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Snakes survive starvation by employing supply- and demand-side economic strategies

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Abstract

Animals vary widely in their abilities to tolerate extended periods of food limitation. Although some snakes are known for their unique ability to survive periods of inanition that last up to 2 years, very little is known about the biological mechanisms that allow them to do this. Consequently, the present study examined physiological, compositional, and morphological responses to 168 days of starvation among three distantly related snake species (i.e., ball python, *Python regius*; ratsnake, *Elaphe obsoleta*; and western diamondback rattlesnake, *Crotalus atrox*). Results revealed that each of these species was able to successfully tolerate starvation by adaptively utilizing supply- and demand-side regulatory strategies. Effective demand-side strategies included the ability of snakes to depress their resting metabolic demands by up to 72%. Moreover, supply-side regulation of resources was evidenced by the ability of snakes to spare their structurally critical protein stores at the expense of lipid catabolism. Such physiological strategies for minimizing endogenous mass and energy flux during periods of resource limitation might help explain the evolutionary persistence of snakes over the past 100 million years, as well as the repeated radiation of snake lineages into relatively low-energy environments. The final section of this study outlines a novel modeling approach developed to characterize material and chemical flux through animals during complete inanition. This approach was used to make comparisons about the efficacy of various supply- and demand-side starvation strategies among the three species examined, but could also be used to make similar comparisons among other types of animals.

Keywords: Body composition; Energetics; Metabolism; Reptiles; Fasting

Introduction

All animals are heterotrophic, and thus face the possibility of environmentally imposed periods of inanition or even starvation-induced mortality. The likelihood that an animal will succumb to starvation depends on the food resources available in its environment as well as its ability to physiologically cope with food limitation. However, just as different environments vary in their food resources, different animals vary in their abilities to survive extended periods of inanition. Over the past 20 years researchers have identified species that are apparently 'well-adapted' to starvation and can survive multiple *months* without food (see reviews by Castellini and Rea, 1992; Navarro and Gutierrez, 1995; Wang et al., 2006); however, some groups of animals, most notably snakes, are inexplicably excluded from comparative studies of fasting and starvation. The exclusion of snakes from these investigations is

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perplexing given the ability of snakes to tolerate multiple *years* of inanition (Martin and Bagby, 1973; Blood, 1993; de Vosjoli et al., 1995; Klauber, 1997; Wang et al., 2006). The present study was conducted to characterize and compare the biological strategies used by different snake species to tolerate prolonged periods of food limitation.

The terms *fasting* and *starvation* have been defined in numerous ways by researchers characterizing physiological responses to inanition among mammals and birds that typically feed continuously or at regular intervals. According to such definitions, the distinction between *starving* and *fasting* states can be based on several metrics including sequential changes in rate of mass loss (Robin et al., 1983, 1988; Cherel et al., 1988) or physiological fuel utilization (Cahill, 1976; Castellini and Rea, 1992), but may also be based on the behavioral and other qualitative changes in animals subjected to food limitation (Le Maho et al., 1981; Bines, 1999; Caloin, 2004). On the other hand, many animals (e.g., snakes) consume relatively large meals infrequently and/or at relatively irregular intervals (Gans, 1983; Greene, 1983), and therefore do not conveniently fit into these existing definitions. Moreover, the underlying causality of their irregular feeding patterns may be voluntary or involuntary. As a result, the terms *fasting* and *starvation* are used throughout this manuscript to differentiate between the causality of not feeding. For example, many snakes will not voluntarily ingest a new meal until they become postabsorptive from their prior meal, a process that generally requires 2 weeks (Hailey and Davies, 1987; Hopkins et al., 1999; Holmberg et al., 2003; Toledo et al., 2003; McCue et al., 2005). Voluntary refusal to eat may also be caused by behavioral or thermal stress, as well as ecdysis or reproductive cycles. Because limitation of available food resources is not the underlying cause of not eating, each of the aforementioned situations exemplifies individuals that are considered to be *fasting*. Conversely, individuals deprived of the opportunity to consume a meal that would otherwise consume food voluntarily are considered to be *starving*, a condition that is not uncommon among wild animals.

