ECOPHYSIOLOGY

Emily N. Taylor · Michael A. Malawy
Dawn M. Browning · Shea V. Lemar · Dale F. DeNardo

Effects of food supplementation on the physiological ecology of female Western diamond-backed rattlesnakes (*Crotalus atrox*)

Abstract Food availability is an important factor in the life histories of organisms because it is often limiting and thus can affect growth, mass change, reproduction, and behaviors such as thermoregulation, locomotion, and mating. Experimental studies in natural settings allow researchers to examine the effects of food on these parameters while animals are free to behave naturally. The wide variation among organisms in energy demands and among environmental food resources suggest that responses to changes in food availability may vary among organisms. Since most supplemental feeding field experiments have been conducted on species with high energy demands, we conducted a supplemental feeding study on free-ranging, female Western diamond-backed rattlesnakes (*Crotalus atrox*), a species with low energy demands and infrequent reproductive investment. Snakes were offered thawed rodents 1–4 times per week. Over two active seasons, we collected data on surface activity, home range size, growth, mass change, and reproduction of supplementally fed and control snakes. Fed and control snakes did not differ in surface activity levels (proportion of time encountered above versus below ground) or home range size. Fed snakes grew and gained mass faster, and had a dramatically higher occurrence of reproduction than control snakes. Also, fed snakes were in better body condition following reproduction than snakes that were not fed. However, litter characteristics such as offspring number and size were not increased by feeding, suggesting that these characteristics may be fixed. These data experimentally demonstrate that food availability can directly impact some life history traits (i.e., growth and reproduction for *C. atrox*), but not others (i.e., surface activity and home range size for *C. atrox*). The relationship between food availability and life history traits is affected in a complex way by ecological traits and physiological constraints, and thus interspecific variation in this relationship is likely to be high.

Keywords Reproduction · Energy · Growth · Snake

E. N. Taylor (✉) · M. A. Malawy
School of Life Sciences, Arizona State University,
Tempe, AZ, 85287-4601 USA
E-mail: entaylor@asu.edu
Tel.: +1-480-9650698
Fax: +1-480-9657599
E-mail: malawy@asu.edu

D. M. Browning
School of Natural Resources, University of Arizona,
Tucson, AZ, 85721 USA
E-mail: dbrownin@ag.arizona.edu
Tel.: +1-520-6217255
Fax: +1-520-6218801

S. V. Lemar
Information Technology, Arizona State University,
Tempe, AZ, 85287-0101 USA
E-mail: shea.lemar@asu.edu
Tel.: +1-480-9651205
Fax: +1-480-9656317

D. F. DeNardo
School of Life Sciences, Arizona State University,
Tempe, AZ, 85287-4501 USA
E-mail: denardo@asu.edu
Tel.: +1-480-9653325
Fax: +1-480-9656899

Introduction

Food availability is one of the most important environmental variables in animal life histories because it can affect organism-level processes such as growth, reproduction, space use and other behaviors, as well as higher-level processes such as food web dynamics and spatial structures of communities. Because many organisms live in food-limited environments, it is of interest to examine the mechanisms by which food limitation affects the above processes. Experimental food supplementation has been a powerful tool in

demonstrating the diversity of mechanisms by which food limitation affects organismal and population function (reviewed in Boutin 1990). The majority of recent research on this topic has been conducted on invertebrates and endothermic vertebrates and has examined the effects of food supplementation on ecological and physiological processes such as space use (e.g., Monadjem and Perrin 1998; Kreiter and Wise 2001), growth and body composition (e.g., McKillup and McKillup 1997; Banks and Dickman 2000; Unangst and Wunder 2004), and reproduction (Richner 1992; Garcia et al. 1993; Pelletier and McNeil 2003; Brommer et al. 2004). Although results of these studies vary, food supplementation generally decreases home range or territory size, and increases growth, mass, and reproductive output (Boutin 1990).

