Copeia, 2005(1), pp. 152–158

Reproductive Ecology of Western Diamond-Backed Rattlesnakes (*Crotalus atrox*) in the Sonoran Desert

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We studied the reproductive ecology of a population of Western Diamond-Backed Rattlesnakes (*Crotalus atrox*) in south-central Arizona for four active seasons using radiotelemetry and portable ultrasonography. Snakes mate in the spring and fall, and females undergo vitellogenesis exclusively in the spring, ovulate in the early summer, and give birth in the late summer. Although parturition occurs at the same time of year in all rattlesnake species studied, females of most species initiate vitellogenesis in the fall, and it is unusual for females to delay this process until the spring. No females gave birth more than once in this study, indicating that reproduction is less than annual. Litter sizes range from 2–7 neonates (mean = 4.5). The sex ratio of the neonates was approximately equal, but male neonates were longer in snout–vent length and heavier than female neonates. There was no significant relationship between maternal snout–vent length and clutch mass, number of neonates, mean neonate mass, or mean neonate snout–vent length. Maternal postparturient mass was positively correlated with mean neonate mass, but not the other variables.

A large proportion of research on snakes focuses on their reproductive biology (Seigel and Ford, 1987). However, as data accumulate on the natural history and reproductive biology of snake species, more questions are generated about geographic variation (Burghardt and Schwartz, 1999), temporal variation (Madsen and Shine, 2001), and the evolution of snake mating systems (Duvall et al., 1993; Aldridge and Duvall, 2002). It is clear that comprehensive knowledge of snake reproduction requires data from long-term studies of multiple populations and species.

The Western Diamond-Backed Rattlesnake (*Crotalus atrox*) is one of the most abundant and geographically widespread rattlesnakes in North America, ranging from western Arkansas to eastern California and central Mexico to northern Arizona, New Mexico, and Texas (Stebbins, 1985). Several studies have documented the reproductive biology of female *C. atrox* in the eastern part of its range (Tinkle, 1962; Fitch and Pisani, 1993) and in Arizona (Rosen and Goldberg, 2002). These studies were conducted primarily on museum specimens or snakes killed at rattlesnake roundups, which provide valuable single-point anatomical data. However, multiyear studies on individual populations are important because they allow examination of patterns of reproduction over time (Parker and Plummer, 1987), yielding more complete data on frequency of reproduction, reproductive output, and population structure.

We studied the reproductive ecology of a population of *C. atrox* in the Arizona Upland region of the Sonoran Desert for four active seasons. Using a combination of radiotelemetry and mark-recapture approaches, we collected data on the reproductive phenology and output of individual snakes.

MATERIALS AND METHODS

Study site.—The study site (N32°36′ W111°08′) is an approximately 1.5 × 1.0 km area of Arizona Upland Sonoran Desert (elevation 800–900 m) located 33 km north-northeast of Tucson, Arizona. The habitat consists of rocky volcanic buttes and sandy plains with intermittent washes.

Field monitoring.—We marked all *C. atrox* encountered at the study site for identification with intramuscularly injected passive integrative transponder (PIT) tags (AVID, Norco, California) and a unique three-color code of acrylic paint injected into the three most-proximal segments of the rattle. At the initial capture, we weighed snakes (± 5 g) with a 1000 g Pesola scale and measured their snout–vent lengths (SVL, ± 0.5 cm) with a cloth measuring tape.

We monitored a total of 32 female snakes with radiotelemetry (SI-2T 11–13-g radiotransmitters, Holohil, Carp, Ontario, Canada). Because of snake death and premature radiotransmitter failure, not all snakes were monitored for the entire four-year study period. Of the 32 snakes, 21 were monitored for at least one year and, therefore, were included in the analyses. The mean time the snakes were monitored was

27.5 consecutive months (range = 12–43). Eight snakes were monitored between 12 and 23 months, seven between 24 and 35 months, and six between 36 and 40 months. During the active season (mid-March to mid-November), we located each snake 1–5 times per week. During the overwintering period (mid-November to mid-March), we checked them 1–2 times per month.

