Environmentally cued parturition in a desert rattlesnake, *Crotalus atrox*

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Received 5 April 2013; revised 8 July 2013; accepted for publication 9 July 2013

Embryonic development in animals is dynamically regulated by physiological, behavioural, and environmental factors (temperature, precipitation, humidity), which in turn influence the timing of birth or hatching. In the present study, we provide evidence that parturition in a large-bodied North American pitviper, the western diamond-backed rattlesnake (*Crotalus atrox*), is environmentally cued. Specifically, we tested the hypothesis of births coinciding with rainfall events during the second-half of the monsoon season (late July to mid September) using randomization modelling. Twenty-one adult females surgically implanted with radio-transmitters were tracked for extended periods from 2001–2010. From 2003 to 2007, the 21 females gave birth to 38 litters, generating sufficient data to test our hypothesis. In all years, births were restricted to a 4-week period from 5 August to 7 September, which spanned between 6 and 19 days (mean ± SD, 15 ± 5.2 days). Most births (92.1%) occurred in August. Births were significantly associated with rainfall events in 2007, although births in 2003 and 2005 occurred closer to rain events than randomly generated births for respective years. However, when birth events across all 5 years were pooled, the model indicated a significance difference in mean rain-days versus random rain-days. Hence, births occurred more closely to rain events than random days. Other variables associated with monsoon events (increases in cloud cover and humidity; changes in barometric pressure) were not measured but constitute potential cues. The present research is the first long-term, individual-based radio-telemetric study of a snake species to investigate environmental cues related to parturition using procedures of randomization modelling. © 2013 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2013, 110, 866–877.


INTRODUCTION

Gestation and the timing of birth in vertebrates are life-history events controlled and modulated by the physiology (e.g. endocrine system) and behaviour of the mother (Stearns, 1992; Roff, 2002; Adkins-Regan, 2005; Norris, 2006). Furthermore, a wide variety of environmental cues, such as photoperiod, temperature, rainfall, and even predation, have important integrative roles (Lourdais et al., 2002). Consequently, births (or hatching) presumably occur when it is optimal both for neonates and their mothers (Olsson & Shine, 1998; Shine & Olsson 2003; Warkentin & Caldwell, 2009; Wapstra et al., 2010; Doody, 2011; DeNardo, Lourdais & Stahlsmich, 2012). Pregnancy and the timing of birth can thus exhibit varying levels of phenotypic plasticity (West-Eberhard, 2003; Doody, 2011).

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There are numerous individual-based studies on gestation length and birth dates in mammals, primarily those that are large, relatively easy to observe, and/or aggregate predictably (Clutton-Brock & Sheldon, 2011). Primarily researched species include great apes (Goodall, 1968), herding ungulates (Clutton-Brock, 1982; Ogutu et al., 2011), elephant seals (Le Boeuf & Reiter, 1988), lions (Schaller, 1972; Packer et al., 1988), and bats (Bumrungsri, Bumrungsri & Racey, 2007). Studies on ungulates and bats, in particular, show that rainfall cues are strongly associated with parturition dates (Cumming & Bernard, 1997; Porter & Wilkinson, 2001; Bumrungsri et al., 2007; Ryan, Knechtel & Getz, 2007; Ogutu et al., 2011; Pfard et al., 2013). In these cases, the causal connection of rainfall to the timing of birth is resource-based (e.g. vegetation and insect abundance) to assure adequate nutrients for lactating mothers.

In other live-bearing vertebrates, such as squamate reptiles (lizards, snakes, and amphisbaenians), small body size, and cryptic lifestyles pose serious challenges to studies of pregnancy and birth in nature (Morafka, Spangenb and Lance, 2000). However, the relatively recent use of surgically implantable radio-transmitters has had pronounced impacts in advancing our knowledge of squamates (Reinert, 1992; Dorcas & Willson, 2009). In oviparous reptiles, there is a growing body of evidence that hatching is environmentally cued and can be early or delayed (Doody, 2011).

In the present study, we investigated whether the timing of parturition in a desert-inhabiting pitviper (Serpentes: Viperidae) is cued via environmental variables. Specifically, we tested the hypothesis that rainfall events during the second-half of the monsoon season are cues for the timing of birth in a population of western diamond-backed rattlesnakes (*Crotalus atrox*) from the Sonoran Desert of southern Arizona.

