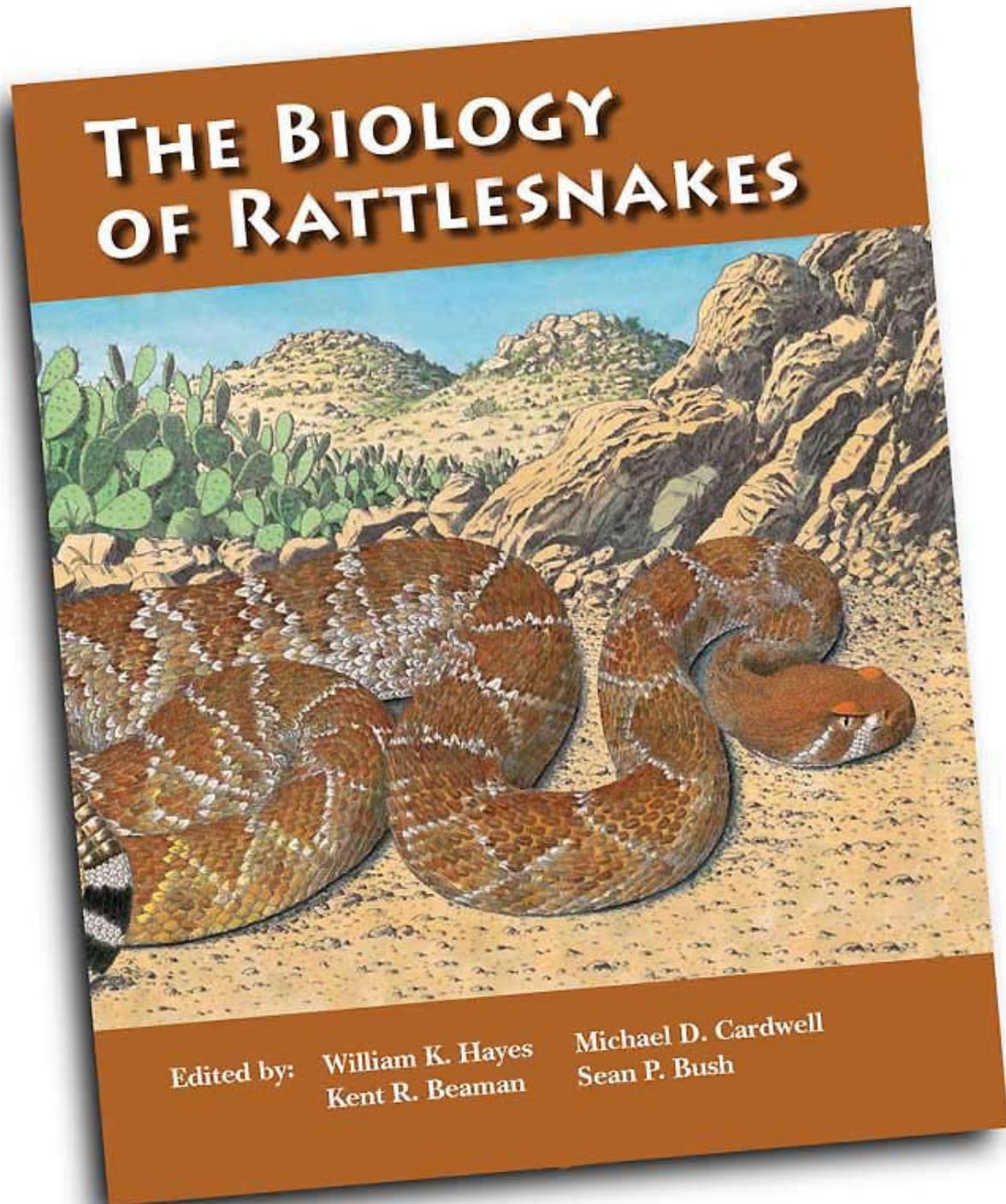


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Behavioral Ecology of Neonate Southern Pacific Rattlesnakes (*Crotalus oreganus helleri*) Tracked with Externally-Attached Transmitters

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ABSTRACT.—Our understanding of the biology of snakes is hampered by a lack of information about the earliest and most vulnerable stage of their life. By externally gluing radio transmitters to the dorsoposterior surface of seven neonate Southern Pacific Rattlesnakes (*Crotalus oreganus helleri*), we monitored the behavior and ecology of this understudied age-class and species. As an alternative to surgical implantation, external transmitter attachment was less invasive, permitted frequent transmitter replacement, and did not appear to affect neonate behavior. Five neonates tracked through several transmitter replacements (48-125 d) increased 10-38% in mass, indicating successful foraging. No mortality was recorded in this group. Neonates predominately occupied introduced grassland and coastal sage scrub habitats, similar to those used by adult males at the same study site. Unlike adults, however, the neonates frequently used arboreal positions (10% of 144 relocations) up to 90 cm above the ground, where they often assumed ambush postures similar to those observed near rodent features (burrows and runways). Mean daily movements decreased over successive months during the period of study (September 2004-February 2005). Neonates undertook short, non-directional movements presumably associated with foraging. Exceptional levels of autocorrelation in successive locations confounded estimates of activity range, as demonstrated for fixed kernel estimates using two different smoothing parameters. The neonates occasionally moved during the winter, with none overwintering communally. These findings demonstrate that snakes can be tracked successfully as neonates and, with further effort, throughout their lifetime. This capacity can one day offer a more complete understanding of a species' natural history and the role of experience in ontogenetic processes.