Reproductive state of females was assessed using a combination of abdominal palpation and portable ultrasonography (Concept/MCV, Dynamic Imaging, Livingston, Scotland). By initially combining both palpation and ultrasonography, we concluded that palpation reliably revealed reproductive activity (either vitellogenesis or pregnancy) but did not effectively distinguish among the various reproductive states. Therefore, we used frequent palpation throughout the year to distinguish reproductive activity of any kind and periodic ultrasonography to verify palpation findings and to ascertain the timing of the various stages of reproduction. We determined the reproductive stages of females based on the following ultrasonic image descriptors (Fig. 1). Nonreproductive snakes had either no detectable follicles or small, previtellogenic (< 6 mm and nonechogenic) follicles. Vitellogenic snakes had enlarged, yolked follicles (> 10 mm and echogenic) clustered and overlapping with each other in a restricted area at midbody. Ultrasonograms of gravid snakes varied depending on date, from large, elongated, echogenic yolk masses arranged linearly throughout the caudal third of the snake, to germinal discs visible as echolucent areas within the larger echogenic yolk masses, to visible fetuses. As pregnancy progressed, fetus size enlarged, and yolk was depleted. The loss of nearly all yolk was used to indicate a periparturient state.

To collect reproductive output data, periparturient snakes were captured and brought into the laboratory one to several weeks prior to parturition. We collected a total of 18 gravid females during the study (eight of these were radiotelemetered, and 10 were encountered randomly in the field). Within two days after parturition, we weighed (± 0.01 g, using an Acculab digital scale), measured (± 0.1 mm, using a foam padded squeeze box, Quinn and Jones, 1974), and determined the sex of offspring by examining tail length and by everting hemipenes in males. Snakes were released at the sites of capture along with their neonates one week after parturition.

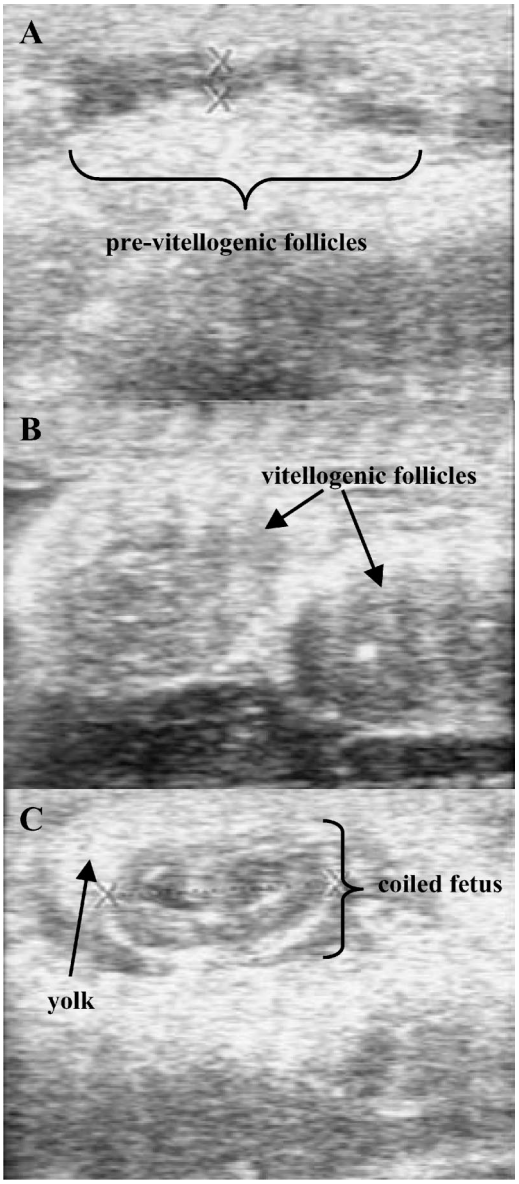

Fig. 1. Ultrasonograms of female *Crotalus atrox* at different points in the reproductive cycle, showing (A) nonvitellogenic follicles; (B) vitellogenic follicles; and (C) a fetus and yolk. In (A) and (C), the distance between the two X marks is the diameter of a single follicle or fetus.