**MATERIAL AND METHODS**

**STUDY SPECIES**

The western diamond-backed rattlesnake (*C. atrox*) is a large-bodied, viviparous (live-bearing) venomous pitviper (Serpentes: Viperidae). In Arizona, *C. atrox* occupies the southern half of the state and inhabits most of the biotic regions found there (Campbell & Lamar, 2004; Amarello et al., 2010). In some regions *C. atrox* is extremely abundant, often the dominant snake species, and sometimes the dominant vertebrate predator (Nowak, Theimer & Schuett 2008).

**STUDY SITE**

The research site, located in Pinal County, Arizona, is 40 km south-south-east of the city of Florence, 8 km west of State Route 79. The focal area encompasses approximately 3 km² at the western edge of the Suizo Mountains (32°40′08″N, 111°07′22″W, Conus 27), a summit that has an elevation of 947 m. The region is designated as Sonoran Desert, Arizona Upland Desertscrub subdivision (Brown, 1994; Phillips & Comus, 2000). In addition to mountainous terrain, the general topography of the Suizo Mountains (SMs) is bajada and desert flats, intersected by dry washes of varying sizes. Annual rain patterns of the Sonoran Desert are bimodal (Mock, 1996; Phillips & Comus, 2000). Gentle to moderate broad frontal storms occur from late fall to early spring (November through March), and strong to violent, often localized, convective storms occur from mid- to late summer (early July to mid-September), the period of the North American monsoon. At our site, the availability of free water is highly unpredictable.

**RESEARCH SUBJECTS**

**Capture and immediate processing**

Twenty-one adult female *C. atrox* were captured from March 2001 through August 2007 (Schuett, Repp & Hoss, 2011). Snakes were captured using conventional snake hooks and plastic grabbers. The capture process involved grabbing a snake and placing it into a clear plastic tube (length 1 m; diameter varied in size). This was carried out gently and quickly (typically less than 1 min) to minimize handling stress (Schuett et al., 2004a). In many cases, adult subjects were located basking at or near the entrances of dens in spring (March to April).

Within 24 h of the initial capture, each subject was measured (snout–vent length, tail length, head dimensions to the nearest 1 mm; body mass to the nearest 1.0 g) and sex confirmed (via probing) under anesthesia (isoflurane). Global Positioning System (GPS) coordinates were collected as Universal Transverse Mercators (UTMs) (Kenward, 2000). Each subject had an appropriately sized (<5% of the total body mass) temperature-sensitive radio-transmitter (models SI-2T and AI-2T, 11–16 g; Holohil Inc.) surgically implanted within the coelom in accordance with the general procedures used for snakes (Reinert, 1992; Schuett et al., 2011). For both short- and long-term identification, each subject was photographed, implanted with a unique PIT-tag (AVID, Inc.), and their proximal rattle segments were coloured using Sharpie pens. After processing, all subjects were released at the exact site of capture.

**Radio-tracking and observations**

All 21 subjects implanted with radio-transmitters were tracked by foot minimally two to four times per month from 2003 to 2007. Tracking was increased...
from late July through mid September, which is the period of birthing. For each radio-tracked subject located, UTM coordinates were recorded using a hand-held GPS unit. These data were useful in re-locating previously used sites and birth locations. Some of these spatial data have been reported elsewhere (Schuett et al., 2013).

Determining reproductive status
The reproductive status of female C. atrox was determined using methods described previously (Schuett et al., 2011, 2013). Briefly, in each year that they were radio-tracked, subjects were assigned a reproductive status of either pregnant (when they produced a litter) or nonpregnant. After parturition, the reproductive status of a female changed to post-partum through the end of that year and, in the subsequent year, was re-assigned as either pregnant or nonpregnant. Similar to their viper relatives, female C. atrox are noticeably robust when pregnant (Rosen & Goldberg, 2002; Taylor & DeNardo, 2005; Schuett et al., 2011, 2013). In the present study population of C. atrox, vitellogenesis and ovulation occur in late spring, and the duration of pregnancy spans from early June to mid-September (Taylor & DeNardo, 2005, 2011; Schuett et al., 2011, 2013). Thus, based on their increased mass, we were able to readily detect reproductive from nonreproductive females by mid- or late June. Births occur from early August to early September at sheltered sites (e.g. Neotoma middens, small mammal burrows or rock shelves) but not at or near winter refugia (Repp & Schuett, 2008; Schuett et al., 2011, 2013). Parturition was deemed imminent when female movements from these sites were greatly reduced or ceased; thus, radio-tracking episodes were often increased to one or two times per day to better pinpoint birth dates. The number of offspring (or their molts) observed determined litter size.

