Journal of Herpetology, Vol. 33, No. 2, pp. 229–234, 1999

Energetic Cost of Predation: Aerobic Metabolism during Prey Ingestion by Juvenile Rattlesnakes, *Crotalus durissus*

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ABSTRACT.—**We investigated the cost of prey ingestion in the South American rattlesnake, *Crotalus durissus*, to see if the capacity to generate energy aerobically could be a constraint on the size of the prey that can be ingested. To accomplish this goal, we measured time and aerobic metabolism (inferred from oxygen consumption) of juvenile *C. durissus* ingesting prey ranging from 10 to 50% of their own body mass. Time needed for prey ingestion increased with prey size, with prey representing 10 and 20% of snake size being ingested with the same effort. Whole animal rates of oxygen consumption increased linearly with prey size, but at a slower pace for snakes ingesting prey larger than 30% of their body mass. Aerobic factorial power input necessary for prey ingestion increased with prey size, and for snakes ingesting prey representing 50% of their body mass it equaled the aerobic factorial scope for exercise. For the maximum prey size tested, the aerobic derived energy necessary for prey ingestion represented 0.02% of the total energy content of the prey. Within the prey size range we studied, the cost of ingestion did not constitute any constraint on the size of the prey that can be ingested. These constraints are set by morphological (gape size), ecological (predation risk), and, probably, by physiological parameters, as suggested by the tendency of $\dot{V}O_2$ during ingestion to increase at a slower pace at relative larger prey sizes.**

Several evolutionary scenarios consider morphological modifications related to dietary demands as the main driving force for the impressive radiation experienced by snakes (Rieppel, 1980; Greene, 1983). Early in the evolution of this group, small modifications of the jaw apparatus permitted them to ingest prey of relatively large mass (Gans, 1961). This modification were associated with a shift in foraging mode, from frequent ingestion of small prey to infrequent ingestion of large prey (Greene, 1983).

The feeding biology of snakes has been examined from several perspectives: predator-prey relationships (Arnold, 1993), kinematics of jaw apparatus during prey handling and ingestion (Cundall, 1987), dietary correlates of evolution (Greene, 1983), and physiological aspects of digestion (Andrade et al., 1997). Despite the attention given to morphological, behavioral, and ecological aspects of predation in snakes, some fundamental questions remain. For example, studies on the energetic correlates of predation in snakes are rare (Feder and Arnold, 1982). In lizards, studies on energetic expenditure associated with ingestion of different prey sizes have provided data that have clarified some aspects related to optimal foraging theory (Pough and Andrews, 1985), the constraints on feeding due to their morphological adaptation for a particular habitat (Andrews et al., 1987), the metabolic support (aerobic or anaerobic) during feeding (Preest, 1991), and the relationship between prey size and sexual size dimorphism (Preest, 1994). Nonetheless, extrapolation of these interpretations to snakes may be misleading, due to fundamental differences in feeding mechanisms between these groups (Gans, 1961).

Herein, we quantify aerobic metabolism and the time expended by juvenile South American rattlesnakes, *Crotalus durissus*, in ingesting prey of relative different sizes. *Crotalus durissus*, like other viperids, possess very derived specializations associated with feeding and ingest prey of a wide size range (S. S. Santana, unpubl. data), which make it a suitable model to test the effects of prey size on feeding energetics in snakes. Since there is a lack of data on the relationship between energetic expenditure and prey ingestion in snakes (but see Feder and Arnold, 1982), we analyzed our data in two ways: (1) by comparing energy expenditure for ingesting different prey size with the maximum aerobic capacity of this species, and (2) by analyzing the relationship between energy input and return associated with the ingestion of different prey sizes. With this approach we attempted to determine how the physiological capabilities, in terms of oxygen consumption, vary with the ingestion of different relative prey sizes. The results will help to determine if these variation sets an upper limit to the size of the prey that can be ingested by juvenile *C. durissus*.

MATERIAL AND METHODS

Experimental Animals.—We used 15 juvenile *Crotalus durissus* of both sexes in this study.

