Unlike most vipers, female rattlesnakes (Crotalus atrox) continue to hunt and feed throughout pregnancy

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Abstract

For various reasons, reduction or cessation of feeding (anorexia) can occur in either sex during periods of reproduction among vertebrates, from cichlids to elephant seals. Anorexia is commonly associated with gestation in snakes. Using radiotelemetry, we investigated the feeding and spatial ecology of a live-bearing viperid snake, the western diamond-backed rattlesnakes (Crotalus atrox). Specifically, from 2001 to 2010, we determined the feeding frequency and home range size of adult females ($n = 27$) during the active season (March–October) in a population from the Sonoran Desert of Arizona. We addressed a central hypothesis: Do hunting and feeding occur throughout pregnancy? Also, we tested a corollary hypothesis: Does pregnancy influence home range size? We documented hunting and feeding from March to October and during pregnancy (June to mid-September). Feeding frequency was significantly greater in late pregnancy, a result that is in sharp contrast to most other large-bodied vipers. Furthermore, home range sizes in gestating subjects did not differ from those in nonreproductive years. Births occurred from mid-August to mid-September and mean litter size was 3.4. Frequent feeding in C. atrox during gestation unquestionably provides energy and nutrients to the mother, which is likely important for survival, but such food consumption does not imply that nutrients are used by the fetuses. There is, however, recent evidence in other snakes, including a pitviper, that amino acids are transferred to fetuses. Feeding during pregnancy in C. atrox may be important for both income and capital mode reproduction. Hunting and feeding throughout gestation might be accomplished by having relatively small litters not burdened by a body cavity filled with fetuses. Reduction in litter size may thus be a life-history (fecundity) trade-off that permits females to survive and maintain pregnancy in regions where drought and high temperatures are often extreme and chronic.

Introduction

Reproduction by individuals is essential to achieve fitness, yet it involves proximate costs such as extensive changes in behavior and physiology (Stearns, 1992; Roff, 2002; Harshman & Zera, 2006). In widely divergent vertebrates, from cichlid fishes to elephant seals, reproductive activities (nest attendance, rearing offspring, territoriality, mate searching), for example, often impose constraints to feeding and movements related to obtaining food (Mrosovsky & Sherry, 1980). Even when prey or other foodstuffs (e.g. vegetation) are readily available, the feeding response is often absent (Mrosovsky & Sherry, 1980; Brivio, Grignolio & Apollonio, 2010). Reduction or cessation of feeding in animals is a condition termed anorexia (Mrosovsky & Sherry, 1980; Gregory, Crampton &

Skebo, 1999; Lourdais, Bonnet & Doughty, 2002). The causes of anorexia in reproducing animals are complex and include behavioral and physiological changes, such as to the endocrine and immune systems (Mrosovsky & Sherry, 1980; Adamo et al., 2010).

In both live- and egg-bearing squamate reptiles (lizards, snakes), anorexia and related costs are commonly associated with gestation (Shine, 1980; Shine & Schwarzkopf, 1992; Gregory et al., 1999; Brischoux, Bonnet & Shine, 2011), particularly in vipers (Klauber, 1956; Keenlyne, 1972; Macartney & Gregory, 1988; Bonnet, Bradshaw & Shine, 1998; Beaupre, 2002; Lourdais et al., 2002; Crane & Greene, 2008; Webber, Glaudas & Rodriguez-Robles, 2012). The causes of anorexia in gestating snakes are not clearly understood, and several hypotheses (nonmutually exclusive) have

been promulgated including physiological changes, thermoregulatory constraints and reduced space in the body cavity (Gregory *et al.*, 1999; Brischoux *et al.*, 2011; Webber *et al.*, 2012). Of these, the 'space constraint hypothesis' is prominent, and it appears that the burden of fetuses can severely reduce locomotor ability (Brodie, 1989; Weeks, 1996; Gregory *et al.*, 1999; Gignac & Gregory, 2005; Winne & Hopkins, 2006; Brischoux *et al.*, 2011). Subsequently, female snakes often show large reductions in movements and hence home range sizes during gestation, which can negatively influence hunting, prey subjugation and predator avoidance (Fitch, 1960; Graves & Duvall, 1995; Smith *et al.*, 2009; Brischoux *et al.*, 2011; Webber *et al.*, 2012).