ASSessment of rainfall
To determine rainfall events and storm systems in the area of our study site, we referred to the Intellicast website (http://www.intellicast.com) on a daily basis. Furthermore, we checked those data against the weather reports at Tucson International Airport (TIA) via the National Oceanic and Atmospheric Administration website (http://www.wrh.noaa.gov/twc/). Importantly, during the birth season (early August through mid-September), we typically made daily visits to the SMs to assess rainfall events and births (Schuett et al., 2011). For the present study, we used our estimates of rainfall frequency and amount of precipitation (collection of rainfall on the ground and natural structures) at the SMs. Our estimates of precipitation are conservative. Also, we checked with nearby weather stations (e.g. Red Rock) for rainfall events and precipitation estimates. Annual and monsoon rainfall at SMs closely match the values reported by the TIA (Table 1).

RANDOMIZATION AND STATISTICAL ANALYSIS
We used randomization procedures (Manly, 1991) to assess whether births were significantly associated with discrete rainfall events during the second-half of the monsoon season (29 July to 14 September).

ASSIGNMENT OF RAIN DAYS AND BIRTHING DAYS
We first determined the dates of the earliest (5 August) and latest (7 September) recorded births across all 5 years (2003–2007) of the present study to
define a general birthing season for our population. To ensure we included rainfall events that might have influenced the earliest and latest births in any given year, we extended this range ±7 days (i.e. 29 July to 14 September). Rainfall events occurring within this range of dates were included in all single-year analyses, irrespective of the earliest and latest births recorded during that particular year.

For each date between 29 July and 14 September, we assigned the smaller of two absolute values representing the number of days before (negative value) and after (positive value) a rain event (termed ‘rain-day’). For example, rain on 10 August and 16 August, with no rain recorded between those two dates, yields both post- and pre-rain day values for the intervening rainless dates, 11–15 August. Specifically, 10 August and 16 August would be assigned the value 0 because it rained on those dates. Dates without rain would be assigned the absolute value representing the minimum number of days post- or pre-rain; for example, 14 August was 4 days post-rain (value = 4) and 2 days pre-rain (value = −2), and thus was assigned the value 2.

To preserve inter-year variation in rain patterns, we calculated rain-day values for each year, independently. Each birth date of the present study was given the corresponding rain-day value for that date.

**RANDOMIZATION PROCEDURES**

POPTOOLS, version 3.2.5 (Hood, 2011), and add-in for EXCEL (Microsoft Corp.), was used to generate 10 000 random birth dates, which could occur on any date between 29 July and 14 September, for each of the 38 observed births (2003–2007) used in our analysis. In total, this resulted in 380 000 random birth dates (i.e. 10 000 random birth dates for each observed birth event).

Each random birth date was assigned a rain-day value (described above) based on the rain pattern for the year in which the birth occurred. Thus, there was a single observed rain-day value and 10 000 random rain-day values for each female that produced a litter during that year. For each year, we calculated the mean observed rain-day value (i.e. mean rain-days for all females who gave birth that year) and 10 000 mean random rain-day values. For example, if six females gave birth in a given year, there would be one mean observed rain-day value, calculated from a sample size of N = 6, and 10 000 mean random rain-day values, each calculated from a sample size of N = 6. We then generated a P-value by dividing the number of mean random rain-day values that were less than or equal to the mean observed rain-day value. Finally, we conducted a global analysis in which we compared the mean observed rain-day value, calculated from all observed births across all years (N = 38), to a distribution of random mean rain-day values, calculated from all random births across all years (N = 38). Our a priori hypothesis was that observed mean rain-day value would be less than the random mean rain-day value; thus, we used a one-tailed design for all analyses. The alpha level for significance was set at α ≤ 0.05.

