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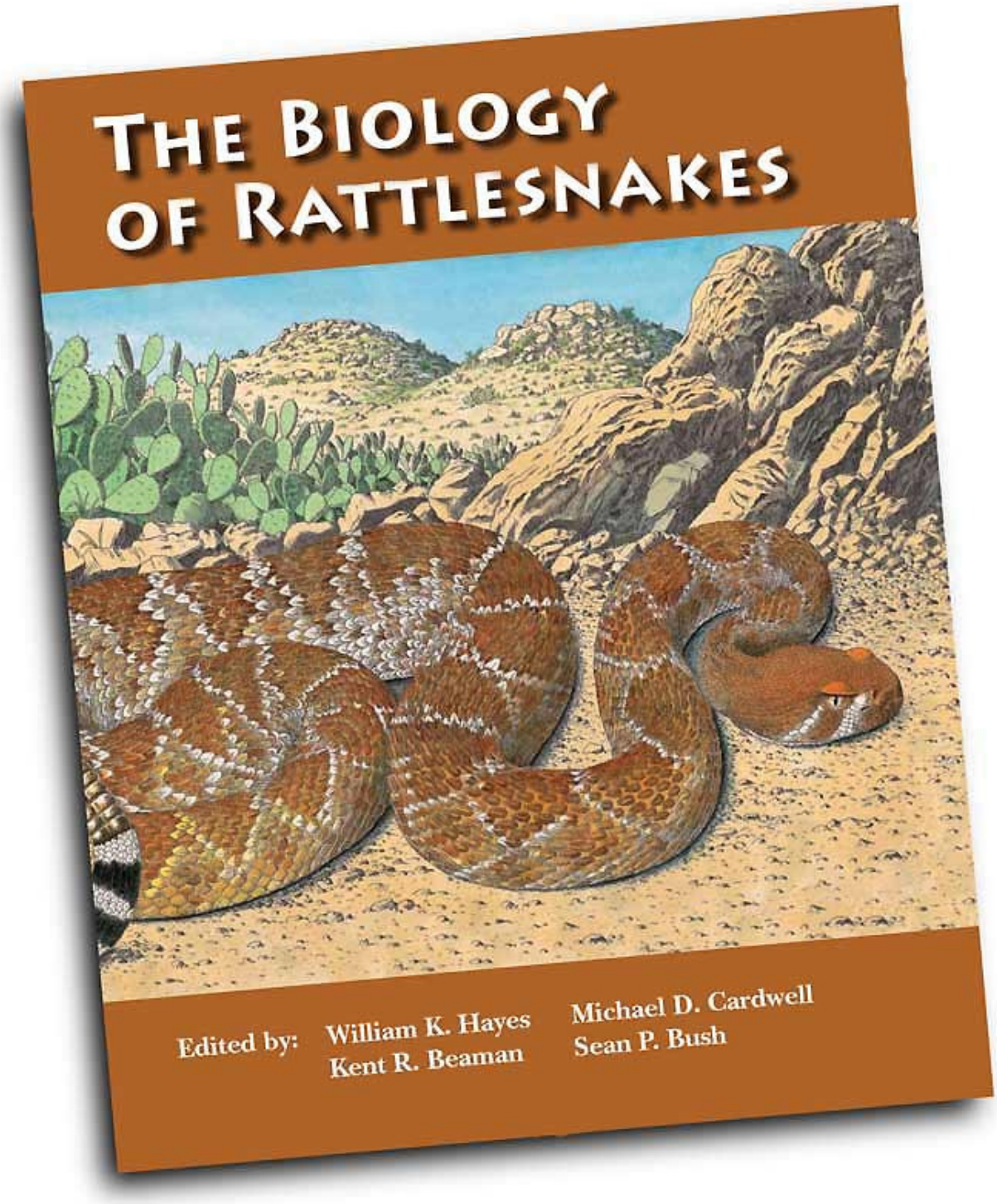

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Home Range Size, Movements, and Mating Phenology of Sympatric Red Diamond (*Crotalus ruber*) and Southern Pacific (*C. oreganus helleri*) Rattlesnakes in Southern California

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Abstract.—Although many sympatric snake species partition food to reduce interspecific competition, rattlesnakes and other vipers, like most vertebrates, typically partition the habitat. To evaluate this generality, we used radiotelemetry to study the home range sizes, movements, and mating phenology of sympatric adult male Red Diamond (*Crotalus ruber*) and Southern Pacific (*C. oreganus helleri*) Rattlesnakes in a coastal valley of southern California. Mean home range sizes and mean daily movements were substantially greater in *C. o. helleri* than in *C. ruber*. Both species occupied much larger home ranges during the two active seasons (March-November) compared to the winter season. Mating seasons differed between the two species, with *C. ruber* engaging in accompaniment, courtship, and copulation exclusively in the spring and *C. o. helleri* exhibiting reproductive behavior during both late summer/fall and spring. Annual movements by *C. o. helleri* spiked in both spring and late summer/fall, whereas movements of *C. ruber* spiked also in spring but less dramatically in late summer/fall. Spatial use and movement differences between the two species likely resulted from distribution of preferred habitats at the study site (limited *Opuntia* cactus patches for *C. ruber*, widespread non-native grassland and riparian habitats for *C. o. helleri*) and differences in mating phenology (*C. o. helleri* males searching for mates in two seasons versus one for *C. ruber*). Thus, these two species, like other sympatric rattlesnakes and vipers studied to date, appear to partition habitat. However, unlike other sympatric rattlesnakes studied to date, *C. ruber* and *C. o. helleri* also differ in their use of spatial and temporal resources, though probably not as a direct result of competitive mechanisms.