The biological strategies that different species can employ to increase their starvation tolerance fall into two general categories. To borrow language from the science of economics, these strategies involve *supply*- and/or *demand-side* regulation. Demand-side strategies are those that involve alterations in metabolic expenditure, whereas supply- strategies deal with the patterns in which different endogenous physiological fuels are mobilized during periods of starvation. Previous research into starvation physiology has revealed numerous supply- and demand-side strategies that allow vertebrates to successfully survive extended periods of inanition. For example, some animals tolerate environmentally imposed bouts of inanition by taking advantage of demand-side regulation and enter inactive periods referred to as hibernation or aestivation (Cramp and Franklin, 2003; Prunescu et al., 2003). Other animals are able to remain relatively active while significantly reducing their energetic demands. Examples of animals that rely on this strategy include marine iguanas which decrease their overall metabolic requirements by 'shrinking' in mass and length (Wikelski and Thom, 2000). While the mass-specific metabolic demands of an animal typically decrease as they increase in size (Schmidt-Nielsen, 1999; West et al., 2000), the converse is not always true during starvation-induced mass loss. In fact, some animals are apparently able to take further advantage of demand-side regulation by reducing their mass-specific metabolic rates even as they lose body mass (Chwalibog and Thorbek, 1989; Wieser et al., 1992; Hervant et al., 2001; Mata et al., 2001; Rios et al., 2002; Leggatt et al., 2003).

The best studied supply-side strategies to cope with starvation involve animals (e.g., penguins, bears, and seals) that are able to survive prolonged periods of starvation by relying on enormous lipid stores that can account for over half of their initial body mass (Cherel et al., 1987; Worthy and Lavigne, 1987; Castellini and Costa, 1990; Reilly, 1991; Nordoy et al., 1993; Atkinson et al., 1996). Interestingly, snakes appear to differ from many of the vertebrates that have previously been identified to be 'well-adapted' to starvation by virtue of their relatively lean body composition (Wharton, 1969; Smith, 1976; Costanzo, 1985; Congdon, 1989; Blem, 1997; McCue, 2007) and their heretofore undocumented ability to adaptively reduce metabolic expenditure during starvation.

What supply- and demand-side accommodations are made by snakes to allow them to survive bouts of starvation that exceed those tolerated by most other vertebrates? This study examined this question by characterizing and comparing the starvation strategies among three distantly related snake species (*Python regius*, ball pythons; *Elaphe obsoleta*, ratsnakes; and *Crotalus atrox*, western diamondback rattlesnakes) subjected to a biologically realistic period of starvation that approximates a complete active season. Measurements of energy expenditure and changes in organic and inorganic body composition were used to examine how these animals ration their endogenous resources using various supply- and demand-side strategies.

Methods

Subadult *P. regius* ($n = 20$), *Elaphe obsoleta* ($n = 22$), and *C. atrox* ($n = 20$) were individually caged and acclimated for 6–12 months to common laboratory conditions (i.e., 12L:12D; 27 ± 1 °C) prior to experimentation in order to minimize differences in their feeding histories and body condition (BC). During the acclimation period, snakes were fed every 5–10 days, and provided water ad libitum. Fourteen days following their last meal, all snakes were postabsorptive (Bennett and Dawson, 1976; McCue, 2006a) and were thus beginning the process of starvation (i.e., starvation day 0). A minimum of four snakes representing each species were randomly assigned to one of four treatment groups and were subsequently euthanized at starvation days 0, 56, 112, or 168. Additional animals were assigned to each of the treatment groups, and were used to serve as replacement animals in the event that some individuals were unable to complete the experiment. Even if no mortalities occurred, these replacement animals were to be monitored through the entire starvation experiment.

The following morphological and physiological measurements were made on all snakes at starvation day 0. Snout-vent-lengths (SVL) were measured to the nearest 0.5 cm using a squeeze-box (Quinn and Jones, 1974; Blouin-Demers, 2003) and body masses were measured to the nearest gram. Mean rates of resting oxygen consumption (RMR; $\mathrm{ml\,O_2\,h^{-1}}$) were quantified over a 24 h period at 30 °C using a Sable Systems FC-1 oxygen analyzer connected to a computer-controlled multiplexer that serially subsampled excurrent gas from eight animal chambers every hour; a detailed process diagram outlining the measurement apparatus is available from McCue (2006b). Rates of oxygen consumption for each snake were calculated using the following equation modified from Withers (1977), where $O_{2\,\mathrm{consumption}}$ is aerobic metabolic rate ($\mathrm{O_2\,ml\,h^{-1}}$), E_{STPD} is mass flow of the gas stream passing through respirometry chambers, and O is the fractional concentration of incurrent (i) and excurrent (e) gas streams:

$$O_{2\,\mathrm{consumption}} = \frac{[O_\mathrm{i} - O_\mathrm{e}] \times E_{\mathrm{STPD}}}{1 - [O_\mathrm{i}]}.$$

