

Timing of reproduction of a cold desert viperid snake from North America, the Great Basin rattlesnake (*Crotalus lutosus*)

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ABSTRACT

In this study, we examined the reproductive tracts of preserved specimens of the Great Basin rattlesnake (*Crotalus lutosus*) to investigate the reproductive strategies used by the only species of rattlesnakes widely occurring in a cold desert. The vitellogenic cycle of female rattlesnakes spanned over two consecutive years: females started vitellogenesis in late spring/early summer, and ovulated in the summer of the next year. This contrasts with the female reproductive cycle of other rattlesnake species from warmer regions of North America, which typically initiate vitellogenesis in summer/fall, and ovulate in late spring of the next year. On the other hand, the reproductive cycle of male *C. lutosus* conformed well to those described for other rattlesnakes; that is, testes were active (i.e., sperm formation) in summer. The sexual segments of the kidneys of males were hypertrophied in summer, suggesting an unimodal summer mating season. Our findings suggests that the relatively short active season (i.e., 4–5 months) experienced by these snakes in the Great Basin of North America has implications for the timing of female reproductive events, such as an early onset of vitellogenesis, a late time of ovulation, and possibly a restricted period for giving birth.

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1. Introduction

The reliance of ectotherms on the physical environment to regulate body temperature has important implications for the ecology and evolution of these organisms, because most developmental, physiological, and behavioral processes are temperature-dependent (Peterson et al., 1993). For example, variation in environmental temperatures can affect many reproductive and life-history traits, including embryonic development (Deeming and Ferguson, 1991; Laugen et al., 2003), offspring fitness and growth rate (Sinervo and Adolph, 1989; Shine, 1999; Brana and Ji, 2000), size and age at maturity (Atkinson, 1994), timing of reproductive cycle and sexual activity (Saint Girons, 1982; James and Shine, 1985; Pizzatto and Marques, 2002), and frequency of reproduction (Saint Girons, 1982). Exposure to varying environmental conditions has consequently generated an immense diversity of reproductive and life-history strategies in ectotherms, including squamate reptiles (Tinkle et al., 1970; Shine, 2005).

In temperate regions, severe seasonal fluctuations in thermal conditions can constrain and prevent year-round activity in reptiles and amphibians (Cowles and Bogert, 1944; Gregory, 1982). Many ectotherms consequently hibernate during the coldest part of the year, and the severity and the length of the winter is a crucial determinant of hibernation duration (Gregory, 1982). A prolonged hibernation period directly affects the time available for activity. Indeed, many ectotherms living at high altitudes or latitudes exhibit shorter activity seasons than conspecifics or congeneric species living in more thermally favorable environments (Goldberg, 1974; Iburgüengoytia and Casalins, 2007). Reduction in the length of the activity season can in turn affect the reproductive characteristics of many ectotherms (McCoy and Hoddenbach, 1966; Tinkle et al., 1970; Leclair et al., 2006). For instance, a shortened annual activity period has been correlated with delayed vitellogenesis, spermiogenesis, age at first reproduction, and decreased female reproductive frequency (Saint Girons, 1957; McCoy and Hoddenbach, 1966; Goldberg, 1974; Martin, 2002).

Rattlesnakes (*Crotalus*, *Sistrurus*) belong to a clade of snakes that includes 32 currently recognized species (Campbell and Lamar, 2004). Although some species inhabit mesic environments, rattlesnakes are typically associated with xeric habitats (Klauber, 1972),

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and are an integral component of the arid ecosystems of North America. Within this clade, the Great Basin rattlesnake (*Crotalus lutosus*) is unique because it is the only species widely occurring in a cold desert, the Great Basin Desert of North America. This desert is the largest and most northerly of the four North American deserts (Brown, 1994). As a high elevation desert, the region is arid, cold, mountainous, and experiences a short growing season (Trimble, 1989). As a result, the activity season of *C. lutosus* is reduced compared to those of rattlesnakes inhabiting the warmer deserts of North America (Fautin, 1946; Diller and Wallace, 1996; Jenkins, 2007; Hamilton, Personal observation). Herein, we relied on examination of *C. lutosus* museum specimens to characterize the reproductive ecology of this unique cold-desert rattlesnake. Our objectives were to determine the timing of the reproductive cycle of *C. lutosus* by inspecting the testis, sexual segment of the kidney and vas deferens of males and the reproductive tracts of females. We then compare our findings to the reproductive cycle of rattlesnake species inhabiting warmer deserts of North America to examine patterns of reproductive variation in this group of snakes.