Owing to their biological diversity, rattlesnakes (genera *Crotalus* and *Sistrurus*) are good candidates for testing life-history hypotheses (Klauber, 1956; Duvall, Arnold & Schuett, 1992; Reiserer, 2001; Spencer, 2003, 2008). All rattlesnakes are viviparous and fetuses use stored yolk (lecithotrophic mode) for nourishment and development (Bull & Shine, 1979; Blackburn & Stewart, 2011; but see Van Dyke & Beaupre, 2012). Furthermore, because most rattlesnakes produce multiple litters over their lifetime on a less-than-annual basis, there is apparent dependence on capital (vs. income) modes to acquire energy (yolk) for reproduction (Jönsson, 1997; Stephens *et al.*, 2009; Harrison *et al.*, 2011), although that pattern is variable among species and populations (Bonnet *et al.*, 1998, 1999, 2001; Gregory *et al.*, 1999; Shine, 2005; Schuett, Repp & Hoss, 2011; Van Dyke & Beaupre, 2011, 2012; Webber *et al.,* 2012).

Using radiotelemetry, we investigated the influence of pregnancy on feeding frequency consumption and home range size in a North American pitviper (Viperidae), the western diamond-backed rattlesnake (*Crotalus atrox*) in a population from the Sonoran Desert of Arizona. Specifically, during the active season (March–October) from 2001 to 2010, we addressed a central hypothesis: Do hunting and feeding occur throughout pregnancy? Also, we tested a corollary hypothesis: Does pregnancy influence home range size? Previous work has demonstrated that pregnant *C. atrox* in southern Arizona both feeds and makes long distant movements (Taylor *et al.,* 2005). Litter size in *C. atrox* from this region is relatively small (Taylor & DeNardo, 2005; Schuett *et al.*, 2011), and we discuss low fecundity as a life-history trade-off that permits maternal survival and maintenance of pregnancy in regions where drought and high temperatures are often extreme and chronic (Dunham, Miles & Reznick, 1988; Stearns, 1992; Cox *et al.*, 2010).

Methods

Study species

The western diamond-backed rattlesnake (*C. atrox*) is a large-bodied pitviper (Serpentes: Viperidae). Throughout its wide distribution in the western US and Mexico (Campbell & Lamar, 2004), *C. atrox* exhibits minor morphological variation (Spencer, 2008) and shallow genetic (mtDNA) differences (Castoe, Spencer & Parkinson, 2007), but adult body size of *C. atrox* varies significantly (Spencer, 2008). Large differences in adult body size in *C. atrox* are documented in Arizona (Amarello *et al.*, 2010), a state that has broad physiographic structure and multiple biotic communities within a relatively narrow latitudinal range (Brown, 1994). In Arizona, *C. atrox* occupies the southern half of the state and inhabits most of these biotic regions (Campbell & Lamar, 2004). Moreover, adults of both sexes are significantly larger snout-vent length (SVL) in regions of Arizona that are wetter and cooler (Amarello *et al.*, 2010), two variables associated with increases in their common prey (e.g. small mammals, birds and lizards). Presumably, this prey response is linked to increases in predation opportunities and opportunities to acquire sufficient reserves for reproduction and growth (Rosen & Goldberg, 2002; Repp & Schuett, 2009; Schuett *et al.*, 2011). In some regions, *C. atrox* is extremely abundant and commonly the dominant snake species, sometimes even the dominant vertebrate predator, and is a mobile ambush predator (Nowak, Theimer & Schuett, 2008).