**RESULTS**

**ANALYSIS OF RAINFALL**

Rainfall data at the study site for the calendar dates 29 July to 14 September (J–S period) from 2003 to 2007 showed variation in both frequency and quantity of rainfall (Table 1). There were 36 discrete rainfall events in the J–S period for all 5 years (range: 3–9, mean = 7.2 ± 2.8). Total rainfall estimates for the J–S period for all years was 56.6 cm (range: 4.4–17.4 cm, mean = 11.3 cm ± 5.5). For all years, August was the peak month for both frequency of discrete rainfall events (N = 25) and total rainfall (35.5 cm), followed by September and July. Total annual rainfall (2003–2007) at the study site (152.1 cm) was slightly greater (28.3 cm) than the total reported by the TIA (123.8 cm).

**TIMING OF BIRTHS**

From 2003 to 2007, 21 females gave births to 38 litters (Table 2). Parturition was restricted to a 4-week period from 5 August to 7 September. Most (92.1%) births occurred in August. The mean range of birth dates across years was 15 days ± 5.2 (minimum − maximum: 6–19 days). In 2006 and 2007, no births occurred in September.

**BIRTH AND RAINFALL ANALYSIS**

In the 5-year period in which we analyzed the association of birth dates and discrete rainfall events, the only year in which births were significantly associated with rainfall events (mean rain-days versus random days) was 2007 (mean rain-days = 0.333, P < 0.001) (Fig. 1, Table 2). Although not statistically significant, births in 2003 and 2005 occurred closer to rain events than randomly generated births for respective years. When births across all 5 years were combined, there was a significant difference in mean rain-days versus random rain-days (mean rain-days = 1.84, P = 0.037). Specifically, births occurred more closely to rain events than random births.

**DISCUSSION**

Our central hypothesis that the timing of births in a desert population of western diamond-backed...
Figure 1. Distribution of mean random rain-day values generated in the present study. Random birth dates ($N = 10,000$) were generated for each of 21 *Crotalus atrox* subjects that produced a litter in a given year. Random birth dates were assigned a rain-day value, which indicated the number of days since or until a rain event occurred, whichever was smallest. Means were calculated across random rain-day values for individual females during each year and for all years combined. The dashed vertical lines denote the position of the mean observed rain-day value calculated from real birth dates. For statistical results, see Table 2 and text.
rattlesnakes (C. atrox) is cued by rainfall events during the second-half of the monsoon season (29 July to 14 September) was supported. Specifically, using randomization procedures, we found that females gave birth on dates that were significantly closer to discrete rainfall events than were randomly selected dates. Despite the fact that statistical significance was not obtained in some years, three of the 5 years had mean observed rain-days that were smaller (i.e. closer to a rain event) than mean random rain-days. Furthermore, our pooled analysis (2003 to 2007), which benefited from a much larger sample size (N = 38 births), revealed that births occurred significantly closer to rain events than expected.

Table 2. Births and rain-days randomization analysis for the 21 adult female Crotalus atrox in the present study

<table>
<thead>
<tr>
<th>Year</th>
<th>ID</th>
<th>Birth date</th>
<th>Rain-days</th>
<th>Mean rain-days</th>
<th>Observed</th>
<th>Random</th>
<th>P-value</th>
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<td>039</td>
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<tr>
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<tr>
<td></td>
<td>042</td>
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<td>2</td>
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<td></td>
<td>061</td>
<td>24 August (?)</td>
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<td></td>
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<td></td>
<td>042</td>
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<td>081</td>
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<td>2006 (N = 9)</td>
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<tr>
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<td>102</td>
<td>11 August (2)</td>
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</table>

Births (N = 38 litters) occurred from 2003 to 2007. Values in parenthesis indicate the litter size (number of progeny). The number of litters is denoted in the year column. ID, subject identification. P-values were generated by comparing mean rain-days with a random distribution of 10 000 mean rain-days. Significant P-values are shown in bold. See also Figure 1 and Table 1.
Significance was only attained in 2007, despite the fact that it did not represent the largest sample size. However, the model performed well (significance was attained) when we combined all 5 years for the analysis, which we attribute to a function of sample size.

