Review

Energetic and physiological correlates of prey handling and ingestion in lizards and snakes

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Abstract

In this review, we summarize the energetic and physiological correlates of prey handling and ingestion in lizards and snakes. There were marked differences in the magnitude of aerobic metabolism during prey handling and ingestion between these two groups, although they show a similar pattern of variation as a function of relative prey mass. For lizards, the magnitude of aerobic metabolism during prey handling and ingestion also varied as a function of morphological specializations for a particular habitat, prey type, and behavior. For snakes, interspecific differences in aerobic metabolism during prey handling seem to be correlated with adaptations for prey capture (venom injection vs. constriction). During ingestion by snakes, differences in aerobic metabolism might be due to differences in cranial morphology, although allometric effects might be a potentially confounded effect. Anaerobic metabolism is used for prey handling and ingestion, but its relative contribution to total ATP production seems to be more pronounced in snakes than in lizards. The energetic costs of prey handling and ingestion are trivial for both groups and cannot be used to predict patterns of prey-size selection. For lizards, it seems that morphological and ecological factors set the constraints on prey handling and ingestion. For snakes, besides these two factors, the capacity of the cardio-respiratory system may also be an important factor constraining the capacity for prey handling and ingestion. © 2001 Elsevier Science Inc. All rights reserved.

Keywords: Energetics; Feeding; Lizards; Metabolism; Snakes

1. Introduction

Among vertebrates, lizards and snakes are considered particularly suitable organisms to study the energetic and physiological correlates of feed-ing. Lizards and snakes are ectothermic animals and their activities, including feeding performance, are constrained by temperature which, in turn, affects their metabolism (Bennett and Dawson, 1976; Bennett, 1978, 1982). Lizards and snakes possess a suite of morphological, ecological and behavioral adaptations to feeding that can be correlated with their physiological traits (Regal, 1983; Cundall, 1987; Lillywhite, 1987).

For lizards and snakes, a feeding bout can be

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divided into four stages: prey search, subjugation (handling), ingestion, and digestion. The search stage of feeding can be described as one of two general strategies, usually referred to as sit-and-wait or widely foraging strategies (Huey and Bennett, 1986; Mushinsky, 1987). Physiological and energetic correlates of foraging strategies have been extensively analyzed, and several reviews are available (e.g. Bennett, 1982; Andrews, 1984; Huey and Bennett, 1986), and the physiological and energetic correlates of digestion are receiving growing attention (cf. Secor, 2001). On the other hand, studies on the energetic and physiological correlates of prey handling and ingestion by squamate reptiles lag behind those related to search and digestion. Also, no study has summarized the available information on this topic. In this review, we have attempted to fill this gap by reviewing current information on the energetic and physiological correlates of prey handling and ingestion in lizards and snakes.

2. Overview and general approach

To the best of our knowledge, only eleven studies have directly investigated the energetic and physiological correlates of feeding in lizards and snakes (Table 1). It is clear that the primary motivation behind each study differs appreciably and that the taxonomic breadth covered is very limited. Thus, attempts to make any generalizations would be premature. Instead, we will focus on a few detailed examples to analyze the absolute and relative contribution of aerobic and anaerobic metabolism during prey handling and ingestion, the extent by which factors such as morphology, behavior, temperature, prey type, etc., affect the absolute contributions of these metabolic pathways, and to what extent prey handling and ingestion require energy utilization close to the limits that the physiological machinery is able to deliver. We will also use the available data to assess questions on feeding energetics, such as: Do the costs of prey handling and ingestion result in relatively large expenses in comparison with energy intake? Do these costs place any constraints on the type (or size) of prey selected?

3. Lizards

Lizards have been regarded as model organ-

isms in ecological studies (Vitt and Pianka, 1993), so it is no surprise that investigations on the energetic correlates of prey handling and ingestion were directed to answering ecological questions. Nevertheless, all studies provided information about the aerobic and anaerobic metabolic rates, how these rates vary ontogenetically, with prey mass, morphological specializations, temperature, and behavior.