At subsequent 56-day intervals (i.e., 56, 112, and 168 days of starvation) identical metrics were quantified on all remaining snakes. BC was calculated using a standard equation, $\mathrm{BC} = 100 \times g/\mathrm{SVL}^3$ (Saiki and Tash, 1978; Barton and Schreck, 1988). On starvation day 0 four snakes were euthanized with an overdose of IsoFlo® (> 5 ml/kg) to provide baseline compositional measurements that were later compared to other treatment groups. A minimum of four snakes of each species were also euthanized at starvation days 56, 112, or 168 according to their treatment group assignment. Following euthanasia the livers and hearts were removed from each snake and weighed to the nearest 0.001 g. After replacing these excised organs into the thoracic cavities of the snakes, the entire body of each animal was individually pureed using a commercial-grade blender. A 100 g subsample of each pureed snake was freeze-dried to determine its moisture content. Once dried, these dried subsamples of each snake were pooled according to their respective species-treatment group and pulverized into a fine powder using a Wiley Mill®. Processed tissues were stored at −20 °C prior to compositional analyses at the University of Arkansas Central Analytical Laboratory (Fayetteville, AR).

Tissue ash content was determined by combusting samples in a muffle furnace (AOAC Official Method 934.01). Crude fat in tissues was quantified by extracting samples with petroleum ether. Crude protein was determined through combustion analyses (AOAC Official Method 990.03) and carbohydrate content was determined by using the addition method (i.e., % lipid + % protein + % ash + % carbohydrate = 100% dry sample mass; Caloin, 2004).

All statistical comparisons were conducted using StatView (SAS). When possible, repeated measures were used for statistical analyses; however, because some of the response variables (e.g., organ masses and proximate analyses) precluded the use of repeated measures, unpaired comparisons were used. Critical significance for *t*-tests, repeated measures analyses of variance (ANOVA), analyses of covariance (ANCOVA), and Fisher's PLSD *post hoc* tests were set at $\alpha < 0.05$. Mean values presented in the text are followed by standard deviations (e.g., $X \pm X$).

Results

At the start of starvation snake masses were 261 ± 53g, 170 ± 19g, and 431 ± 82 g for pythons, ratsnakes, and rattlesnakes, respectively. Snakes lost total body mass at a rate that was dependent on their initial mass and is best described by the linear equation $y = 0.2688x - 21.148$ ($p = 0.012$, $R^2 = 0.790$), where y represents mass loss at 168 days and x represents the initial body mass (Fig. 1). ANOVA and *post hoc* tests revealed that the *relative* rates of mass loss experienced by snakes differed among the species ($p < 0.0001$). For example, following 168 days of starvation, ratsnakes ($n = 8$), pythons ($n = 6$), and rattlesnakes ($n = 5$) had lost 9.3%, 18.3%, and 24.4% of their initial masses, respectively. According to ANOVA, the initial (i.e., prestarvation) BC of the snakes significantly differed among the three species ($p < 0.0001$). Repeated-measures ANOVAs comparing BC at starvation day 0 with day 168 revealed that the BC of all three species had decreased significantly (ratsnakes, $p < 0.0001$; pythons, $p < 0.0001$; rattlesnakes, $p = 0.0075$).

All three snake species increased their SVL over the 168-day period (Fig. 2); however, the relative increase in SVL did not differ among the species ($p = 0.5605$). The average increase in SVL for all three species was 4.3 ± 2.1% of initial SVL.

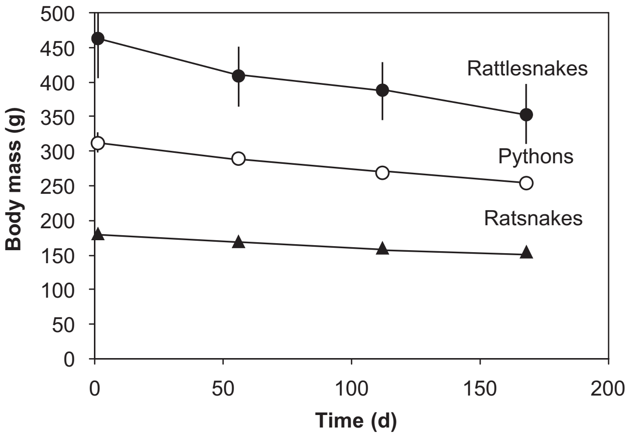

Fig. 1. Snakes lose mass during starvation. Data points represent repeated measures of rattlesnakes ($n = 5$), pythons ($n = 6$), and ratsnakes ($n = 8$), and error bars denote ± 1 standard error. It should be noted that in some cases the symbols used are larger than the error bars.