Study site

The research site, located in Pinal County, Arizona, is 40 km SSE of the city of Florence, 8 km W of State Route 79. The focal area encompasses ≈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; Epple & Epple, 1995; Phillips & Comus, 2000). In addition to mountainous terrain, the general topography 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–March), and strong to violent, often localized, convective storms occur from mid- to late summer (from early July to mid-September), the period of the North American monsoon. At our site, availability of free water is highly unpredictable.

Subject processing

Twenty-seven adult female *C. atrox* (SVL: 70.5–94.5 mm, mean = 85.76 ± 1.35 standard error of the mean) used in this study were collected from 15 March 2001 to 23 May 2009, and radio-tracked through 2010. See Supporting Information Table S1 for radio-tracking history and fate of subjects. 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 was confirmed (via probing) while under anesthesia (isoflurane). Global Positioning System coordinates were collected as Universal Transverse Mercator (UTM) (Kenward, 2001). 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., Carp, Ontario, Canada) surgically implanted within the coelom following general procedures used for snakes (Reinert, 1992; Schuett *et al.*, 2011).

Radiotelemetry and recent feeding status

We located the subjects with radio transmitters via telemetry on a weekly basis throughout each given year, but here restricted our analyses to the active season (March–October) when reproductive activities occur (Taylor & DeNardo, 2005, 2011; Repp & Schuett, 2008; Schuett *et al.*, 2011). When radio-tracked subjects were visible, we recorded whether they had recently fed as determined by a conspicuous food bolus. Thus, a conspicuous food bolus was used as a proxy for feeding frequency. From 2001 to 2002, we examined subjects for a food bolus by gently lifting them with a snake hook, but this was abandoned in all subsequent years as we developed our visual skills for detecting recent feeding. A conspicuous food bolus is typically associated with the consumption of large prey (e.g. adult *Neotoma* sp.) or multiple prey (e.g. *Dipodomys* sp.). We recognize that predation of small prey, such as lizards, is not uncommon in adult *C. atrox* (Nowak *et al.*, 2008; Repp & Schuett, 2009); however, we did not include such observations in this analysis. Even with a large bolus, digestion is rapid and its presence is typically undetectable within 3–7 days (Beaupre & Duvall, 1998; G. Schuett & R. Repp, pers. obs.). Thus, recounting ('double dipping') the same feeding event was highly unlikely.

Determining reproductive status

The reproductive status of females was determined by previous methods (Schuett *et al.*, 2011). Subjects were assigned a reproductive status of pregnant when they produced a litter, or nonpregnant in each year they were radio-tracked. Following parturition, their reproductive status changed to postparturient through the end of that year, and in the following year it was reassigned as pregnant or nonpregnant. Briefly, as in nearly all snake species, but especially in vipers, reproductive female *C. atrox* is noticeably robust (Rosen & Goldberg, 2002; Taylor & DeNardo, 2005). In this population, vitellogenesis and ovulation occur in late spring, and duration of pregnancy spans from approximately early June to mid-September (Taylor & DeNardo, 2005, 2011; Schuett *et al.*, 2011). Based on their increased mass, we were able to detect reproductive from nonreproductive females by mid- or late June. All births occurred from mid-August to mid-September at sheltered sites (e.g. *Neotoma* middens, small mammal burrows, or rock shelves), but not at or near hibernacula (Repp & Schuett, 2008). During this period, parturition was deemed imminent when female movements from these sites were greatly reduced or ceased; thus, radio-tracking episodes were often increased to one to two times per day to better pinpoint birth dates. The number of offspring (and or their molts) observed determined litter size. All mothers remained at birth sites until their progeny underwent ecdysis, which occurred from 5 to 7 days post birth. Maternal attendance is a common feature in temperate pitvipers (Greene *et al.*, 2002; Reiserer *et al.*, 2008).