Introduction

Niche theory predicts that closely-related sympatric species should partition resources to avoid or reduce interspecific competition (Pianka, 1981; Walter, 1991). Niche separation can be achieved via differences in food (type or size) or in use of spatial (macrohabitat or microhabitat), temporal (diel or seasonal activity patterns), or thermal resources (Schoener, 1974; Saint Girons, 1978). Snakes have been considered atypical among vertebrates because sympatric species usually partition food rather than habitat (Toft, 1985; Vitt, 1987; Luiselli, 2006a). However, sympatric viper species apparently adhere to the typical vertebrate pattern, primarily partitioning habitat (Luiselli, 2006a,b; Luiselli et al., 2007).

Rattlesnakes (genera *Crotalus* and *Sistrurus*) represent an ideal group for exploring niche separation in vipers. The ranges of many species often overlap broadly, particularly in the arid and semi-arid regions of southwest North America, where species richness is highest (Klauber, 1972; Beaman and Hayes, this volume). The few studies of this group support the view that sympatric rattlesnake species primarily partition habitat. Pough (1966), Reynolds and Scott (1982), and Mendelson and Jennings (1992) demonstrated differences in habitat use of *Crotalus atrox*, *C. molossus*, and *C. scutulatus* in the Sonoran Desert of southeast Arizona, southwest New Mexico, and northern Chihuahua, Mexico. Beck (1995) determined that sympatric *C. atrox*, *C. molossus*, and *C. tigris* in southeast Arizona use different habitats, but otherwise exhibit similar home range sizes, activity patterns, thermal ecology, and annual food intake. Waldron et al. (2006b) found that sympatric *C. adamanteus* and *C. horridus* in coastal South Carolina prefer different habitats, but occupy similar home range sizes. Steen et al. (2007) also showed that sympatric *C. adamanteus* and *C. horridus* in coastal Georgia use different habitats. Reinert (1984) determined that *C. horridus* and another sympatric viper, *Agkistrodon contortrix mokeson*, prefer different habitats in eastern Pennsylvania.

Differences in space use and movements by sympatric rattlesnakes could be expected for many reasons apart from competitive mechanisms. The distribution and abundance of critical resources greatly influence the movement patterns of snakes (Gregory et al., 1987). Critical resources for rattlesnakes include required habitat, food, access to potential mates, protection from predators, and suitable thermoregulation and overwintering sites (e.g., Reinert and Zappalorti, 1988; Secor, 1992; Duvall and Schuett, 1997). Temporal variation in resources and needs also influences movements by snakes (Seigel and Pilgrim, 2002). Some crotaline snakes, for example, mate only in spring, some mate only in late summer/fall, and others exhibit a bimodal mating phenology, with copulations occurring during both late summer/fall and spring (i.e., interrupted by hibernation; Aldridge and Duvall, 2002; Schuett et al., 2002). During mating season,

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males frequently undertake extensive searches for mates (e.g., Duvall et al., 1992; Secor, 1992; Aldridge and Brown, 1995; Prival et al., 2002; Sealy, 2002; Ashton, 2003; Marshall et. al, 2006; Waldron et al., 2006a; Jellen et al., 2007; Cardwell, 2008; Brown et al., this volume; Goode et al., this volume). Rattlesnake activity also shifts dramatically with seasonal changes in temperature and rainfall (e.g., Prival et al., 2002; Goode et al., this volume). Thus, differences in space use and movements by sympatric rattlesnakes could result from differences in preferred habitats and species-specific eco-physiological constraints.

The Red Diamond Rattlesnake (*C. ruber*) is a large-bodied pitviper distributed from southern California southward throughout the Baja peninsula and several of its associated islands (Grismer, 2002). *Crotalus ruber* can be found from the desert slopes to the coastline, and preys predominately on rodents (Klauber, 1972; Dugan, unpubl. data). The Red Diamond rattlesnake is currently listed as a species of special concern by the State of California (Jennings and Hayes, 1994). To date, no published accounts exist detailing the biology of this species (Beaman and Dugan, 2006); however, recent research has begun to address this void in our knowledge (Greenberg, 2002; Brown et al, this volume; Halama et al., this volume).

The Southern Pacific Rattlesnake (*C. oreganus helleri*; Ashton and De Queiroz, 2001) is another large-bodied pitviper, distributed from central California southward into northern Baja (Grismer, 2002). This snake is considered a habitat generalist (Stebbins, 2003), as it inhabits a wide range of habitats from montane coniferous forests to coastal sage scrub along the coast. The Western Rattlesnake complex (*C. viridis* + *C. oreganus* + *C. cerberus*) is one of the most extensively studied group of snakes (Diller and Wallace, 2002; Beaman and Hayes, this volume). However, no quantitative data have been published on movements and habitat use of *C. o. helleri*.

The close phylogenetic relationship and extensive overlap of the ranges, habitat, and general life histories makes these two species ideal candidates for studies of niche separation and interspecific variation in natural history. In California, coastal populations of both species coexist in a rapidly-fragmenting environment, placing many remaining populations in danger of genetic isolation and local extirpation (Halama et al., this volume). Accordingly, we need a better understanding of the ecology of these two broadly sympatric species, not just for behavioral and ecological theory, but also for conservation concerns. The data presented herein address the following questions as they relate to potential niche separation. 1) Do home ranges of sympatric *C. ruber* and *C. o. helleri* differ in area and by season? 2) Do movements of sympatric *C. ruber* and *C. o. helleri* differ in magnitude and by season? And finally, 3) does the phenology of reproductive activity differ between *C. ruber* and *C. o. helleri*? Additional data collected during this study on habitat use, diet, and survival will be presented in a separate manuscript.