Our study has two important implications. First, investigating the reproductive characteristics of taxa inhabiting extreme environments provides a better understanding of the strategies used by organisms to reproduce and persist in the face of severe environmental challenges. Further, an understanding of a species reproductive biology is an essential component of wildlife management and conservation biology. Many rattlesnake species have experienced declines or local extirpations (e.g. Brown, 1993), and reptiles living in thermally challenging environments typically exhibit reduced reproductive output compared to species living in more favorable environments (Vial and Stewart, 1985; Dunham et al., 1994; Cree and Guillette, 1995). Consequently, information on reproduction is necessary to assess likelihood of persistence, potential for reestablishment, and management of habitat and human activities.

2. Methods

2.1. Study region and species

The distribution of *C. lutosus* approximates the boundaries of the biological Great Basin (Stebbins, 2003), defined by the boundaries of contiguous sagebrush (*Artemisia* spp.) plant communities, an area of over 492,100 km² (Trimble, 1989). Located in the rain shadow of the Sierra Nevada, the Great Basin is arid, mountainous, and cold, with most precipitation falling as snow (Trimble, 1989). Climate varies with topography and higher elevations are cooler and receive more precipitation than lower elevations. In Great Basin National Park, located in eastern White Pine County, Nevada, mean annual temperature and precipitation vary from 10 °C and 19 cm at 1600 m to 0 °C and 80 cm at 3960 m (Western Regional Climate Center, unpublished data). As a hydrologically closed system, the Great Basin is composed of a series of north to south trending valleys and mountain ranges created through crustal extension (Grayson, 1993). The Great Basin has been anthropogenically altered by overgrazing, fire suppression, and non-native plants and large areas are now dominated by annual grasses (Thompson et al., 2006; Chambers et al., 2007). Plant production peaks in late spring early summer when soil moisture is high (Smith and Nowak, 1990).

Within the Great Basin, *C. lutosus* typically inhabits arid and semiarid plains, desert areas, and talus slopes of mountainous, rocky areas (Klauber, 1972). (The systematic relationships of *C. lutosus*, a taxon belonging to the *Crotalus viridis* species complex, have been recently studied by several authors (Pook et al., 2000; Ashton and de Queiroz, 2001; Douglas et al., 2002), and herein we

recognize this snake at the species level, following the recommendation of Douglas et al. (2002).) Individuals can grow up to 135 cm in total length (Ernst and Ernst, 2003), although adult body sizes average 73.9 cm and 65.3 cm in snout-to-vent length (SVL) in males and females, respectively (Glaudas et al., 2008). As with most viperid snakes, *C. lutosus* is a sit-and-wait predator that typically selects an ambush site based on the presence of chemical cues left by potential prey (Reinert et al., 1984; Greene, 1992, 1997), which are mostly rodents and lizards (Glaudas et al., 2008).

2.2. Data collection

We examined 275 *C. lutosus* collected between 1893 and 2003 from the Monte L. Bean Life Science Museum, Brigham Young University, Provo (BYU), California Academy of Sciences, San Francisco (CAS), Field Museum of Natural History, Chicago (FMNH), Los Angeles County Museum of Natural History (LACM), Museum of Vertebrate Zoology, University of California, Berkeley (MVZ), San Diego Natural History Museum (SDNHM), Utah Museum of Natural History, University of Utah, Salt Lake City (UMNH), Marjorie Barrick Museum of Natural History, University of Nevada, Las Vegas (MBM), and Museum of Biology, University of Nevada, Reno (UNR). We avoided type and soft, brittle, or otherwise fragile specimens. Whenever possible, for each snake we recorded the following variables: complete locality data, date of collection, body size (snout-vent length [± 1 cm]), body mass (± 0.1 g), sex and reproductive maturity. Females were considered mature if they were gravid, had thickened muscular oviduct, or if they had enlarged vitellogenic follicles (≥ 10 mm). For mature females, we recorded the diameter of the largest ovarian follicles, as well as the number of enlarged follicles, oviductal eggs or embryos. Males were defined as mature if they had enlarged testes or opaque and convoluted vas deferens (Shine, 1977). Whenever possible, we recorded the length, width, and the thickness of each testis. Additionally, we removed 5 mm sections of the middle portion of the testis, anterior portion of the kidney (to examine the sexual segment of the kidney [SSK], which is involved in the production of seminal fluid; Prasad and Reddy, 1972), and distal vas deferens (where sperm is typically stored; Almeida-Santos et al., 2004) of 43 males collected throughout the activity season in eastern Nevada and western Utah for histological examination. Tissues were embedded in paraffin and cut into 5–10 μ m sections. Slides were stained with Harris' hematoxylin followed by eosin counterstain (Presnell and Schreibman, 1997). We took measurements of 10 round to nearly round seminiferous and SSK tubules using axiovision 4.0 microscopy software (Carl Zeiss, Germany), and averaged these measurements per specimen. The measurements recorded were seminiferous tubule diameter (STD) and sexual segment of the kidney tubule diameter (SSKD). We were unable to obtain all measurements for all individuals due to differences in preservation and histological preparation, resulting in different sample sizes among tissue analyses. Finally, we examined the testis slides to determine the stage of the testicular cycle. We slightly revised the criteria provided by Goldberg and Parker (1975) to classify the testes as follow: (1) Regression – the germinal epithelium consists of several layers of cells made up primarily of spermatogonia and Sertoli cells; (2) Early recrudescence – a proliferation of cells (mainly primary spermatocytes) for the next period of sperm formation is underway; (3) Late recrudescence – an increased number of cells consisting of primary and secondary spermatocytes, some spermatids, but no spermatozoa; (4) Spermiogenesis – the lumina are lined with spermatozoa or bundles of metamorphosing spermatids. The observer was blind to the time of year each specimen was collected throughout the histological analysis. We performed statistical tests using STATISTICA (version 6.0; StatSoft Inc., 2000). Values given are