To analyze the available data for lizards, we considered some pitfalls and adopted the following protocol: (1) Measurement of metabolic rate in lizards includes the sum of the aerobic and/or anaerobic metabolism during prey handling and ingestion. As handling and ingestion are different behavioral events, this may constitute a problem when the energetic cost of the entire feeding bout is to be quantified, especially if the handling phase is more expensive than the ingestion phase (Preest, 1994). (2) The first paper that directly measured metabolic rates during prey handling and ingestion found that up to 93% of the oxygen consumed in excess of resting levels occurred after ingestion (Pough and Andrews, 1985a). Based on this observation, several subsequent studies included rates of metabolism measured after ingestion in the total cost of feeding (Andrews et al., 1987; De Queiroz et al., 1987; Grimmond et al., 1994). However, all these studies were done with a single species (*Chalcides ocellatus*). Aerobic metabolism following feeding was apparently not elevated for the skink, *Eumeces inexpectatus*, even when large prey were eaten (Andrews et al., 1987). Thus, whether or not the oxygen debt is a generalized phenomenon associated with feeding in lizards is not known, and we opted not to include these values in the subsequent analysis. (3) We relied heavily on data for two species of lizards, *C. ocellatus* and *E. inexpectatus*, to highlight some of our points. We chose these species either because they were intensively used or because allometric equations were available for them, allowing us to predict some trends. In this regard, all the values for these species presented throughout the text, in tables and in the figures, are calculated on the basis of such allometric equations. Moreover, since these species are nearly identical in terms of body mass, most of our interpretations will not be confounded by allometric effects. (4) Based on the last consideration, we expressed rates of aerobic metabolism during prey handling and ingestion as

Table 1
Physiological and energetic correlates of prey handling and ingestion in lizards and snakes[a]

Species	Variable measured	Principal motivation
1. Lizards		
Chalcides ocellatus (Pough and Andrews, 1985a)	Aerobic and anaerobic metabolism	Quantify the costs of prey handling and ingestion
Sceloporus virgatus (Pough and Andrews, 1985b)	Anaerobic metabolism	Use of anaerobic metabolism during activity in natural conditions
Chalcides ocellatus and *Eumeces inexpectatus* (Andrews et al., 1987)	Aerobic metabolism	Correlated effects of morphological specializations on the costs of prey handling and ingestion
Chalcides ocellatus (De Queiroz et al., 1987)	Aerobic metabolism	Thermal dependence of the aerobic costs of prey handling and ingestion
Scincella lateralis (Preest, 1991)	Aerobic and anaerobic metabolism	Relative contribution of the aerobic and anaerobic metabolism for prey handling and ingestion
Chalcides ocellatus (Grimmond et al., 1994)	Aerobic metabolism	Effects of prey type on the aerobic metabolism for prey handling and ingestion
Anolis carolinensis (Preest, 1994)	Aerobic and anaerobic metabolism	Role of sexual head size dimorphism on the costs of prey handling and ingestion
2. Snakes		
Thamnophis elegans (Feder and Arnold, 1982)	Anaerobic metabolism	Verify the use of anaerobic metabolism during predatory encounters
Coluber constrictor (Stinner and Ely, 1993)	Blood pressure and heart rate	Characterize pulmonary and systemic blood pressure and heart rate during feeding
Crotalus durissus (Cruz-Neto et al., 1999)	Aerobic metabolism	Effects of prey size on the energetic costs of handling and ingestion; extent by which this costs approach metabolic limits
Boa constrictor (Canjani et al., unpublished data)	Aerobic metabolism	Effects of prey size on the energetic costs of handling and ingestion

[a] Variable measured refers to the parameter used by the authors to analyze the physiological and energetic aspects of prey handling and ingestion. Aerobic metabolism inferred from rates of oxygen consumption and anaerobic metabolism from rates of lactate production. The principal motivation was extracted from the main objectives of the study as reported by the authors.

the amount of oxygen (ml O_2) consumed in excess of pre-feeding (Preest, 1994). This value is taken to represent aerobic metabolism during prey handling and ingestion and, hereafter, will be referred to as $V_{O_{2HI}}$. We used relative prey mass (as % of lizard body mass) for most of the analysis.