These snakes came from the same litter as those used in our previous study on the energetics of digestion in rattlesnakes (Andrade et al., 1997). Protocol for maintenance of the snakes in captivity are in Andrade et al. (1997). We fasted snakes for at least 10 d before the experiments in order to raise the level of hunger, and used only healthy snakes that were not in shedding phase.

Experimental Protocol.—We assessed the aerobic cost of ingestion by measuring rates of oxygen consumption before and during prey swallowing. All experiments were carried out in a constant temperature room at 30 C. After weight measurements, we placed a snake in a metabolic chamber (volume = 1.2–1.8 L). The snakes were left overnight in this condition and during this time room air was pumped through the chamber. On the next morning, the pump was shut off, the chamber sealed, and rates of oxygen consumption were measured for the next two hours by taking a 10 ml sample every 30 min. To assure mixing, we pushed air back and forth several times with a syringe before taking a sample. After removing CO_2 and water vapor, we injected the air sample into an Applied Electrochemistry S3A Oxygen Analyzer. Oxygen concentration was read directly from the digital output of the O_2 analyzer and whole-animal rates of oxygen consumption ($\dot{V}O_2$) were calculated according to Vleck (1987).

Following baseline measurements, we opened the chamber and introduced a live mouse weighing 10, 20, 30, or 50% (±1% for all cases) of the body mass of the snake in the respirometer. Each of the fifteen snakes used in this experiment were tested with each of the four prey sizes, with an interval of 10–20 d between measurements. We randomly determined the order of prey presentation to avoid possible effects of training on prey ingestion ability and to balance, as closely as possible, the snake masses among experimental groups (see below).

In all cases, following the introduction of the prey in the respirometer, the snakes immediately struck and released the prey. The prey often died in less than 5 min, and the snake started to ingest it after 2–10 min. When the swallowing phase of ingestion started, we took a first 10 ml sample and injected it into the O_2 analyzer. A second 10 ml air sample was taken when the prey had just disappeared into the snake mouth and the tongue first protruded. During this procedure, we pushed air back and forth several times with a syringe before taking a sample in order to assure perfect mixing. We recorded with a stop-watch the time elapsing between these stages, and calculated whole-animal rates of oxygen uptake as described above. Only snakes that swallowed prey head-first were included in the analysis.

Data Handling and Analysis.—We assumed that the average of the two lowest values recorded before the feeding trials was the standard metabolic rate (SMR). For the feeding trials we assumed that the oxygen consumed and time elapsed between the first and second sample represented, respectively, the oxygen consumption (VO_{2ing}) and time expended (T_{ing}) during prey ingestion.

We transformed VO_{2ing} and prey mass to energetic equivalents by estimating the following parameters: (1) Energy content of the prey, by assuming that each g of a mouse (wet mass) yields 8.95 kJ (Smith, 1976); (2) the net energetic cost of ingestion by assuming that each ml of O_2 consumed during prey ingestion (after subtracted the cost of maintenance during this period, calculated from SMR values) was equivalent to 0.0198 kJ (Gessman and Nagy, 1988). The percentage of the total energy content of the prey that is used for ingestion was found by the following formula:

(net energetic cost of ingestion
÷ total energy content of the prey) * 100

For statistical purposes, we defined four groups, based on the weight ratio of prey / snake body mass (hereafter referred as G10%, weight ratio = 0.1; G20%, weight ratio = 0.2; G30%, weight ratio = 0.3, and G50%, weight ratio = 0.5). Comparisons of the variables (body mass, SMR, VO_2, VO_{2ing}, T_{ing}, and so on) were carried out between these groups. Because each individual was measured repeatedly for each prey size, we employed a one way repeated-measure ANOVA with univariate-corrected probabilities (Potvin et al., 1990). Before running this test, we checked for the assumptions of normality and homogeneity of variances. If these assumptions failed, we first attempted to log-transform the variables prior to analysis. A parametric ANOVA was used in the cases where the log-transformation helped to achieve normality and homogeneity. In situations where this was not the case, a Friedman Repeated Measures Analysis of Variance on Ranks was used with the raw data. Since we had equal number of observations for each group, a Student Newman-Keuls (SNK) post-hoc test was used to distinguish differences between experimental groups. We present all values as mean ±1 SD and designate the level of statistical significance as $P \leq 0.05$.

