

The reproductive ecology of Mohave rattlesnakes

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Keywords

Crotalus scutulatus; reproduction; mating systems; growth; movement; home range; drought; radiotelemetry.

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Abstract

The reproductive ecology of Mohave rattlesnakes *Crotalus scutulatus* was investigated in the western Mohave Desert using radiotelemetry from August 2001 to November 2004. This paper documents reproductive behavior across successive seasons in the context of seasonal timing, mean daily movement, home range, body temperature and relationship with abiotic factors such as time of day, temperature, precipitation, photoperiod and microhabitat. This population of *C. scutulatus* used a bimodal mating system, with reproductive behavior occurring in late summer/fall (21 August to 7 October), interrupted by 4 months of cold weather, and concluding in the spring (16 March to 16 May). Drought apparently curtailed courtship and copulation during the 2002 activity season, but the pregnancy rates in 2002 and 2003 were not significantly affected. Communal denning was not detected and there was no indication of seasonal migration. Autumnal and vernal movements appeared to be driven by reproductive effort, predominantly males engaged in prolonged mate searching. Sexual maturity was achieved at 2.0 years/600 mm snout–vent length (SVL) for females, and 1.5 years/400 mm SVL for males.

Introduction

Previous investigation of the reproductive biology of the Mohave rattlesnake, *Crotalus scutulatus* (Kennicott, 1861), has been accomplished using analyses of museum specimens (Goldberg & Rosen, 2000; Schuett *et al.*, 2002) and behavioral, histological and hormonal analyses of individuals derived from nature (Schuett *et al.*, 2002). However, comparatively little investigation has been devoted to the natural history of *C. scutulatus*.

This paper is the first to document the reproductive ecology of a population of *C. scutulatus* across multiple seasons in the context of seasonal timing, mean daily movement (MDM), home range, body temperature and abiotic factors such as time of day, temperature, precipitation, photoperiod and microhabitat.

Materials and methods

Study site

Field work was conducted in the western Mojave Desert near Victorville, San Bernardino County, CA, USA (34°36'N, 117°10'W). The study site is dominated by creosote bush *Larrea tridentata* and covers *c.* 150 ha at the confluence of two bajadas demarcated by an ephemeral wash. The median elevation is *c.* 975 m.

Radiotelemetry

An attempt was made to maintain seven telemetered adult rattlesnakes of each sex. When a telemetered animal was

lost, it was replaced by the next suitable subject encountered. The first transmitter was implanted in male C_{ss}02 on 23 August 2001 and the last new subject, male C_{ss}64, was implanted on 28 March 2004. Routine data collection was discontinued on 22 November 2004, when a blanket of snow ensured the end of the activity season. The remaining telemetered snakes were recaptured for transmitter removal during April 2005; this activity resulted in five new animals (C_{ss}81–85) and five additional reproductive pairs being encountered, as well as the recapture of three non-telemetered animals. Although 2005 observations of reproductive behavior and morphological data are included in these analyses, movement and home range estimates are based on data collected through November 2004 only.

In total, 10 male and 10 female adults (> 180 g) *C. scutulatus* were surgically implanted (Reinert & Cundall, 1982; Reinert, 1992; Hardy & Greene, 1999, 2000) with temperature-sensing radio transmitters (model SI-2T by Holohil Ltd., Ontario, Canada) and radiotracked for periods ranging from 9 to 1015 days (mean = 570 ± 362 SD). Transmitters did not exceed 5% of body mass.

With few exceptions, all telemetered animals were located and documented at least once during each field day. Excluding one absence of 15 days in July 2004, the mean interval between field days (calendar dates) during the combined activity seasons (March–November) was 1.05 day (± 1.35 SD, range 0–8, *n* = 459). Field effort was generally timed to coincide with environmental temperatures favorable for activity, although some visits were intentionally carried out during temperature extremes. Although study animals were monitored during all seasons, more time was

spent in the field when reproductive activity was detected or anticipated. Variations in monthly field hours did not produce a significant effect on the number of reproductive pairs encountered ($r = 0.333$, $P = 0.072$).

Data collection

All nontelemetered subjects encountered (both new and recaptures) were removed from the field for processing, except animals that were *in copulo* and those that had been processed within the previous few months. Telemetered animals were processed annually during transmitter replacement. All animals, including post-surgical subjects, were released as soon as possible at their capture locations, often within 24 h.

In addition to standardized serial data recorded at the time of capture, processing involved determination of mass (± 0.5 g; Ohaus decigram balance), precise snout-vent (SVL) and tail length (under general anesthesia), verification of sex by probing (Schaefer, 1934), rattle condition and dimensions, identification photos and colored marking of proximal rattle segments. All references to numbers of segments in 'complete' or 'unbroken' rattle strings include the button. All animals captured after 2001, except late-term pregnant females, were permanently implanted with a passive integrated transponder (PIT) tag (Avid Identification Systems, Norco, CA, USA) in the posterior abdomen.

A standardized serial dataset was recorded at each encounter, including date, time, geographic location, activity, body position, sun exposure and transmitter pulse interval, as well as environmental factors including sun and shade air temperature, overhead environment, photoperiod, recent precipitation and proximity to vegetation and animal burrows. Statistical calculations were carried out with SPSSTM, Students' v.12 for Windows (SPSS Inc., Chicago, IL, USA) and ExcelTM, v.2002 (Microsoft Corp., Redmond, WA, USA).