Starvation-induced changes in resting metabolic rates were apparent in all three species (Fig. 3). Ratsnakes and rattlesnakes demonstrated significant starvation-induced metabolic depressions (Table 1). Rattlesnakes and ratsnakes demonstrated the greatest metabolic reductions (i.e., 72% and 45%, respectively) at 168 days of starvation. On the other hand, the pythons demonstrated their greatest metabolic reductions (i.e., 41%) at 112 days. By 168 days of starvation, their metabolic rates partially recovered to levels that were only 23% lower than their initial rates. Nevertheless, the metabolic rates of pythons at 168 days of starvation were still significantly lower than their initial values ($p = 0.0012$).

Measurements of body water revealed that all three snake species increased the relative moisture content of their tissues by an average of $5.9 \pm 2.0\%$ during the experiments (Fig. 4). The starvation-induced increase in relative moisture content did not differ significantly among the species, despite the fact that the initial and final moisture content differed significantly among the species ($p = 0.3347$ and 0.0001, respectively).

The relative wet masses of cardiac and/or hepatic tissues were generally influenced by starvation. Ratsnakes demonstrated significant decreases in relative liver mass at 168 days of starvation ($p = 0.0096$), but did not demonstrate significant changes in cardiac mass. Conversely, pythons demonstrated no significant change in relative liver mass during starvation, but did demonstrate significant reductions in relative heart mass ($p = 0.0222$; Table 2). Significant starvation-induced changes in the organ masses of rattlesnakes were previously reported in McCue (2007), and are thus not further discussed here.

Because body tissues were pooled using an equal weighting procedure prior to compositional analyses, the measured values reflect only mean values for each species at each experimental time point and could not be characterized statistically. Nevertheless, clear patterns of starvation-induced changes in body composition were observed among the snakes (Fig. 5). For example, relative protein content generally increased in all species during starvation. Lipid and carbohydrate content generally decreased during starvation, whereas relative ash content either increased or remained the same.

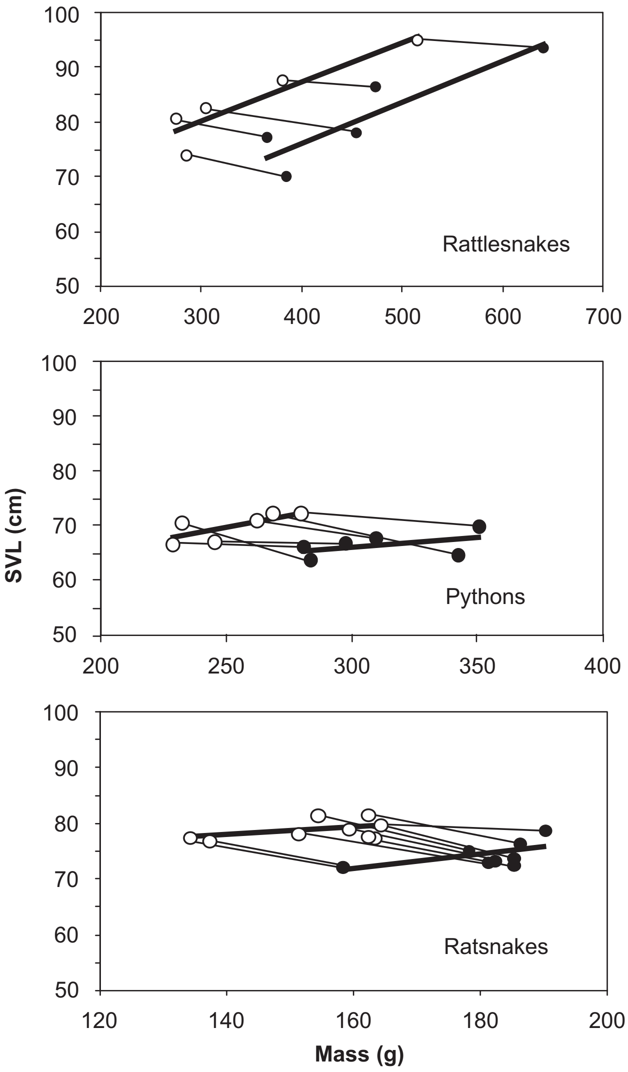

Fig. 2. Snakes can increase body length during starvation. Closed and open data points represent SVL at 0 and 168 days of starvation, respectively. Data points for each individual are connected with a thin line. Comparisons of starvation treatment (thick lines) were made using repeated-measures ANCOVAs (see text for details).