Because organisms vary dramatically in their life history strategies and because environments differ in the abundance of food resources, we would expect that food availability would affect different organisms in different ways (e.g., endotherms vs. ectotherms, herbivores versus carnivores, temperate versus tropical, etc.). Most food manipulation experiments have been conducted on small, herbivorous mammals occupying temperate habitats, presumably because of the ease with which food can be manipulated (Boutin 1990). However, how food availability effects an endotherm might be quite different than how it affects an ectotherm, since ectotherms have lower energetic demands. Unfortunately, food manipulation studies on ectotherms are scarce (reviewed in Boutin 1990; see also Eifler 1996; Abell 1999; Brown and Weatherhead 2000; Blouin-Demers and Weatherhead 2001). Desert reptiles represent an extreme of low energy availability and demand, and food supplementation studies on such species would be very informative for testing the hypothesis that food availability directly limits life history traits such as body size, growth, and reproduction, and for examining the relative degree to which these traits are plastic to perturbations in food availability.

Desert rattlesnakes are particularly well-suited for such studies for physiologic, ecologic, and technical reasons. Rattlesnakes have extremely low metabolic rates (Beaupre and Duvall 1998) and reproductive frequencies (Taylor and DeNardo 2005), and energy demands can be minimal. Additionally, rattlesnakes feed on large meals at highly infrequent intervals and thus supplemental feeding can have a substantial impact on total food consumption with limited disturbance. Lastly, the Western diamond-backed rattlesnake (*Crotalus atrox*) is abundant and spends much of its time above ground, making a manipulative study such as this feasible.

Several studies have documented that high food intake leads to increased reproductive output in snakes. These studies are comprised of two main types of investigation, those that control food intake in the laboratory and measure reproductive output (e.g., Ford and Seigel 1994), and those that correlate food availability in the wild with reproductive output (e.g., Goldberg and Rosen 2000; Diller and Wallace 2002; Rosen and Goldberg 2002; Lourdais et al. 2002). The effect of food on growth in snakes has also been documented in laboratory studies (Madsen and Shine 1993; Forsman and Lindell 1996; Scudder-Davis and Burghardt 1996; Bonnet et al. 2001a). While laboratory experiments are useful in isolating the effects of food on growth and reproduction, subjects are not allowed to behave naturally (e.g., thermoregulation, locomotion, foraging, etc.), so results might not be wholly indicative of what occurs in the wild. Similarly, correlational field studies help elucidate the relationship between food availability and physiological processes in natural situations, but the causation of this relationship is clouded since other variables may affect growth and reproduction.

In this study, we conducted a field experiment to test the hypothesis that food availability limits life history traits such as reproductive output and growth, by supplementing the diets of free-ranging, female *C. atrox*. We predicted that supplementally fed snakes would show higher growth rates, mass gain, and reproductive output than control snakes. Furthermore, because activity and spatial distribution may be influenced by foraging behavior, we predicted that food supplementation would reduce the need to forage and thus lead to a reduction in surface activity and home range size.

Materials and methods

Field site

The field site is a 1.5×1.0 km area of Arizona Upland Sonoran Desert (elevation 800–900 m) located approximately 33 km NNE of Tucson, Arizona. The habitat consists of rocky volcanic hillsides and sandy plains with intermittent washes. During the snake active season, ambient temperatures typically range between 5°C and 30°C in spring and fall (mid-March through mid-May and mid-September through mid-November) and 20–40°C in summer (mid-May through mid-September). Additionally, a limited but reliable summer rainy season (approximately 10 cm of rain) occurs between mid-July and early September.

Experimental design

The study took place from March 2002 until October 2003. We implanted a total of 17 female *C. atrox* with 11–13 g radiotransmitters (#SI-2T, Holohil, Carp, ON, Canada). Nine of the snakes were randomly designated as supplementally fed snakes (=*fed*), while the other eight were *control* snakes. Based on a previous descriptive natural history study (Taylor and DeNardo 2005), most of the snakes (*n* = 13) did not reproduce the

year before the study (2001), but one did (she was randomly assigned to the *fed* group). We do not know the reproductive histories of the other three snakes since they were added when this study commenced. *Fed* snakes were offered thawed rodents as often as possible over the course of the study (1–4 times per week). Feeding occurred throughout the active season (mid-March through mid-November, primarily April through October). Snakes sometimes immediately struck and ingested rodents in front of the experimenter. At other times, the experimenter left the rodent in front of the snake, oftentimes but not always returning to see if the rodent was gone. Therefore, it was not possible to keep track of exactly how much food each snake ate; however, our goal was not to examine the effects of specific amounts of supplemental food, but rather to provide the experimental group with dramatically increased food availability in comparison to the control group. All snakes ate at least four extra meals per year, and most consumed more. Since the annual energy budgets of rattlesnakes tend to be very low (e.g., approximately equal to their body mass, or to only several meals a year; Secor and Nagy 1994; Beck 1995), the *fed* snakes likely consumed considerably more food than the *control* snakes.