We were somewhat surprised to find how close birth dates were clustered in any given year. Although birth ‘synchrony’ has been reported in other snakes, including rattlesnakes (Graves & Duvall, 1993, 1995), no previous studies have provided longitudinal information on individually marked females or formally explored environmental variables (e.g. rainfall) as cues using the procedures of randomization modelling.

Although we directly observed mothers and neonates (or their natal sheds), the actual birth process was never directly observed. Nonetheless, the birth dates are highly precise estimates based on frequent use of radio-tracking (Schuett et al., 2011). Furthermore, based on several lines of evidence, we are confident that we observed mother–offspring associations and that litter sizes were assessed accurately. First, communal birthing (e.g. rookeries), which occurs in other rattlesnakes and pitvipers (Graves & Duvall, 1993, 1995), was not observed in the present study (Price, 1988; Schuett et al., 2011, 2013). Second, based on our DNA-based (microsatellite) parentage analyses (R. W. Clark, G. W. Schuett, R. A. Repp & H.-W. Herrmann, unpubl. data), all progeny or their sheds were matched to identified mothers. Neonate rattlesnakes associated with adult females may not be progeny or kin-related (Graves & Duvall, 1993; Parker, Spear & Oyler-McCance, 2012). Lastly, other studies show that litter sizes of C. atrox in the region of the study area are small (Rosen & Goldberg, 2002; Taylor & DeNardo, 2005); thus, we do feel that our values are underestimates.

STUDIES OF THE TIMING OF BIRTH IN OTHER SNAKES

Our inspection of the literature on rattlesnakes and other live-bearing snake species detected no studies similar to the present one, and only in rare cases is an environmental variable (temperature, rainfall) noted to be associated with the timing of birth. Estimates of parturition dates, however, are commonly reported in wild rattlesnakes (Klauber, 1972; Price, 1988; Martin, 1992; Graves & Duvall, 1993; Butler, Hull & Franz, 1995; Ashton & Patton, 2001; Diller & Wallace, 2002; Greene et al., 2002; Holycross & Fawcett, 2002; Reiserer, Schuett & Earley, 2008; Setser et al., 2010) and other live-bearing snakes (Fitch, 1960; Ford & Seigel, 1989; Seigel, Ford & Mahrt, 2000; Seigel & Ford, 2001). Despite the fact that several of these studies were longitudinal and individual-based (sensu Clutton-Brock & Sheldon, 2011), none provided a formal, hypothesis-based analysis of rainfall or other environmental cues for the timing of birth. Furthermore, several of these accounts were anecdotal and based on very small sample sizes (e.g. N = 1) or involved bringing females into captivity (Price, 1988; Butler et al., 1995; Setser et al., 2010). Nevertheless, other studies (Price, 1988; Greene et al., 2002; Setser et al., 2010) have implicated rainfall as a potential environmental cue for the timing of birth in rattlesnakes.

GESTATION LENGTH AND CONTROL OF PARTURITION

Pregnancy in vertebrates, primarily in mammals, has been dominated by studies emphasizing the role of endocrine and paracrine systems (Challis et al., 2000; Weiss, 2000; McLean et al., 2007; Smith, 2007; Wada, 2008), although recent studies have revealed that the length of gestation and the timing of birth are often controlled and modulated by abiotic factors such as photoperiod, temperature, and rainfall (Cumming & Bernard, 1997; Bumrungsri et al., 2007). This new perspective is presently extended to live-bearing reptiles, especially in lizards (Atkins, Jones & Guillette, 2006; Rock, 2006; Atkins, Swain & Jones, 2007; While, Jones & Wapstra, 2007; Cadby et al., 2010; Le Galliard, Marquis & Massot, 2010).