Discussion

All three-snake species demonstrated potentially adaptive supply- and demand-side regulation of mass

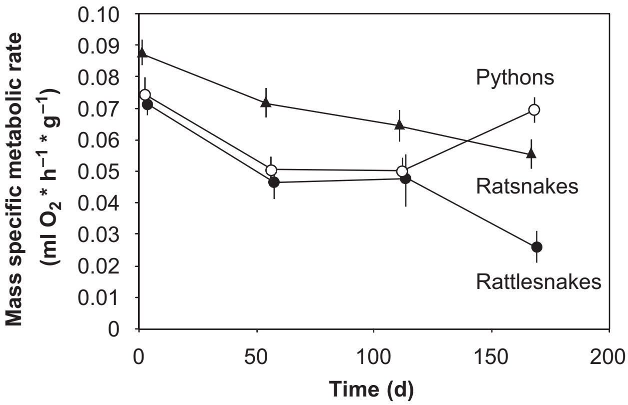

Fig. 3. Starving snakes undergo adaptive metabolic depression. Note that the symbols are slightly staggered to better illustrate the standard error bars.

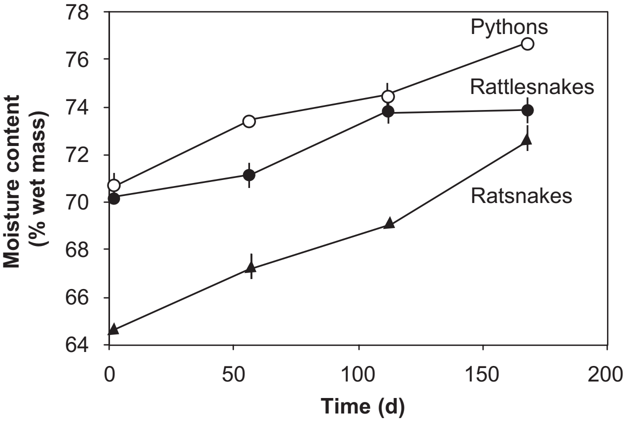

Fig. 4. Moisture content increases in starving snakes. Data points represent relative moisture content (% water) measured in four snakes of each species at each time point. Vertical bars indicate ±1 standard error.

Table 1. Starvation-induced reductions in metabolic rates

Species	Slope (*p*-value)	Intercept (*p*-value)
Rattlesnake	0.5536	0.0023
Python	0.3677	0.1092
Ratsnake	0.5576	0.0073

Repeated measures ANCOVAs comparing $\log_{10}$ metabolic rate as a function of $\log_{10}$ body mass in snakes at the beginning and the end of the starvation experiment.

Table 2. Organ masses change in response to starvation

Species	Starvation (day)	Cardiac index	Hepatic index
Python	0	0.17	1.75
Python	0	0.35	2.02
Python	0	0.20	1.77
Python	0	0.20	1.73
Python	0	0.35	2.43
Python	56	0.15	1.24
Python	56	0.23	1.65
Python	56	0.20	1.79
Python	56	0.15	1.70
Python	112	0.16	1.81
Python	112	0.18	1.94
Python	112	0.19	1.48
Python	112	0.20	2.05
Python	168	0.15	2.08
Python	168	0.14	1.77
Python	168	0.18	1.81
Python	168	0.17	1.81
Ratsnake	0	0.20	1.70
Ratsnake	0	0.27	2.41
Ratsnake	0	0.19	1.95
Ratsnake	0	0.18	1.90
Ratsnake	56	0.27	1.40
Ratsnake	56	0.24	1.25
Ratsnake	56	0.24	1.49
Ratsnake	56	0.21	1.48
Ratsnake	112	0.20	1.27
Ratsnake	112	0.22	1.80
Ratsnake	112	0.14	1.91
Ratsnake	112	0.16	1.24
Ratsnake	168	0.18	1.24
Ratsnake	168	0.16	1.21
Ratsnake	168	0.17	1.45
Ratsnake	168	0.16	1.02
Ratsnake	168	0.13	1.46
Ratsnake	168	0.22	1.20
Ratsnake	168	0.15	1.57

Cardiac and hepatic indices (organ mass/body mass) calculated for two snake species undergoing starvation.

and energy during starvation. For example, all snakes reduced their overall metabolic demands, and preferentially mobilized lipid stores to meet their energy requirements. Interestingly, the degree to which these strategies were adopted differed among the species examined. The following sections outline the calculations that were used to generate these conclusions.