means ± 1 S.E., and all p values are two-tailed. Significance level for all tests was determined at $\alpha = 0.05$.

3. Results

All snakes under 50 cm SVL were immature. The smallest mature male and female examined were 50.8 cm and 51.4 cm SVL, respectively. All snakes above these sex-specific minimum body sizes at first reproduction were not all unequivocally mature but all snakes above 70 cm SVL were. Mature males were significantly larger than mature females (ANOVA; males: 72.8 ± 0.8 cm, range: 50.8–97.8, $n = 130$; females: 65.6 ± 0.7 cm, range: 51.4–83.5, $n = 103$; $F_{1,231} = 36.9$, $p < 0.0001$).

3.1. Female reproductive cycle

Females initiated secondary vitellogenesis (i.e., follicles ≥ 10 mm) as early as mid-May but more commonly in the early summer months, indicating that the onset of the vitellogenic cycle occurs in late spring/early summer (Fig. 1). The development of follicles continued throughout the active season, presumably paused during hibernation, and resumed the following spring. One female collected in mid-May had oviductal eggs, suggesting that fertilization can occur in mid-spring. However, ovulation seemed to occur more generally in summer because 94% (16/17) of the reproductive females collected from April to late June had not yet ovulated. Only one female collected on 9 September 1930 had full term embryos (i.e., snakes fully formed). The proportion of reproductive females did not vary among size categories (10 cm-increment intervals; 50–60, 60.1–70, 70.1–80, 80.1–90; $\chi^2 = 0.6$, $df = 3$, $p = 0.89$). Finally, 40 of 89 (45%) mature females were reproductively active.

We used the number of enlarged follicles ($n = 40$), oviductal eggs ($n = 2$), and embryos ($n = 1$) to investigate the relationship between body size and litter size. Larger females produced larger litters (linear regression; $y = -5.33 + 0.17 \cdot x$, $r^2 = 0.28$, $n = 43$, $p = 0.0002$; Fig. 2). Even though this relationship was highly significant, female body size only explained 28% of the variance in clutch size, suggesting that other important factors are at work. Finally, females with enlarged vitellogenic follicles (≥ 10 mm) were heavier than those that were not vitellogenic (ANCOVA; covariate: SVL; $F_{1,106} = 20.24$, $p < 0.0001$).

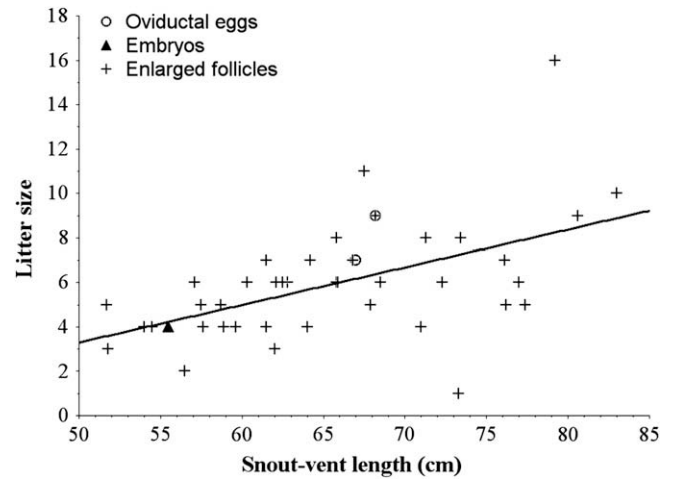


Fig. 2. Relationship between litter size and the body size (SVL) of female *Crotalus lutosus*. See legend for definitions of symbols.