Geographic locations were determined with handheld global positioning system (GPS) receivers. Before April 2003, a Garmin[®] 12XL GPS receiver (Garmin International Inc., Olathe, KA, USA) yielded indicated errors between 2.7 and 6.7 m (mean = 3.7). Beginning 2 April 2003, a Garmin[®] 72 GPS receiver was used and consistently yielded <3.0 m error.

Terrain NavigatorTM software, v.5.01 (Maptech[®] Inc., Andover, MA, USA), was used to create a 'route' for each telemetered animal. The location of each successive observation was entered as a 'waypoint' on the animal's route and the length of the resulting route 'legs' yielded the straight-line distance moved between observations. MDM was calculated as

$$\frac{\text{Distance (m) between observation}}{\text{Time (day) between observation}}$$

Due to evidence that kernel home range estimators produce inconsistent results for organisms (e.g. many reptiles) that move relatively short distances and return to certain locations repeatedly (Row & Blouin-Demers, 2006), estimated seasonal home ranges for this study are reported

as 100% minimum convex polygons (MCP), calculated with CALHOME software, v.1.0 (Forestry Sciences Lab., Fresno, CA, USA).

Air temperature at each encounter was measured in sun (T_{su}) and shade (T_{sh}) with an Hg cloacal thermometer (Miller & Weber Inc., Ridgewood, NY, USA) about 1 cm above the substrate and recorded to the nearest 0.5 °C. Background temperature data were collected continuously at 1 h intervals near the center of the study area with data loggers (model 'RHTemp101' by Pacific Transducer Corp., Los Angeles, CA, USA <26 August 2002; model 'HOBO Water Temp Pro' by Onset Computer Corp., Bourne, MA, USA, thereafter) in shade at 1 cm above the substrate and at the bottom of an artificial rodent burrow (north-facing opening, length 3 m, terminal depth 1 m, inside diameter 3.8 cm, two 90° bends, polyvinylchloride tubing). Photoperiod was recorded as 'day,' 'night' or 'twilight' based on sunrise and sunset times, as well as the duration of 'nautical twilight,' as determined for each date from the United States Naval Observatory website (<http://www.usno.navy.mil/>).

Overhead environment indicated the material directly above a snake: 'clear' indicated unobstructed sky, 'foliage' indicated that the subject was under the branches of a perennial shrub, 'in burrow' was used when an animal was inside a subterranean burrow and 'debris' was used when a snake was under man-made material. When a snake's body extended from one overhead environment to another, the location of the snake's head was used.

Body temperatures were estimated to the nearest 1 °C for each observation by timing transmitter pulse intervals three times with a stopwatch, and then comparing the mean with a chart supplied by the transmitter manufacturer. Before implantation, each transmitter was tested in an H₂O bath at room temperature and the result was compared with the manufacturer's chart. The pulse interval-to-temperature conversion charts supplied by the manufacturer were found to yield values up to 1.5 °C greater than the measured temperatures, resulting in body temperatures calculated from many transmitters being reduced accordingly.

Reproductive behavior was categorized as accompaniment, courtship or copulation, as defined by Duvall, Arnold & Schuett (1992), in addition to 'trailing,' wherein a male was observed following the scent trail of a female.

Recent and historical precipitation data were obtained from the National Oceanic and Atmospheric Administration for its 'Victorville Pump Plant' station (COOP ID 049325), located 14 km southwest of the study area (National Climatic Data Center, 2001–2002, 2002).

All times are reported in Pacific Standard Time (GMT minus 8 h).

Results

Number of observations

More than 3550 individual encounters with 20 free-ranging telemetered *C. scutulatus* were recorded, in addition to >150 chance encounters with 60 non-telemetered animals.

Table 1 Body size data

Cohort	<i>n</i>	SVL (mm)			Body mass (g)		
		Mean	SD	Range	Mean	SD	Range
All ♂ and ♀	80	617	174	183–870	184.7	109.6	8.5–439.5
All ♂	37	611	191	262–870	182.5	122.6	12.5–439.5
All ♀	43	622	159	183–778	186.7	98.4	8.5–352.0
Mature ^a ♂ and ♀	50	728	61	612–870	252.8	70.7	125.0–439.5
Mature ^a ♂	19	762	74	612–870	280.3	80.3	146.0–439.5
Mature ^a ♀	31	706	38	620–778	236.0	59.4	125.0–352.0

^a ≥ 600 mm SVL (see 'Size at sexual maturity').

SD, standard deviation; SVL, snout–vent length.