Since some snakes died or were lost due to premature radiotransmitter failure, not all snakes were monitored for the entire 19-month study period. All 17 snakes were monitored for at least 6 months, and the mean time the snakes were monitored was 12.7 months (range: 6–19 months). The mean time monitored did not differ between *fed* and *control* snakes (*fed*: mean = 15.0 months; *control*: mean = 11.6 months; $t = 1.46$, $P = 0.16$).

Field monitoring

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. We weighed (± 1 g, using a 1,000 g Pesola scale) the snakes once a month. At these times, we also examined the snakes with portable ultrasonography (Concept/MCV, Dynamic Imaging, Livingston, Scotland) to examine reproductive activity. We measured (± 0.5 mm) their snout-vent lengths (=SVL) twice per year with cloth measuring tape while snakes were anesthetized with isoflurane. To collect reproductive output data, pregnant snakes were captured and brought into the laboratory one to several weeks prior to parturition. Within 2 days after parturition, we weighed (± 0.01 g, using an Acculab digital scale), measured SVL (± 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 within 2 weeks of parturition.

As part of a separate study (Taylor and DeNardo 2005), we collected data from 2000 to 2003 on an additional 49 adult female snakes using mark-recapture and radiotelemetry, including data on 18 litters from the females (=*non-fed* females). Note that *non-fed* females are a different cohort than *control* females, but both represent a natural, non-fed state. Our analyses of litter characteristics include data on these *non-fed* females as well as the experimental *fed* and *control* females in order to facilitate statistical comparisons (see below).

Surface activity and home range size

When radiotracking snakes, we recorded whether snakes were above or below ground. We define surface activity as the proportion of time encountered above versus below ground. We calculated home range estimates using global positioning system (GPS) point locations and the fixed kernel method (Worton 1989) to ascertain whether *fed* and *control* snakes differed in home range size during 2002 and 2003. The fixed kernel method generates a nonparametric estimate of the distribution of an animal's position across a plane based on densities of locations, and applies a fixed smoothing factor to the entire evaluation area (Worton 1989; Kernohan et al. 2001). We derived the 50% and 95% contours of the utilization distribution and selected the optimal smoothing factor (h) using the least squares cross-validation (LSCV) option embedded in the Animal Movement Extension (Hooge and Eichenlaub 1997) for Arcview (v. 3.3, Environmental Systems Research Institute 2000). Some snakes traveled long distances to overwinter while some snakes overwintered in their summer ranges, resulting in tremendous interindividual variation in home range size. Since our aim was to examine whether home range size was affected by food supplementation, which only occurred during the active season, we also calculated active season 95% and 50% kernel home ranges using all fixes for each snake in the months of April through October. Two snakes were removed from the home range analyses because they had fewer than 30 fixes (Seaman et al. 1999), so analyses include data from seven *fed* snakes and eight *control* snakes.

Calculations

We calculated the mean monthly growth in SVL of snakes as the change in SVL between the first and last captures divided by the number of active season months between these dates. One *fed* snake was lost after 6 months in the experiment but before we could obtain a second measurement of SVL; the growth analysis is therefore on eight snakes in each group. We also calculated the mean monthly mass change of *fed* and *control* snakes as the average change in mass during each month in the active season. Not all snakes were weighed

every month of the study because they were often underground and therefore inaccessible. In such cases, we calculated the change in mass between the two available measurements and divided this value by the number of months between measurements. We deleted values for months spanning parturition events because pregnant snakes dropped significantly in mass when they gave birth, and we did not want this to interfere with detecting overall patterns of mass gain and loss. We then calculated the grand mean of the mean monthly changes in mass for *fed* and *control* snakes. We also compared the body conditions of *fed* and *control* snakes at the end of the experiment. We regressed ln-transformed SVL and mass data from initial captures of 49 female snakes marked at the field site but not a part of this study. Using this regression equation, we calculated the residual value for each *fed* and *control* snake at the end of the experiment as its body condition. We also divided residual values by predicted mass and multiplied values by 100 to find the percentage above or below the predicted mass for the snakes' SVL.