3.2. Male reproductive cycle

Our histological analysis revealed that testes are regressed or exhibit signs of early recrudescence (i.e., renewal of germinal epithelium) in spring. Spermiogenesis occurred from mid-June to mid-September (Fig. 3). The seminiferous tubules were significantly larger during spermiogenesis compared to the other stages of the spermatogenic cycle (spermiogenesis: $281.8 \pm 11.9 \mu\text{m}$, $n = 15$; other spermatogenic stages: $196.6 \pm 16.4 \mu\text{m}$, $n = 13$; ANOVA, $F_{1,26} = 18.23$, $p < 0.001$; Fig. 4). The vas deferens of the snakes examined contained sperm in all months, with dense amounts present in spring.

We compared testis length among spermatogenic stages in 31 snakes to investigate if testis morphometry correlates with spermatogenic cycle. Testis length consistently increased from the recrudescence stages to spermiogenesis (regression: 15.7 ± 0.59 mm; early recrudescence: 14.02 ± 1.05 mm; late recrudescence: 17.22 ± 2.09 mm; spermiogenesis: 18.38 ± 1.05 mm; ANCOVA; covariate: SVL; $F_{3,26} = 3.1086$, $p = 0.04$), indicating that this trait is a reliable predictor of spermatogenic activity. We then used our larger sample of snakes to examine seasonal variation in testis length. We used the residual scores of a regression of testis length

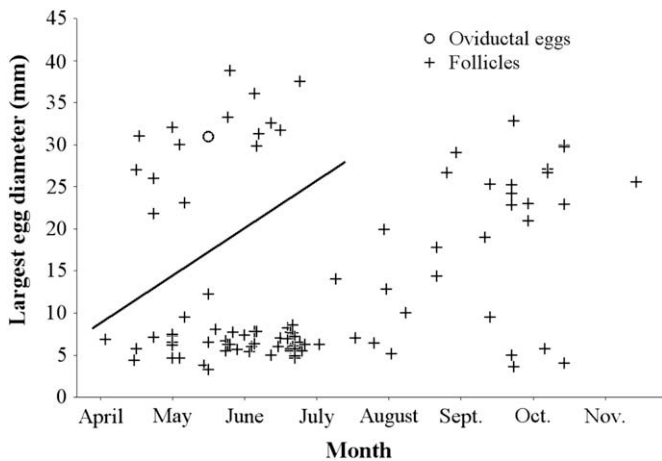


Fig. 1. Seasonal variation in the diameter of the largest follicle of adult female *Crotalus lutosus*. The line on the graph differentiates females that are starting vitellogenesis in spring/summer (below the line) from those that are completing vitellogenesis and would presumably give birth a few months later (above the line).

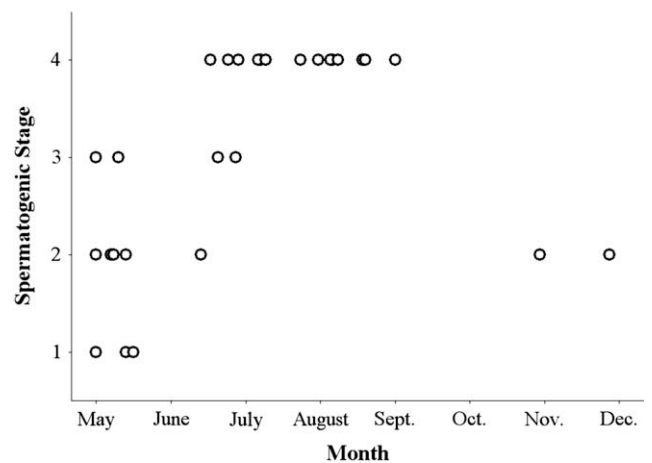


Fig. 3. Spermatogenic stage of *Crotalus lutosus*. The stages depicted on the Y axis are: (1) Regression; (2) Early recrudescence; (3) Late recrudescence; (4) Spermiogenesis. See text for definitions.