Results

Mean body mass of the snakes varied only about 1% among the experimental groups, ranging from 49.8 to 50.4 g (Table 1). There was no difference between snake body mass among the

TABLE 1. Snake body mass (grams), meal mass (grams), meal energy (kJ), cost of ingestion, quantified as kJ and as a percentage of total energy content of prey for juvenile *Crotalus durissus* ingesting mice equalling 10%, 20%, 30%, and 50% of snake body mass (experimental groups). The calculations for meal energy, total energy content of prey and costs of ingestion are explained in the text. All values presented are mean ± 1 SD for 15 observations. Values in parentheses denote range of observations.

Experimental groups	Snake body mass	Meal mass	Meal energy (kJ)	Cost of ingestion (kJ)	Cost of ingestion/meal energy (%)
G1 (WR = 0.1)	49.9 ± 19.2 (23.5–85.6)	5.06 ± 1.9 (2.4–8.6)	45.3 ± 17.4 (19.4–69.2)	0.0013 ± 0.0002 (0.0003–0.002)	0.003 ± 0.001 (0.001–0.005)
G2 (WR = 0.2)	50.4 ± 18.5 (26.6–85.1)	10.03 ± 3.7 (5.2–16.6)	89.8 ± 34.1 (41.4–133.1)	0.008 ± 0.007 (0.0016–0.026)	0.008 ± 0.004 (0.003–0.02)
G3 (WR = 0.3)	49.03 ± 18.7 (25.3–79.3)	14.8 ± 5.6 (7.8–23.8)	132.5 ± 51.9 (61.9–190.3)	0.018 ± 0.015 (0.003–0.047)	0.01 ± 0.007 (0.004–0.02)
G4 (WR = 0.5)	49.8 ± 16.9 (27.8–80.4)	24.8 ± 8.5 (13.6–40.6)	221.5 ± 78.7 (108.8–324.8)	0.042 ± 0.035 (0.009–0.126)	0.02 ± 0.009 (0.007–0.03)

four experimental groups ($F_{3,59} = 0.49$, $P = 0.69$). VO_2 before feeding trials (SMR) followed the same pattern as described for snake body mass. There was no difference in SMR among experimental groups ($F_{3,59} = 0.86$; $P = 0.47$), with average values ranging from 0.044 to 0.046 $mlO_2 \cdot g^{-1} \cdot h^{-1}$ (Fig. 1A).

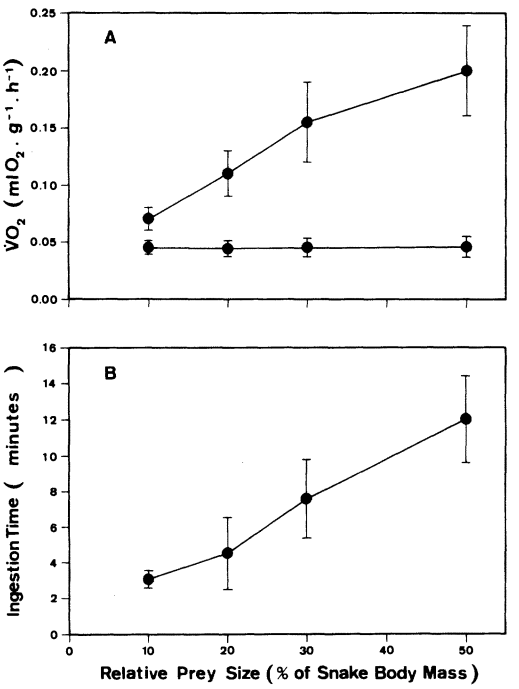

FIG. 1. Variations in oxygen consumption (A) and ingestion time in relation to the prey weight/snake weight ratio. Prey weight/snake weight ratio is represented as relative prey size (10, 20, 30 and 50%). Dots and transversal bars represent mean values and ±1 SD. Lower trace in A indicate the mean SMR values for the experiemental subjects.