To examine how food supplementation affected reproductive output, we compared the number of *fed* and *control* snakes that reproduced, and we compared the number of neonates produced by *fed* and *control* snakes. However, since only one *control* snake reproduced (see Results), it was not possible to statistically compare the litter characteristics of *fed* and *control* snakes. Instead, we compared data from *fed* litters to those from the 18 *non-fed* females from the same site. The fact that these litters occurred in different years may confound the data with factors such as climate and food availability, but, despite this limitation, this comparison is valuable because it allows us to examine the effects of food supplementation on more detailed aspects of reproductive output.

Data analysis

We analyzed data using SAS (v. 8.2, SAS Institute) and Systat (v. 10.0). We checked to see that the data conformed to assumptions of parametric tests prior to inference, and ln-transformed response variables when necessary. We analyzed mean home range size and monthly growth in SVL of *fed* and *control* females using ANCOVA (with initial SVL as the covariate), and mean monthly change in mass using ANCOVA (with initial mass as the covariate). We used t-tests to compare the body condition (residual scores) of *fed* and *control* snakes at the end of the experiment, the litter characteristics of *fed* and *non-fed* females, and the mean proportion of time encountered above ground in *fed* and *control* snakes. We did not adjust litter characteristics for maternal size because they are unaffected by maternal SVL in this population (Taylor and DeNardo 2005). We compared the number of *fed* and *control* snakes that reproduced using a Chi-square contingency table. All values reported are means ± 1SEM.

Results

Growth, mass, and body condition

Fed females had a significantly higher mean monthly growth rate than *control* females (*fed*: 0.39 ± 0.08 cm/month; *control*: 0.06 ± 0.10 cm/month; $R^2 = 0.54$, $F = 7.20$, $P = 0.019$; Fig. 1a). In terms of overall growth over the 19-month experiment, the mean total growth of *fed* females was 3.75 cm (range: 1–7 cm), while the mean total growth of *control* females was 0.90 cm (range: −1.5 to 3.5 cm). Three *control* females appeared to shrink over the course of the study (two shrank 1.5 cm, and one shrank 0.5 cm). *Fed* females had a significantly higher mean monthly mass gain than *control* females (*fed*: 21.34 g/month, *control*: 1.36 g/month; $R^2 = 0.71$, $F = 17.33$, $P = 0.003$; Fig. 1b). *Fed* snakes were in slightly better body condition at the end of the experiment than *control* snakes, but the difference between groups was not significant (*fed*: 0.14, *control*: 0.03; $R^2 = 0.20$, $t = -1.88$, $P = 0.08$). Similarly, there was no significant difference in body condition when assessed relative to size (*fed*: −0.44%, *control*: −2.31%; $R^2 = 0.18$, $t = -1.76$, $P = 0.08$).
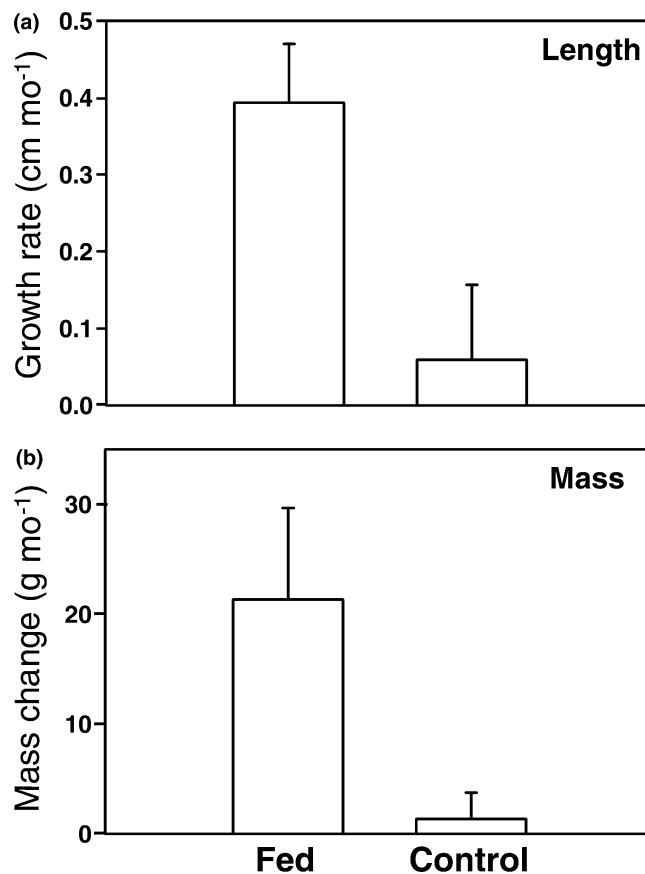
Fig. 1 Supplementally *fed* female Western diamond-backed rattlesnakes (*C. atrox*) ($n = 8$) have **a** a higher mean monthly growth rate than *control* females ($n = 8$), and **b** a higher mean monthly mass change than *control* females. Values shown are means ± 1SEM
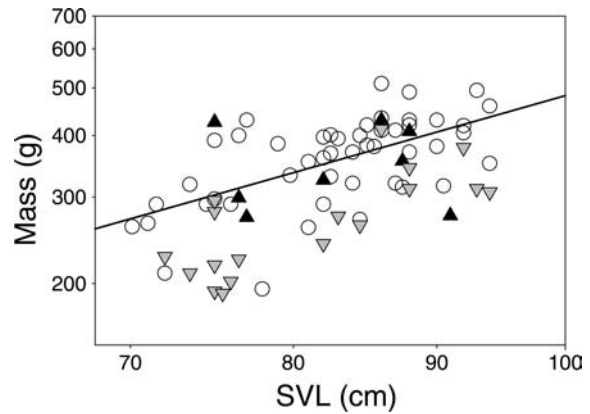
Reproduction

