

Fifteen Consecutive Years of Successful Reproduction in a Captive Female Sidewinder (*Crotalus cerastes*)

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Life history (LH) theory postulates that natural selection exerts its influence on the life cycle of organisms, predominantly growth, reproduction, and survivorship. Accordingly, life histories influence and provide linkages between the phenotype (behavior and morphology) and genotype. Specific LH traits include measurement of juvenile development (e.g., size), age at sexual maturity, age of first reproduction, number and size of offspring per litter, level of parental investment (vitellogenesis, egg attendance, post-birth care), age of reproductive senescence, and lifespan (Lack 1954; Williams 1966; Stearns 1992; Roff 1992, 2002; Scharf et al. 2015). Not only do these LH traits have genetic-epigenetic components (Martinez et al. 2015), but they are also strongly influenced and constrained by the environment (abiotic and biotic components), which includes climate, prey and water availability, shelter, and predator abundance (Stearns 1992; Roff 1992, 2002). Environmental effects can be more pronounced in ectothermic vertebrates such as reptiles, and they are not

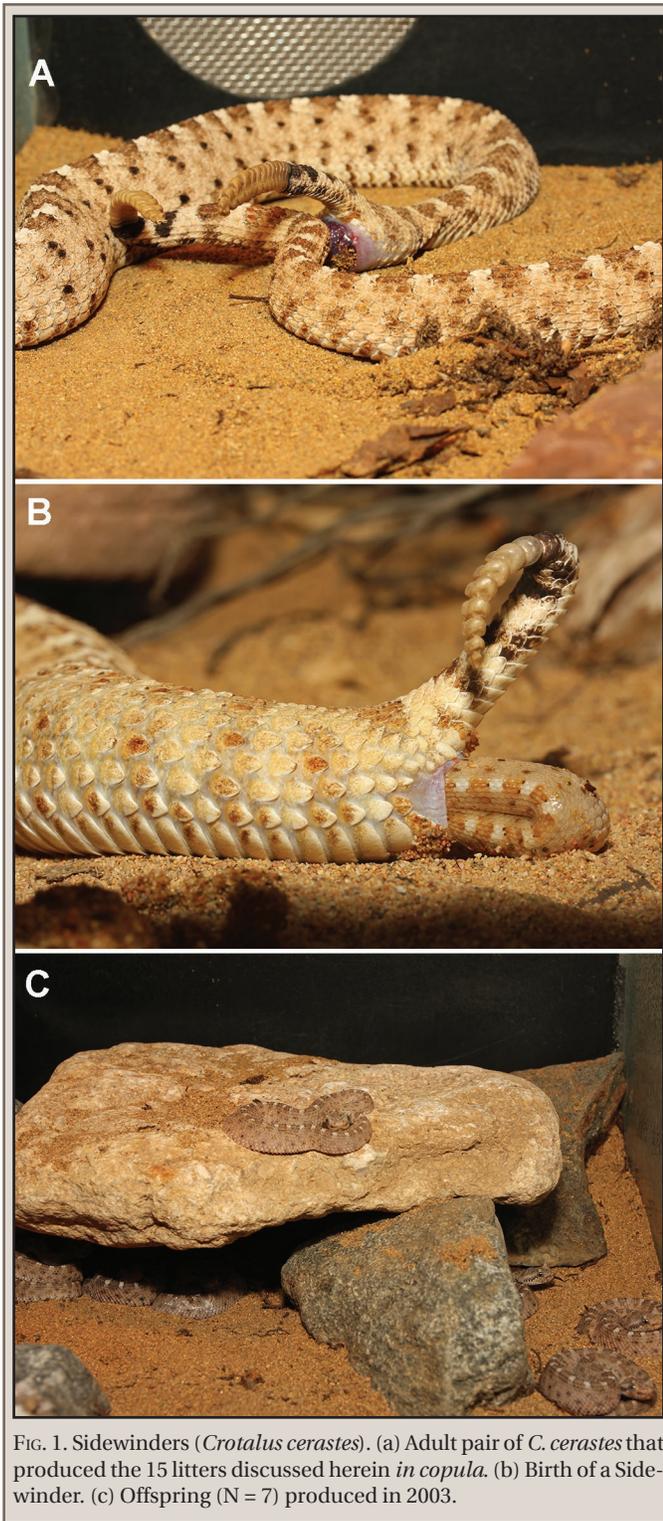


FIG. 1. Sidewinders (*Crotalus cerastes*). (a) Adult pair of *C. cerastes* that produced the 15 litters discussed herein *in copula*. (b) Birth of a Sidewinder. (c) Offspring (N = 7) produced in 2003.

necessarily predictable; hence, stochasticity plays a role in life history evolution (Dunham et al. 1988).