Spatial analyses

Home (activity) range size was calculated from the UTM data using the Animal Movement Extension in ArcView 3.2 (Hooge, Eichenlaub & Solomon, 1999) and was estimated in hectares (ha) using the 100% minimum convex polygon (MCP) method (Kenward, 2001; Row & Blouin-Demers, 2006). UTM data were analyzed by season (Season 1: 1 March–30 June; Season 2: 1 July–30 September; Season 3: 1 October–30 November), by reproductive state (pregnant vs. nonpregnant) and by year.

Feeding analyses

To accommodate several potential biases, we used a mixed model where the subject (ID) was a random variable (to account for nonindependence of locations of individuals), number of observations was as a response variable, and reproductive status was a predictor variable to determine whether pregnant subjects were located more frequently than nonpregnant subjects. Because we could only determine whether individuals had recently fed if they were visible (e.g. not in burrows), we used a mixed model with ID as a random variable (to account for nonindependence of locations of individuals), whether or not they were visible as a response variable, and reproductive status as a predictor variable to ascertain whether pregnant subjects were visible more frequently than those that were nonpregnant. To determine whether pregnant subjects fed less than nonpregnant or postparturient, we used a binomial mixed model. We included date (to account for serial autocorrelation) and ID (to account for nonindependence of locations of individuals) as random variables, presence of a food bolus as a response variable, and reproductive status as a predictor variable. For this analysis, we did not include locations when subjects were not visible, or when feeding and reproductive status could not be determined for other reasons.

We tested for seasonal differences in feeding frequency in pregnant, postparturient and nonpregnant females. Also, we tested whether subjects that became pregnant fed more frequently early in the year (March–May) than those individuals that failed to reproduce (nonpregnant). We used a linear mixed model with ID as a random variable. Furthermore, we tested whether pregnant subjects had conspicuous food boluses significantly more often in spring (March–May, the period of vitellogenesis) than in summer (June–September, the period of pregnancy).

Similarly, we tested for overall differences in home range size (MCP) in pregnant and nonpregnant females, including differences in home range size prior to pregnancy (March–May) and during pregnancy (June–September). We used linear mixed models with ID as a random variable.

The R statistical program (R Development Core Team, 2010) with packages lme4 (Bates & Maechler, 2009) and nlme (Pinheiro *et al.*, 2010) was used for all analyses. Graphics were created using the R package ggplot2 (Wickham, 2009). Our experiment-wide alpha level was 0.007 (Bonferroni correction: $0.05/7 = 0.007$).

Results

We radio-tracked 27 adult female *C. atrox* 1828 times during the active season (March–October) from 2001 to 2010. A

Table 1 Proportion of observations where adult female *Crotalus atrox* (*n* = 27) had conspicuous food boluses

ID	Years sampled									
	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010
1	0.25	0.29 (3)	0.40	0.50 (5)	0.50	0.75 (4)	0.42 (3)			
2	0.28 (3)	0.26	0.22 (5)	0.50	0.64	1.00				
14		0.20	0.50 (2)	0.75	0.33					
16			0.31 (?)	0.55	0.42 (3)	0.33	0.40 (3)			
29			0.13	0.21 (3)						
30			0.44 (3)	0.64	0.50 (?)	0.33 (7)				
39			0.22 (4)	0.00						
42			0.36 (4)	0.43	0.44 (3)					
44			0.25 (3)	0.78	0.61 (1)	0.60	1.00			
46			0.25 (3)	0.73 (1)	0.41 (1)	0.67	0.40 (4)			
47			0.25 (3)	0.57	0.53 (?)	0.47 (6)	0.56 (3)	0.27	0.47 (?)	
49				0.75						
58				0.48 (4)		0.25 (9)	0.27 (3)			
59				0.60 (4)						
61				0.50 (?)	0.53	0.37 (1)				
62				0.00						
64				0.58 (?)	0.36					
66				0.57 (?)	0.56 (?)					
81					0.53 (2)	0.67				
93					0.43	0.43 (2)				
94					0.33	0.50 (3)				
95					1.00	0.53 (?)				
100						0.36				
102						0.38 (2)	0.45 (?)	0.29		
120									0.59 (?)	0.24
121									0.57	0.36 (3)
124										0.53 (5)

Shaded boxes represent birth years and parenthetical values denote litter size (? = indeterminable). Litters = 46 (*n* = 118 progeny, min–max = 1–9, mean = 3.4, standard error of the mean ±1.66). See Fig. 1

general summary of feeding frequency and reproduction is provided in Table 1. See Supporting Information Table S1 for radio-tracking history and fate of subjects.