During the experiment, only one *control* snake reproduced (in 2003), while seven *fed* snakes reproduced (two in 2002 and six in 2003; one of these snakes reproduced in both years of the experiment as well as in 2001 and 2004, for a total of four years in a row), showing that supplemental feeding led to a significantly increased incidence of reproduction ($\chi^2 = 6.25$, $P < 0.025$). In terms of overall reproductive output, the single *control* snake that reproduced had two neonates, while the number of neonates produced by *fed* snakes was 37 (mean litter size = 4.6 neonates). This considers data from the single *control* snake and six of the *fed* snakes that reproduced (the seventh *fed* snake went underground several weeks before parturition, so we were unable to capture her neonates). Therefore, the actual number of neonates produced by *fed* snakes was greater than 37.

Litter characteristics of *fed* and *non-fed* females are shown in Table 1. Although *fed* snakes had higher mean total and live clutch masses and mean neonate mass than *non-fed* snakes, these differences were not significant. *Fed* snakes had a significantly higher mean postparturient body mass and body condition than *non-fed* snakes (Fig. 2, Table 1), indicating that they were heavier relative to length than *non-fed* snakes following reproduction. Postreproductive *fed* snakes were only 0.51% below the predicted mass, meaning that for a given SVL they were almost as heavy as the reference group; this shows that supplemental feeding essentially gave the snakes a "free" reproductive bout. In contrast, postreproductive *non-fed* snakes were on average 4.48% below predicted mass, significantly lower than *fed* snakes ($R^2 = 0.11$, $t = 1.71$, $P = 0.005$). There was no effect of feeding on relative clutch mass, litter size, or mean neonate SVL.

Surface activity and home range size

The proportion of time encountered above ground did not differ between *fed* and *control* snakes (*Fed*: 0.45; *control*: 0.55; $R^2 = 0.10$, $t = 1.26$, $P = 0.23$). *Fed* and *control* snakes did not differ in home range size

Fig. 2 Regression of SVL and mass of reference female *C. atrox* (*open circle* and regression line, $n = 49$), showing higher postreproductive body condition of supplementally *fed* females (*filled triangle*, $n = 7$; one snake reproduced twice and is shown twice) than *non-fed* females (*filled inverted triangle*, $n = 18$). Note the log axes

(Table 2), and SVL did not significantly affect home range size.