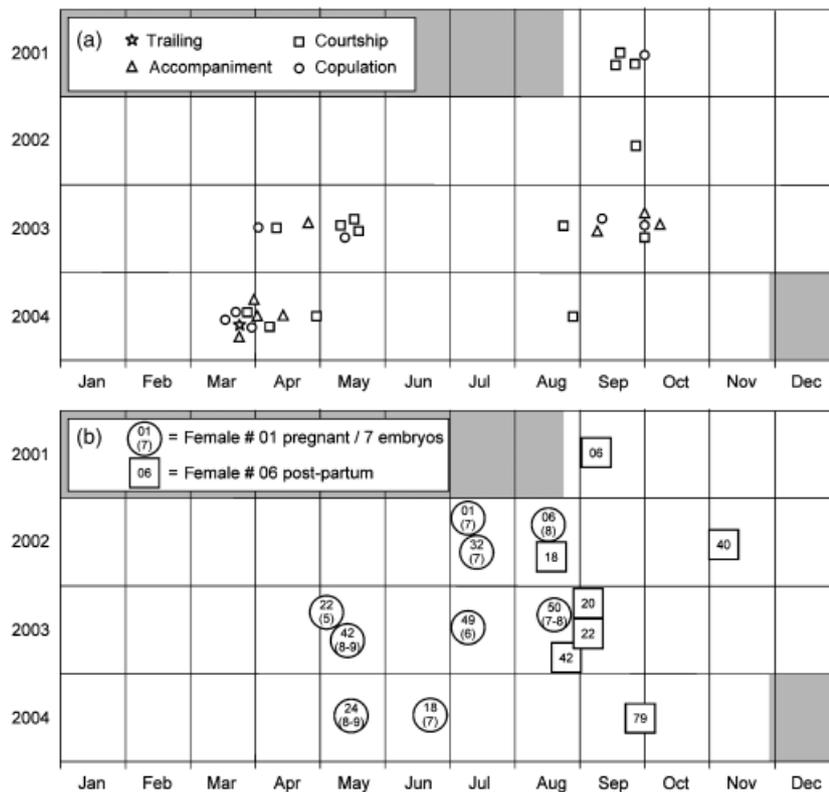


Figure 1 Temporal distribution of observations of *Crotalus scutulatus* reproductive behavior (a), and reproductive females (b). Shaded areas denote periods for which data were not collected.

These observations were made in all seasons, at all times of day and under a wide variety of weather conditions. Of the telemetered animals, three (C_{ss}11, 16, and 36) were eaten by mammalian predators, probably coyotes. Two (C_{ss}09 and 19) were found dead with no cause determined at necropsy, and seven (C_{ss}02, 03, 15, 30, 32, 43 and 64) disappeared without explanation. Eight rattlesnakes were monitored to hibernation in November 2004.

Body size

SVL and body mass data in Table 1 are based on measurements from initial captures. Three *in copulo* animals (not captured – C_{ss}12, 54 and 60) and two badly damaged road

kills (C_{ss}13 and 63) are not included. Mature (> 600 mm SVL) males were significantly larger than mature females, both in mean body mass ($P = 0.030$) and in mean SVL ($P = 0.008$) (independent *t*-tests).

Sexual activity

Thirty-one pairs of Mohave rattlesnakes were encountered while engaged in reproductive behavior. These observations were clustered between 21 August and 7 October ($n = 13$) and between 16 March and 16 May ($n = 18$), consistent with the bimodal mating system suggested by Schuett *et al.* (2002) for *C. scutulatus* (Fig. 1a). Details of these observations are summarized in Table 2.

Table 2 Detail of individual observations of *Crotalus scutulatus* reproductive pairs

Date	Time PST	Male		Female		Behavior	Air Temp	Photo-period	Overhead	Distance to shrub	Comments
		Css	T _b	Css	T _b						
14 September 2001	2040	03	24	Unid	Unk	Ct	25.0	N	Clear/foliage	0.0	Male trailing new female – nose to rattle, male tail-wagging; 20 min later, in <i>Larrea</i> bush with male hj and rtf on top of female; 15 min later, female gone
18 September 2001	2100	03	19	09	Unk	Ct	19.5	N	Clear	4.0	Male almost motionless on top of female, occasional hj & rtf; new female captured after 1.5h
26 September 2001	1912	03	27	11	Unk	Ct	27.0	N	Foliage	0.0	Male almost motionless on top of female under edge of <i>Larrea</i> , occasionally hj and rtf; new female captured
30 September 2001	1834	03	23	12	Unk	Cp	23.5	N	Clear	3.0	Male hj, rtf and slowly undulating cloacal area; intromission obvious; observed until 2018 PST
25 September 2002	1846	02	26	10	Unk	Ct	24.5	N	Clear	0.2	Female in pancake coil with male hj, cr and rtf vigorously on top of her; female recaptured
02 April 2003	1813	23	15	22	15	Cp	7.0	T	In burrow	0.0	Tails of both telemetered snakes visible c. 5 cm inside rodent burrow, coitus visually confirmed
10 April 2003	1755	15	21	Unid	Unk	Ct	18.0	D	Foliage	0.0	Male on top of female under edge of <i>Larrea</i> bush, engaged in hj, cr and rtf; 3.5 h later, male is underground nearby and female is not visible
27 April 2003	1808	23	18	19	19	Ac	15.0/15.0	D	In burrow	0.0	Telemetered, underground, out of sight
10 May 2003	1601	14	Unk	09	36	Ct	26.5	D	Foliage	0.0	Both snakes in the center of <i>Larrea</i> bush with male hj and cr on top of female; 1909 PST – little change (♀ T _b = 18, T _e = 16.0); 0953 PST – snakes in a pile in sun c. 125 m away, male is hj, cr and rtf (♀ T _b = 26.0, T _e = 33.0) (male IDed from marked rattle – not collected)
12 May 2003	1040	23	32	28	Unk	Cp	25.5	D	Foliage	0.0	Both snakes in center of <i>Larrea</i> bush and obviously <i>in copulo</i> . (Female IDed from marked rattle)
15 May 2003	2014	02	Unk	40	26	Ct	17.5	N	In burrow	0.0	Css40 tracked to rodent burrow but tail visible inside not hers; 0841 PST, snakes outside same burrow with male on top and occasionally hj; male Css02