INTRODUCTION

What do snakes do early in their lives? Relatively little is known concerning the ecology of free-ranging neonate and juvenile snakes compared to adults (Morafka et al., 2000; Újvári and Korsós, 2000). Our understanding of snakes at the earliest and most vulnerable stage of their life is based largely on laboratory studies, anecdotal observations, and data collected using mark-and-recapture techniques. Radiotelemetry has proven superior for behavioral studies, as it allows for repeated relocations of free-ranging individuals, reduces observational bias associated with sampling, and is particularly useful for studying secretive animals (Reinert, 1992). However, neonates are nearly always excluded from radiotelemetry studies due to their small size and constraints on transmitter design. Only a small number of published articles exist involving radiotelemetry of neonate or juvenile snakes, and all of these have been relatively recent (e.g., Conner et al., 2003; Cobb et al., 2005; Reinert, 2005; Himes et al., 2006; Blouin-Demers et al., 2007; Jellen and Kowalski, 2007; Durbian et al., 2008; Gibson et al., this volume).

Movements and habitat use have long been recognized as critical components of snake behavior. Because spatial patterns and movements of snakes reflect variation in the spatiotemporal distribution of resources, movements of individuals are often nonrandom (Gregory et al., 1987). Since movement incurs a higher risk of mortality and greater en-

ergy expenditure than remaining sedentary (Gibbons and Semlitsch, 1987), snakes engage in activity when potential benefits of being at another point in space and time outweigh the costs of remaining in the same place. These costs may be more pronounced in neonates, who are naïve to their environment. Neonates and juveniles are alleviated from behaviors associated with reproduction and, therefore, face different selection pressures than adults (Gibbons and Semlitsch, 1987). In rattlesnakes, ontogenetic shifts in diet (Klauber, 1972; Mackessy, 1988; Holycross and Mackessy, 2002) and vulnerability to environmental fluctuations and predators (e.g., Brown et al., 2007; Brown, this volume) often accompany the maturation process. Accordingly, the way young snakes interact with their environment will differ from that of adults (Altwegg et al., 2005; Blouin-Demers et al., 2007). Moreover, experiences early in life can profoundly influence survival, growth, age at first reproduction, maximum adult body size, habitat preference, locomotor efficiency, and foraging behavior (Charland, 1989; Madsen and Shine, 2000; Krause and Burghardt, 2001; Aubret and Shine, 2008). Clearly, a more complete understanding of spatial use and resource acquisition in snakes will require studies of all age-classes (Macartney et al., 1988).

We employed radiotelemetry to monitor the movements and behavior of neonate Southern Pacific Rattlesnakes (*Crotalus oreganus helleri*) for up to six months following parturition. The Southern Pacific Rattlesnake inhabits coastal and mountainous habitats from San Luis Obispo and Kern counties, California, south into the San

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Table 1. Summary of body size (initial snout-vent length, SVL, in millimeters; mass in grams, excluding transmitter) and tracking dates (during the period September 2004–February 2005) for individual neonate Southern Pacific Rattlesnakes (*Crotalus oreganus helleri*; M = male, F = female) with up to three successive externally-attached radiotransmitters. Mass (and percent change) was recorded on day of transmitter attachment or replacement.

Snake	SVL	Transmitter # 1		Transmitter # 2		Transmitter # 3	
		Dates	Mass	Dates	Mass	Dates	Mass
CH58 (M)	259	28 Sep-12 Oct ^a	18.5	13 Oct-5 Nov	25 (+35%)	11 Nov-24 Dec ^b	26 (+4%)
CH71 (M)	300	28 Sep-11 Oct ^a	21	—	—	—	—
CH76 (F)	304	10 Oct-31 Oct	21.5	7 Nov-26 Nov ^b	27 (+26%)	—	—
CH77 (M)	313	15 Oct-5 Nov	18	7 Nov-10 Dec ^a	20 (+11%)	—	—
CH78 (M)	291	15 Oct-5 Nov	13	11 Nov-16 Feb ^c	18 (+38%)	—	—
CH79 (M)	320	15 Oct-5 Nov	20	11 Nov-16 Feb ^c	22 (+10%)	—	—
CH83 (F)	353	16 Nov-13 Dec ^a	39	—	—	—	—

^a Transmitter became detached from snake

^b Transmitter battery failed prematurely

^c Transmitter battery failed after weather disrupted access to study site

Pedro Martir Mountains in Baja California (Klauber, 1972; Grismer, 2002; Campbell and Lamar, 2004). Until recently (Dugan et al., this volume; Labonte, this volume), detailed behavioral and ecological research has been absent for this species, with most information based on anecdotal observations or on inferences from congeners and other subspecies, including *C. v. viridis* and *C. o. oreganus* (Klauber, 1972; Grismer, 2002; Ernst and Ernst, 2003; Campbell and Lamar, 2004). Neonates are born in the late summer or early autumn and are frequently encountered in southern California (Klauber, 1972).

We elected to attach transmitters externally to the dorsal surface of the snake's skin (Ciofi and Chelazzi, 1991; Gent and Spellerberg, 1993; Cobb et al., 2005; Jellen and Kowalski, 2007; McGowan and Madison, this volume). Unfortunately, the only transmitters small enough to implant in neonates of most snake species have only a few weeks of battery life. Neonates implanted with transmitters would, therefore, require frequent handling and surgery to replace the exhausted batteries. Attaching transmitters externally offers several advantages for smaller organisms and/or short-term studies, including ease of attachment for the investigator and avoidance of surgical trauma to the animal. We hoped that, compared to neonates of sympatric colubrid taxa, the relative stoutness and presumed sedentary behavior of this species would render it suitable for external transmitter attachment (Cobb et al., 2005).

Our objectives for this study were to examine: 1) the utility of external transmitter attachment, as indicated by foraging success and survival; 2) habitat use relative to adults at the same study site; 3) whether movements were random or directional; 4) individual variation in activity range, as compared by several measures influenced by autocorrelation; and 5) whether neonates overwintered in communal hibernacula.