Determining reproductive status

From 2001 to 2010, the 27 subjects we radio-tracked produced 46 litters, resulting in 118 progeny (litter size: min–max, 1–9, x = 3.4, standard error ± 1.66 progeny; Table 1). Frequency of reproduction was typically less than annual (e.g. biennial), but production of annual litters occurred on multiple occasions in different females (Schuett *et al.*, 2011).

Feeding analysis

Subjects were not located more frequently when they were pregnant (mixed model with ID as a random variable; pregnant: $\beta = 0.015 \pm 0.07$, $z = 0.21$, $P = 0.8$), nor were pregnant individuals tracked more frequently than those that were nonpregnant within a given year (mixed model with year as a random variable; pregnant: $\beta = 0.015 \pm 0.07$, $z = 0.21$, $P = 0.8$). Pregnant individuals were not visible more frequently than those that were nonpregnant (mixed model with ID as a

grouping variable; pregnant: $\beta = -0.189 \pm 0.12$, $z = -1.62$, $P = 0.105$); postparturient individuals were visible more frequently than those that were pregnant or nonpregnant (postparturient: $\beta = 0.909 \pm 0.17$, $z = 5.27$, $P < 0.001$).

Pregnant subjects had conspicuous food boluses significantly more often than nonpregnant ones (Table 1, Fig. 1; pregnant: $\beta = 0.49 \pm 0.15$, $z = 3.18$, $P = 0.001$). Of 417 observations, pregnant subjects had conspicuous food boluses 218 times (52.3%) and no food boluses 199 times (47.7%). Of the 366 observations, nonpregnant subjects had conspicuous food boluses 155 times (42.3%) and no food boluses 211 times (57.6%) ($F_{1,781} = 7.76$, $P = 0.005$). Postparturient and nonpregnant subjects showed no significant difference in the frequency of food boluses (postparturient: $\beta = -0.502 \pm 0.19$, $t = -2.66$, $P = 0.008$). Also, pregnant subjects had conspicuous food boluses significantly more often in summer (June–September) than in spring (March–May) ($\beta = 0.23 \pm 0.04$, t = 4.89, $P < 0.0001$).

Spatial analysis

Home range size (MCP) was not significantly different in pregnant versus nonpregnant subjects (Fig. 2; see Supporting
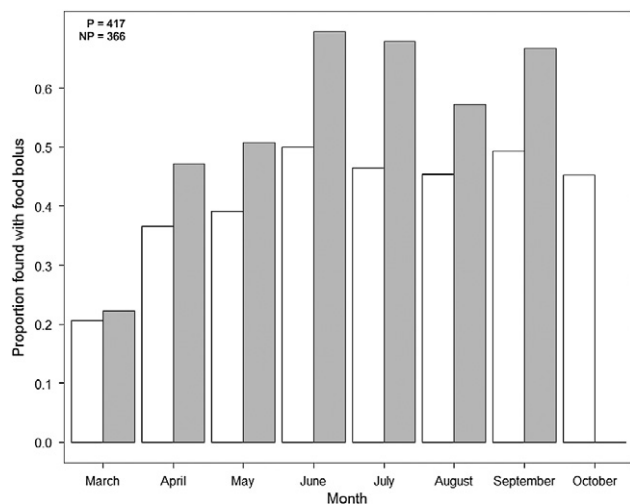
Figure 1 Feeding frequency in 27 radio-tracked adult female *Crotalus atrox* from 2001 to 2010. Pregnant (gray bars) and nonpregnant (open bars). P = number of observations of pregnant subjects, NP = number of observations of nonpregnant subjects.
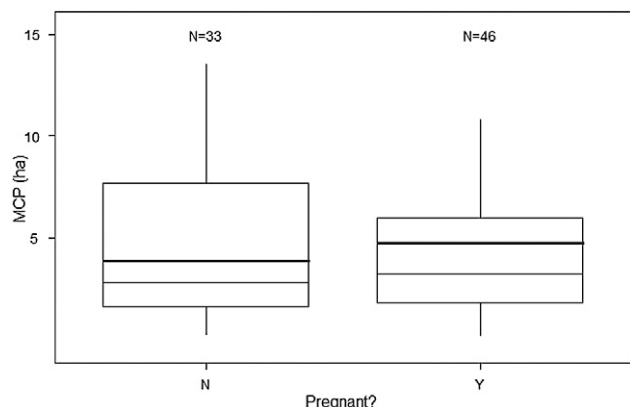