16 May 2003	2302	43	Unk	31	Unk	Ct	13.5	N	Foliage	0.0	New male hj, cr and rtf on top of marked female
21 August 2003	2034	51	Unk	42	26	Ct	24.0	N	Clear	0.8	Male actively hj, cr, rtf and ts – cloacae in apposition but no copulation; new male was captured
09 September 2003	1833	43	31	19	31	Ac	19.5	T	In burrow	2.5	Telemetered, underground, out of sight
10 September 2003	1917	25	30	54	Unk	Cp	22.5	T	In burrow	1.7	Both visible just inside rodent burrow, coitus obvious
30 September 2003	1859	15	26	42	32	Ac	24.0	N	Foliage/burrow	0.0	Female in burrow at entrance, male outside, touching her
30 September 2003	1914	03	26	60	Unk	Cp	24.0	N	Foliage	0.0	Coitus visible in the center of dense <i>Larrea</i> bush
30 September 2003	2022	25	32	24	31	Ct	22.0	N	In burrow	1.8	Both tails visible inside rodent burrow, ts observed
07 October 2003	2119	15	27	Unid	Unk	Ac	19.0	N	In burrow	0.0	Both faces visible inside rodent burrow, no movement, impossible to tell whether (presumed) female was marked
16 March 2004	2003	25	13	Unid	Unk	Cp	12.0	N	Clear/burrow	0.5	Male coiled on open ground, <i>in copulo</i> with small female in burrow under him
19 March 2004	2035	15	15	55	Unk	Cp	15.0	N	Foliage	0.0	<i>In copulo</i> under <i>Larrea</i> overhang, not disturbed
20 March 2004	0849	23	31	24	32	Tr	19.5/26.0	D	Various	Various	Male scent-trailing female c. 20 m behind; her path was relatively direct bush to bush; his was neither straight nor direct - just like SICS; after 45 min, clear that he would not catch up until she stopped
20 March 2004	0958	34	Unk	22	28	Ac	28.0/36.0	D	Foliage	0.0	Male on top of female under <i>Larrea</i> overhang, both motionless; male recaptured
25 March 2004	1744	25	20	55	Unk	Ct	17.5	D	Foliage	0.0	Male on top of female under small desiccated shrub, engaged in hj, cr and rtf
27 March 2004	0953	64	Unk	40	24	Cp	12.0/28.0	D	Foliage	0.0	New male hj and rtf on top of female; male captured/released at capture site 2.5 days later with new transmitter, female then 71 m away; <24 h later he had found her and they are <i>in copulo</i> under <i>Ephedra</i> bush; next day (1 April 2004) he is hj, rtf and ts on top of her

Table 2. Continued

Date	Time PST	Male			Female			Air Temp	Photo-period	Overhead	Distance to shrub	Comments
		Css	T _b	T _e	Css	T _b	T _e					
29 March 2004	1934	02	23	27	32	27	18.5	N	In burrow	0.0	Telemetered snakes together, underground, out of sight; no change next day (March 30, 1327 PST) (T _b = 29/29, T _e = 37.0/35.5)	
01 April 2004	1106	34	Unk	29	19	29	25.0/26.0	D	Foliage	0.0	Coiled next to each other touching; 15 days later and 9 m away, male on top of female, both motionless, female's head hidden under own coils; together again (still?) 9 days later, touching, motionless; 2 days later (27 April), female found dead on surface, no trauma, male gone. Cause not obvious upon necropsy	
08 April 2004	1727	23	23	Unk	65	Unk	21.0	D	Clear	0.1	New female captured for processing	
14 April 2004	1814	15	22	26	20	26	18.5	D	In burrow	0.0	Telemetered, underground, out of sight	
29 April 2004	1212	02	29	Unk	Unid	Unk	26.0/36.0	D	In burrow	0.0	Male in rodent burrow; visible c. 3 cm inside were coils, one face (believed not to be male's), and male's tail – vigorously engaged in ts behavior	
27 August 2004	2055	78	Unk	22	24	22	23.5	N	Clear	0.5	New male cr and rtf on top of female; tails appositioned but no coitus; male fled hissing and rattling – unusual behavior for courting male; male was captured	

Behavior = most advanced step observed from 'Trailing > Accompaniment > Courtship > Copulation' continuum. Air temp = shade/sun (°C); single values indicate no sun. Distance to shrub = distance (m) to overhang of the nearest shrub. Ac, Accompaniment; Cp, copulation; cr, chin rubbing; Css, animal number; Ct, courtship; D, day; hj, head jerking; N, night; PST, Pacific Standard Time; rtf, rapid tongue flicking; SICS, strike-induced chemosensory searching; T, twilight; T_b, body temperature (°C); T_e, air temperature (°C); Tr, trailing; ts, tail searching; unid, unidentified; unk, unknown.