We found that the rate of oxygen consumed during prey ingestion (VO_2) varied among the four experimental groups ($F_{3,59} = 100.8$; $P < 0.001$; Fig. 1A). VO_2 varied from 0.07 $mlO_2 \cdot g^{-1} \cdot h^{-1}$ for snakes in G10% to 0.21 $mlO_2 \cdot g^{-1} \cdot h^{-1}$ for snakes in G50%. VO_2 increased with the increase in prey size (Fig. 1A), so that the values recorded for the G50% > G30% > G20% > G10% (SNK: $P < 0.05$ for all comparisons). Time needed for ingesting a prey also varied among the experimental groups ($F_{3,59} = 69$; $P < 0.0001$; Fig. 1B), ranging from three minutes for snakes in G10% to 12 min for snakes in G50%. Snakes in group G50% took more time to ingest than snakes in other groups (SNK: $P < 0.05$ for all comparisons). Also, snakes in G30% needed more time to ingest than those in G20% or G10% (SNK: $P < 0.05$ for both comparisons). Snakes in G10% and G20% did not differ from each other in respect to time needed for ingestion (3 and 4.2 minutes—SNK: $P > 0.05$).

Data on ingestion cost are found in Table 1. Both the total energetic content of the prey ($F_{3,59} = 115.8$; $P < 0.0001$) and the net energy spent for ingestion ($F_{3,59} = 281.3$; $P < 0.0001$) increased with increasing prey size (SNK: $P < 0.05$ for all pairwise comparisons). The energy allocated for ingesting a prey varied with prey mass ($X^2 = 42.9$, df = 3; $P < 0.001$), representing only 0.003–0.02% of the total energy content of the prey.

DISCUSSION

Rates of oxygen consumption and time needed for ingestion increased with increasing relative prey size for juvenile *C. durissus*, but in a different fashion. VO_2 increased more sharply from G10% to G30% than from G30% to G50%, i.e., O_2 consumption rate did not increase proportionately with the increase in relative prey

size. Thus, our data suggest a tendency for the $\dot{V}O_2$ to increase at a slower pace as snakes took larger prey. Due to their lung morphology, the O_2 extraction efficiency of snakes is very low (Stinner, 1982). Moreover, it has been suggested that the rates of gas exchange of crotaline and viperine snakes are further constrained by the lower capacity of their cardio-respiratory systems (Lillywhite and Smits, 1992), which seems to be more pronounced in juveniles than in adults (Pough, 1977). Taken together, these limitations may account for the slow increase in $\dot{V}O_2$ as *C. durissus* were ingesting relative prey sizes above 30%. These limitation may be further enhanced because, during ingestion, the airway was blocked for most of the time. The extent by which O_2 stores present in air sacs could be used to accommodate the increased demand for O_2, and offset the problem of blocked airways during ingestion, is debatable (Brattstrom, 1959; McDonald, 1959). Thus, it seems that juvenile *C. durissus* have difficulty in supplying an adequate amount of O_2 during ingestion of relative large prey.