MATERIALS AND METHODS

Study site.—We conducted the study in the eastern portion of Chino Hills State Park (CHSP), California (33°54' N; 117°42' W), which occupies 5,039 ha of the Puente-Chino Hills in Los Angeles, Orange, Riverside, and San Bernardino Counties. Topography at the site consists of large areas of rolling hillsides with scattered steep, vertical cliffs, and elevation up to 543 m (Sampson, 1985). Six plant communities are recognized (Sampson, 1985): riparian woodland along banks and streams (1% of area); southern oak woodland on north-facing slopes and bottoms of tributary ravines (11%); chaparral on the shallow, rocky soil of south-facing slopes (5%, but not occurring in our study area); coastal sage scrub on the clay soils of south-facing slopes, dry hillsides, and hilltops (13%); native valley grassland (<1%); and introduced annual pastureland ("introduced grassland" hereafter; 70%, but also abundant in understory of some other communities).

The Park experiences a Mediterranean climate, with cool wet winters, warm dry summers, and annual precipitation averaging 350–460 mm (Sampson, 1985). However, unseasonably cool temperatures and exceptional rainfall occurred during much of the study period (September 2004 to February 2005; see Figueroa, 2006). Local flooding was so severe in February that the roads into the study area were closed, thus interrupting and terminating the study.

Body measurements and transmitter attachment.—Prior to attaching radio transmitters, we anesthetized neonates with 0.5 ml of sevoflurane (Halocarbon Products Corp., River Edge, New Jersey, USA) and individually marked snakes with a passive integrative transponder (PIT tag; AVID Identification Systems, Inc., Norco, California, USA) for identification. We measured snout-vent length (SVL, nearest millimeter) of anesthetized snakes using a cloth measuring tape and weighed them to the nearest gram with a 100 g Pesola scale (Pesola AG, Baar, Switzerland).

Snakes were sexed by relative tail length and subcaudal scale counts (males > females; Dugan, unpubl. data). With each recapture for transmitter replacement, we re-weighed individuals to monitor growth. To avoid repeated anesthesia, we chose not to re-measure body length. To avoid undo disturbance, we did not palpate food boli in the gut or collect fecal material from telemetered snakes.

We attached transmitters (SOM-2011, 0.6 g; SOM-2028, 1.5 g; or SOM-2038, 2.0 g; Wildlife Materials International Inc., Murphysboro, Illinois, USA) to seven neonate snakes subsequent to their first ecdysis. Two neonates (CH58 and CH71) were taken from wild-caught gravid females that gave birth in captivity, and these neonates were released 2 wk after ecdysis. The remaining five neonates were wild-caught snakes found separately on different occasions. Transmitters were glued (Super Glue Corp., Rancho Cucamonga, California, USA) to the dorsoposterior skin surface at approximately 75% of the snake's SVL (Fig. 1; see Figueoa et al., 2006, for discussion of gluing methods). We first used the 0.6 g transmitters to stay within 5% of the snake's body mass; however, battery life expectancy was only 23 d. Although the larger transmitters were up to 10% of the neonate's body weight, their longer expected battery life (57-80 d) was deemed advantageous. The antennae (100 mm long) trailed posteriorly behind the snake. Neonates were released at the site of capture (or mother's capture). Transmitters remained attached >15 d for all but one snake; CH83 lost its transmitter after 9 d, but remained stationary another 20 d (without attachment of another transmitter), permitting additional locations (i.e., "fixes"). When transmitters neared their battery life expectancy, we recaptured the neonates, brought them to the lab to replace the transmitter unit, and then released them at the site of capture. We used non-acetone nail polish remover to detach the transmitters. In some instances, several scales sloughed off at the transmitter attachment site but the snakes otherwise suffered no obvious injury.

Radio-tracking proceeded from 28 September 2004 through 16 February 2005. We located transmittered snakes using a Telonics TR2 receiver (Telonics, Mesa, Arizona, USA) and a two-element Yagi antenna. Weather permitting, we often relocated snakes daily, but intervals between fixes were uneven for most snakes. 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 remained in one location between successive fixes, we assigned the UTM coordinates of the previous fix to minimize GPS measurement error. We observed no obvious locomotory or other behavioral impairments to the snakes other than stiffness immediately adjacent to the transmitter attachment site.

Habitat and microhabitat use.—For each fix, we recorded the habitat and microhabitat occupied by the neonate. We recorded snakes in only four habitats: introduced grassland, coastal sage scrub, riparian woodland, and

southern oak woodland. We also recorded occurrence in three microhabitats: underground (within a burrow), above-ground, or arboreal (above the ground in vegetation.). For each snake, we computed separately the proportions of both total and unique (only those following a movement by the snake) fixes in each habitat and in each microhabitat. Percentage of total fixes reflected time use, whereas percentage of unique fixes reflected discrete decisions about habitat and microhabitat use.

Movements.—We calculated for each snake the following movement variables derived from straight (Euclidean) distances between successive GPS locations: 1) mean distance moved per day for each fix = distance moved divided by number of days between successive fixes (Gregory et al., 1987; Macartney et al., 1988; Diffendorfer et al., 2005); 2) monthly mean distance = mean distance moved per day averaged for all fixes for each month; 3) mean distance moved per day averaged for all fixes; 4) dispersal distance = distance from first to last location; 5) total distance traveled = sum of all distances moved between successive fixes; and 6) index of relative dispersal = ratio of dispersal distance to total distance traveled. We applied circular statistics to analyze movement directionality, using the Animal Movement Extension (Hooze and Eichenlaub, 1997) in ArcView 3.3 (ESRI, Redlands, California, USA), to compute mean bearing, angular concentration (r), and Rayleigh's z (Zar, 1996).