Table 3 Temperature summary for initial observations of (top to bottom) all, *in copulo*, surface and underground reproductive pairs

All ($n=30$)	T_b – male ($n=23$)	T_b – female ($n=15$)	T_b – all ($n=38$)	δ – \varnothing T_b SD ($n=8$)	T_e ($n=30$)	T_b minus T_e ($n=30$)
Mean	24	27	25	1.50	20.8	+4.3
range	13–32	15–36	14–34	0.00–4.24	7.0–28.0	–1.5–12.0
sd	5.62	5.43	5.47	1.58	5.03	3.92
<i>In copulo</i> ($n=8$)	T_b – male ($n=7$)	T_b – female ($n=2$)	T_b – all ($n=9$)	δ – \varnothing T_b SD ($n=1$)	T_e ($n=8$)	T_b minus T_e ($n=8$)
Mean	22	20	21	–	17.7	+4.6
range	13–32	15–24	14–28	–	7.0–26.0	–1.0–12.0
sd	7.75	6.36	7.21	–	7.01	4.55
Surface ($n=19$)	T_b – male ($n=13$)	T_b – female ($n=7$)	T_b – all ($n=20$)	δ – \varnothing T_b SD ($n=1$)	T_e ($n=19$)	T_b minus T_e ($n=19$)
Mean	23	28	25	–	21.8	+2.7
range	13–32	22–36	18–34	–	12.0–28.0	–1.5–12.0
sd	5.60	4.78	5.67	–	4.85	1.5
Underground ($n=10$)	T_b – male ($n=9$)	T_b – female ($n=7$)	T_b – all ($n=16$)	δ – \varnothing T_b SD ($n=6$)	T_e ($n=10$)	T_b minus T_e ($n=10$)
Mean	25	25	26	1.18	18.6	+7.2
range	15–32	15–31	15–32	0.00–2.83	7.0–26.0	3.0–11.5
sd	6.04	5.97	5.40	1.32	5.07	2.61

Temperatures, °C; sd, standard deviation; T_b , body temperature; T_e , air temperature.

On five occasions, pairs of rattlesnakes were partially visible inside rodent burrows and were scored as accompaniment unless courtship behavior or coitus could be specifically observed. Four of the eight recorded observations of accompaniment involved telemetered male–female pairs located together by their respective radio signals underground and out of sight. In each case, the origins of their radio signals were precise and identical. Because pairs were never found together outside of the bimodal mating season and two animals of the same sex were never found in close proximity during any season, these encounters were recorded as accompaniment.

Embryos were palpated in nine females between 2 May and 21 August, and seven post-partum females were observed between 18 August and 9 November (Fig. 1b).

Winter behavior

Seventeen individuals (8♂/9♀) were monitored over one or more winters, totaling 30 ‘snake/winters.’ They used mammal burrows (*Dipodomys* sp., *Ammospermophilus leucurus* and *Vulpes macrotis*) exclusively for hibernacula and, with the exception of C561 (♂), who spent the winters of 2003/2004 and 2004/2005 in the same abandoned *Vulpes* burrow, they did not use a hibernaculum more than once. There was no evidence of communal denning or seasonal migration. Individuals appeared to simply cease surface activity when the weather turned cold, remaining in any convenient mammal burrow until spring, when they emerged and resumed activity as if uninterrupted. Hibernation ingress and egress dates were not well-defined, with large (50 days) variation between individuals and no detectable difference between sexes.

Body temperatures

Of 31 reproductive pairs observed, body temperatures (T_b) are available for the male only in 15 cases, for the female

only in seven cases, for both sexes in eight cases and for neither animal in one case (Table 3). Two reproductive pairs interacting at burrow entrances with one animal inside and the other outside are excluded from the surface and underground temperature summaries in Table 3. Of 20 Mohave rattlesnakes engaged in reproductive behavior on the surface for which T_b values are available, all but three were found to be warmer than the surrounding T_{sh} . The greatest differential was found between T_{sh} and underground pairs. Temperatures recorded at the bottom of the artificial rodent burrow disclosed a very stable underground thermal environment that changed gradually in response to multi-day trends outside but was unaffected by the daily solar cycle. The mean T_b was warmer than the mean T_{sh} by 4.3, 4.6, 2.7 and 7.2 °C for all, *in copulo*, surface and underground cohorts, respectively.

Seasonal movements and environmental conditions

Males were much more motile than females, particularly during the bimodal mating season. Utilizing only data from animals monitored for entire activity seasons (six males, with four tracked for two seasons each = 10 snake/seasons; seven females, with five tracked for two seasons each = 12 snake/seasons), seasonal home ranges utilized by males were found to be *c.* 5.6 times larger than those used by females (independent *t*-test, $P < 0.001$), with mean estimated seasonal home ranges of 31.6 ha (± 12.54 sd, range 14.6–52.6, $n = 10$) and 5.6 ha (± 2.71 sd, range 2.0–10.5, $n = 12$), respectively (Fig. 2).

During the 2003 and 2004 activity seasons (March–November), MDM of males ($38 \text{ m day}^{-1} \pm 24.7$ sd, range 1–89) was more than three times that of females ($12 \text{ m day}^{-1} \pm 7.9$ sd, range 2–29) (independent *t*-test, $P < 0.001$). When controlled for body size (SVL = covariate), ANCOVA confirmed the