Hormonal profiles of pregnancy have been described for lizards (Guillette, 1979; Jones & Guillette, 1982; Guillette, Dubois & Cree, 1991) and snakes (Schuett et al., 2004b; Taylor & DeNardo, 2011; Smith, Schuett & Hoss, 2012) and, in both groups, profound hormonal changes occur throughout pregnancy and post-partum periods (Smith et al., 2012). Similar to studies of mammals, recent research on lizards emphasizes the importance of an integrative approach to the investigation of gestation length and the timing of birth. One genus in particular, the Old World skink Niveoscincus has been extensively studied (Girling, Jones & Swain, 2002; Atkins et al., 2006; Girling & Jones, 2006; Cadby et al., 2010; Wapstra et al., 2010). These studies reveal the complex and dynamic role of temperature and hormones [e.g. corticosterone, arginine vasotocin (AVT)] on gestation length and the timing of birth. Studies of other live-bearing lizard species show similar relationships (Rock, 2006; While et al., 2007; Meylan, Haussy & Voituron, 2010; Cree & Hare, 2011). One striking result is that parturition in these lizards can be either accelerated or delayed, often by weeks, when temperature conditions are not optimal (e.g. low) and inhibit the action of hormones associated with parturition, such as AVT (Girling et al., 2002; Girling & Jones, 2006; While et al., 2007). Accordingly, females show a highly plastic response to gestational length and the timing of birth, which
indicates a high level of dynamic control between physiological systems and environment with respect to the timing of birth.

To the best of our knowledge, studies similar to the present one have not been conducted on other species of snakes. Rattlesnakes, including tropical taxa (Almeida-Santos et al., 2004), and other vipers (Lourdais et al., 2004; Smith et al., 2012) are prime candidates for parallel analyses. The present study provides compelling evidence that females of C. atrox are capable of controlling the timing of parturition to a certain extent, which appears to be based, in part, on exogenous factors such as rainfall and perhaps other variables (e.g. relative humidity, barometric pressure) that were not measured in the present study. Among snakes, C. atrox is one of the few species for which steroid hormone profiles of pregnancy and post-partum periods have been reported (Schuett et al., 2004b; Taylor & DeNardo, 2011; Smith et al., 2012), which makes this species conducive to future work investigating how the interaction between exogenous and endogenous factors influence the timing of parturition.

**Timing of birth and rainfall events**

Why give birth during or near rainfall events? Based on empirical studies, the timing of birth in wild animals, including reptiles, occurs when it is apparently optimal for the survival of neonates. For example, rainfall is often linked to the availability of important resources such as food (e.g. vegetation, insects, rodents). Furthermore, rainfall can provide important environmental conditions for newborns, especially during their natal (first) ecdysis. In many snakes, neonates undergo their first shed (natal ecdysis) shortly after birth (Tu et al., 2002; Agugliaro & Reinert, 2005). In most temperate rattlesnakes, including C. atrox (Price, 1988), the natal ecdysis occurs within 5–10 days after birth (Schuett et al., 2011, 2013; Greene et al., 2002; Agugliaro & Reinert, 2005; Reiserer et al., 2008) and maternal attendance and care commonly occur during this pre-shed period (Greene et al., 2002; Reiserer et al., 2008; G. W. Schuett and R. A. Repp, unpubl. data). After shedding, neonates disperse and maternal care is terminated (Greene et al., 2002; Reiserer et al., 2008).

If ecdysis is not completed successfully, a serious health threat is presented to the neonate (Harvey-Clark, 1995; Harkewicz, 2002). For example, in newborn rattlesnakes, retention of the natal shed (dysecdysis), including the eye caps, interferes with locomotion, feeding, defence, and development of the rattle (G. W. Schuett, unpubl. data). Retention of the shed can also lead to secondary bacterial and fungal infections (Harvey-Clark, 1995; Harkewicz, 2002). Presumably, ecdysis problems in newborn snakes also would increase vulnerability to predation. Numerous studies have noted the vulnerability of pre-shed neonate snakes to predators (Price, 1988; Butler et al., 1995; Graves & Duvall, 1995; Greene et al., 2002). A leading cause of dysecdysis in snakes and lizards is desiccation and insufficient ambient moisture (Harkewicz, 2002).

**Birth-sites and post-birth maternal care**

Although we have no direct empirical evidence, we suggest that female C. atrox at our study site selected birth-site locations that were optimal for natal ecdysis, which we presume would increase offspring survival. In hot and xeric environments, such as the Sonoran Desert, rainfall produces environmental conditions (e.g. high humidity, ground moisture, lower temperatures) that are ideal for the neonates to undergo their first ecdysis (Harkewicz, 2002). Birth sites include small mammal burrows (e.g. Kangaroo rats), wood rat (Neotoma albigularis) nests (middens) or shallow areas beneath rocky structures (Schuett et al., 2011, 2013). During rainfall events, these sites exhibit prolonged, high moisture and humidity, as well as lower temperatures (G. W. Schuett and R. A. Repp, unpubl. data), which is conducive to ecdysis. By contrast, high temperatures and low humidity contribute to cutaneous water loss in snakes (Cohen, 1975; Dmi’el, 1985) and thus are contributing factors in neonates failing to shed properly.