Calculations and data analysis.—Data from the 18 captive-born litters were used to calculate clutch mass, litter size, mean neonate SVL, and mean neonate mass (Table 1). Because four females produced undeveloped ova along with neonates, we calculated two values each for clutch mass and clutch size: Total clutch mass and size reflect both neonates and undeveloped ova,

TABLE 1. MEAN VALUES (± 1 SD) OF REPRODUCTIVE MEASUREMENTS FOR *Crotalus atrox* ($N = 18$ LITTERS).

Characteristic	Definition	Value
Total clutch mass	Mass (g) of all neonates and undeveloped ova	88.5 ± 24.0
Live clutch mass	Mass (g) of all neonates	86.6 ± 25.7
Maternal postparturient mass	Mass (g) of females within two days following reproduction	271.3 ± 64.6
Relative clutch mass	Total clutch mass divided by maternal postparturient mass	0.33 ± 0.13
Total litter size	Number of neonates and undeveloped ova	4.72 ± 1.56
Live litter size	Number of neonates	4.50 ± 1.58
Mean neonate SVL	Grand mean of mean neonate SVL (cm) in each litter	28.6 ± 1.5
Mean neonate mass	Grand mean of mean neonate mass (g) in each litter	20.00 ± 3.6

whereas live clutch mass and size assess fully formed neonates only. We also calculated the relative clutch mass as the total clutch mass divided by the postparturient mass of the female. We used linear regression analysis to determine whether maternal SVL affected total clutch mass, live clutch mass, total litter size, live litter size, mean neonate SVL, and mean neonate mass. We performed similar regressions with postparturient mass as the factor to determine whether maternal mass affected litter characteristics.

We compared the SVL of male and female neonates with ANCOVA (with family as the covariate). We compared mass in the same way. We did not determine the sex of neonates from the three litters in 2001; thus, the analyses comparing male and female neonates use data on the 15 litters from 2000, 2002, and 2003. We analyzed the sex ratio of neonate snakes with Chi-square goodness-of-fit tests to determine whether the ratio was different from 1:1. All tests were performed using SAS (vers. 8.2) or Systat (vers. 10.0), and alpha was 0.05 for all analyses.

RESULTS

Timing of reproductive events.—We observed snakes consorting, courting and mating in the spring (March through April) and late-summer/fall (August through October, see Appendix 1). We define consortship as a male and a female within 1 m of one another. Annual and seasonal differences in the frequency of these observations may result from differences in sampling effort, number of snakes with radios, and/or climatic factors such as rainfall. For example, no consortships or copulations were observed in spring 2002, but we had few snakes to observe at this time because a large number of radiotransmitters had failed in fall 2001. The outcomes of the 12 observed copulations ($N = 10$ females) were as follows: three snakes were lost before the following summer, two females became gravid in the following summer, and five females did not become gravid the following summer. Thus, copulation does not necessarily imply that females will become gravid. Two females copulated with two different males in September 2002; copulations were three and four days apart.

In 2001, ultrasonography of 14 adult females on 14 April revealed six females with no detectable follicles and eight females with small, nonvitellogenic follicles 2–5 mm in diameter. Ultrasonography on 17 May 2001 revealed 12 females with no detectable follicles, two females with small, nonvitellogenic follicles, and two females with large (35 and 37 mm diameter), vitellogenic follicles. One of the females with large, vitellogenic follicles on 17 May had only 5 mm nonvitellogenic follicles in April, whereas the other vitellogenic female did not undergo an ultrasonic exam because she was added to the study after the 14 April date. A third ultrasonographic examination conducted on 5 and 9 July 2001 revealed no significant reproductive activity in 13 females and pregnancy in the two females that had large, vitellogenic follicles in May. In 2002 and 2003, because palpation reliably detected vitellogenesis, we mostly limited ultrasonography to midsummer to best estimate parturition date. Regardless, overall ultrasonographic results of females who gave birth in the following summer consistently demonstrated no detectable or very small (< 6 mm), nonvitellogenic follicles in the fall (September and October, $N = 3$ females) and early spring (March and early April, $N = 3$). The first visible evidence of vitellogenesis appeared in the latter