Although the animals used in these experiments differed somewhat in body size, the relatively narrow range of body masses examined herein allowed the observed morphological and compositional responses to be corrected to a common body size (i.e., 300 g). This mass correction was necessary to permit comparisons of starvation strategies among the three species. Below, I use raw data from the pythons to explain the calculations that I used to reconstruct the total energy requirements for snakes. The mean mass of pythons at starvation day 0 was 311 g. Their RMRs averaged $22.9\,\mathrm{ml\,O_2\,h^{-1}}$ at day 0, and was best described by the equation $\mathrm{RMR} = 0.717W^b$ where W is body mass in grams, and b is some allometric scaling coefficient

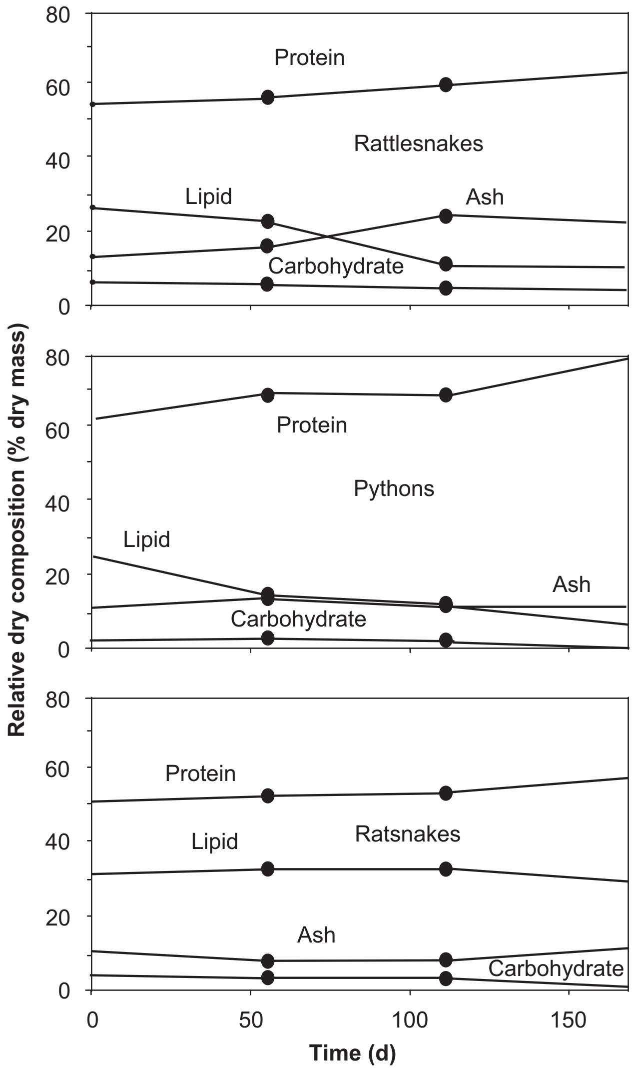

Fig. 5. Body composition changes in starving snakes. Data points represent non-repeated, equally weighted, pooled measurements made on four snakes representing each species.

(typically valued between 0.6 and 0.8). Assuming an allometric scaling coefficient '*b*' of 0.70 (Andrews and Pough, 1985; Dmi'el, 1986; Beaupre, 1993; Nagy et al., 1999; McCue and Lillywhite, 2002), the aforementioned power function predicts that the RMR of a 300 g python would be 22.5 ml $O_2\,h^{-1}$ measured at 30 °C. However, because all snakes were kept at 27 °C during the experimental trials, a Q_{10} correction factor was also required (McCue, 2004). A factor of 2.0 (Chappell and Ellis, 1987; Beck, 1995; Beaupre and Zaidan, 2001; McCue and Lillywhite, 2002; Dorcas et al., 2004) was applied to the following equation to estimate RMRs at a temperature of 27 °C (e.g., 18.3 ml $O_2\,h^{-1}$):

$$Q_{10} = \frac{[\mathrm{RMR}_{30\,^\circ\mathrm{C}}]^{10/\Delta\mathrm{temp}}}{[\mathrm{RMR}_{27\,^\circ\mathrm{C}}]}.$$

Because snakes were continually losing mass while starving, identical allometric and temperature corrections were made on the subsequent metabolic measurements made at 56, 112, and 168 days.

In order to estimate the total energy expended over the entire starvation experiment, the 168-day trial was divided into three temporal segments over which individual estimates of energy consumption were integrated. For example, during the first 56 days, energy expenditure was assumed to represent the average RMRs measured on days 0 and 56. Similarly, between days 56 and 112, the energy expenditure was assumed to represent the mean RMRs measured on days 56 and 112, and the metabolic expenditure during the final 56 days was estimated as the mean RMR measured on days 112 and 168. The total oxygen consumed during each of these three time periods was summed. The resulting model predicted that a 300 g ratsnake, python, and rattlesnake would require 864, 977, and 933 kJ of energy, respectively, to survive 168 days of starvation under the given experimental conditions (Fig. 6).