Activity ranges.—We use the term "activity range" in place of "home range," since neonates have yet to establish or perceive a defined home range. Using all fixes obtained, we estimated activity ranges for each neonate based on 100% minimum convex polygon (MCP) using Calhome 1.0 (Kie et al., 1994) and 100%, 95%, and 50% fixed kernel (FK) using the default options in Home Ranger 1.5 (Hovey, 1999). Opinions remain contentious as to which estimate (MCP vs. FK) performs better (e.g., Row and Blouin-Demers, 2006; Laver and Kelly, 2008). Minimum convex polygon uses all known locations to outline the maximum area used by an animal, but ignores the internal structure of



Figure 1. Neonate Southern Pacific Rattlesnake (*Crotalus oreganus helleri*), illustrating external transmitter attached directly to the snake's skin.

Table 2. Percentage of total (and unique) fixes of individual neonate Southern Pacific Rattlesnakes (*C. o. helleri*) occurring in four habitats and three microhabitats.

Snake	Number of fixes	Habitats				Microhabitats		
		Introduced grassland	Coastal sage scrub	Riparian woodland	Southern oak woodland	Under ground	Above ground	Arboreal
CH58	38 (21)	0 (0)	100 (100)	0 (0)	0 (0)	0 (0)	76 (76)	24 (24)
CH71	13 (5)	100 (100)	0 (0)	0 (0)	0 (0)	38 (20)	54 (60)	8 (20)
CH76	22 (18)	59 (71)	0 (0)	27 (12)	14 (18)	27 (11)	59 (78)	14 (11)
CH77	18 (12)	100 (100)	0 (0)	0 (0)	0 (0)	0 (0)	94 (92)	6 (8)
CH78	23 (16)	100 (100)	0 (0)	0 (0)	0 (0)	4 (6)	96 (94)	0 (0)
CH79	24 (14)	92 (88)	0 (0)	8 (13)	0 (0)	4 (7)	92 (86)	4 (7)
CH83	6 (1)	0 (0)	0 (0)	100 (100)	0 (0)	0 (0)	100 (100)	0 (0)
Mean	21 (12)	64 (66)	14 (14)	19 (18)	2 (3)	10 (6)	82 (84)	8 (10)

an activity range, thus disregarding patterns of space use (Powell, 2000). The FK estimator is a better descriptor of space use because it places contours around different intensities of use and, when combined with least-squares cross-validation (h_{iscv} , the bandwidth with the least estimated error), generally provides more accurate estimates (Seaman et al., 1999; Powell 2000). However, when fixes are autocorrelated, h_{iscv} often undersmooths the contours, resulting in underestimates of activity range by creating numerous small, fragmented contours around clumped observations (Powell, 2000; Hemson et al., 2005). In such cases, it may be more appropriate to use an alternative smoothing parameter, such as the reference (or optimal) bandwidth (h_{ref} ; Kernohan et al., 2001), although this has a tendency to oversmooth, resulting in overestimates of activity range and concealing fine-scale detail (Powell, 2000; Hemson et al., 2005). To better understand the effect of bandwidth, we computed FK estimates using both h_{iscv} (the default selection) and h_{ref} .

Autocorrelation, when combined with FK activity range estimates, serves as a measure of space use since independence of observations is biologically unrealistic (de Solla et al., 1999; Blundell et al., 2001; Row and Blouin-Demers, 2006). Autocorrelation values, represented by Schoener's ratio (t^2/r^2 ; Swihart and Slade, 1985a), were computed for each snake using Home Ranger 1.5. When autocorrelation exists (i.e., $t^2/r^2 < 2.0$), the distance moved between consecutive observations decreases, resulting in underestimates of activity range (Swihart and Slade, 1985b). Because the six fixes from CH83 were all at the same location, this individual was eliminated from movement and activity range analyses.

Statistical analyses.—We analyzed the data using SPSS 15.0 for Windows (SPSS, 2006), testing significance at $\alpha = 0.05$. Because the data met parametric assumptions, we used a paired *t*-test (Zar, 1996) to evaluate changes in mass between transmitter replacements. For other analyses, we relied on nonparametric tests (Conover,

1999). We used Friedman analyses of variance (Friedman ANOVAs) to compare use of the four different habitats and three microhabitats (SPSS provided only asymptotic, and not exact, *P* values). We also computed Spearman rank correlation coefficients among the measures of movement, activity range, and autocorrelation. However, we expressed the correlations as coefficients of determination (r_s^2), which are more informative because they indicate effect size (i.e., proportion of variance in one variable explained by another variable). Although the multiple correlations inflated experimentwise error, we chose not to reduce alpha because the effect sizes were often sufficiently large (Cohen, 1988) that we considered them to be meaningful in spite of the small sample sizes ($N = 6$ for each). Rayleigh's test for directionality was used to evaluate the hypothesis that neonate movements were non-random (Zar, 1996).

RESULTS

Radio-tracking.—At least two and up to seven snakes were tracked during each month between 28 September 2004 and 16 February 2005 (Table 1). The number of relocations per individual ranged from 6-38. Five of the seven snakes were tracked for a sufficient duration to receive at least one replacement transmitter. One snake (CH58) received a total of three transmitters. Radio-tracking ended due to premature transmitter battery failure ($N = 3$), transmitter becoming detached from snakes ($N = 2$), or disrupted access to the study site because of unusually wet weather ($N = 3$).

Foraging success.—Three types of evidence confirmed that telemetered neonates were successful at foraging. First, all five snakes receiving replacement transmitters gained mass (Table 1). The differences in mass between first and last measurements were significant ($t = 4.13$, $df = 4$, $P = 0.014$). Snake CH58 realized a 7.5 g (41%) increase, which seems unlikely from a single meal and suggests foraging success on more than one occasion. Second, apparent food boli (distended gut region) were observed on one occasion

Table 3. Movement data for individual neonate Southern Pacific Rattlesnakes (*C. o. helleri*; see text for descriptions of variables). Rayleigh's z = test for directionality; all $P > 0.05$.