Materials and Methods

Study site.—The study site encompassed ca. 30 ha in the southeastern portion of Chino Hills State Park (CHSP), California (33º54' N, 117º42' W). A north-south running canyon with a small semi-perennial creek dominates the site's topography. The CHSP system comprises ca. 5,039 ha in Los Angeles, Orange, Riverside, and San Bernardino counties, and ranges in elevation from 131-543 m (Keller, 1992; Goodman, 1997; http://www.stateparks.com/chino_hills.html).

We identified five major habitats at the study site: cactus, coastal sage scrub (CSS), non-native grassland, riparian, and oak woodland. Cactus patches of Coastal Pricklypear (*Opuntia littoralis*) were found exclusively on south-facing slopes and represented the habitat with the smallest distribution at our site. The distribution of CSS was patchy, primarily on south-facing slopes. Non-native grassland was the most widespread, occurring on both hillsides and in canyon bottoms. The riparian system was largely confined to the creek channel, but penetrated into damper drainages of the grassland. Oak woodland was found primarily on north-facing slopes, but was not used by any of the telemetered snakes in this study. The study site was devoid of rock outcroppings, as the soil is predominately clay. Sampson (1985) provided further details on relative abundance and species composition of these plant communities.

The site experiences a Mediterranean climate. Average annual precipitation ranges from 35-46 cm, with the majority of rainfall occurring during the winter and spring months (Sampson, 1985). Winters are mild (average daily low in January = 5.6°C) and summers hot and dry (average daily high in July = 31.7 °C), with temperatures occasionally exceeding 38°C.

Radio-telemetry.—We began collecting, marking, and implanting snakes with radio-transmitters in March 2003. Individuals were tracked from March 2003 through December 2004. Visual searches and road surveys were used to obtain snakes of both species. Snakes were anesthetized with sevoflurane (Halocarbon Products Corp., River Edge, New Jersey, USA) while restrained within clear plastic tubes (Hardy and Greene, 1999) to allow collection of various measurement data. We recorded snout-vent length (SVL), total length, mass, rattle number, number of subcaudal scales, and sex for each snake. Adult snakes were sexed using Neosporin-lubricated sexing probes. All individuals were marked with a passive integrative transponder (PIT) tag (AVID Identification Systems, Inc., Norco, California, USA). PIT tags allowed us to permanently identify individuals as part of a long-term mark-recapture effort.

We used SI-2T temperature-sensitive transmitters (Holohil Systems Ltd., Ontario, Canada) to monitor up to six males of each species simultaneously. Transmitters weighed 9 g and always represented <5% of an individual's body mass (Hardy and Greene, 1999). Surgical procedures followed the guidelines and methods described by Reinert

and Cundall (1982) and Hardy and Greene (1999). Snakes were released at their collection site 24-36 h post-surgery. Minimizing time in captivity has been shown to increase post-surgical survival (Hardy and Greene, 1999). Sampling effort varied seasonally as snake activity patterns changed. Individuals were located 1-4 times/wk throughout the active season (March-November) and less often (bi-monthly) during the winter period (December-February). Telemetered snakes were relocated using a Telonics TR2 receiver (Telonics, Mesa, Arizona, USA) and a hand-held four-element yagi antenna. Upon each relocation, we visually located each snake if possible and recorded the universal transverse mercator (UTM) coordinates with a handheld GPS unit (Garmin GPS Plus III; Garmin Ltd., George Town, Cayman Islands). When snakes were located in dense, impenetrable cactus patches, coordinates were taken at the closest location possible (within 5 m of presumed location).

Data presented herein were collected from nine adult male *C. o. helleri* (84-103 cm SVL) and seven adult male *C. ruber* (98-156 cm SVL). Snakes were lost (predation, transmitter battery failure) or added opportunistically throughout the study, resulting in variable tracking periods (202-905 d) for different individuals.

Home range size and movements.—Based on location data, we computed two estimates of home range size, one estimate for autocorrelation, and one movement variable (see below). We compared each of these dependent measures for the two species and for three seasons: active season (March-November) 2003, winter season (December-February) 2003-2004, and active season (March-November) 2004.

We computed seasonal home range sizes using both minimum convex polygons (MCP) and fixed-kernel (FK) methods. We used Calhome 1.0 (Kie et al., 1994) and HomeRanger 1.5 (Hovey, 1999) to obtain 100% MCP and 95% FK, respectively. We used all fixes obtained from each individual for our analyses and software defaults, including least-squares cross-validation as the smoothing factor for FK. Although FK estimates are increasingly preferred (Powell, 2000), MCP estimates continue to be reported and are more available in the literature for comparisons between studies. Both estimates are sensitive to sample size, with MCP increasing asymptotically and FK decreasing asymptotically with increasing number of fixes (Seaman et al., 1999). Opinions remain contentious as to which estimate (MCP vs. FK) performs better (e.g., Row and Blouin-Demers, 2006; Laver and Kelly, 2008). HomeRanger also computed autocorrelation (t^2/r^2) for each snake, a measure of temporal independence between successive fixes. When autocorrelation exists ($t^2/r^2 < 2$), the distance moved between consecutive observations decreases, resulting in underestimates of FK (Swihart and Slade, 1985).

We considered movements at three time levels: daily, monthly, and seasonal. We used the mean distance moved per day as our fundamental unit of measurement for individual snakes. This was computed from the distance moved between each two consecutive fixes divided by the number of days between the two fixes (Gregory et al., 1987). To obtain mean daily movements per month, we calculated the mean of all such measurements procured within a given month for each snake. To avoid bias from uneven sampling across months, mean daily movements per season were computed as the average of all monthly estimates (rather than the mean from all fixes) for those months within a given season.