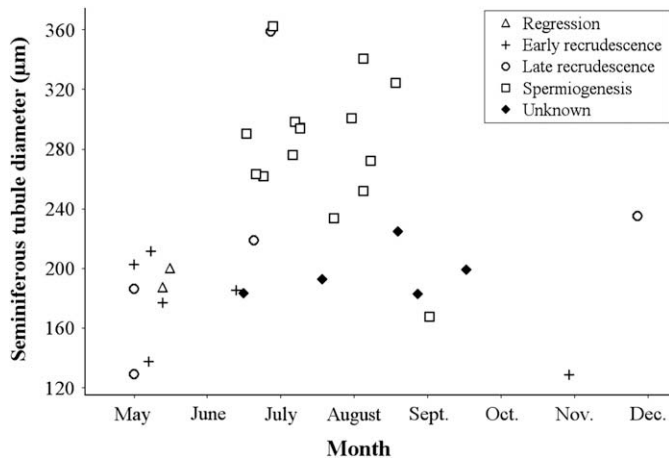


Fig. 4. Seasonal variation in seminiferous tubule diameters of *Crotalus lutosus*. Each point represents the average of 10 measurements per snake. The different symbols depicted represent the different stages of the spermatogenic cycle. See legend for definitions of symbols.

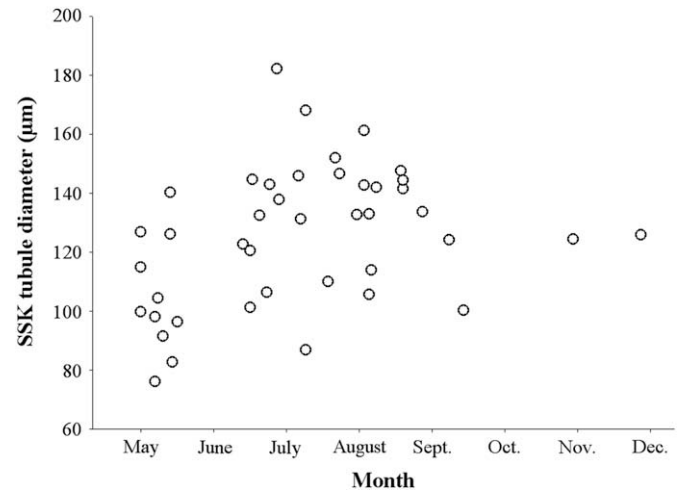


Fig. 6. Seasonal variation in the diameters of the sexual segment of the kidney of *Crotalus lutosus*. Each point represents the average of 10 measurements per snake.

on SVL to control for the relationship between the two variables (linear regression; $y = -0.61 + 0.22 \cdot x$, $r^2 = 0.35$, $n = 152$, $p < 0.0001$). Relative testis length varied between months (ANOVA; $F_{6,125} = 2.54$, $p = 0.02$; Fig. 5). Multiple comparisons between monthly means using Fisher LSD test revealed that relative testis length was significantly higher in August and September than in April, May, and June.

The diameters of the SSK showed an unimodal peak in summer (Fig. 6). We classified the specimens examined by season of collection to statistically test seasonal variation in SSK hypertrophy. Because our sample size for fall was small ($n = 2$), we compared snakes collected in spring (21 March–20 June, $n = 15$) and summer (21 June–20 September, $n = 24$). The SSK diameters of snakes collected in spring were smaller than those of snakes collected in summer (spring: $111.8 \pm 5.6 \mu\text{m}$; summer: $134.6 \pm 4.4 \mu\text{m}$; ANOVA, $F_{1,37} = 10.11$, $p = 0.003$).

4. Discussion and conclusions

Our study reports the reproductive cycle of the only rattlesnake species widely inhabiting a cold desert, the Great Basin rattlesnake

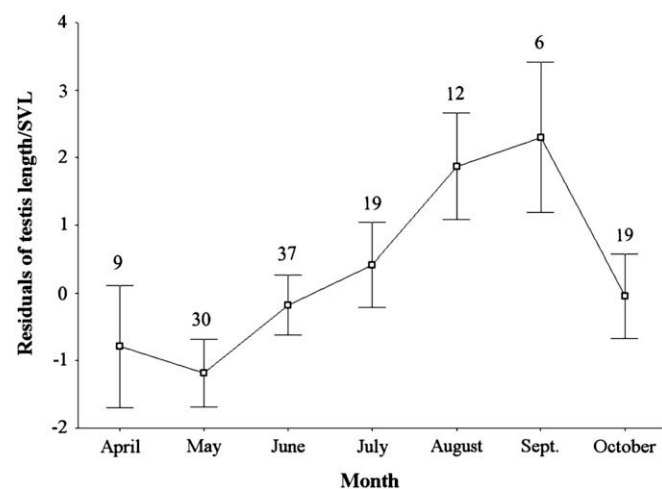


Fig. 5. Seasonal variation (mean \pm SE) in relative testis length (residual scores of a regression of testis length on SVL) of *Crotalus lutosus*. Numbers above the bars refer to sample size.