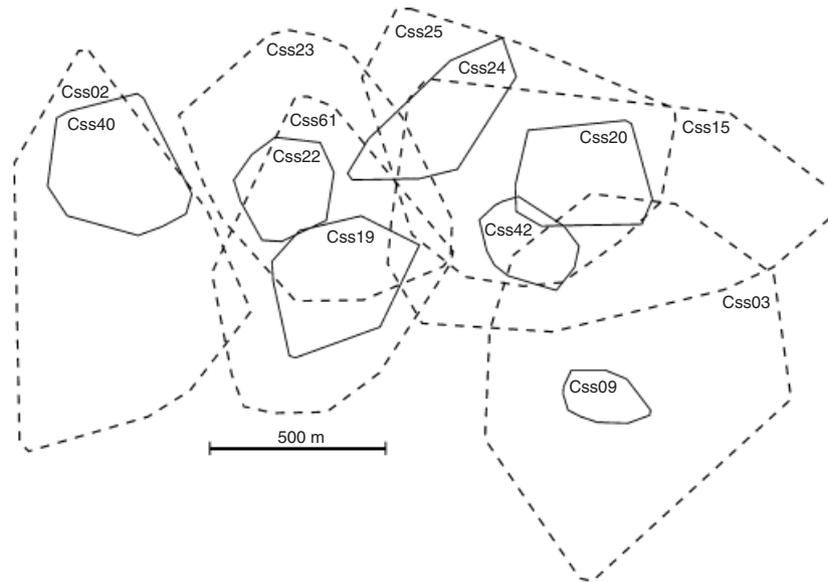


Figure 2 Relative multi-season home ranges for six male (dashed lines) and seven female (solid lines) adult *Crotalus scutulatus*, based on 100% minimum convex polygon analyses. An additional 58 conspecific animals were recorded in this area (excluding neonates), but were either not telemetered or yielded less than a complete season's movement data. Numbers, animal identifiers.

strong effect of sex on MDM ($F_{1,208} = 46.80$, $P < 0.001$, partial $\eta^2 = 0.184$), while the effect of body size was minimal ($F_{1,208} = 3.07$, $P = 0.081$, partial $\eta^2 = 0.015$). Compared with 2003 and 2004, MDM was dramatically reduced for both sexes during the drought of 2002 (Fig. 3), and only one incidence of reproductive behavior (September courtship) was observed that season. Pooling data from all 3 years, male MDM showed a much stronger correlation ($r = 0.638$, $P < 0.001$) with the number of reproductive pairs observed per month than female MDM ($r = 0.381$, $P = 0.050$), although both were significantly correlated (Fig. 4).

The 2002 activity season coincided with a storm season that produced only 28.6% of the mean (1971–2000) seasonal precipitation. In 2002, virtually no perennial plants flowered at the study site, there was no annual plant growth and nocturnal *Dipodomys* sightings became far less common compared with their previous (and subsequent) abundance. The drought was broken on 15–16 March 2003 with a substantial overnight storm and reproductive behavior resumed *c.* 2 weeks thereafter.

Size at sexual maturity

The youngest (based on the length of an unbroken rattle) females observed *in copulo* ($n = 3$) possessed unbroken rattle strings of six segments (Ccss28 on 12 May 2003, Ccss54 on September 10, 2003 and Ccss84 on 13 April 2005). These females were not captured for processing when they were observed copulating however, Ccss28 had been processed and released 8 days before, having measured 582 mm SVL with a mass of 161 g. Ccss84 was captured and processed the day after being observed *in copulo* and measured 597 mm SVL with a mass of 183 g. My dataset contains one addi-

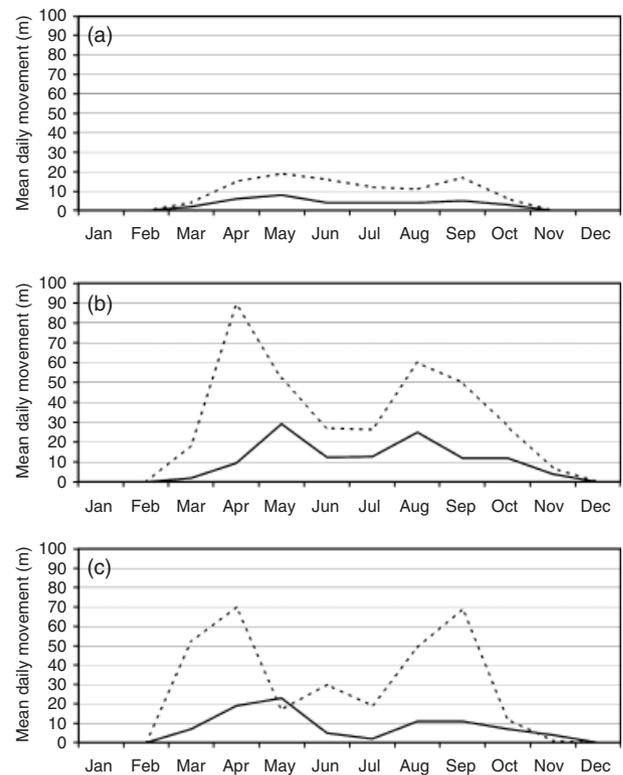


Figure 3 Mean daily movement for 2002 (a), 2003 (b) and 2004 (c); dotted lines, males; solid lines, females.

tional female with an unbroken rattle string of six segments (Ccss37 on 15 September 2002) that measured 620 mm SVL with a mass of 125 g. The youngest male involved in