Snake	Total Fixes	Number of moves	Tracking duration (d)	Distance per day (m/d)	Dispersal distance (m)	Total distance traveled (m)	Index of relative dispersal	Mean bearing	Angular concentration (r)	Rayleigh's z
CH58	38	20	88	6.0	31	394	0.08	305	0.14	0.41
CH71	13	4	14	5.6	14	49	0.28	197	0.12	0.06
CH76	22	17	48	6.4	172	257	0.67	268	0.40	2.65
CH77	18	11	57	4.5	60	186	0.32	179	0.14	0.22
CH78	23	15	125	2.9	31	106	0.29	236	0.31	1.40
CH79	24	13	125	1.8	18	114	0.16	162	0.24	0.74
Mean	23.0	13.3	76.2	4.5	54.5	184.6	0.30	225	0.23	0.91
(1 SD)	(8.4)	(5.5)	(44.6)	(1.9)	(59.9)	(125.3)	(0.20)	(55)	(0.11)	(0.97)

Table 4. Estimated activity ranges (ha) and autocorrelation values (t^2/r^2 , Schoener's ratio) for individual neonate Southern Pacific Rattlesnakes (*C. o. helleri*). MCP = minimum convex polygon; FK = fixed kernel (h_{lscv} = least-squares cross-validation bandwidth; h_{ref} = optimum bandwidth; 100%, 95%, and 50% areas used).

Snake	FK using LSCV					FK using reference h					t^2/r^2
	MCP100	FK100	FK95	FK50	LSCV score	h_{lscv}	FK100	FK95	FK50	h_{ref}	
CH58	0.303	0.172	0.081	0.010	-2.90	2.3	1.109	0.531	0.091	12.2	0.61
CH71	0.009	0.224	0.001	<0.001	-3.90	0.9	0.073	0.033	0.005	5.6	1.16
CH76	0.343	0.149	0.070	0.016	-0.69	0.9	2.262	1.170	0.286	5.4	0.11
CH77	0.068	0.054	0.024	0.004	-2.92	2.8	1.214	0.599	0.150	16.8	0.41
CH78	0.040	0.028	0.014	0.003	-0.93	1.0	0.180	0.091	0.020	5.5	0.46
CH79	0.037	0.012	0.005	0.001	-1.47	0.6	0.171	0.087	0.020	3.5	0.70
Mean	0.133	0.106	0.033	0.006	-2.10	1.4	0.835	0.418	0.095	8.2	0.58
(1 SD)	(0.149)	(0.087)	(0.034)	(0.006)	(1.29)	(0.9)	(0.861)	(0.442)	(0.109)	(5.2)	(0.35)

each in CH58, CH71, CH77, and CH79. Third, CH58 added one rattle segment during monitoring as a result of ecdysis, which is normally associated with growth (Klauber, 1972). Although ecdysis might have resulted from skin irritation caused by the transmitter, one of the wild-caught snakes, CH79, similarly added a rattle segment prior to, and not as a consequence of, transmitter attachment.

Habitat use and arboreal behavior.—Friedman ANOVAs revealed that evenness of neonate distribution among the four habitat types depended on whether total fixes ($\chi^2 = 8.27$, $df = 3$, asymptotic $P = 0.041$) or unique fixes ($\chi^2 = 7.41$, $df = 3$, asymptotic $P = 0.060$) were analyzed; however, the percentage differences between total and unique fixes were trivial (see Table 2). Five of the seven neonates primarily occupied introduced grassland habitats. Snake CH58 used only coastal sage scrub and CH83 was found 100% of the time beneath a metal watering trough within riparian woodland. As CH76 dispersed, it moved from introduced grassland into riparian woodland and southern oak woodland before continuing into more introduced grassland.

Friedman ANOVAs indicated uneven usage of the three microhabitats (total fixes: $\chi^2 = 11.39$, $df = 2$, asymptotic $P = 0.003$; unique fixes: $\chi^2 = 12.33$, $df = 2$, asymptotic $P = 0.002$), with the majority of positions (82–84%) being aboveground. Snakes were observed in arboreal positions on 15 (10%) of 144 fixes, up to 90 cm high in shrubs (Table 2). By comparison, adult conspecifics at the same study site were found in arboreal positions in only three (0.4%) of 717 fixes (Dugan, unpubl. data). Snake CH58 occupied arboreal positions 24% of the time. The arboreal positions assumed by neonates often resembled ambush postures characteristic of foraging pit-vipers (Reinert et al., 1984). Neonates also assumed foraging positions along rodent trails and animal burrows (not quantified).

Movements.—Each of the six neonates analyzed provided 13–38 fixes (mean = 13; Table 3). The snakes moved between successive fixes on 31–77% of occasions (mean = 57%). For the entire duration of tracking, the snakes averaged 1.8–6.4 m of movement per day (mean = 4.5; Table 3). However, mean daily movements, compared on a

monthly basis, clearly declined as the study progressed into the cooler winter months (Fig. 2). Because the mean monthly distances in Fig. 2 included both independent (different snakes) and related data (same snake) from month-to-month (i.e., pseudoreplication), we did not statistically evaluate the data. The total distance traveled by neonates ranged from 50-394 m (mean = 184) and reflected the number of movements per individual ($r_s^2 = 0.60$, $P = 0.072$). For most neonates, dispersal distances between first and last fixes were small (14-60 m). However, CH76 traveled 172 m. The index of relative dispersal, which describes the ratio of dispersal distance to total distance traveled, indicated that movements by this individual took it far from its original location (0.67 versus 0.08-0.32 for other individuals). Movements were random in bearing rather than directional, with all Rayleigh's z values non-significant (all $P > 0.05$). Total distance and dispersal distance were positively but not significantly associated with each other, though the effect size was large ($r_s^2 = 0.60$, $P = 0.072$). Neither total distance nor dispersal distance were associated with index of relative dispersal ($r_s^2 < 0.36$, $P > 0.21$).