Mating phenology.—Data were collected opportunistically from both telemetered and non-telemetered snakes throughout the duration of the study. We recorded two types of sexual activities: accompaniment (pairs coiled next to or within 0.5 m of each other, often with males chin-rubbing and/or pursuing females in courtship; c.f. Duvall et al., 1992; Duvall and Schuett, 1997) and copulations. Nonsexual accompaniment during the winter months (overwintering at same site, November-February) was excluded. We also gleaned additional observations from the existing literature on *C. ruber* and *C. o. helleri*.

Statistical analyses.—Our primary interest was to examine the effects of species and season on spatial use and movements. For home range and movement data, we subjected each of the four dependent variables (100% MCP and 95% FK estimates of home range size, mean daily movements, and autocorrelation values) to three analyses.

First, to evaluate species and season simultaneously, we conducted 2 × 3 analyses of variance (ANOVAs; Mertler and Vannatta, 2004), treating species (two levels) as a between-subjects factor and season (three levels) as a within-subjects factor. Because some telemetered snakes were lost during the study (one of the initial six *C. ruber* became ill; three of the initial six *C. o. helleri* were predated) and then replaced by others, only five *C. ruber* and three *C. o. helleri* were tracked continuously over the three seasons, rendering a small sample size. Effect sizes from the ANOVAs were obtained as partial η^2 values (Cohen, 1988), indicating the approximate proportion of variance in the dependent variable explained by each independent variable or interaction, with values >0.25 generally considered large. When multiple effect sizes within a model summed to >1, we adjusted the values by dividing each partial η^2 by the sum of all partial η^2 values. Second, we conducted independent-samples *t*-tests to compare the two species for each of the three seasons, and computed Cohen's *d* (Cohen, 1988) for effect sizes using pooled standard deviation. Cohen's *d* values >0.8 are generally considered large effects. This within-season paired-comparison approach utilized all of the available subjects, increasing the sample size for the two active seasons ($N = 6$ for each species). Third, we used Pearson correlation coefficients of determination (r^2)to examine associations among the home range estimators (MCP and FK), number of fixes, autocorrelation, and movements.

Data used in these analyses were examined to determine whether parametric assumptions were met, and the fit was found to be acceptable in all cases. We also conducted

Table 1. Summary of number of locations (fixes), home range estimates (100% minimum convex polygon, MCP; 95% fixed kernel, FK; in hectares), mean daily movements (m/d), and Schoener's autocorrelation (t^2/r^2) per each of three seasons for individual male Red Diamond (*Crotalus ruber*, CR) and Southern Pacific (*C. oreganus helleri*, CH) Rattlesnakes.

Species-	Active Season 2003					Winter Season 2003-2004					Active Season 2004				
Snake	Fixes	MCP	FK	m/d	t^2/r^2	Fixes	MCP	FK	m/d	t^2/r^2	Fixes	MCP	FK	m/d	t^2/r^2
CR1	29	4.05	7.53	9.42	1.02	11	0.17	0.20	0.85	2.59	29	3.72	1.62	5.40	0.62
CR2	32	3.80	1.77	5.45	0.67	8	0.01	0.05	1.07	2.76	6	4.50	127.02[a]	16.46	0.89
CR8	27	1.26	0.73	6.02	1.89	6	0.06	0.03	1.58	1.21	7	0.63	0.52	26.06	2.46
CR12	23	2.36	1.57	6.22	1.46	10	0.10	0.02	2.21	2.67	40	3.58	1.11	9.50	1.52
CR13	23	1.58	0.60	5.76	1.95	9	0.02	0.03	1.04	0.87	39	1.96	1.16	11.96	1.45
CR19	23	0.34	0.15	2.93	1.59	-	-	-	-	-	-	-	-	-	-
CR36	-	-	-	-	-	-	-	-	-	-	13	0.93	0.61	5.39	1.47
Mean	26.2	2.23	2.06	5.97	1.43	8.8	0.07	0.07	1.35	2.02	22.3	2.55	1.00	12.46	1.40
±	±	±	±	±	±	±	±	±	±	±	±	±	±	±	±
1 SE	1.6	0.60	1.12	0.85	0.20	0.9	0.03	0.03	0.25	0.40	6.4	0.66	0.20	3.21	0.26
CH1	10	3.22	2.90	12.18	0.86	-	-	-	-	-	-	-	-	-	-
CH2	27	4.82	0.92	13.23	2.07	-	-	-	-	-	-	-	-	-	-
CH3	34	3.46	2.14	14.13	1.32	-	-	-	-	-	-	-	-	-	-
CH5	25	1.98	2.81	4.70	1.16	10	0.01	0.06	0.88	2.80	10	6.10	0.22	25.83	1.94
CH7	23	8.53	15.28	21.79	1.80	10	0.19	0.26	3.69	1.06	37	23.02	9.73	17.39	1.26
CH8	24	6.13	12.38	34.70	1.71	10	0.05	0.05	3.40	1.47	12	4.45	16.39	37.18	2.47
CH33	-	-	-	-	-	-	-	-	-	-	8	0.90	2.60	21.78	1.44
CH39	-	-	-	-	-	-	-	-	-	-	19	3.54	0.17	27.06	0.80
CH42	-	-	-	-	-	-	-	-	-	-	32	3.70	0.84	14.28	1.49
Mean	23.8	4.69	6.07	16.79	1.49	10.0	0.08	0.12	2.66	1.78	19.7	6.95	5.00	23.92	1.57
±	±	±	±	±	±	±	±	±	±	±	±	±	±	±	±
1 SE	3.2	0.96	2.50	4.21	0.18	0.0	0.05	0.07	0.89	0.53	5.0	3.29	2.72	3.31	0.24

[a] Regarded as an outlier and excluded from analyses.

non-parametric equivalents of *t*-tests and Pearson coefficients, but because the conclusions were identical, we report only the parametric outcomes.