Figure 2 Box-and-whisker plot of annual home range [minimum convex polygon (MCP)] in square hectares for 27 adult female *Crotalus atrox* (pregnant and nonpregnant). Subjects were tracked for multiple years; thus, sample sizes denote snake years (1 year per subject). Lower end of the whisker = lower + 1.5 inner quartile range; lower hinge (box bottom) = first quartile (25th percentile); midline = median (50th percentile); upper hinge (box top) = 75th percentile; upper whisker = upper hinge + 1.5 inner quartile range; thick gray bars = arithmetic mean; diamonds = outliers.

Information Table S2 for data on individual subjects; mixed model with ID as a random variable; pregnant: $\beta = 0.112 \pm 0.69$, $t = 0.16$, $P = 0.87$). We found home range size to be significantly larger in spring (March–June) than in summer (July–September) (home range size: $\beta = -1.71 \pm 0.41$, $t = -4.10$, $P = 0.0001$, based on 27 subjects and 138 observations, but there was no difference between pregnant and nonpregnant subjects (pregnant: $\beta = 0.17 \pm 0.46$, $t = 0.37$, $P = 0.71$).

Discussion

We provide robust support for our central hypothesis that female *C. atrox* continues to hunt and feed throughout pregnancy. This result was expected based on the results of a supplementary feeding study in this species (Taylor *et al.*, 2005). However, unexpectedly, we found that pregnant subjects were found with conspicuous feeding boluses more frequently than females scored as nonpregnant or postpartum. Furthermore, pregnant subjects had significantly more food boluses in summer than in spring, with feeding frequency significantly greater in late pregnancy. These findings are in sharp contrast to results reported in other viviparous snakes (Gregory *et al.*, 1999; Brischoux *et al.*, 2011) including vipers (Klauber, 1956; Keenlyne, 1972; Macartney & Gregory, 1988; Bonnet *et al.*, 1998; Beaupre, 2002; Lourdais *et al.*, 2002; Crane & Greene, 2008; Webber *et al.*, 2012). In the present population of *C. atrox*, vitellogenesis is largely restricted to spring (Beaupre & Duvall, 1998; Taylor & DeNardo, 2005; G. Schuett, unpubl. data), which is rare in North American rattlesnakes and other pitvipers (Webber *et al.*, 2012). We expected that females undergoing vitellogenesis would show greater feeding frequency than nonpregnant, pregnant or postparturient individuals (Van Dyke & Beaupre, 2011), but that was not detected. Our results imply that maintenance of pregnancy is metabolically expensive (Birchard *et al.*, 1984; Schultz, Webb & Christian, 2008), perhaps more than vitellogenesis (Beaupre & Duvall, 1998; Van Dyke & Beaupre, 2011). Following birth, postparturient subjects continued to hunt and feed throughout October, just prior to entering hibernacula (Schuett *et al.*, 2011). Overall, the frequency of feeding we describe in female *C. atrox* is greater than that which has been reported in females of other rattlesnake species (Beck, 1995; Beaupre, 2002).