Discussion

Fed snakes gained more mass per month than *control* snakes (Fig. 1b), showing that, despite the lack of actual prey consumption data, the food manipulation in this experiment had the desired outcome of providing *fed* snakes with a much greater amount of prey than *control* snakes. That is, *control* snakes that hunted on their own were not able to obtain as much food as the *fed* snakes that were fed experimentally. The greater energy intake of *fed* snakes led to increased monthly growth rates in comparison to *control* snakes (Fig. 1a), similar to the results of studies on birds, mammals, and lizards (reviewed in Boutin 1990). Several laboratory studies have documented similar effects of food intake on growth of juvenile snakes (Forsman and Lindell 1996; Scudder-Davis and Burghardt 1996; Bonnet et al. 2001a), although the effects of increased food intake on growth in adult snakes are less clear.

Table 1 Comparison of litter characteristics of supplementally *fed* female *C. atrox* and *non-fed* female *C. atrox* from the same field site

Characteristic	Definition	Fed	Non-fed	R^2	t	P
N	Number of litters	8	18	NA	NA	NA
Total clutch mass (g)	Mass (g) of all neonates and undeveloped ova	107.0	88.5	0.118	−1.79	0.086
Live clutch mass (g)	Mass (g) of all fully formed neonates	103.0	86.6	0.082	−1.46	0.157
Maternal postparturient mass (g)	Mass (g) of females within 2 days following reproduction	348.9	271.3	0.248	−2.81	0.01
Maternal postparturient body condition	Residuals from regression of ln-transformed SVL on ln-transformed mass	−0.03	−0.26	0.283	3.08	0.005
Relative clutch mass	Total clutch mass divided by maternal postparturient mass	0.30	0.33	0.024	0.76	0.453
Litter size	Number of live neonates	4.6	4.5	0.002	−0.19	0.849
Mean neonate SVL (cm)	Grand mean of mean neonate SVL (cm) in each litter	28.2	28.6	0.006	0.39	0.699
Mean neonate mass (g)	Grand mean of mean neonate mass (g) in each litter	22.9	20.0	0.099	−1.62	0.119

Table 2 There is no difference between mean home range size (hectares) of supplementally *fed* ($n = 7$) and *control* ($n = 8$) female *C. atrox*

Home range	*Fed* mean	*Fed* SEM	*Control* mean	*Control* SEM	Type III sum of squares	*F*-value	*P*-value
95% Kernel (Total)	6.96	3.63	7.66	2.81	0.02	0.01	0.92
50% Kernel (Total)	1.21	0.75	1.32	0.60	< 0.01	< 0.01	0.99
95% Kernel (Active season)	3.22	0.76	3.29	0.76	0.17	0.16	0.69
50% Kernel (Active season)	0.40	0.11	0.39	0.10	< 0.01	< 0.01	0.97

Total home range size uses all fixes, whereas active season home range size uses only those fixes from the active season (April through October)

This study was conducted during a period of relatively low rainfall at our study site (based on Tucson rainfall data from National Oceanic and Atmospheric Administration web-site, http://www.noaa.gov/), when food availability was likely to be relatively low. Low food availability may have been responsible for the low reproductive rate and possible shrinking observed among *control* snakes. Although our measurements were carefully taken on anesthetized snakes, the shrinking in size up to 1.5 cm is likely within the range of measurement error (Blouin-Demers 2003), and careful, repeated measurements will be necessary to confirm that rattlesnakes can shrink. Shrinking has been reported in several reptiles, and may be the result of measurement error (Madsen and Shine 2001; Blouin-Demers et al. 2002) or result from such processes as absorption of bone minerals during nutritional stress (Wikelski and Thom 2000).