**Climate change and drought in South-western North America**

Most climate-change models project that widespread areas of south-western North America will be negatively impacted by elevated temperatures and protracted drought (Cayan et al., 2010; Woodhouse et al., 2010; Munson et al., 2011). Since 2000, most areas of Arizona, especially the Sonoran Desert (Weiss & Overpeck, 2005), have had severe drought and record-breaking high temperatures (National Oceanic and Atmospheric Administration; http://www.wrhl.noaa.gov/twc/). This has been termed the Early 21st Century Drought (Cayan et al., 2010). Forecasts based on paleoclimate records and present-day modeling show that plant and animal populations will be affected in ways that are both predictable and unpredictable (Munson et al., 2011; Lawing & Polly, 2011; Notaro, Mauss & Williams, 2012).

For example, the North American monsoon is a dramatic climatic feature of the south-west from early July to mid September, especially in generating cloud cover, elevated relative humidity, and violent thunderstorms centred in the late afternoon and evening.
These storms produce significant amounts of rainfall. Up to 50% of the annual rainfall occurs during this period (Sheppard et al., 2002). Recent trends in climate change may disrupt the North American monsoon, particularly with respect to decreasing the frequency of storms and levels of precipitation (Sheppard et al., 2002). Subsequently, this may negatively impact reproductive activities in animals such as the timing of birth in desert rattlesnakes. This view is not unprecedented because other studies have demonstrated negative impacts of drought on reproduction in other vertebrates (Ogutu et al., 2011).

CONCLUSIONS
In studies of wild animals, especially in species that are iteroparous and long-lived, monitoring recognizable individuals over extended periods (successive years, decades) provides a wealth of ecological and evolutionary information that is otherwise unobtainable (Clutton-Brock & Sheldon, 2011). Examples include life-history information such as age-related changes in reproductive performance, differential fitness, social structure (e.g. kinship), selection responses (phenotypic changes), and linkages of reproductive phenology to climate change (Visser et al., 2010; Clutton-Brock & Sheldon, 2011).

The phenomena of gestation (incubation) length and the timing of birth (hatching) in vertebrates comprise basic and fundamental life-history problems that remain to be investigated. We thus contend that robust ecological and evolutionary models will require detailed information on all major lineages. Given that reptiles exploit a wide variety of reproductive strategies (Shine, 2003, 2005) and the sister group of mammals (Janes et al., 2010), further study of development and birth in this group is warranted. Importantly, Doody (2011) outlines future prospects for the study of environmentally cued hatching in reptiles that are directly applicable to birth events in live-bearing taxa. Furthermore, owing to the life-history attributes of many vipers (e.g. large body size, tendencies to aggregate), obtaining information on gestation, birth, and post-birth events is possible (Greene et al., 2002; Lourdais et al., 2004; Reiserer et al., 2008; Schuett et al., 2011), especially with the use of radio-telemetry (Dorcas & Willson, 2009). Accordingly, we expect to see more studies similar to the present one.

ACKNOWLEDGEMENTS
We are especially grateful to Douglas Deutschman, San Diego State University, who provided invaluable statistical and modelling counseling. Many individuals provided invaluable assistance in the field, especially Martin Feldner, Ryan Sawby, and John Slone. Dale DeNardo (Arizona State University) was always helpful with surgeries and addressing our questions. Arizona State University, Zoo Atlanta, and Georgia State University (Center for Behavioral Neuroscience) funded the present study. We also appreciate the generous financial support of Dr David L. Hardy Sr and Kent Jacobs. We thank two anonymous reviewers for their helpful comments. The Institutional Animal Care and Use Committee (IACUC) of Arizona State University approved this study (protocol 98-429R) and appropriate scientific permits were obtained from the Arizona Game and Fish Department.

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