In most viperid snakes, including rattlesnakes, home range size tends to be severely reduced during gestation (Fitch, 1960; Graves & Duvall, 1995; Greene *et al.*, 2002; Winne, Willson & Gibbons, 2006; Smith *et al.*, 2009). Consequently, in spring and throughout pregnancy, females either remain at their winter hibernacula or move to nearby sites (e.g. rookeries) where they give birth in summer (Graves & Duvall, 1995; Greene *et al.*, 2002). Feeding is greatly reduced or ceases during this period, which is based on several lines of evidence (Klauber, 1956; Keenlyne, 1972; Macartney & Gregory, 1988; Greene *et al.*, 2002). In sharp contrast, our results show that overall home range size did not change during pregnancy. In fact, we found no significant difference in home range size on a year-to-year basis or whether subjects were pregnant or nonpregnant.

As in many species of snakes, female *C. atrox* is iteroparous and produces multiple litters over their lifetime, but generally on a less-than-annual basis (e.g. biennial pattern); hence, they skip reproductive opportunities (Bull & Shine, 1979; Dunham *et al.*, 1988; Rosen & Goldberg, 2002). However, in the population we studied, production of annual litters was not infrequent (Schuett *et al.*, 2011), and we attributed this to high levels of feeding success, even during pregnancy (Schuett *et al.*, 2011; this study).

A prominent hypothesis to explain anorexia and impaired locomotor ability in snakes is obstruction of the digestive tract due to the presence of fetuses or eggs (Weeks, 1996; Gregory *et al.*, 1999; Lourdais *et al.*, 2002; Brischoux *et al.*, 2011; Webber *et al.*, 2012). Previously (Schuett *et al.*, 2011), and in this study, we report mean litter size to be relatively small (3.4), which is severalfold smaller than litters produced by similar-sized female *C. atrox* in other regions of Arizona and elsewhere in the US (Klauber, 1956; Fitch, 1970; Fitch & Pisani, 1993; Rosen & Goldberg, 2002; Spencer, 2003; Campbell & Lamar, 2004). Small litter size also has been reported in a population of *C atrox* close (3 km) to the one we studied (Taylor & DeNardo, 2005). Although we have no experimental evidence, we suggest that decreasing the number of fetuses relaxes spatial constraints in the body cavity (Johnson *et al.*, 2010; Brischoux *et al.*, 2011), which thereby reduces the possibility of obstruction by a large food bolus (Weeks, 1996; Gregory *et al.*, 1999; Schuett *et al.*, 2011). Furthermore, because *C. atrox* is a mobile ambush predator (Nowak *et al.*, 2008), having fewer fetuses likely permits greater capacity for locomotion and selection of optimal hunting sites (Seigel, Huggins & Ford, 1987; Brodie, 1989; Brischoux *et al.*, 2011).

Why do female *C. atrox* continue to hunt and feed throughout pregnancy, which is presumed be high-risk activities? We offer two provisional explanations for future testing.