(*C. lutosus*). Our findings suggest that the thermal conditions experienced by these snakes in the Great Basin of North America have implications for the timing of reproductive events in females.

4.1. Female reproductive cycle

The female reproductive cycle of *C. lutosus* is similar to the pattern observed in almost all rattlesnake species, in which completion of vitellogenesis is achieved over two consecutive years (see Taylor and DeNardo, 2005 for a unique and rapid vitellogenic development in this group of snakes). However, there are subtle differences with other rattlesnakes exhibiting this pattern. First, female *C. lutosus* initiate vitellogenesis in late spring/early summer whereas closely-related species of the *C. viridis* complex (to which *C. lutosus* belongs; Pook et al., 2000; Douglas et al., 2002) do so in summer/fall (*C. viridis*: Aldridge, 1979; *Crotalus oreganus*: Diller and Wallace, 1984; Fig. 7). Other more distantly-related species from the warm deserts of North America, such as the sidewinder (*Crotalus cerastes*) and the Mojave rattlesnake (*Crotalus scutulatus*), also exhibit a delayed vitellogenic cycle compared to *C. lutosus* (Goldberg and Rosen, 2000; Goldberg, 2004; Fig. 7). Second, many rattlesnakes ovulate in late spring (*Crotalus enyo*: Goldberg and Beaman, 2003; *Crotalus horridus*: Gibbons, 1972; Keenlyne, 1978; *Crotalus molossus*: Goldberg, 1999; *C. oreganus*: Diller and Wallace, 1984). Although ovulation can occur as early as mid-May in *C. lutosus* (e.g. one female collected in mid-May had oviductal eggs), females typically do not ovulate before early summer, as concluded by Cobb (1994). Consequently, despite the early onset of vitellogenesis, *C. lutosus* ovulates relatively late.

In many ectotherms including reptiles, the physiological onset of vitellogenesis (e.g. hormone production) is largely controlled by environmental conditions, such as food availability (Ballinger, 1977; French et al., 2007), temperature and/or photoperiod (Marion, 1970; Pancharatna and Patil, 1997; Hilder and Pankhurst, 2003; Yoneda and Wright, 2005). Female *C. lutosus* significantly reduces feeding during follicular development and pregnancy (Glaudás, unpublished data), suggesting that this species mainly rely on stored body fat to fuel reproduction (i.e., capital breeder; Jönsson, 1997; Bonnet et al., 1998). In a capital breeder, food intake should affect intervals between reproductive events rather than the length of the vitellogenic cycle, because the resources allocated to reproduction have supposedly already been collected when a female