The mass-corrected estimates of energy expenditure were then coupled with information about the net compositional changes measured in snakes in order to understand how the different species relied on individual physiological fuels during starvation. Again, I use data

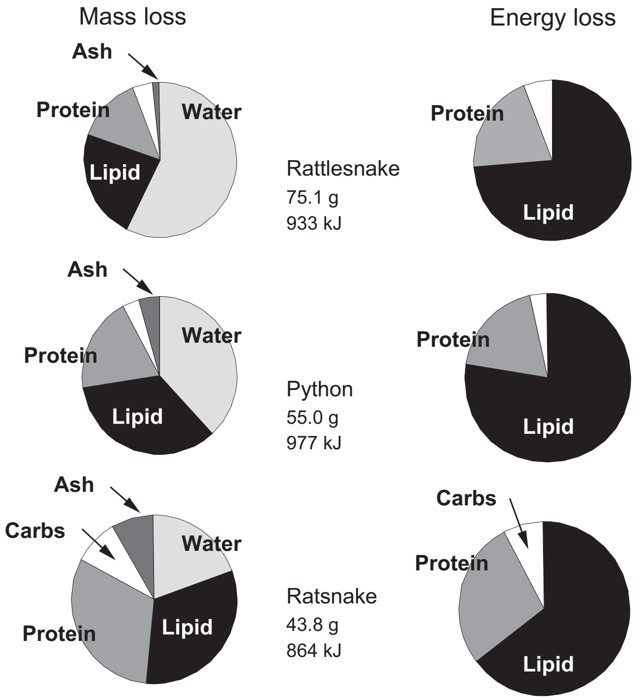

Fig. 6. Snake species differ with regard to starvation responses. Results are extrapolated from measured changes in total mass and organic and inorganic composition as well as metabolic expenditure during starvation. Values were corrected to a common body mass (i.e., 300 g; see Discussion for details).

from the python trials to explain how I reconstructed the compositional changes for a hypothetical 300 g python faced with 168 days of starvation. Because pythons lost 18.3% of body mass during the experiment, a 300 g python would be expected to lose 55 g of total mass. Although the pythons were losing total body mass, their relative body water content increased from 70.2% to 77.3%, and net water loss thus accounted for approximately 21 g of the total loss. The remaining 34 g was necessarily lost as dry mass (i.e., protein, lipid, carbohydrate, and ash). Given the observed changes in total mass, water content, and dry composition, hypothetical snakes representing each species could be reconstructed at each respective time point (e.g., pythons at days 0 and 168 are described in Table 3). Finally, assuming energetic equivalents of 17.58 and 39.94 kJ for the oxidation of carbohydrates/proteins and fats, respectively (Kleiber, 1975; Nagy, 1976), losses in organic mass could be equated with each species' energetic demand (Fig. 6) to understand how they were mobilizing their limited resources during starvation.

Because the resultant models describing mass-energy utilization in starving snakes involved numerous response variables and multiple assumptions, they are precluded from formal statistical analyses. Nevertheless, this modeling approach offers a novel tool for qualitative comparisons of starvation strategies among different animal species. The subsequent comparisons of starvation strategies among snakes revealed subtle similarities and differences with regard to the starvation responses among them that might otherwise be difficult to detect. For example, despite their comparatively lean body composition prior to food deprivation, all three species chiefly relied on lipid oxidation followed by protein and carbohydrate oxidation to meet their energetic demands. Other similarities included the fact that relative losses of water and protein were inversely related to one another, relative rates of ash loss were directly proportional to losses in protein, and energy reliance on lipid oxidation was inversely proportional to that on carbohydrates. One of the most obvious differences among the species was in their rates of mass loss. Moreover, the models revealed that the majority of the differences in total body mass loss experienced during starvation could be explained by water loss, which was highest in rattlesnakes and lowest in ratsnakes. This finding was not initially predicted given the comparatively xeric habitats typically inhabited by western diamondback rattlesnakes, and raises additional questions about the underlying causality and potential benefits of starvation-induced changes in tissue water content (see discussions in Blasco et al., 1992; Cherel et al., 1992; Hardy et al., 2000; Hervant et al., 2001; Simpkins and Hubert, 2003).