Activity ranges.—We used three methods for estimating the activity range of each snake, as summarized in Table 4. The FK method using h_{ref} gave the largest estimates, followed by MCP and then FK using h_{lscv} . The two different smoothing parameters had a dramatic impact on FK estimates (Fig. 3), raising the question of which would be most suitable (see Discussion). The 100% FK computed by h_{lscv} for snake CH71, which occupied just five locations during the 13 fixes, was an obvious computational outlier, being far larger than all other estimates for this snake. With the exception of this individual, FK estimates based on h_{ref} were typically 5-30 times larger than FK estimates based on h_{lscv} .

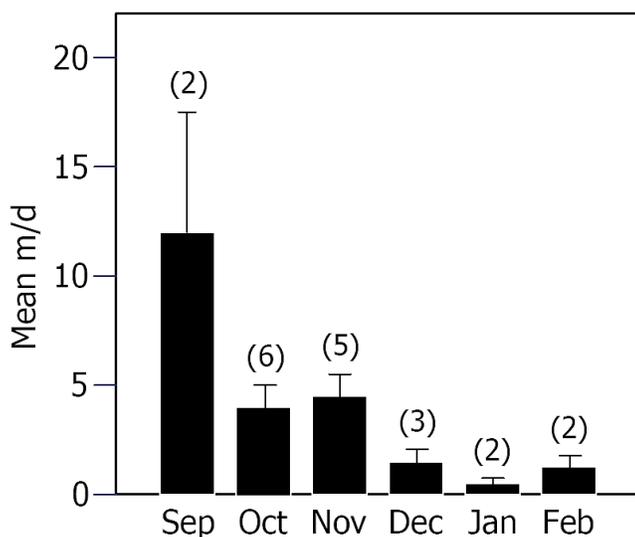


Figure 2. Decrease in mean (+1 SE) movements per day (m) by neonate Southern Pacific Rattlesnakes (*C. o. helleri*) for each month tracked (September-February). Sample size for each mean is shown in parentheses.

Of the two most frequently reported estimators (Laver and Kelly, 2008), MCP estimates (mean = 0.13 ha) averaged four-fold greater than 95% FK estimates based on h_{lscv} (mean = 0.03 ha). Core areas (50% FK) represented a small fraction of the 95% FK activity ranges (18% based on h_{lscv} , 23% based on h_{ref}). Autocorrelation values were all well below 2.0, ranging from 0.11-1.16 (mean = 0.58), indicating strong time-dependence between successive observations and likely underestimation of activity range.

Spearman rank correlations among individuals indicated that MCP, 100% FK computed by h_{ref} , 95% FK (both bandwidths), and 50% FK (both bandwidths) were all positively correlated with each other and with dispersal distance (all $r_s^2 > 0.68$, $P < 0.05$). In contrast, estimates for 100% FK computed by h_{lscv} showed no association with other measures of activity range size and movements (all $r_s^2 \leq 0.02$), essentially because of the outlier represented by CH71. Autocorrelation (corresponding to smaller t^2/r^2 ratios) was positively associated with all activity range estimates (other than 100% FK and 95% FK computed with h_{lscv}) and dispersal distance (all $r_s^2 > 0.68$; $P < 0.05$). Autocorrelation was also positively, though not significantly, associated with 95% FK, total distance, and dispersal index ($r_s^2 = 0.29-0.59$; these were still large effect sizes). Number of fixes did not substantially influence dispersal distance ($r_s^2 = 0.01$), activity range estimates (all $r_s^2 < 0.24$), or autocorrelation ($r_s^2 < 0.01$). Within individuals, we did not assess the influence of number of fixes on these estimates.

Overwintering behavior.—None of the neonates overwintered together or with other conspecifics. In fact, none remained stationary at a single location. Sporadic movements were exhibited during each month of tracking.

DISCUSSION

Radio-tracking and foraging success.—Ideally, attaching radio transmitters to free-ranging organisms should provide reliable tracking over an extended period of time without interfering with normal behavior. We tracked individuals up to 125 d and through several transmitter replacements necessitated by size constraints on battery life. All five neonates that received replacement transmitters gained weight, indicating foraging success. Four of these appeared to have food boli in their guts on at least one occasion. No obvious abnormal behaviors were seen, and no mortalities occurred. There were, however, several shortcomings, with transmitters detaching from some of the snakes and some body stiffness observed in the vicinity of the transmitter.

Our success with externally-attached transmitters mirrored that of two other studies involving rattlesnakes. Cobb et al. (2005) glued transmitters to four neonate Timber Rattlesnakes (*C. horridus*) in Tennessee. The neonates were tracked 39-42 d, during which three neonates moved 320 m to a communal hibernaculum, presumably following conspecific odor trails, and the fourth moved >300 m in the opposite direction. Jellen and Kowalski (2007) simi-

larly glued transmitters to 16 neonate Eastern Massasaugas (*Sistrurus c. catenatus*) in Pennsylvania. Twelve neonates were tracked up to 56 d prior to hibernation, two lost their transmitters within 2 d of release, one was predated, and one died after the antenna became entangled in vegetation. Males gained significantly more mass than females during this period, but changes in body length were similar. In both studies, some neonates exhibited coordinated movements along their mother's path, suggesting pheromonal trailing.