Facing the limitations discussed above, it is plausible that some of the energy needed by *C. durissus* to ingest relative large prey could be provided by anaerobic metabolism. Feder and Arnold (1982) reported that for *Thamnophis elegans* eating a salamander (*Plethodon jordani*) with a relative prey mass of about 14%, the total amount of energy derived from the anaerobic pathway may be as much as 26% of the total energy devoted to ingestion. Similar patterns, albeit with a lower proportion (ca. 8%), have been reported for lizards swallowing prey whole (Pough and Andrews, 1985; Preest, 1991). Anaerobic pathways may become important when animals reach a certain threshold where the demands for activity exceed levels than can be met by aerobic pathways (Taigen and Beuchat, 1984). In snakes, the upper limit of this threshold is normally associated with the aerobic factorial scope for activity (Ruben, 1976; Cruz-Neto and Abe, 1997), which, for juveniles rattlesnakes, is 4.4 (Andrade et al., 1997). The aerobic factorial power input necessary for juveniles *C. durissus* to eat prey representing 10, 20, 30, and 50% of their body mass is respectively, 1.6, 2.4, 3.4, and 4.3. This means that during ingestion of relative prey size ranging of 10, 20, 30, and 50%, *C. durissus* uses about 36, 55, 77, and 98% of their total aerobic factorial scope for activity. Notwithstanding the problem in comparing muscles that might have different oxidative capacities (see also Andrade et al., 1997; Secor and Diamond, 1997), it seems probable that *C. durissus* incur anaerobiosis when ingesting relative large prey, especially in the prey mass range above 30%. The use of anaerobic metabolism, however, has a serious drawback, since it is not very efficient in generating energy and is often correlated with rapid exhaustion (Glesson, 1991). Thus, a snake cannot rely on the use of this pathway for long periods, since exhaustion may jeopardize the ability to engage in other activities.

Ingestion time increased in an approximately linear way with relative prey size, with larger prey requiring more time to be ingested than smaller ones. Thus, the time for prey ingestion, contrary to that observed for $\dot{V}O_2$, continues to increase as relative prey size increases. Presently it is very difficult to determine if ingestion of large prey could be constrained by the longer time needed for its ingestion. However, as prey size increases, more time is needed for its ingestion, and the snake, during this process, may be at risk of predation. After ingestion, snakes that feed on large prey have their locomotion ability impaired (Garland and Arnold, 1983) which further increases the risk of predation. Given this considerations, it seems plausible that, together with morphological (e.g., gape size: see Forsman, 1996) and physiological limitations (discussed above), ecological factors (e.g., ingestion time) could make the large energetic return provided by a large prey less profitable.

In energetics terms, a given relative prey size might become limiting for a snake if the costs associated with all phases of predation (cf. Taylor, 1984) exceed the net profit provided by the prey. Considering only prey ingestion, we have shown that the aerobic cost to ingest prey ranging from 10 to 50% of the snake body mass represents only 0.003 to 0.02% of the total energy content of prey. These results, however, could represent only a fraction of the total ingestion cost, because we did not include the costs associated with the use of anaerobic metabolism, as well as the costs associated with a possible oxygen debt. Moreover, data on assimilation efficiency for rattlesnakes are not available. Feder and Arnold (1982) estimated that the total energetic cost of prey ingestion in *T. elegans* eating *P. jordani* was equivalent to 0.76% of the total energy content of the prey. If we only consider the amount of energy aerobically derived, *T. elegans* will spent ca. 0.3% of the total energetic content of the prey to ingest it (Feder and Arnold, 1982; Arnold, 1993). This value is aproximately 45 times higher than the energy expenditure expected for a rattlesnake ingesting a prey of same mass ratio. At present, we can relate this difference to three factors: (1) The aerobic cost of prey ingestion in *T. elegans* was estimated and not directly quantified; (2) the lower energy content of salamanders, compared to mice, causes an increase in the relative cost of

prey ingestion as expressed in percentual terms; (3) the specialized cranial morphology of viperid snakes (see Pough and Groves, 1983) could reduce the energetic cost of prey ingestion as compared to colubrids.

In summary, our data have highlighted some ways in which physiology, ecology, and morphology could interplay during prey ingestion in snakes. However, our data interpretation is far from being complete for two main reasons. First, to gain a complete overview of the energetic correlates of feeding in snakes we need to quantify the costs of prey pursuit and capture. Second, more data on other species of snakes are needed to verify if the pattern described here is restricted only to viperid snakes or constitutes a common feature for other snakes as well. The study of the aerobic and anaerobic metabolism during prey ingestion in snakes with variable feeding strategy and different degrees of morphological and ecological specializations for feeding would be very helpful. Also, the study of the possible variation that occur in the physiological parameters involved with prey ingestion during snakes' ontogeny, and the way this variation interacts with morphology (e.g., Forsman, 1996) and ecology (e.g., Greene, 1983, 1992), may help to understand some of the observed patterns of prey size—snake size relationship (Pough and Groves, 1983; Shine, 1991; Arnold, 1993).