Frequency data for sexual behavior were compared between the two species for the spring and late summer/fall seasons. The resulting 2 × 2 contingency table had too few cells with expected frequency ≥5 to use Chi-square tests. Thus, we evaluated the strength of asymmetry between species and seasons using Cramer's *V* (Conover, 1999).

Analyses were conducted using SPSS 12.0 for Windows (SPSS, 2003) with alpha set at 0.05.

Results

Home range size.—The two estimates of home range size (100% MCP and 95% FK) are summarized in Table 1 for each snake during each of the three seasons (the FK estimate for CR2 in the active season 2004 was deleted from analysis as an obvious outlier). Individual home range estimates varied from 0.15-23.02 ha during the active season and from 0.01-0.26 ha during the winter. Comparisons between species and seasons are depicted in Fig. 1. The main effect of species in the ANOVA model was not significant for either MCP or FK (both $P \geq 0.16$ and partial $\eta^2 \leq 0.32$; Table 2). However, the main effect of season was significant for both MCP and FK ($P = 0.041$ and 0.033, respectively), with each measure having a large effect size (partial $\eta^2 = 0.47$ and 0.43, respectively; Table 2). As expected, the snakes occupied much smaller home ranges during the winter, with *C. ruber* and *C. o. helleri* averaging 3.6% and 1.8% of their active-season home ranges, respectively (computed using species means in Table 1, with active-season home range calculated as the average for the two estimators, and averaged again for the two active seasons). No interactions between season and species were detected (both $P > 0.20$ and partial $\eta^2 = 0.25$; Table 2). Given the relatively large effect sizes (Cohen, 1988) for species and for interaction of species × season, larger samples may well have yielded significance. When the two species were compared for each season by *t*-tests, no species differences were detected in any season (all $P \geq 0.056$). However, the effect sizes (Cohen's *d*) were large (active 2003: MCP, $d = 1.25$, FK, $d = 0.85$; winter 2003-2004: MCP, $d = 0.14$, FK, $d = 0.58$; active 2004: MCP, $d = 0.76$, FK, $d = 0.85$), especially during the active seasons, further suggesting that *C. o helleri* occupied larger home ranges than *C. ruber*. Mean home range estimates were two- to five-fold greater for *C. o. helleri* (Table 1).

Table 2. Summary of analysis of variance (ANOVA) results for home range estimates (100% minimum convex polygon, MCP; 95% fixed kernel, FK), mean daily movements, and autocorrelation (t^2/r^2) for two species of rattlesnake over three seasons (see Table 1). Results include degrees of freedom (df), *F*-value, probability (*P*), and effect size (adjusted partial η^2).

Dependent Variable	Season				Species				Interaction			
	df	*F*	*P*	η^2	df	*F*	*P*	η^2	df	*F*	*P*	η^2
MCP	2,8	8.89	0.041	0.47	1,4	2.08	0.223	0.29	2,8	1.66	0.250	0.25
FK	2,8	5.39	0.033	0.43	1,4	2.96	0.160	0.32	2,8	1.97	0.201	0.25
Movements	2,12	15.35	0.001	0.41	1,6	7.14	0.037	0.39	2,12	2.18	0.156	0.20
t^2/r^2	2,8	0.51	0.621	0.11	1,4	0.49	0.524	0.11	2,8	0.62	0.562	0.13

The 100% MCP and 95% FK estimates from individual snakes were positively correlated during the first two seasons (active 2003: N = 12, $r^2 = 0.74$, P < 0.001; winter 2003-2004: $N = 8$, $r^2 = 0.70$, $P = 0.009$), but not during the third (active 2004: $N = 11$, $r^2 = 0.22$, $P = 0.15$). Although individual MCP estimates were usually larger than corresponding FK estimates during the active season (73.9% of 23 estimates), the FK estimates were more often larger during the inactive season (62.5% of 8 estimates, excluding one tie). In all seasons, the MCP (all $r^2 < 0.26$ and $P \geq 0.20$) and FK (all $r^2 < 0.27$ and $P \geq 0.19$) estimates were independent of number of fixes.

Autocorrelation.—Autocorrelation values (Schoener's t^2/r^2 statistic) varied from 0.62-2.80 for individual home range estimates, with means for the six cells (2 species × 3 seasons) ranging from 1.40 to 2.02 (Table 1). Schoener values substantially <2.0 are indicative of time dependence between successive relocations (Swihart and Slade, 1985). The ANOVA showed that autocorrelation values were similar for the two species and three seasons, with no interaction (all $P \geq 0.52$; all partial $\eta^2 < 0.13$; Table 2). Likewise, independent *t*-tests for each of the three seasons revealed no species differences (all $P \geq 0.65$) and effect sizes were small (all Cohen's $d \leq 0.27$). Autocorrelation values during each of the three seasons were independent of both MCP (all $r^2 < 0.02$, $P \geq 0.65$) and FK (all $r^2 < 0.14$, $P \geq 0.26$), and number of fixes (all $r^2 < 0.10$, $P \geq 0.32$).

Movements.—Mean daily movements of individual snakes varied from 2.93-37.18 m/d during the active season to 0.85-3.69 m/d during the winter (Table 1). From the ANOVA, the significant main effect of species ($P = 0.037$, partial $\eta^2 = 0.39$) indicated that *C. o. helleri* moved greater distances on average than *C. ruber* (Table 2). The differences were most evident during the active seasons, with *C. o. helleri* moving 2.8-fold further in 2003 and 1.9-fold further in 2004 (using species means in Table 1). The main effect of season was also significant ($P = 0.001$, partial $\eta^2 = 0.41$), with snakes moving considerably less during the winter compared to the active seasons (*C. ruber* = 14.7% and *C. o. helleri* = 13.1% of their respective active-season movements, calculated from species means in Table 1 averaged for the two active seasons). There was no interaction between season and species (Table 2). When the two species were compared for each season by *t*-tests, mean daily movements differed for each of the two active seasons (active 2003: $t_{10} = 2.52$, $P = 0.031$, Cohen's $d = 1.45$; active 2004: $t_{10} = 2.48$, $P = 0.032$, Cohen's $d = 1.43$), but not for the winter season ($P = 0.12$), though the effect size was substantial (Cohen's $d = 1.13$).