Several investigators have also tracked neonate rattlesnakes using surgically-implanted transmitters. Reinert (2005) monitored the movements of 16 neonate *C. horridus* in Pennsylvania and New Jersey (Reinert, pers. comm.) from four litters up to a maximum of 100 d post-parturition. Fifteen individuals were tracked up to 1.7 km until they entered hibernacula, while the remaining snake was lost due to either transmitter failure or predation. Correlated movements among siblings were frequent. David Hardy (pers. comm.) followed six neonate Black-tailed Rattlesnakes (*C. molossus*) in Arizona. Four of the snakes soon died (presumably from predation), the battery failed prematurely in the fifth, and the transmitter was removed from the remaining snake after three months of tracking. This tracked individual grew in length but not in mass. Durbian et al. (2008) obtained sufficient data to compute MCP estimates from 12 of 28 implanted neonate *S. c. catenatus* in Wisconsin (fates of the other 16 snakes were omitted). The neonates had substantially smaller activity ranges and range lengths than adult snakes; however, differences could have resulted from an unequal number of fixes used to obtain estimates (criteria for inclusion: ≥ 3 fixes for neonates and ≥ 30 fixes for adults; further details not provided) or from differences in duration or season of tracking (details not provided). Batteries in the transmitters used by these investigators were exhausted before hibernation ended.

Collectively, these studies support the emerging view that juvenile rattlesnakes (Brown et al., 2007; Brown, this volume), and juvenile reptiles in general (Pike et al., 2008), have much higher annual survival rates than previously believed. We suggest that, in spite of any shortcomings, external attachment for longer-term tracking is preferable for neonate rattlesnakes because of the advantage of using larger transmitters with longer-lived batteries and to avoid repeated surgeries to replace transmitters with expired batteries.

Habitat use and arboreal behavior.—Neonates in our study primarily occupied introduced grassland, the dominant habitat at our study site (Sampson, 1985), and frequently exhibited arboreal behavior. Habitat use was similar to adult male conspecifics studied at the same site (Dugan et al., this volume), but arboreality was far more prominent in neonates (10% of all observations) than adult males (0.4%; Dugan, unpubl. data). Differences in body and gape size require that neonates often feed on different prey than adults and occupy specific microhabitats to meet such requirements (Macartney et al., 1988; Ford and Burghardt, 1993; Reinert, 1993; Shine et al., 2002). Thus, one might expect

neonates and adults to partition the landscape, reducing intraspecific competition for foraging sites and prey. Ambush postures by both neonates and adults were frequently observed along rodent trails and near rodent burrows at our study site. However, unlike adults, the neonates appeared to adopt similar positions in arboreal habitat, presumably to ambush lizards and/or rodents. The diet of *C. o. helleri* shifts ontogenetically from primarily lizards to rodents, with corresponding changes in venom (Mackessy, 1988). We frequently observed lizards in the vegetation used by the neonate snakes, and neonate *C. o. helleri* are attracted to odors deposited by lizards (LaBonte, this volume). Trapping studies also confirm that rodents frequently use arboreal habitats in southern California (Laakkonen, 2003). Higher levels of arboreality in juveniles compared to adults have been reported in other viperid species (*Bothrops* spp.:

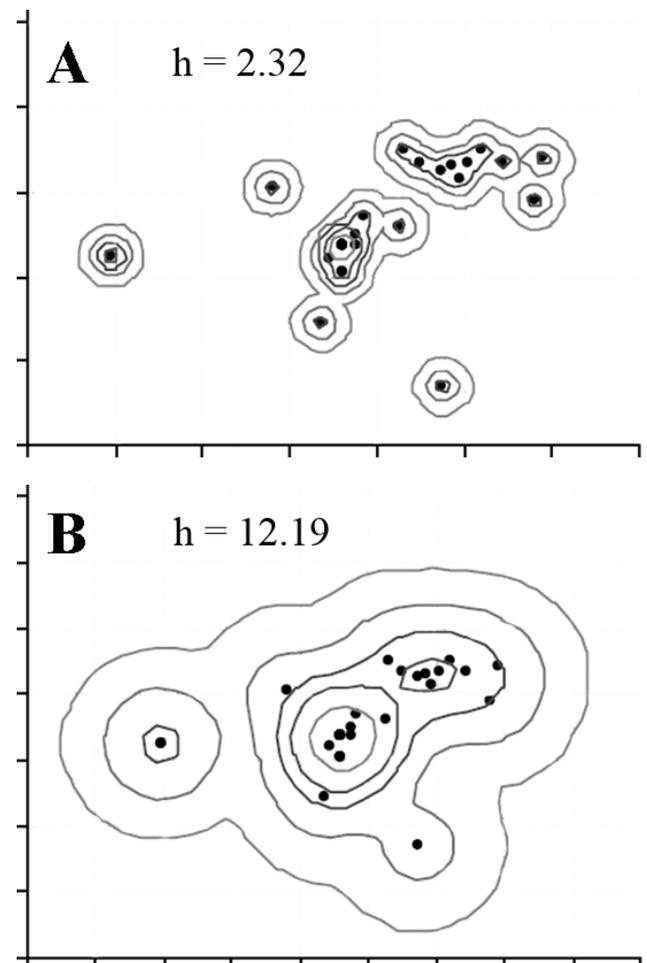


Figure 3. Fixed kernel contours (100%, 95%, 75%, 50%, and 25% from outermost to innermost on 100 m² grid) for snake CH58 using two different bandwidths (h). (A) Bandwidth selected by least-squares cross-validation (LSCV), resulting in numerous small, fragmented contours around clumped observations. (B) Bandwidth is reference h , resulting in apparent oversmoothing. The preferred activity range estimate likely requires an intermediate h .

Martins et al., 2001; *C. horridus*: Gibson et al., this volume; *Gloydus shedaoensis*: Shine et al., 2002).

Movements and activity ranges.—Independent and behaviorally naive from birth, neonates are unfamiliar with their surroundings and have yet to establish an activity range. Movements varied considerably among individuals and declined as the study progressed into the winter months (Fig. 2), undoubtedly due to thermal constraints. Movements also were random rather than directional. One might expect directional movements if the neonates were moving from the birthing site to a communal hibernaculum (Cobb et al., 2005; Reinert, 2005), or if foraging was conducted in a patchy environment (Duvall and Schuett, 1997). None of the neonates occupied communal hibernacula (see below), but we do not know how patchy the food base is at the study site.

