0.38-17.97
	Z	-3.30	-0.35	1.20	0.97
	P	**0.001**	0.723	0.232	0.333
Rocky slope	Odds ratio	1.31	4.90	0.50	7.03
	SE	0.61	3.26	0.16	3.84
	Cl	0.53–3.27	1.33–18.09	0.27–0.93	2.40–20.53
	Z	0.59	2.39	-2.21	3.57
	P	0.556	**0.017**	**0.027**	**<0.001**

Table 2. Habitat selection by *Crotalus ornatus* and *C. atrox* at IMRS as count and percent of total observations per species.

Habitat	*C. atrox* (%)	*C. ornatus* (%)
Arroyo	91 (33.9)	17 (15.9)
Bajada	50 (18.7)	4 (3.7)
Disturbed	22 (8.2)	5 (4.7)
Rocky slope	105 (39.2)	**81 (75.7)**

Table 3. Shelter types used by *Crotalus ornatus* and *C. atrox* at IMRS as count and percent of total observations per species.

Shelter type	*C. atrox* (%)	*C. ornatus* (%)
Burrow	51 (19.5)	9 (8.7)
Crevice	48 (18.3)	**48 (46.6)**
None	39 (14.9)	11 (10.7)
Rock	5 (1.9)	6 (5.8)
Shrub	**114 (43.5)**	29 (28.2)
Yucca	5 (1.9)	0 (0)

Table 4. Slope aspect used by *Crotalus ornatus* and *C. atrox* at IMRS as count and percent of total observations per species.

Slope aspect	*C. atrox* (%)	*C. ornatus* (%)
Slope	168 (60.9)	**82 (75.9)**
Flat	108 (39.1)	26 (24.1)

Table 5. Slope direction used by *Crotalus ornatus* and *C. atrox* on IMRS as count and percent of total observations per species.

Slope direction	*C. atrox*	*C. ornatus*
S	28 (16.8)	**19 (23.2)**
N	9 (5.4)	8 (9.8)
E	**12 (7.2)**	1 (1.2)
W	50 (29.9)	**27 (32.9)**
SE	**8 (4.8)**	2 (2.4)
NE	**7 (4.2)**	0 (0)
SW	41 (24.6)	**24 (29.3)**
NW	12 (7.2)	1 (1.2)

ionality of the slope, with *C. ornatus* primarily associated with the southwestern quadrant, occurring most frequently on western, southern, and southwestern slopes and *C. atrox* primarily associated with the eastern quadrant, occurring most frequently on eastern, northeastern, and southeastern slopes ($X^2 = 15.05$, $df = 7$, $P = 0.035$; Table 5).

DISCUSSION

Although no statistically significant differences were detected in any space use metric between *C. ornatus* and *C. atrox* at IMRS, *C. atrox* home ranges were on average larger than *C. ornatus*. Factors that influence interspecific variation in home range remain unclear (Macartney et al. 1988; Fiedler et al. 2021), however a positive correlation with body size has been demonstrated at the intraspecific level (Blouin-Demers et al. 2007). Individuals of *C. atrox* are on average larger than *C. ornatus* and so this may partially explain this difference. Daily distances moved were on average much larger for *C. ornatus* than *C. atrox* despite no statistically significant difference. This is likely explained by the tendency of some individual *C. atrox* to utilize resource hot spots in the form of man-made refugia as demonstrated by DeSantis et al. (2019). This may also explain the slightly larger movement frequency of *C. atrox* as individuals utilizing these refugia likely move frequently within and between these areas over shorter distances.

There is currently only one published study on the spatial ecology of *C. ornatus* (Emerson et al. 2022), likely because it was only recently revalidated to full species status from *Crotalus molossus* by Anderson & Greenbaum (2012). There is also limited information for *C. molossus* as now envisioned. Given this relatively recent taxonomic treatment, we compare our study population to both *C. ornatus* and *C. molossus*. Emerson et al. (2022) reported a much higher MCP home range (33 ha) but a much lower daily distance moved (11.63 m/day) for male *C. ornatus*. Our results on *C. ornatus* were different from those reported by Beck (1995), Hardy & Greene (1999a), and Nowak (2009) for *C. molossus* in Arizona. Movement rate reported here for *C. ornatus* was less than that of male and female *C. molossus* (41.6 m/day) reported by Beck (1995), and our result for MCP home range was larger than that reported by Beck (1995; 3.49 ha). The home range estimates for male *C. molossus* conveyed by Hardy & Greene (1999a) and Nowak (2009) were both larger than our findings (21 ha and 18.05 ha, respectively). In New Mexico, Smith et al. (2001) reported a home range of < 0.1 ha for the single male *C. molossus* in their study.