Movements were positively correlated with MCP in one season (active 2003: $r^2 = 0.62$, $P = 0.002$), but not in the others (both $r^2 < 0.18$ and $P \geq 0.30$). Movements were similarly associated with FK in one season (active 2003: $r^2 = 0.64$, $P = 0.002$), but not in the others (both $r^2 < 0.26$ and $P \geq 0.11$). Movements were independent of number of fixes in all seasons (all $r^2 < 0.26$ and $P \geq 0.09$), but were weakly positively associated with autocorrelation in one season (active 2004: $r^2 = 0.33$, $P = 0.049$; other seasons: $r^2 < 0.21$ and $P \geq 0.25$). Although not amenable to statistical analysis, monthly patterns of activity (Fig. 2) revealed peaks in both spring and late summer/fall, with relatively less activity occurring during the summer months. The late summer/fall peak in movement appeared to be more pronounced for *C. o. helleri* than for *C. ruber*.

Individuals of both species moved on occasion during the winter, demonstrating a lack of overwintering single-site fidelity. Neither species used communal hibernacula.

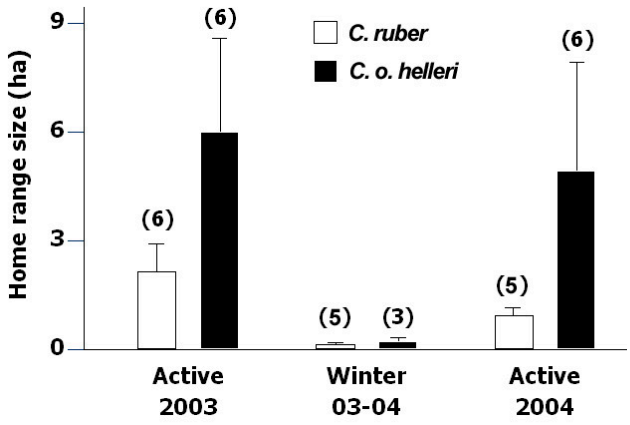

Figure 1. Mean (+ 1 SE) 95% fixed kernel estimates of home range size for adult male Red Diamond Rattlesnakes (*Crotalus ruber*) and Southern Pacific Rattlesnakes (*C. oreganus helleri*) during three seasons at Chino Hills State Park, California. Sample sizes for each mean are within parentheses.

Table 3. Number of sexual interactions observed in Red Diamond (*Crotalus ruber*) and Southern Pacific (*C. oreganus helleri*) Rattlesnakes, including male-female pairs interacting (accompaniment, sometimes including courtship) or copulating at our study site during spring and late summer/fall. Numbers in parentheses represent sum of our observations and reports from existing literature.[a]

Sexual Interactions	Spring		Late Summer/Fall	
	C. ruber	*C. o. helleri*	*C. ruber*	*C. o. helleri*
Accompaniment	10 (19)	8 (8)	0 (0)	3 (3)
Copulation	9 (27)	5 (6)	0 (0)	2 (5)
Totals	19 (46)	13 (14)	0 (0)	5 (8)

[a]Sources: Linsdale (1932), Armstrong and Murphy (1979), Klauber (1972), Grismer (2002), Brown et al. (this volume).

Mating phenology.—At our study site, we observed distinctly different use of mating seasons in the two species (Table 3). *Crotalus ruber* exhibited accompaniment, courtship, and copulation only during spring (2 February-7 April), whereas *C. o. helleri* exhibited sexual behaviors during both spring (16 February-24 April) and late summer/fall (11 September-3 October). For total observations (accompaniment and copulations), the asymmetry between species and season was significant (Cramer's $V = 0.41$, $P = 0.013$). When additional data from existing literature were added to our observations (Table 3), the asymmetry was even stronger (Cramer's $V = 0.53$, $P < 0.001$).

Discussion

We expected to see seasonal differences in home range size and movements, with both species occupying larger home ranges and moving greater distances during the active season than during the winter. However, we had no *a priori* expectations of finding the species differences that were detected. In the sections that follow, we emphasize these species differences, but also render comparisons to other studies when relevant.

Home range size.—Although we did not detect a statistical difference in home range size between the two species, effect sizes were large enough to suggest that a disparity exists, with *C. o. helleri* occupying two- to five-fold larger home ranges than *C. ruber* at our study site. Unfortunately, the relatively small sample size resulting from high levels of predation on *C. o. helleri* (see Methods) reduced the power of our statistical analyses, but practical significance (effect size) is often more meaningful, as it can be interpreted apart from sample size effects (Cohen, 1988). During winter, the two species likely occupied similarly-sized home ranges, and these were much smaller than those used during the active season. Although we did not track females during this study, *C. ruber* females use significantly smaller home ranges than males (Greenberg, 2002; Brown et al., this volume). We attribute species differences in home range size to the different preferred habitats, as discussed in the next section.