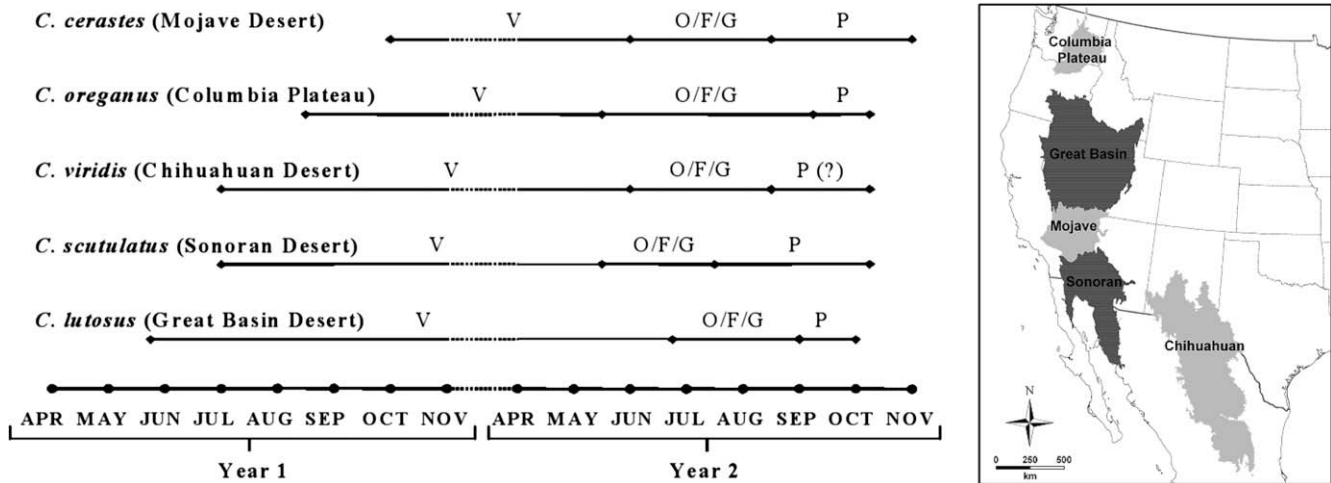


Fig. 7. Schematics of the female reproductive cycles of *Crotalus lutosus* and other rattlesnake species (*C. cerastes*, *C. oreganus*, *C. scutulatus*, *C. viridis*) from the Columbia Plateau and the three warm deserts of North America. V refers to secondary vitellogenesis. O/F/G refers to ovulation, fertilization, and gestation. P refers to parturition. Timing of reproductive events represents data from this study, (Aldridge (1979); *C. viridis*), (Diller and Wallace (1984); *C. oreganus*), (Goldberg (2004); *C. cerastes*), (Goldberg and Rosen (2000); *C. scutulatus*), and Klauber (1972). The physiographic regions depicted on the map are from Omernik (1987).

decides to reproduce. For this reason, the length of the active season – largely a function of environmental temperatures in ectotherms – likely causes these interspecific differences in timing of reproductive events among the rattlesnake species. Consistent with this idea, *C. cerastes*, *C. oreganus*, *C. scutulatus*, and *C. viridis* exhibit shorter vitellogenic cycles and longer active season (from 6 to 9 months; Diller and Wallace, 1984; Secor and Nagy, 1994; Cardwell, 2008; Painter, Personal communication) compared to *C. lutosus* (4–5 months; Fautin, 1946; Diller and Wallace, 1996; Jenkins, 2007; Hamilton, Personal observation).

Our hypothesis assumes that genetic differences for the rate of vitellogenesis are minor among *Crotalus* species exhibiting the lengthened vitellogenic cycle (i.e., the vast majority of rattlesnake species). This idea is seemingly supported by our comparative figure (Fig. 7). That is, *C. lutosus*, a snake occurring at high altitudes and latitudes, possesses a longer vitellogenic cycles compared to rattlesnakes from the warmer regions of North America. Further, because of the presumably high costs associated with reproduction in most female viperid snakes (e.g. increased metabolic rate: Beaupré and Duvall, 1998; locomotive impairment: Kissner et al., 1997; seasonal anorexia: Madsen and Shine, 1993; Lourdais et al., 2002), one would expect natural selection to have decreased genetic variation for rate of vitellogenesis. Consequently, we believe that our study demonstrates that the climatic conditions of a cold desert significantly constrain and lengthen the reproductive cycle of female rattlesnakes. This idea is supported by the fact that – unlike many other rattlesnakes from the warmer regions – parturition seems to be restricted to ca. a month at the end of the active season in *C. lutosus* (late August to early October; Wright and Wright, 1957; Klauber, 1972; Diller and Wallace, 1996), but also in populations of *C. oreganus* inhabiting the high latitudes (but comparatively low altitudes) of the Columbia Plateau (Diller and Wallace, 1984; Fig. 7).

4.2. Male reproductive cycle

The seasonal cycle of spermatogenesis in *C. lutosus* is essentially the same described for all other North American crotaline snakes. Males had regressed testes in late April–May only, and testes were in recrudescence throughout the year except during the summer. We found spermiogenic males from June to September, which is consistent with the summer/fall pattern of sperm formation in the

genus *Crotalus*. The vas deferentia of males contained sperm in all months of the year examined. The dense amounts of sperm in spring could indicate that mating occurs during this period. Nevertheless, reports of mating in the wild are only in July and August (Wright and Wright, 1957; Jenkins, Personal communication). Further, our analysis of the sexual segment of the kidney (SSK) showed enlarged tubules in summer. This result supports the idea that *C. lutosus* mates only in summer – at least in the central part of its range (i.e., where the specimens we used for histological analysis came from) – because SSK hypertrophy is associated with the mating period in almost all snakes studied to date (Bishop, 1959; Aldridge, 1993, 2002; Clesson et al., 2002). However, the timing of mating in rattlesnakes varies within and among species (Aldridge and Duvall, 2002) and is overall poorly known. Meticulous field observations are required to thoroughly characterize when mating occurs at the population and species level. A study examining seasonal variation in SSK size and its correlation with mating activity for all mating patterns known in rattlesnakes (i.e., spring only, summer only, spring and summer; Aldridge and Duvall, 2002) is also needed to assess whether SSK size is an absolute predictor of mating activity.