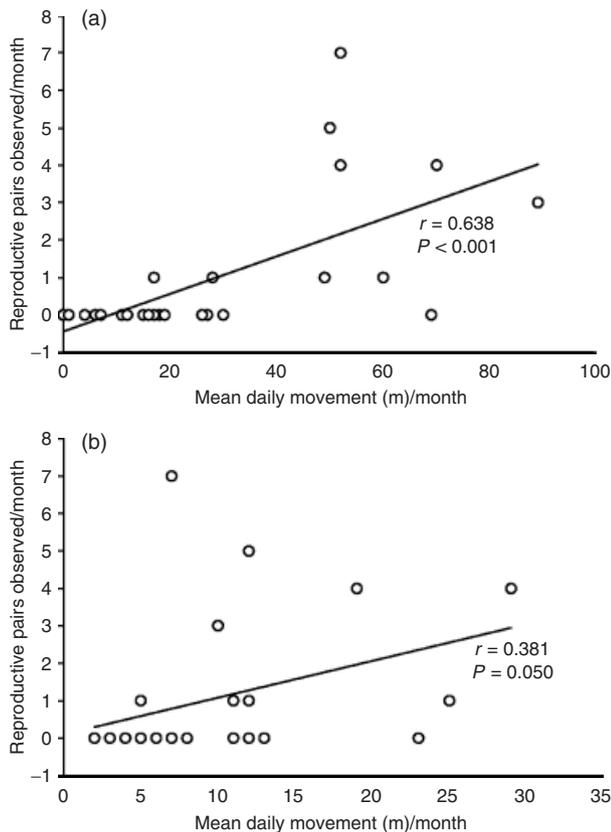


Figure 4 Correlation between the mean daily movement of males (a) and females (b) with reproductive pairs observed. Note difference in x-axis scales.

reproductive behavior was C_{ss}82, observed courting C_{ss}40 on 12 April 2005. Upon processing, C_{ss}82 measured 614 mm SVL with a mass of 146 g and an unbroken rattle of six segments. The data set contains four additional males with complete six-segment rattles with SVL/mass (mm/g) of 559/142, 573/118, 592/115 and 612/169 (C_{ss}53, 34, 80 and 83), respectively.

Probing for hemipenes identified 37 male rattlesnakes. Using the probe depth as a measure of hemipenis length (usually only one side was probed), hemipenis development was found to be clustered between 27.3 and 30.6% (mean = 28.5) of tail length ($n = 6$) with corresponding SVLs of 262–302 mm (mean = 276) and between 51.5 and 93.8% (mean = 66.8) of tail length ($n = 30$) with corresponding SVLs of 467–870 mm (mean = 687). Only one animal fell between these clusters (C_{ss}45 at 44.4% and 361 mm). A strong correlation was demonstrated between SVL and hemipenis length ($r = 0.768$, $P < 0.001$, $n = 37$).

Sexual size dimorphism

Analyses of \log_{10} -transformed SVL and body mass of mature animals (> 600 mm SVL) indicate that females tend

to gain more body mass per unit of length but the difference is not significant at $\alpha = 0.05$ (independent t -test, $P = 0.163$), but male body length exceeds that of females, both in mean (independent t -test, $P = 0.008$) and maximum SVL values (see Table 1 for details). Similar analyses of immature animals (< 600 mm SVL, $n = 18\text{♂}/12\text{♀}$) yielded indistinguishable regression models.

Neonates and timing of parturition

Nine neonatal *C. scutulatus* (defined by a rattle consisting of the button only) were encountered in the study area and an additional nine were encountered on roadways near the study site (and not considered elsewhere in this study), including 12 born in 2001 (earliest encounter 2 September), one in 2002 (encountered 9 October), one in 2003 (encountered 14 September) and four in 2004 (earliest encounter 14 August). These were isolated encounters with no evidence that any were siblings, and all had completed postpartum ecdysis.

Three telemetered females produced litters during the study, as indicated by an abrupt loss of an estimated 30–50% of body mass, resulting in significant lateral posterior skin folds. All births occurred in 2003. While embryos were palpated in C_{ss}22 and 42 in May (see Fig. 1b), pregnancy was not noted when C_{ss}20 was processed on 27 April 2003. When observed on 21 August while still pregnant, C_{ss}42 was coiled on open ground with a male (C_{ss}51) actively courting her. C_{ss}51 was collected for processing and C_{ss}42 was found postpartum on 25 August, 74 m away. C_{ss}20 and 22 were both obviously pregnant when observed on 28 August. On 3 September C_{ss}20 was found, clearly postpartum, coiled near a rodent burrow into which she quickly fled upon my approach – atypical behavior compared with many other encounters. On 3 September, C_{ss}22 was found to be postpartum and was observed to kill and eat a kangaroo rat, *Dipodomys merriami*. While C_{ss}22 remained at the same location for 9 days before and 4 days after 3 September both C_{ss}20 and 42 continued to change locations frequently both before and after parturition. The interiors of burrows were repeatedly checked for visible neonates or neonatal exuvia, in these and many other instances, but always without success.

Male fighting

Multiple male rattlesnakes were never encountered together, however, on the evening of 21 August 2003, I moved C_{ss}15 (♂) about 100 m and introduced him to a pair (C_{ss}51♂ and C_{ss}42♀) naturally engaged in courtship. Immediately upon tongue-flicking each other, the males commenced classic male–male fighting that continued for nearly 10 min, covering an area of $c. 50 \text{ m}^2$ before C_{ss}15, who was about the same length but less mass, crawled away. C_{ss}51 did not pursue C_{ss}15, but returned immediately to find the female. C_{ss}15 was returned to his previous location and C_{ss}51 (a new animal) was captured for processing.

Discussion

My data, derived from a California population of *C. scutulatus*, support the bimodal mating system hypothesis for this taxon as proposed by Schuett *et al.* (2002); however, the late summer/early fall mating season did not correspond to a well-defined monsoon, as noted for Arizona populations (Schuett *et al.*, 2002). Sexual behavior was observed during two distinct periods: 21 August – 7 October and 16 March – 16 May.