half of April (echogenic follicles > 10 mm, $N = 6$), and greatly enlarged, yolked follicles did not appear until May ($N = 6$). Females became gravid in June ($N = 7$), and in July fetuses were visible and yolk steadily became depleted ($N = 15$). In August ($N = 18$), fetal heartbeats were often visible, and very little yolk was present, which indicated imminent parturition. All females that initiated vitellogenesis in late April ($N = 6$) proceeded to produce clutches. Parturition in a given year predominantly occurred over a short period (three weeks) in August (Appendix 1). Females in this study never reproduced more than once, indicating that reproduction is less than annual. Only a subset of radiotelemetered females reproduced in a given year: 2000 (five of 10), 2001 (two of 17), 2002 (none of 14), 2003 (two of 11).

Litter characteristics.—A total of 81 neonates were born in 18 litters (Table 1). The mean litter size was 4.5 (range = 2–7 neonates). Mean neonate mass was 20.0 g, and mean neonate SVL was 28.6 cm. Among the 61 neonates for which we have sex data, the sex ratio was 33:28 males:females and was not significantly different from a 1:1 sex ratio ($\chi^2 = 0.4$, $P > 0.4$). There was a significant effect of family on neonate SVL and mass (SVL: $F = 13.60$, df = 14, $P < 0.0001$; mass: $F = 34.69$, df = 14, $P < 0.0001$), and male neonates were significantly longer (male mean = 28.97 cm; female mean = 28.38 cm; $F = 3.91$, $P = 0.05$) and heavier (male mean = 18.89 g; female mean = 18.73 g; $F = 10.02$, $P = 0.003$) than female neonates. Moreover, the ANOVA model only detected a significant sex difference in mass when family was used as a covariate. Otherwise, the sex difference in mass was masked by the large variability among families.

Females had a high relative clutch mass (mean = 0.34, range = 0.13–0.61). Maternal SVL was not correlated with total clutch mass ($R^2 = 0.004$; $P = 0.81$), live clutch mass ($R^2 = 0.004$; $P = 0.80$), total litter size ($R^2 = < 0.001$; $P = 0.96$), live litter size ($R^2 = < 0.001$; $P = 0.96$), mean neonate SVL ($R^2 = 0.006$; $P = 0.76$), or mean neonate mass ($R^2 = 0.04$; $P = 0.41$). Similarly, maternal postparturient mass was not related to the total clutch mass ($R^2 = 0.08$; $P = 0.27$), live clutch mass ($R^2 = 0.07$; $P = 0.29$), total litter size ($R^2 = 0.08$; $P = 0.26$), live litter size ($R^2 = 0.11$; $P = 0.19$), or mean neonate SVL ($R^2 = 0.012$; $P = 0.66$). However, maternal postparturient mass was significantly related to mean neonate mass ($R^2 = 0.23$; $P = 0.05$).

Discussion

In this study, we characterize the reproductive ecology of an Arizona Upland Sonoran Desert population of *C. atrox*. We found snakes copulating during the spring and late-summer/fall. This observation agrees with other reports on *C. atrox* as well as several other species of North American pitvipers (reviewed in Aldridge and Duvall, 2002; see also Rosen and Goldberg, 2002). Females that mate in the fall store sperm over the winter (Schuett, 1992), and fertilization occurs at ovulation the following spring or summer. *Crotalus atrox* likely stores sperm over the winter (Schuett, 1992) but may also breed again in the spring. This suggests that *C. atrox* litters have the potential for multiple paternity (Schuett and Gillingham, 1986).

Copulations were observed exclusively in the sandy plains. In contrast to many species of rattlesnakes (Landreth, 1973; Gregory, 1984), snakes in this population do not appear to den communally and do not mate at the entrances of overwintering sites. Instead, snakes overwinter solitarily and locate mates following egress from their overwintering sites in spring (March through April) and/or in the late-summer or fall (September). Geographic variation in occurrence of communal denning may relate to abiotic factors such as temperature and distribution of suitable overwintering sites (Gregory, 1984). However, other populations of *C. atrox* in Arizona Upland show communal denning (Repp, 1998), leaving the question of why some snakes den communally and others do not, a potentially interesting research topic.