Here, we describe unusual reproductive competence of a pair of captive Sidewinders (*Crotalus cerastes*), which provides important information on the reproductive potential of this species when certain environmental constraints (e.g., low prey availability, excessively high temperatures, drought) often present in their natural setting (Sonoran Desert) are eliminated.

TABLE 1. Reproductive history of the present female Sidewinder (*Crotalus cerastes*). UO = undeveloped ovum (yolk plug). SB = stillborn. Total: 111 healthy young, 12 deformed or stillborn young, and 8 UO.

Copulation	Birth	Litter
08-29-00	07-09-01	8 normal; 1 UO
10-11-01	—	—
03-02-02	08-10-02	6 normal; 0 UO
09-22-02	—	—
02-05-03	07-01-03	7 normal; 0 UO
09-28-03	—	—
—	07-27-04	11 normal; 0 UO
09-25-04	—	—
03-02-05	07-31-05	10 normal; 1 UO
09-26-05	—	—
04-11-06	08-19-06	10 normal; 0 UO
10-24-06	—	—
—	08-08-07	4 normal; 6 SB
—	—	—
—	07-28-08	8 normal; 1SB
09-05-08	—	—
—	08-01-09	10 normal; 1 SB
09-24-09	—	—
02-26-10	07-21-10	7 normal; 0 UO
09-21-10	—	—
07-25-11	—	5 normal; 4 SB; 1 UO
09-20-11	—	—
—	07-21-12	5 normal; 2 UO
09-14-12	—	—
—	07-29-13	9 normal; 0 UO
—	08-28-14	6 normal; 3 UO
02-21-15	09-28-15	5 normal; 0 UO

SUBJECTS AND HUSBANDRY

Subjects.—A young adult pair (both estimated to be about three years old based on complete rattles; see Reiserer 2001, *in press*) of *C. cerastes* was road-collected in the evening by two of us (GWS, MH) on Sun Valley Parkway (Maricopa Co., Arizona, USA), approximately 10 km W of Phoenix, in early August 1999. The snakes were transported to Sweden for captive studies.

Captive housing.—The cage used to house the adult snakes was 80 cm wide, 50 cm deep, and 26 cm high. A 40-W incandescent bulb was used to create a hotspot (35–38°C) at one end of the enclosure. The hotspot was close to refugia (“hiding sites”) created by a rock pile. The opposite end of the cage was cooler (daytime temperature: 25–27°C) and followed the temperature in the room. The cage was well ventilated. Substrate was natural sand and small rocks. The pair were housed together year-round.

Neonates and juveniles were housed in separate cages (16 cm wide, 20 cm deep, and 10 cm high) and substrate was sand and small rocks; however, moistened sphagnum was introduced to assist newborns with their first shed. All of the juveniles were housed separately owing to problems associated with cannibalism.

Feeding schedule.—Food was exclusively domestic mice of varying sizes (newborn to adult). The feeding schedule was moderate to avoid obesity. Specifically, during summer months,

the adult pair was offered sub-adult mice once every four weeks, and during spring and fall every second week. About every second or third feeding, a small quantity of a commercially available calcium and vitamin D₃ powder (Namiba CalViRep® D3⁺) was sprinkled lightly on the mice. Newborns and juveniles were fed more frequently (weekly) based on defecation rates.

Water.—All of the captive Sidewinders were housed without providing water in water bowls. Rather, water was sprayed on the walls of the cages and the snakes themselves when they were visible. This was done once every two weeks during summer and once a week during spring. During late summer and fall, water was sprayed once a week and every time a storm passed. Surprisingly, sprayed water was largely ignored by the snakes; the exception was during summers when the female was pregnant.