A comparison of 100% MCP estimates from three locations in southern California suggests that coastal populations of *C. ruber* occupy smaller home ranges than those of desert populations. At our coastal site, the seven adult males averaged 2.4 ha, with individuals occupying 0.3-4.5 ha (based on 6-40 fixes during the 9-month active season over 2 yr; Table 1). Five telemetered adult males at a coastal San Diego County location averaged 2.8 ha, with individuals ranging from 1.1-4.4 ha (based on 18-79 unique fixes during up to a 4-yr duration; Brown et al., this volume). In contrast to coastal populations, five telemetered adult males at a desert location in Riverside County averaged 25.8 ha, with individuals ranging from 7.2-52.5 ha (based on an unknown number of fixes over 381-1,000 d; Greenberg, 2002). Intraspecific variation in home range size could be attributed to differential availability and distribution of resources in coastal and desert environments (Gregory et al., 1987). One might expect that reliance on communal hibernacula would increase home range size, with snakes often dispersing great distances during the active season to reduce interspecific competition (Reinert and Zappalorti, 1988; Martin, 1992; Brown, 1993; Jørgensen et al., this volume; see further comments below). However, whereas snakes at our site and at the desert Riverside County location (Greenberg, 2002) did not use communal overwintering sites, those at the coastal San Diego County site did so, and their home ranges were relatively small (Brown et al., this volume). Unfortunately, we cannot compare our results from *C. o. helleri* to other locations due to the absence of such studies.

In our study, MCP and FK estimates showed close correspondence (with CR2 being the one exception in Table 1). Although both home range estimators are sample size-dependent (MCP increasing and FK decreasing with increasing sample size; Seaman et al., 1999) and FK estimates are especially sensitive to autocorrelation (Powell, 2000), we found no overt influence of number of fixes or autocorrelation on our estimates. The consequences of autocorrelation are frequently ignored in studies of home range size, though the sedentary nature of snakes, and reptiles in general, can often result in autocorrelation (Row and Blouin-Demers, 2006; Figueroa et al., this volume).

Movements and mating phenology.—*Crotalus ruber* not only used a smaller home range size than *C. o. helleri*, but also moved significantly less. We hypothesize two as-

pects of the biology of each species that likely contributed to the differences observed in active-season movements: habitat use and the timing and frequency of mating seasons.

The availability and distribution of preferred habitat have been shown to affect both annual (Reinert, 1993) and seasonal (Marshall et al., 2006) movements of rattlesnakes. At our site, *C. ruber* and *C. o. helleri* exhibited significant differences in habitat use (Dugan and Hayes, 2005, unpubl. data). Preferred habitat of *C. ruber* at our site—cactus primarily, and chaparral—is sparsely distributed and restricted to a series of south-facing hillsides. Movements of *C. ruber* throughout the study period were primarily confined to moves between and within clusters of *Opuntia* cactus patches. Several individuals spent virtually an entire active season within a single cactus patch. In contrast, preferred habitat of *C. o. helleri*—grassland and riparian—is widely and more continuously distributed throughout the site. The greater mean distances moved annually by *C. o. helleri* may be associated with the less-restricted abundance of grassland and riparian habitats.

Reproductive condition also dramatically affects the movements of both male and female rattlesnakes. During mating season, male rattlesnakes search extensively for females to mate (e.g., Duvall et al., 1992; Secor, 1992; Aldridge and Brown, 1995; Prival et al., 2002; Sealy, 2002; Ashton, 2003; Marshall et. al, 2006; Waldron et al., 2006a; Jellen et al., 2007; Cardwell, 2008; Brown et al., this volume; Goode et al., this volume). Female rattlesnakes, in contrast, do not actively search for mates (Duvall and Schuett, 1997), and typically exhibit smaller home ranges and reduced movements, with gravid individuals being most sedentary. At our study site, male *C. o. helleri* moved significantly greater distances than male *C. ruber*. The difference may result, in part, from the different mating phenology of the two species. *Crotalus ruber* at our site appears to mate exclusively in the spring (Table 3). A comprehensive review of the literature suggests that this is a range-wide phenomenon (Klauber, 1972; Goldberg, 1999; Aldridge and Duvall, 2002; Greenberg, 2002; Grismer, 2002; Campbell and Lamar, 2004; Brown et al., this volume), as we were unable to locate any published records of reproductive activity in *C. ruber* outside of the well-documented spring mating period. *Crotalus o. helleri*, in contrast, mates during both spring and late summer/fall at our site (Table 3), and probably does so throughout its range (Aldridge, 2002). Males of both species at our study site exhibited increased movements during the spring mating season, but late summer/fall movements by *C. o. helleri* appeared to be greater than those of *C. ruber* (Fig. 2). Thus, the finding that *C. o. helleri* moves significantly greater distances than *C. ruber* during the active season may reflect the additional late summer/fall mating season of *C. o. helleri*.

The reason for the marked difference between *C. ruber* and *C. o. helleri* in the timing and frequency of mating seasons remains unclear. A similar disparity exists for sympatric *C. atrox* (late summer/fall and spring mating) and *C. molossus* (spring mating) in Arizona, with *C. atrox* exhibiting two corresponding peaks in testosterone and *C. molossus* only one (Schuett et al., 2005). Thus, the differences may be physiologically based if the behaviors are hormonally dependent, but clearly do not derive from ambient environmental factors (e.g., photoperiod, temperature, precipitation) and more likely relate to evolutionary history (Aldridge and Duvall, 2002; Schuett et al., 2002, 2005). However, because reproductive isolation between sympatric rattlesnakes almost certainly results from pheromone differentiation (Shine et al., 2002, 2004), and the costs borne by males to locate females by following pheromone trails can be high (Aldridge and Brown, 1995; Aldridge and Duvall, 2002; McGowan and Madison, this volume), temporal segregation of mating seasons may have originated from competitive mechanisms if the costs for discriminating conspecific from heterospecific female pheromone trails are high. Such costs might be expected to be higher during the late summer/fall mating season, as both *C. ruber* and *C. o. helleri* at our study site often overwinter in relatively close proximity on south-facing slopes (Dugan and Hayes, unpubl. data), where mate location would be facilitated in spring.