There are also few investigations reporting movement data for *C. atrox*, and a majority of those were conducted in Arizona. Additionally, due to nonstandard protocols among studies, detailed comparisons are not possible (Gregory et al. 1987). Therefore, we present only broad comparisons because the studies differed in the type of movement data recorded, and whether habitat modifications had occurred, such as translocation or construction of manmade refugia. Our results for movement rate and MCP home range were both higher than in studies of *C. atrox* in Arizona conducted by Nowak et al. (2002; 7.65 m/day, 17.84 ha) and Clark et al. (2014; 17.6 ha). In Oklahoma, Landreth (1973) found movement rates to be much higher (55.4 m/day). At IMRS, where our study took place, DeSantis et al. (2019) reported higher values for movement rate (51.1 m/day) and 95% KD home range (42.6 ha), but a lower value for MCP home range (22.7 ha), and a similar value for 50% KD home range (7.35 ha) as our study.

Few studies have directly measured habitat use for either species. However, habitat use at IMRS for both species was similar to previous reports in Arizona (Pough 1966; Beck 1995) and New Mexico (McInnes 2013). We observed a similar effect of season as in Beck (1995) as both species increased utilization of rocky slopes during winter. We also observed the same seasonal shift in habitat use between species as *C. atrox* moved from rocky slopes to bajada and arroyo habitats during spring and summer. During this time, *C. ornatus* also made use of these habitats, however much less frequently than *C. atrox*, as they still displayed an affinity to rocky slopes, which was also noted by Beck (1995) as well as more recently by Emerson et al. (2022). This is further supported by the shelter use data in which *C. ornatus* were most frequently observed in crevices and *C. atrox* in shrubs as in both Beck (1995) and Emerson et al. (2022). In all studies, including ours, *C. atrox* displays a tendency toward using flat habitats dominated by creosotebush during the active season. In Pough (1966), Beck (1995), Emerson et al. (2022), and our study, the *C. molossus/ornatus* complex shows affinity for upland rocky habitats during all parts of the year.

We recognize that our study is somewhat limited in scope due to small sample size, tracking duration differences between the species, low tracking duration overall, and our evaluation of only male individuals. For comparison, DeSantis et al. (2019) and Emerson et al. (2022) recorded nearly twice the number of relocations as our study and both studies were a year longer in duration than ours. These two studies also had three to four times the number of individuals and much greater numbers of females (approximately half the total individuals were female). Beck et al. (1995) reported similar individual numbers as our study but greater tracking frequencies (more similar to those of DeSantis et al. (2019) and Emerson e al. (2022)).

Weather conditions during our study period were largely average for the study area (Mata-Silva et al. 2018; DeSantis et al. 2019; Emerson et al. 2022). Despite this, 2004 was notably a very wet year for the area with 480 mm precipitation. The year was also slightly cooler on average with a daily temperature of 23.8°C during the active season. Beck (1995) noted similar levels of precipitation during their study period although higher average temperatures during the active season (28.8°C). Precipitation during all these studies varied widely between each year ranging from 142.9 to 480 mm.

We accept that other factors, such as differential predation or thermal ecology, as in the intraspecific example provided by Goiran et al. (2020), may also have contributed to the difference in habitat use seen between the two species. Future research into this system should seek to collect temperature and diet data from each species and each habitat to examine niche partitioning more closely.

Despite the caveats, our study represents a novel look at niche partitioning between these two species as no previous study has evaluated this in the northern Chihuahuan Desert or assessed slope directionality as an explanatory factor of habitat use. Additionally, our study adds to the growing body of literature on the spatial ecology of *C. ornatus*.

ACKNOWLEDGMENTS

We thank T&E, Inc., UTEP Graduate School, and IMRS Research Fund for partially financing our fieldwork. We thank Hector Riveroll, Jr., Vicente Mata-Silva, G. Walker Johnson, Helen Brewer, Brett Johnson, Elizabeth Walsh, James Emerson, and Carl Lieb for assistance with study design, data collecting, and useful comments on the manuscript. The UTEP IACUC (Protocol A-1780) approved all research procedures used by JDJ and JPH.

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