Acknowledgments.—Financial support for this work was provided by CNPq (proc. 530339/93-5), FAPESP (proc. 94/6026-9) and FUNDUNESP (proc. 589/92-DFP) grants awarded to A. S. Abe. A. P. Cruz-Neto is in receipt of FAPESP graduate grants. E. M. Venticinque helped with statistical analysis and S. S. Santana allowed us access to unpublished data. M. Martins, R. A. Anderson and two anonymous reviewer provided valuable comments on an earlier version of this manuscript. J. Somera provided the figure.

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Accepted: 15 January 1999.

Journal of Herpetology, Vol. 33, No. 2, pp. 234–240, 1999

Effects of Post-hatching Maintenance Temperature on Desert Tortoise (*Gopherus agassizii*) Shell Morphology and Thermoregulatory Behavior

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ABSTRACT.—**Effects of post-hatching maintenance temperature on growth, morphology, and behavioral thermoregulation were studied in the desert tortoise (*Gopherus agassizii*). Tortoises were held at one of three temperatures (19, 28, 37 C) during the four months following hatching, then placed into a control temperature of 28 C. Body mass, maximum plastron width, height, and length ratios were determined monthly for the following year. Nine months post-hatching, cloacal and shell temperatures were determined while animals were allowed to behaviorally regulate their temperature in a thermal gradient ranging from 23–45 C. Animals held at 37 C had a greater surface area-to-volume ratio (flat morphology) than animals maintained at 19 or 28 C (round morphology). These morphological changes were correlated with thermoregulatory behavior. Animals with a greater surface area-to-volume ratio (37 C) had a lower cycle frequency (movement between minimum and maximum temperatures) and higher mean core temperature than 19 and 28 C animals. These experiments indicate the existence of a window during juvenile development in which temperature will influence morphological and behavioral characteristics.**

During the summer months the desert tortoise exhibits a bimodal activity period, with animals more active during the early morning and late afternoon. Animals retreat to shallow burrows during the hottest part of the day, where they are protected from the sun and can take advantage of the lower subsurface temperatures (Nagy and Medica, 1986). Even with activity limited during mid-day these animals must tolerate harsh temperature regimes and limited water availability. This tortoise has evolved a number of interesting behavioral and physiological mechanisms that allow it to survive in such a harsh environment (Auffenberg, 1969; Voight and Johnson, 1976; Bailey et al., 1995). Some of the less understood adaptations to hot, arid environments occur during development (embryonic and juvenile) when physiological set-points and behavioral thermoregulatory patterns can be established.

Environmental parameters have been shown to play a significant role in determining both morphological and physiological characteristics in a number of amphibian and reptilian species (Barber and Crawford, 1979; Burggren and Mwalukoma, 1983; Pinder and Burggren, 1983; Spotila and Standora, 1986). For example, incubation temperature influences the duration of development, sex ratios, and hatchling mass (Miller et al., 1985; Spotila and Standora, 1986; Gutzke and Packard, 1987; Packard and Packard, 1988; Spotila et al., 1994; Birchard and Reiber, 1995; Lewis-Winokur and Winokur, 1995). Incubation temperature has also been shown to alter long-term physiology and behavior in pine snakes (*Pituophis melanoleucus*), black racers (*Coluber constrictor*), kingsnakes (*Lampropeltis getulus*) (Burger, 1989, 1990) crocodiles (*Crocodylus siamensis*) (Lang, 1985), scincid lizards (*Bassiana duperreyi*) (Shine et al., 1997), water pythons