Adaptive modulation (*sensu* Bock, 1980) of metabolic expenditure is the primary mechanism for regulating *demand-side* mass-energy flux during starvation, and examples of mass-specific metabolic depression have been previously reported in starving animals (Mata et al., 2001; Rios et al., 2002; Chwalibog et al., 2004; Ehrhardt et al., 2005; McCue, 2006c). Interestingly, this adaptive response is far from ubiquitous among vertebrates (Roberts, 1968; Shapiro and Weathers, 1981; Worthy and Lavigne, 1987), and can thus be used as a criterion to determine whether or not a particular species is evolutionarily suited to tolerate starvation (Worthy and Lavigne, 1987; Mehner and Wieser, 1994). While metabolic depression was observed among the three snakes examined here, they differed with regard to the extent to which they did this. Considering the current paradigm (see discussions in Secor and Diamond, 2000; Beaupre and Montgomery, in press) that foraging strategy is highly correlated with feeding frequency among snakes (e.g., ambush foraging snakes consume meals less frequently and thus experience starvation more often), I expected that ratsnakes would exhibit a reduced capacity to adaptively reduce energy expenditure compared to the pythons and rattlesnakes. As the data reveal, this was not necessarily the case. Additional studies that characterize physiological responses to starvation among additional active and ambush foraging snake species as well as appropriate

Table 3. How do snakes 'spend' their mass and energy during starvation?

	Day 0			Day 168			Total		
	Dry (%)	Wet (%)	Wet (g)	Dry (%)	Wet (%)	Wet (g)	Mass loss (g)	Conversion (kJ/g)	Energy (kJ)
Protein	**60.6**	18.1	54.2	**77.9**	17.7	43.3	10.9	17.6*	191.0
Fat	**26.1**	7.8	23.3	**7.9**	1.8	4.4	18.9	39.9*	753.2
Carbohydrate	**2.3**	0.7	2.1	**0.4**	0.1	0.2	1.9	17.6*	32.6
Ash	**11.1**	3.3	9.9	**13.4**	3.0	7.5	2.4	–	–
Water	–	**70.2**	210.0	–	**77.3**	189.5	20.5	–	–
Total	**100**	100	300	**100**	100	245	55.0	–	976.9

An example of the mass-energy changes in a hypothetical 300 g python at starvation days 0 and 168. Values in bold were measured directly and values with asterisks are constants; all other values were calculated from measurements made on actual pythons (see Discussion for details).

squamate reptile outgroups will be required to further examine this hypothesis.

Starvation-induced reductions in the standard length of fishes have been previously reported (Boetius and Boetius, 1985), but the present study is the first to document that snakes can increase their SVL during starvation. The apparent 'growth' during starvation was surprising, primarily in light of published and unpublished accounts of starvation-induced reductions in reptile body length by herpetologists (Wikelski and Thom, 2000; Taylor et al., 2005; personal communications: R.F. Hoyer, J.M. Ray, and R.W. Applegate). Given this unexpected finding, the author conducted a parallel study to quantify the measurement error involved in repeatedly measuring SVL using the squeeze-box method. That study revealed that coefficients of variation were less than 0.5% for an 80 cm snake, a variance similar to that reported by other researchers using similar measurement techniques (Madsen and Shine, 2001; Blouin-Demers, 2003). It should be noted that increase in SVL observed in the snakes could be related to the fact that subadult animals were measured. Nevertheless, when one considers the energetic costs of mobilizing endogenous material resources that must occur during growth (Peterson et al., 1996; Nagy, 2000; Beaupre and Zaidan, 2001; McCue, 2006b), the finding that food-limited subadult snakes 'grow' at all raises questions about the fitness implications associated with increased body length among subadult snakes (see discussion in Blouin-Demers et al., 2002).

Starvation is known to be a leading cause of mortality among many wild animal populations (Cherel et al., 1987; Cooper and Laurie, 1987; Pontes et al., 1988; Madsen and Shine, 1993; Plisetskaya et al., 1994; Halat and Lehman, 1996; Boersma, 1998; Lillywhite et al., 2002; Lowe, 2002; McConkey et al., 2004), and undoubtedly poses challenges to countless others. A better understanding of the strategies that allow snakes to survive extreme bouts of starvation promises to provide valuable insight into low-energy lifestyles that have allowed snakes to persist in resource-limited environments and successfully radiate into over 3000 species since the Upper Cretaceous (Pough, 1980; Gans, 1983; Greene, 1983; Pough and Groves, 1983; Rage, 1997), and might lead to new techniques to monitor nutritional stress and/or provide prophylactic treatments that increase starvation tolerance in other animals.

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