3.1. Intraspecific variations: ontogeny and sexual size dimorphism

Small individuals of *C. ocellatus* (mean mass =

5.1 g) consumed, on average, the same amount of oxygen and required the same amount of time as large individuals (mean mass = 7.6 g) to handle and ingest relatively small prey (Pough and Andrews, 1985a). In fact, for small prey (approx. 2.5% of lizard body mass) rates of $V_{O_{2HI}}$ for both size classes were only 0.03 ml O_2. Moreover, prey with this relative mass required 38 and 35 s to be handled and ingested by large and small lizards, respectively. As prey size increases, $V_{O_{2HI}}$ and time required for handling and ingestion (T_{HI}) were slightly higher for small lizards than large
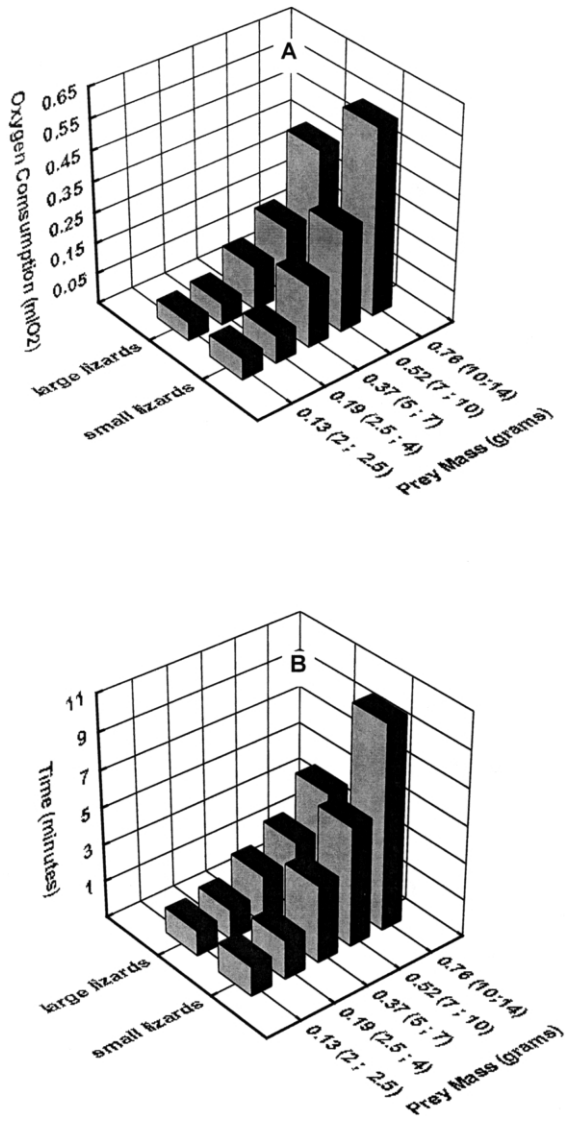
Fig. 1. Effects of prey mass on rates of oxygen consumption (a) and time (b) during handling and ingestion for small (5.1 g) and large (7.6 g) *Chalcides ocellatus*, as a function of the absolute prey. Number in parenthesis on the *x*-axis denotes equivalent relative prey mass for large and small lizards, respectively (after Pough and Andrews, 1985a).

ones (Fig. 1a,b), although the difference was not significant (Pough and Andrews, 1985a). Variations in T_{HI} during ontogeny in *C. ocellatus* probably can be ascribed only to morphological differences, although some degree of experience (naive vs. non-naive) has been reported to affect handling time in lizards (O'Connell and Formanowicz, 1998). Ontogenetic trends in Vo_{2HI} might be due to a trade-off between morphology and physiology. Small individuals need to con-

sume more oxygen than large ones to handle and ingest a given prey type because of morphological constraints. On the other hand, the absolute increase in Vo_{2HI} in juveniles is limited by its low resting mass-independent metabolic rate and low aerobic scope (Bennett, 1978) so that, in terms of relative increase, both juveniles and adults consumed the same relative amount of oxygen to eat a given prey size.

Intraspecific variations in Vo_{2HI} was also reported as being a consequence of sexual size dimorphism. Sexual dimorphism in lizards is often associated with differences in behavior, size and shape (Stamps et al., 1997), and it is supposed that differences in head size affect feeding performance. Preest (1994) investigated the feeding energetics related to sexual size dimorphism in the iguanid lizard *Anolis carolinensis* and found that, for a given prey mass, females (mass range: 1.45–4.00 g) subdued and ingested more slowly (two times) and required more oxygen (five times) than males (mass range: 2.01–6.12 g). These differences in feeding performance and costs were ascribed to differences in head size between males and females.