In summary, our study suggests that living in a cold desert can affect the timing of reproduction in a rattlesnake species. The short active season experienced by *C. lutosus* has implications for the timing of reproductive events of females, such as an early onset of follicular development, a late time of ovulation, and therefore a lengthened vitellogenic cycle, and possibly a restricted period for giving birth. Our findings are in agreement with other studies of ectotherms living at high altitudes/latitudes. That is, female reproductive cycle is typically lengthened in cooler climates, which is likely a consequence of the thermal dependency of reproductive processes (Cree and Guillette, 1995; Iburgüengoytia and Casalins, 2007). On the other hand, males seem relatively unaffected and their reproductive cycle conforms well to those described for other rattlesnake species.

4.3. Conservation implications

The prolonged reproductive cycle of females indicates that intervals between pregnancies are long, as demonstrated by a mark-recapture study (3–5 years; Jenkins, 2007). Decreased reproductive frequency is a key factor in explaining vulnerability to

extirpation (Meffe and Carroll, 1994). *C. lutosus* is still abundant across its range, likely because the Great Basin experiences low human population pressure. Yet this species hibernates communally and local extirpations have been associated with indiscriminate killing by humans at hibernacula (Hall, 1929; Parker and Brown, 1974). Consequently, preventing local extirpation of *C. lutosus* over the long term may require legal protection of snakes at communal hibernacula as a conservation measure, particularly around urban centers of the Great Basin.

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Appendix A. List of the museum specimens examined

BYU: 346, 584, 1306, 2759, 2841, 14 692, 17 971–17 973, 17 975, 17 976, 17 978, 17 981–17 989, 17 991, 17 993, 17 995, 17 996, 17 998–18 000, 18 002–18 005, 18 007–18 014, 22 220, 30 778, 30 781, 30 788, 30 789, 43 147, 46 663, 46 664, 46 666, 46 667, 46 856, 46 857.

CAS: 27 196, 30 921, 37 997, 38 439, 44 221, 47 751, 54 017, 55 226, 55 227, 55 233, 63 908, 63 909, 64 120–64 122, 64 195, 64 208, 64 210, 65 912, 85 699, 91 623, 91 624, 93 785, 93 787, 93 789–93 792, 98 551, 170 412, 170 415, 170 427, 170 429, 170 478, 170 479, 170 481, 170 513, 192 637, 192 647, 192 649, 195 041, 195 840, 201 282, 202 955, 202 964–202 967, 202 974, 227 957.

CAS-SU: 1662, 6542, 7234, 14 367, 15 119, 19 914, 19 915, 21 619–21 623, 21 625, 21 627, 21 628, 21 630–21 632, 21 634, 21 635, 21 638–21 642, 21 645, 21 646.

FMNH: 6961, 6962, 11 261, 18 422, 26 034, 28 591, 40 813.

LACM: 20148, 67 733, 105 200, 105 206–105 208, 120 976, 132 123, 134 050.

MBM: 1932, 1934, 1961, 7516.

MVZ: 1510, 1511, 11 363, 11 364, 11 367, 11 368, 11 376, 12 003, 12 005, 12 006, 12 179, 12 323, 12 755, 12 756, 13 099, 13 100, 14 302, 14 305, 14 307–14 309, 15 961, 15 962, 16 252, 16 253, 16 695, 16 696, 17 135, 18 227, 18 467, 18 468, 20 631, 24 658, 28 574, 31 859, 32 106, 39 176, 42 826, 44 686, 54 595, 57 607, 61 817, 65 568, 67 611, 78 073, 97 147, 180 284, 200 844, 228 733, 228 735–228 737, 235 919.

SDNHM: 1855, 4466, 4471, 4473, 4484, 5050, 5051, 8649, 8651, 17 138, 17 139, 23 790, 25 844, 27 993, 27 995, 29 100, 29 102, 29 104, 29 107, 29 108, 30 244, 31 761, 33 931, 33 938, 36 372–36 375, 36 627, 36 628, 36 630, 36 631, 36 637, 36 639–36 645, 36 647–36 654, 36 657, 38 375, 38 376, 39 041, 39 042, 39 064, 39 248, 39 253, 39 270, 39 272, 39 273, 38 283, 39 284, 42 162, 42 199, 42 200, 43 393, 43 730, 43 731, 44 332.

UMNH: 635, 680, 681, 909, 914, 942, 944, 2199–2201, 2203, 2204, 2206–2208, 2219, 2220, 2222, 2223, 2228, 2480, 2825, 3117, 3249, 19 602.

UNR: 441, 467, 496, 500, 501, 505, 870, 876, 877, 919–922, 948, 950, 987, 2024–2032, 2064, 2065, 2073, 2269, 2736, 3539, 4044, 4057, 5101, 6443, 7194, 7283.

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