Increases in MDM by both sexes corresponded to the months when sexual behavior was observed however, males moved more than three times farther than females, with male movement having a much stronger relationship than female movement to reproductive activity, based on the number of reproductive pairs observed. The corresponding seasonal home ranges of males were found to be *c.* 5.6 times larger than those of females.

Seasonal movement appears to be driven by reproductive effort and I found no evidence of communal denning or seasonal migration between den sites and summer habitat. Although freezing winter temperatures are common at the study site, suitable winter shelters are numerous in the form of rodent and *Vulpes* burrows. As a result, these snakes appear to have no environmental incentive, as described by Gregory (1984) and Aldridge & Duvall (2002), to aggregate at hibernacula.

These data confirm that *C. scutulatus* uses prolonged mate-searching polygyny (indiscriminate mate selection is not inferred; *cf.* Rivas & Burghardt, 2005), a particularly non-gregarious mating system in which males search competitively for receptive females that are widely distributed and spatially unpredictable (Duvall *et al.*, 1992).

MDM for both sexes was reduced during the drought year (2002) to less than one-third of the non-drought years (2003, 2004), with only one observation of sexual behavior in 2002. However, both MDM and observations of sexual behavior resumed as soon as the drought was broken. Nonetheless, seasonal numbers of reproductive females in my sample remained relatively unchanged throughout the 40-month study.

This study suggests that *C. scutulatus* sexually matures sooner than many other viviparous vipers (summarized by Parker & Plummer, 2001), although investigators have documented sexual maturity in some temperate rattlesnakes by late in their second year (e.g. Fitch, 1970). None of the marked and released neonates in this study were recaptured. The relative scarcity of animals between *c.* 300 and 500 mm SVL suggests that they grow through this stage rapidly, as has been reported for other species of *Crotalus* (e.g. Gibbons, 1972; Macartney, Gregory & Charland, 1990; Fitch, 2002). Males were observed courting and females were observed copulating at *c.* 600 mm SVL with unbroken rattles of six segments, a size that probably corresponds to the later part of their second summer and *c.* 2 years of age for both sexes. But my analysis of male hemipenis length suggests that hemipenes are well developed shortly after 400 mm SVL, or potentially 1.0–1.5 years of age. These data

complement the findings of Goldberg & Rosen (2000), who reported that the smallest vitellogenic female *C. scutulatus* was 611 mm SVL and the smallest male with sperm was 411 mm SVL.

The uninterrupted production of offspring in 2003 is interesting due to the lack of reproductive behavior observed in 2002 and studies that suggest that the reproductive condition of rattlesnakes and other vipers may be significantly affected by reduced precipitation (e.g. Goldberg & Rosen, 2000; Schuett *et al.*, 2005) and reduced prey density the previous year (e.g. Diller & Wallace, 2002). Although the viability of these offspring cannot be assumed, my observations suggest that *C. scutulatus* is quite secretive regarding parturition, potentially giving birth in deep mammal burrows, and often without maternal attendance. Additional study is needed to identify the factors that affect the reproductive cycle of *C. scutulatus* and to document maternal behavior.

The only other reports of male–male fighting in *C. scutulatus* are provided by Schuett *et al.* (2002) and R. Reiserer (unpubl. data) of spring and fall observations, respectively.

The population of *C. scutulatus* I studied exists in a prey-rich environment where I observed their principal prey, *Dipodomys*, to be abundant (except during the drought) and homogeneously distributed throughout the study area. With rodent burrows available for thermal shelter under almost every shrub, these sit-and-wait predators have little need to move about to find food or avoid thermal extremes. Previous investigators have suggested that male snakes are more susceptible to predation during increased movement driven by prolonged mate-searching (e.g. Aldridge & Brown, 1995; Bonnett, Naulleau & Shine, 1999). In my sample, 63% more sexually mature (>600 mm SVL) females than males ($n = 31♀/19♂$) were recorded, despite the immature cohort being dominated by males ($n = 18♂/12♀$). Open habitats with widely spaced shrubs and little intervening ground cover, as preferred by *C. scutulatus*, exacerbate the snakes' susceptibility to both mammalian and avian predators. Furthermore, rigorous mate-searching brings the males into contact with humans, resulting in mortality to the snakes (Aldridge & Brown, 1995) and envenoming of humans (Cardwell *et al.*, 2006).

Previous investigators (e.g. Aldridge & Duvall, 2002) have also suggested that female movement is necessary to lay down pheromone trails, thereby advertising to passing males. Such behavior may explain the increased MDM in spring and late summer/fall by females, albeit much less than males, in my study (Fig. 3).

The goal of this study was to document a broad suite of behaviors of a wild population of *C. scutulatus*. Consequently, it was designed to minimize disturbance to the snakes. As a result, females were only palpated to assess reproductive condition when being handled for other reasons; more frequent assessments would have provided more context to these observations. A longer-term study is needed to determine the effect of various abiotic factors on reproduction, but any such effort should include a dedicated

weather station located within the study area, as summer desert rainstorms are typically limited in area and duration, rendering data recorded even a few kilometers away questionable. Future studies must also include more intensive monitoring of the animals for entire seasons, ideally incorporating emerging technologies (e.g. iButton[®] implantable data loggers; see Taylor, DeNardo & Malawy, 2004). Furthermore, it will be important to study populations in diverse parts of the species' range, because considerable geographic variation has been documented in the natural history of other rattlesnakes, and regional variation in *C. scutulatus* venom composition (summarized by Wilkinson *et al.*, 1991) is likely to be related to differences in diet or foraging habits.

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