In most species of North American pitvipers, the fall mating period coincides with the onset of vitellogenesis in females (reviewed in Aldridge and Duvall, 2002). In this system, females deposit yolk into their developing follicles during the fall, either continue to deposit yolk or remain quiescent during the winter, complete vitellogenesis in the spring, and ovulate in the early summer. *Crotalus atrox* have previously been reported to exhibit this reproductive pattern (Tinkle, 1962; Rosen and Goldberg, 2002). However, we found that female *C. atrox* in this population initiate vitellogenesis in the spring rather than in the prior fall. Snakes palpated and monitored by ultrasound showed no evidence of yolk deposition in follicles during the fall or at emergence in March; rather, they commenced vitellogenesis during the latter half of April. Reproductive female *C. atrox* in this population have been previously shown to have increased levels of estradiol, the key hormone responsible for stimulating vitellogenesis (Ho et

al., 1982), in April but not in the fall or in March (Taylor et al., 2004), supporting our ultrasonographic findings. Therefore, it appears that there is geographic variation in the seasonal timing of commencement of vitellogenesis in *C. atrox* but not in the timing of parturition. The fact that female *C. atrox* can complete vitellogenesis in a couple months as demonstrated by our population raises the question as to why many other populations of rattlesnakes commence the process much earlier.

Aldridge and Duvall (2002) present a model of the evolution of North American pitviper mating systems based on the assumption that ''estrus,'' or the mating period, occurs when females are vitellogenic and produce pheromones in skin secretions that make them attractive to males. However, most of the matings in this study occurred when snakes were not vitellogenic and estradiol levels were low (Taylor et al., 2004), calling the generality of this assumption into question. This suggests that factors responsible for attractivity (e.g., skin pheromones) and receptivity may not be regulated by estradiol. The cause of the variation in the timing and control of both mating behavior and vitellogenesis among populations of *C. atrox* is unknown, and compilation of environmental and physiological data from other populations is required to examine potential factors that affect this variation in this wide-ranging species.

Over the course of the four-year study, individual females never gave birth more than once. Rosen and Goldberg (2002) also reported that *C. atrox* shows less-than-annual reproduction, and, indeed, this trend is observed in nearly all other species of rattlesnakes (reviewed in Aldridge and Duvall, 2002). Because the female *C. atrox* at our study site can complete an entire reproductive event (i.e., vitellogenesis through parturition) in less than five months, annual reproduction could be feasible. In fact, certain populations of *C. atrox* may be capable of reproducing annually (Fitch and Pisani, 1993), and this capability may be facilitated by high resource availability. Our study occurred during a period of low rainfall (based on Tucson rainfall data from National Oceanic and Atmospheric Administration web site, http://www.noaa.gov), when food availability was likely low. This may account for the low frequency of reproduction we observed. Rattlesnakes are capital breeders, meaning that females will not reproduce until they have stored enough energy to fuel a costly reproductive bout (Bonnet et al., 1998). If food availability is high, then postreproductive snakes may attain sufficient energy reserves to fuel reproduction again the following year. Indeed, several species of rattlesnakes show increased reproductive output the year after a season of high prey abundance (Goldberg and Rosen, 2000; Diller and Wallace, 2002; Rosen and Goldberg, 2002). However, the relationship between food availability and reproduction in free-ranging snakes remains to be tested experimentally.

The mean litter size in this study was 4.5 neonates (range: 2–7), somewhat smaller than that reported by Rosen and Goldberg (2002) for *C. atrox* from various localities in Arizona (8.3 when calculated from enlarged follicles in museum specimens, and 5.6 when calculated from oviductal ova in museum specimens or live births). Estimates of litter size based on enlarged follicles may overestimate the realized litter size because some follicles may be reabsorbed rather than ovulated (Klauber, 1972). Rosen and Goldberg's (2002) estimate based on only oviductal ova and live young is similar to ours, and both are substantially smaller than estimates in other studies (reviewed in Rosen and Goldberg, 2002). The high litter sizes reported in these papers probably result from two main factors: overestimation of litter sizes by including enlarged follicles in estimates, and surveying *C. atrox* in the eastern parts of its range where snakes appear to have larger litter sizes than in Arizona (e.g., Tinkle, 1962).