Over two active seasons, only a single *control* snake reproduced. In contrast, seven *fed* snakes reproduced, and one of them reproduced during both years of the study as well as the years before and after the study. Food supplementation studies of bird and mammal species generally show similar results, with an increased proportion of breeding females. Other effects include advancement or extension of the breeding season and lower age at first reproduction (reviewed in Boutin 1990). To our knowledge, this study is the first to experimentally demonstrate that food availability is the proximate factor limiting reproductive frequency in free-ranging snakes. Our results agree with other studies that have examined the effects of food intake on reproduction in the laboratory and the field. Ford and Seigel (1994) found that corn snakes raised on a high intake diet matured earlier than those raised on a low intake diet. Other studies have noted a positive relationship between snake reproductive output and prey abundance during the previous year (Goldberg and Rosen 2000; Diller and Wallace 2002; Rosen and Goldberg 2002; Lourdais et al. 2002).

Although food supplementation dramatically increased the frequency of reproduction in *C. atrox*, it did not increase litter size, clutch mass, or mean neonate size. *Fed* snakes were in better body condition following reproduction than *non-fed* snakes. So, in effect, *fed* snakes completed reproductive bouts in similar body condition to non-reproductive snakes, and in much better body condition than post-reproductive, *non-fed* snakes. This suggests that the litter characteristics

(Table 1) of *C. atrox* may be somewhat fixed, such that additional energy is funneled into fat storage rather than into producing more and/or larger neonates. Supplementally fed *Anolis* lizards similarly increased their mass but not clutch size (Rose 1982); however, Guyer (1988a, b) found that supplementally fed *Norops* lizards had higher clutch sizes than control lizards. Results are also mixed for food supplementation studies on birds and mammals. While birds tend to have relatively constant clutch sizes, some mammal species showed increases in clutch size and some showed no change (reviewed in Boutin 1990). It appears that enhanced food resources may be used differentially to increase fitness, either by increasing clutch mass and thus increasing current reproductive effort or by increasing postreproductive body condition and decreasing interclutch interval, which would increase lifetime fecundity (Beaupre 2002). Rattlesnakes are long-lived (Klauber 1972), so it is not surprising that they invest extra energy into storage to use for future reproduction rather than spending all the energy on a current reproductive bout, as a short-lived species might. In this study, we fed snakes throughout the active season and therefore during all periods of the reproductive cycle, including before, during, and after vitellogenesis and pregnancy. Other studies have shown that the timing of food intake in relation to the reproductive cycle may affect how snakes allocate energy into offspring (Bonnet et al. 2001b; Lourdais et al. 2003). More detailed studies in which snakes are fed only at certain times of the reproductive cycle are needed to examine these possible relationships in free-ranging snakes.

We were unable to detect any effects of food supplementation on surface activity or home range size in female *C. atrox*, although our results are limited by the sample size, the frequency of our observations, and the length of time snakes were monitored. Snakes tended to go underground following meals, but they did not remain underground long enough to constitute statistically significant differences between *control* and *fed* snakes. Studies have generally shown decreased home range size in supplementally fed animals (reviewed in Boutin 1990), but most of these studies were performed on small herbivores. Since these animals tend to actively forage for food, supplementation reduces the home range size necessary to meet nutritional needs. However, rattlesnakes are sit-and-wait predators (Klauber 1972), and supplementation did not affect the size of their home ranges, which varied tremendously

among individuals. It therefore appears that home range size in *C. atrox* may be determined by factors other than food availability.

In conclusion, we found that food supplementation of free-ranging female rattlesnakes led to greater mass gain, growth rates, occurrence of reproduction, and postreproductive body condition relative to females that did not receive supplemental food. However, surface activity, home range size, and litter characteristics such as litter size and neonate size were not affected by food supplementation. Food supplementation studies in the wild allow researchers to experimentally observe energy allocation decisions, as well as physiological processes such as thermoregulation (Brown and Weatherhead 2000; Blouin-Demers and Weatherhead 2001), of organisms that are free to behave naturally. This study demonstrates that life history characteristics of a desert reptile, including growth and reproduction, are limited by low resource availability. Further, it demonstrates that organisms with different physiological and life history characteristics (e.g., metabolic rate, activity patterns, frequency of reproduction, etc.) respond in different ways to food supplementation. Conducting such studies using different species and varying quantities of food supplementation would be a powerful tool in understanding the relationship between energy allocation decisions and life history strategies.

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