First, in snakes and most other squamates, vitellogenesis is not initiated until a critical threshold of energy and nutrient accumulation is achieved (e.g. body lipids), which may require more than a single active season. This is termed capital breeding (Jönsson, 1997) and has been discussed extensively in viperid snakes (Bonnet *et al.*, 1998, 1999, 2001; Beaupre, 2002; Lourdais *et al.*, 2002; Shine, 2005; Schuett *et al.*, 2011). In contrast, income breeding involves immediate fueling to fetuses by way of feeding, which is common in eutherian mammals (Jönsson, 1997). However, once thought to be trivial, innovative research over the past 20 years has radically altered dogmatic views regarding placental complexity and nutrient transfer in squamates, especially in several groups of scincid lizards (Thompson & Speake, 2006; Blackburn & Stewart, 2011; Murphy & Thompson, 2011; Blackburn & Flemming, 2012). In snakes, studies on viviparous species imply a greater role of the placenta with respect to the transfer of energy and nutrients to fetuses (Stewart *et al.*, 1990; Blackburn & Stewart, 2011), including amino acids (Van Dyke & Beaupre, 2012). Our results here suggest a more complex relationship than capital mode alone (Taylor & DeNardo, 2005; Taylor *et al.*, 2005; Schuett *et al.*, 2011), and it is plausible that reproduction in a given season is simultaneously fueled by both stored and current sources of energy and nutrients (Winne *et al.*, 2006; Stephens *et al.*, 2009; Van Dyke & Beaupre, 2012). Nevertheless, the role of the placenta in nutrient transfer in *C. atrox* and other rattlesnake species is not known and remains to be tested.

The second explanation concerns the role of feeding in maintaining water balance (McCue, 2007; Schuett *et al.*, 2011). The present population of *C. atrox* is from an extremely hot and xeric region (Sonoran Desert) that lacks permanent free water (Brown, 1994; Phillips & Comus, 2000;

Schuett *et al.*, 2011). Measurable precipitation can be absent for successive weeks, even during the summer monsoon (Mock, 1996; Repp & Schuett, 2008). Consequently, in addition to energy and nutrients, consumption of prey (e.g. rodents and other small mammals) likely provides an important source of preformed and metabolic water (Cloudsley-Thompson, 1971; Nagy, 1987; Bradshaw, 1997; Ladyman & Bradshaw, 2003). Importantly, in viviparous snakes and lizards, there is significant water transport across the placenta to embryos (Thompson & Speake, 2006; Murphy & Thompson, 2011). Water deprivation and loss, for example, can have profound effects on development in the embryos and offspring of mammals (Ross & Desai, 2005). Although the effects of maternal dehydration on the embryonic development have not been reported in viviparous squamates (D. F. DeNardo, pers. comm.), we assume that water balance is necessary for successful development, offspring quality and postbirth survival (Bradshaw, 1997; Ladyman & Bradshaw, 2003; Gardner-Santana & Beaupre, 2009; Tate *et al.*, 2012).

Water loss in squamates and other reptiles that occupy xeric environments is strongly dependent on several environmental variables (Nagy, 1987), such that there are presumed trade-offs between preferred body temperatures during pregnancy, movements and dehydration. Because pregnant snakes tend to have elevated body temperatures (Charland & Gregory, 1990; Gardner-Santana & Beaupre, 2009) and higher metabolic rates (Birchard *et al.*, 1984; Schultz *et al.*, 2008), there is a likely increase in water loss via respiration. In a future analysis, we will report on body temperatures of pregnant, nonpregnant and adult male *C. atrox* (Schuett *et al.*, unpubl. data).

In conclusion, we hypothesize that hunting and feeding throughout pregnancy in *C. atrox* from hot deserts may be driving a life-history trade-off between low fecundity (per litter) and maternal survival (Stearns, 1992; Roff, 2002; Cox *et al.*, 2010; Schuett *et al.*, 2011). By having annual litters, however, female reproductive success (fitness) is presumably increased. Clearly, additional long-term, individual-based studies in this system are needed to address this idea (Stephens *et al.*, 2009; Clutton-Brock & Sheldon, 2010; Harrison *et al.*, 2011). Such research on reproduction in female *C. atrox* in other types of environments (e.g. wetter, cooler) in Arizona and other regions of their range would likely yield important insights on behavior and life history.

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Supporting information

Additional Supporting Information may be found in the online version of this article:

Table S1. Tracking history and fate of subjects we studied.

Table S2. Annual home range size in hectares (minimum convex polygon) for each female *Crotalus atrox* subject ($n =$ 27). Shaded boxes denote years when individuals produced litters. See Table 1 and Fig. 2 in main text.