The accumulation of recent studies provides for some comparisons, though differences in study methods and activity range computations encourage caution (Laver and Kelly, 2008). Neonate *C. o. helleri* in our study dispersed an average of 54.5 m, moving a mean of 4.5 m/d within an activity range (MCP) averaging 0.13 ha. The neonates likely dispersed further, since most were initially caught having already departed from their birth site. Being smaller in size, neonates are expected to cover shorter distances than adults and occupy smaller activity ranges, as reported in *S. c. catenatus* (Jellen and Kowalski, 2007; Durbian et al., 2008). Movements and activity ranges of adult male *C. o. helleri* at our study site (Dugan et al., this volume) averaged 16.8 m/d and 4.69 ha during the active season (March–October 2003) and 2.7 m/d and 0.83 ha during the winter (November–February 2003–2004). Because we did not track adults simultaneously, we cannot conclude with certainty how neonate space use compares with adults. Prior to hibernation, neonate *S. c. catenatus* in Wisconsin dispersed an average of 64 m, occupying a mean MCP of 0.6 ha (Durbian et al., 2008; movement per day was not reported). Neonate *S. c. catenatus* in Pennsylvania dispersed an average of 177 m, moving a mean of 5.3 m/d within an MCP averaging 0.36 ha (Jellen and Kowalski, 2007). Neonate *C. horridus* moved substantially farther than *C. o. helleri* and *S. c. catenatus* before hibernation, traveling >300 m in Tennessee (Cobb et al., 2005) and up to 1.7 km in Pennsylvania and New Jersey (Reinert, 2005). Other measures of space use were not provided by the latter authors.

Exceptional levels of autocorrelation confounded activity range estimates in our study, with I^2/r^2 values ranging from 0.11–1.16 and averaging 0.58. These values are well below the criterion for independence (≥ 2.0 ; Swihart and Slade, 1985a) and those obtained from movements of adult male *C. o. helleri* at our study site (means for active seasons: 1.49 and 1.57; winter: 1.78; Dugan et al., this volume). Our brief (often 1 d) and uneven sampling intervals undoubtedly influenced the autocorrelation values. High levels of autocorrelation, resulting from multiple observations at or near the same location, usually lead to small bandwidths, multiple disjunct contours, and smaller FK estimates com-

puted by h_{1scv} (Powell, 2000; Hemson et al., 2005). For this reason, we also computed FK estimates using h_{ref} as an alternative approach, though it is prone to overestimating activity ranges. We suspect that the preferred estimates were somewhere between those derived from the two smoothing parameters. Row and Blouin-Demers (2006) recommend using the MCP as the area of the home range and adjusting the smoothing factor (h) until the area of the 95% kernel equals the area of the MCP, providing an objective approach for selecting an appropriate smoothing factor (see also Wauters et al., 2007, for an alternative approach). Fixes characterized by no movement are sometimes excluded from computation of activity range using kernel methods, but we included all fixes in our analyses because periods devoid of movement feature prominently in snake behavior (e.g., foraging, thermoregulation, digestion, ecdysis), and eliminating these data may obscure important patterns of movements and space use (de Solla et al., 1999; Powell, 2000; Blundell et al., 2001). With the exception of 100% FK estimates, the activity range estimates and dispersal distance showed high covariance, as expected. Autocorrelation was also positively associated with larger activity ranges, an unexpected finding also reported from another study (Blundell et al., 2001). Despite its problems for estimating activity ranges, autocorrelation reflects biological reality. Unfortunately, autocorrelation is seldom reported in snake studies, so its effect on activity range estimates remain unclear, not just for snakes but for amphibians and reptiles in general (Row and Blouin-Demers, 2006).

Overwintering behavior.—Rattlesnakes do not use communal hibernacula at our study site. None of the neonates overwintered at a single location, and none were associated with a conspecific. Adult *C. o. helleri* and *C. ruber* at our study site also winter independently rather than within communal dens (Dugan et al., this volume), though several *C. o. helleri* are sometimes encountered beneath a single cattle watering trough and several *C. ruber* may transiently occupy the same cactus patch. In marked contrast, *C. o. helleri* at higher elevations in southern California use hibernacula for overwintering (Klauber, 1972). Adult *C. ruber* in Escondido, California, <115 km from our study site, also occupy communal dens in large rock outcrops (Brown et al., this volume).

Neonates can be expected to remain above ground, as seen in our subjects, in areas experiencing mild winter conditions (May et al., 1996; Grismer, 2002; Diffendorfer et al., 2005). The coldest temperature (ambient or surface) recorded for a surface-active neonate in our study was 5°C. At our study site, neonates constitute the most frequently observed surface-active age-class during the fall and winter months. The reason why neonates often remain on the surface rather than in burrows during the winter months (like adults) remains unclear. However, given the evidence that neonates were foraging successfully well into the cooler months, we suggest that they continue opportunistic foraging when conditions permit throughout the winter.

Future possibilities and suggestions.—Although long-term detrimental effects are recognized in snakes (Weatherhead and Blouin-Demers, 2004), radiotelemetry has provided an invaluable means by which many gaps in our knowledge of snake behavior and ecology can be studied within a theoretical background. Successful use of radiotelemetry with neonate snakes suggests that much can be learned about this vulnerable age class. The possibility of monitoring a snake from birth into adulthood offers hope that we can one day have a more complete understanding of a species' natural history and ontogenetic processes. By documenting the role of experience and responses to the environment, we can form a clearer picture of when, why, and where snakes move, and how the activity range is established, used, and the resources within it exploited. External transmitter attachment can serve as a viable alternative to surgically implanting transmitters into snakes. Until smaller, longer-lasting implantable transmitters become available, external attachment may be used—unless precluded by morphology, habitat, or behavior—for short-term tracking of snakes of any size, for studying small species, and for studying young snakes until they reach a size suitable for implantation.

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