Recreating winter: hibernation.—The adult pair was cooled every year to simulate “hibernation” (Murphy and Collins 1980; Warwick et al. 1995). The entire room where the snakes were held was cooled and thus the snakes remained in their cages throughout the hibernation. By the end of October or beginning of November, food was offered one last time before getting them prepared for winter. Initially, the artificial lighting in the cage provided heat (25–27°C) during daylight hours, but temperatures at night dropped to ambient conditions in the room (12–15°C). In early December, the artificial light was no longer used, and temperatures ranged from 12–15°C on a 24-h basis. By the end of January, the temperature cycle was gradually returned to spring conditions, and in mid-March the offering of food was resumed. By the end of March, hotspots (35–38°C) and normal feeding cycles were resumed.

Reproduction.—Courtship, mating, and the production of litters by the present adult pair were documented annually (2000–2015). Reproductive events are summarized in Table 1.

DISCUSSION

Here, we provide unequivocal evidence that Sidewinders in captivity are not only capable of longevity that exceeds estimates for wild snakes (Reiserer 2001), but show no sign of reproductive incompetence or senescence (Bonnet 2011). Furthermore, although *C. cerastes* can exceed 20 years of age under captive conditions (G. Schuett, pers. observ.), none of the best of our knowledge have demonstrated extreme reproductive competence as we describe in this paper. Accordingly, our observation is undoubtedly a record for reproduction in *C. cerastes* and perhaps for other rattlesnake species (D. DeNardo and W. Booth, pers. comm.).

In female snakes, commonly studied life history traits concern the frequency of reproduction and fecundity (Seigel and Ford 1987, 1992, 2001; Shine 1989; 2003; Reiserer 2001; Schuett et al. 2011, 2013a, b; Ford and Seigel 2015). Early attempts to lay the foundations of reproductive frequency of wild female snakes were based primarily on mark-recapture methods and analysis of museum specimens (e.g., Rahn 1942; Blem 1982; Aldridge 1979; Seigel and Ford 1987; Goldberg 2004; Taylor and Booth, *in press*). These and other authors have postulated that reproductive cycles are annual, biennial, triennial, or even longer, and are either obligate or facultative (Schuett et al. 2011, 2013a, b). Of particular interest is the high representation of non-reproductive vs. reproductive individuals in museum collections (Reiserer 2001). Female rattlesnakes tend to reduce their activity when reproductive, especially after ovulation (Reiserer 2001; but see Schuett et al. 2011, 2013a, b); thus, the most prevalent

collection method, namely road-hunting, tends to over represent non-reproductive females in museum collections. Consequently, less-than-annual reproductive cycles have been reported for many species based on the frequencies of reproductive females found in preserved materials (Goldberg 2004; Taylor and Booth, *in press*).

According to Reiserer (2001), wild female *C. cerastes* from the Mojave Desert reproduce annually when energy acquisition permits, but they may have a reproductive cycle that is less-than-annual when energy procurements are inadequate. Furthermore, Reiserer (2001, p. 156) reported life table values, which indicate high mortality for females after they attain maturity. Accordingly, 52% of wild females do not survive beyond a single reproductive episode, suggestive of semelparity (reviewed by Bonnet 2011). Using museum-based female *C. cerastes*, Goldberg (2004) cautiously stated that reproductive frequency data he generated was indicative of a biennial cycle.

Long-term (> 10 yr) radio-telemetric studies of rattlesnakes (Schuett et al. 2011, 2013a, b), have begun to hint at the extent to which erratic mark-recapture and museum data have introduced some biases into our interpretation of female reproductive cycles (Reiserer 2001; Schuett et al. 2002). Based on a long-term (10 yr) radio-telemetric study in the Sonoran Desert of Arizona, Schuett et al. (2011, 2013a, b) demonstrated that the Western Diamond-backed Rattlesnake (*C. atrox*) is capable of annual reproduction (e.g., three consecutive litters). Based on multiple lines of evidence, other viperids (pitvipers and vipers) reproduce on an energy dependent annual schedule (Taylor and Booth, *in press*).

In the wild, female Sidewinders are short-lived and sometimes skip reproductive opportunities (Reiserer 2001). In nature, stochastic energy availability and environmental hazards truncate natural lifespan, but in our captive *C. cerastes* these factors were essentially eliminated. Energy itself appears to be a necessary, but not sufficient proximate determinant of longevity and reproductive frequency in wild *C. cerastes*. Longevity records for reptiles and other vertebrates in captivity are reported in a variety of journals and records (Bowler 1977; Jones 1979; Sherman and Jarvis 2002), but information on reproductive extremes, such as frequency of reproduction, are less common. Our observations on extreme reproduction and longevity in a rattlesnake are unusual and important.

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