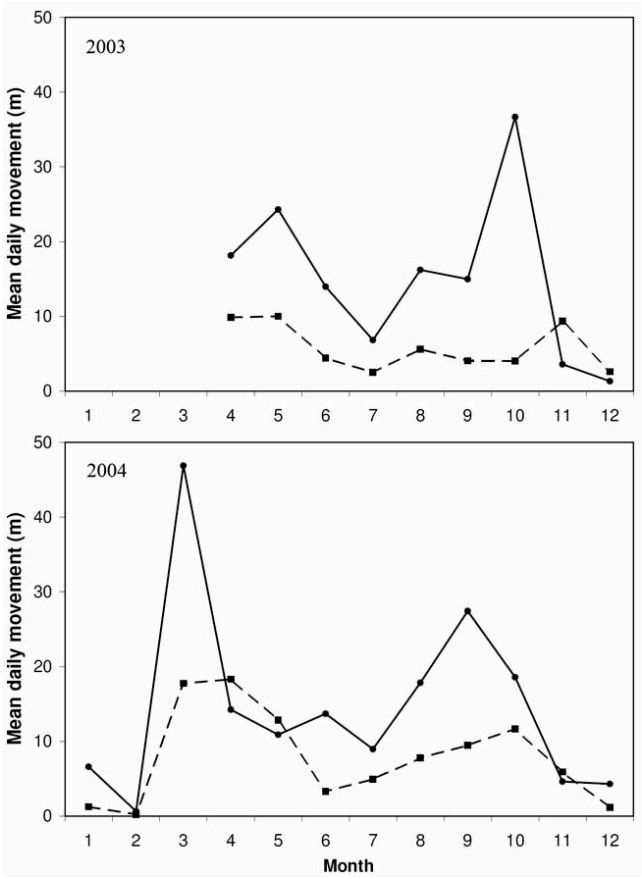

Figure 2. Mean daily movements per month (numbered January-December) of adult male Red Diamond Rattlesnakes (*Crotalus ruber*; dashed lines) and Southern Pacific Rattlesnakes (*C. oreganus helleri*; solid lines) during each of two years. For each mean, $N = 2$-6.

The annual movements of rattlesnakes vary substantially across species and may relate to intraspecific competition. Some populations are clearly migratory, typically moving substantial distances between their communal hibernaculas and their active-season home ranges (e.g., Macartney et al., 1988; Brown, 1993; Duvall and Schuett, 1997; Jørgensen et al., this volume). Migratory populations generally inhabit regions that experience extreme winter temperatures with limited suitable overwintering sites (for an exception, see Harvey and Weatherhead, 2006). However, rattlesnake populations in milder climates, such as those at our study site, frequently hibernate solitarily without strong site fidelity and lack annual unidirectional movements (e.g., Secor, 1992; Greenberg, 2002). Home range size may also be smaller in non-migratory populations. We concur with Greenberg (2002) that differences in movements and spatial use by individuals in these populations likely arise from differences in competition. Snakes at communal hibernacula face higher levels of intraspecific (and often interspecific) competition and, therefore, must disperse to a greater extent than snakes that hibernate solitarily.

Niche partitioning.—Niche separation between closely-related sympatric species can be achieved via differences in food (type or size) or in use of spatial (macrohabitat or microhabitat), temporal (diel or seasonal activity patterns), or thermal resources (Schoener, 1974; Saint Girons, 1978). Our findings suggest that sympatric populations of *C. ruber* and *C. o. helleri*, like other sympatric rattlesnakes (Pough, 1966; Reynolds and Scott, 1982; Mendelson and Jennings, 1992; Beck, 1995; Waldron et al., 2006b; Steen et al., 2007) and vipers (Reinert, 1984; Luiselli, 2006a,b; Luiselli et al., 2007) studied to date, primarily partition the habitat to reduce interspecific competition. However, unlike other sympatric rattlesnakes investigated thus far, *C. ruber* and *C. o. helleri* also differ in their use of spatial and temporal resources, though probably not as a direct result of competitive mechanisms. Although diet may vary among sympatric rattlesnakes (e.g., Clark, 2002; Holycross et al., 2002), including between *C. ruber* and *C. o. helleri* at our study site (Dugan, unpubl. data), rattlesnakes are often opportunistic feeders (within broader categories of preferred prey types, such as lizards and mammals; e.g., Klauber, 1972; Clark, 2002; Holycross et al., 2002; Campbell and Lamar, 2004; Avila-Villegas et al., 2007), and dietary differences may relate primarily to prey availability in the different preferred habitats and, secondarily, to size differences (gape-limited constraints) between adults (Reynolds and Scott, 1982). We imagine that diet might be partitioned more so than habitat among some sympatric rattlesnakes that differ substantially in adult size and coexist in environments with limited habitat variability (e.g., *C. atrox* and *C. cerastes* in Creosote [*Larrea tridentata*] desert flats). Apart from differences in mating seasons, we found no evidence that *C. ruber* and *C. o. helleri* further partition temporal resources. In terms of diel activity, we found both species active primarily during morning and evening hours, with some shift to nocturnal activity during hot weather (Dugan, unpubl. data). In terms of seasonal activity, we found *C. ruber* to be relatively sedentary compared to *C. o. helleri*, but the timing and duration of the active season were similar. Although we have not yet examined body temperature data, we are doubtful that thermal resources are partitioned between these two species. Perhaps further study of other sympatric rattlesnakes will reveal examples wherein food, temporal, or thermal resources are substantially partitioned to facilitate coexistence.

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