Rosen and Goldberg (2002) found that larger female *C. atrox* had larger litter sizes when samples based on enlarged follicles were included; there was no relationship when only snakes with embryos or live young were considered. Similarly, we found no relationship between maternal SVL and litter size or other characteristics comprising fecundity, including clutch mass, mean neonate SVL, and mean neonate mass. It is possible that maternal mass may be correlated with reproductive output because mass incorporates the potentially important contribution of energy reserves. However, there was no effect of maternal postparturient mass on clutch mass, litter size, or mean neonate SVL, but females that were heavier following parturition had heavier neonates. Females that were heavier following reproduction may have had more energy at their disposal during vitellogenesis, allowing them to deposit more yolk in follicles and thereby produce heavier neonates, but this assertion is only speculative without prereproductive measurements.

By collecting gravid females and allowing them to give birth in the lab, we were able to examine the sex ratios and sizes of neonates immediately following parturition. The sex ratio of the 61 neonates in this study was roughly 1:1, similar to that of many snakes (Shine and Bull,

1977; Ashton and Patton, 2001). We found that male neonates were both larger and heavier than females, which conflicts with the conclusions from a study that took place approximately 160 km northwest of ours (Beaupre et al., 1998). However, in a previous study, we collected 32 neonates from a road 5 km from our study site (unpubl.) and found that neonates were not sexually dimorphic in SVL or mass. In the current study, we were able to account for familial variation, which allowed us to observe a sex difference in mass that would have been masked if family has not been included in the model.

In this study, we have provided data on the reproductive ecology of *C. atrox* in the Sonoran Desert that will contribute to the growing body of knowledge on the mating systems and environment-organism interactions in North American pitvipers (Duvall et al., 1993; Aldridge and Duvall, 2002). We have shown that the reproductive ecology of *C. atrox* is similar to that reported for the species in other parts of its range, as well as other species of rattlesnakes. However, the data in this paper are novel in several respects. First, we show that *C. atrox* females at our study site, unlike most other rattlesnakes including certain populations of *C. atrox*, do not begin vitellogenesis until spring yet give birth at the same time as other populations. Second, we show *C. atrox* neonates show slight but significant sexual size dimorphism, a result that contradicts other studies on *C. atrox* (e.g., Beaupre et al., 1998; unpubl.). These results demonstrate that life-history traits of a given species cannot be inferred from studies on one population alone, or from a single year, because considerable geographic and temporal variation can occur. This variation offers the opportunity to examine how genetic and environmental factors affect phenotypes.

Acknowledgments

Numerous people helped collect snakes in the field, including X. Bonnet, T. Brennan, M. Feldner, S. Hussein, O. Lourdais, M. Malawy, J. Miller, and J. Slone. We particularly thank M. Feldner and M. Malawy for help with fieldwork. This manuscript benefited from the input of members of the DeNardo laboratory. This work was funded by an Arizona State University Faculty Grant-in-Aid Award (to DFD) and a National Science Foundation Graduate Research Fellowship (to ENT). All animal use was approved by the Arizona State University Institutional Animal Care and Use Committee (protocol 01–617R). Snakes were collected under Arizona Game and Fish Commission scientific collection permits SP907288, SP606726, SP683705, and SP739250 (to ENT) and SP909328, SP607365, SP683420, and SP739769 (to DFD).

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APPENDIX 1.

DATES OF OBSERVED CONSORTSHIPS, COPULATIONS, AND PARTURITIONS OF *Crotalus atrox* IN THE STUDY POPULATION

Consortship: 2001; April (2,14), August (27), September (15), October (5,13,16). 2002; August (28), September (1,3,10,13,14,17,18,21), October (1,8). 2003; March (15,22), April (6,9), September (7,20,24,28), October (4).

Copulation: 2001; April (2), September (11). 2002; September (10,13,14,17). 2003; March (29), September (19,24), October (4).

Parturition: 2000; July (28), August (6,7,8,12,19). 2001; August (18,21). 2002; September (2). 2003; August (13,17,24,28).