3.2. Effects of morphological specializations

Interspecific differences in Vo_{2HI} may be a consequence of specializations for a particular habitat. For example, fossoriality is often associated with a relatively small head and limited skull kinesis and gape (Gans, 1975) which, presumably, may compromise feeding efficiency. This hypothesis was tested by comparing Vo_{2HI} and T_{HI} in the sand-swimming lizard *C. ocellatus* with the terrestrial skink *E. inexpectatus* (Andrews et al., 1987). *Chalcides ocellatus* were unable to consume as large relative prey sizes as *E. inexpectatus*. Moreover, despite the fact that both species have the same mass (average mass: 11 g), for any relative prey size (except the small ones) *C. ocellatus* took longer and required more oxygen than did *E. inexpectatus* (see Fig. 2a,b) to handle and ingest it. The relative magnitude of the difference in Vo_{2HI} and T_{HI} between these two species might be confounded by factors such as head size dimorphism in *E. inexpectatus,* different source of animals (laboratory reared colonies vs. field captured individuals), and phylogenetic constraints (Andrews et al., 1987). Preest (1991) suggested that morphological differences may also explain
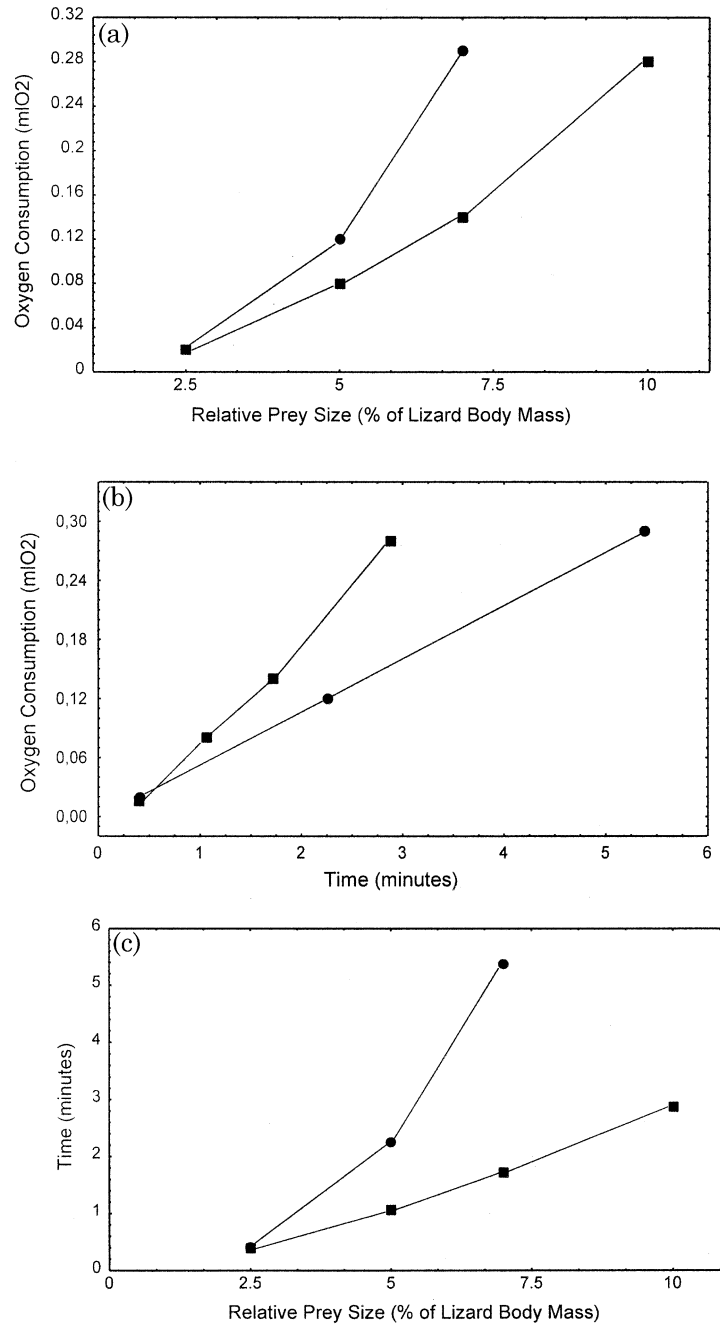
Fig. 2. Relationship between rates of oxygen consumption during handling and ingestion and relative prey size (a) and time (b), and between time and relative prey size (c) for the skinks *Chalcides ocellatus* (●) and *Eumeces inexpectatus* (■). Values for oxygen consumption and time calculated by the equations provided in Table 3 of Andrews et al. (1987), assuming a body mass of 11.1 g for both species (after Andrews et al., 1987).

why the ground skink *S. lateralis* showed a small increase in $V_{O_{2HI}}$ when compared with *C. ocellatus,* even though this species feeds on preys that are twice the relative size as those consumed by *C. ocellatus*. Although this explanation might be

correct, it should be noted that *C. ocellatus* is three times heavier than *S. lateralis* (body mass range: 0.93−2.46 g) and some of the difference can reasonably be ascribed to allometric effects on metabolic rate.

3.3. Effects of prey type and behavior

One problem in interpreting the results from studies that measured Vo_{2HI} is the potential confounding effects of behavior. Although almost all the studies listed in Table 1 did report the behavior of their experimental animals while inside the metabolic chamber, few attempt to analyze its effects on the results. For example, several studies reported that lizards stop ingestion and breathe deeply. This behavior has consequences both for time as well as for oxygen uptake, but seems to be regarded as a random, uncontrolled, variable (Pough and Andrews, 1985a; Andrews et al., 1987). Also, some studies listed in Table 1 used dead prey, although others offered live prey for the lizards. Dead prey may lack particular cues and thus may elicit different behaviors. Furthermore, dead prey will reduce T_{HI} and, perhaps, also Vo_{2HI}.

Besides these considerations, it is well known that a combination of prey mass, type, shape and firmness of exoskeleton affects feeding behavior (number of bites, head-first ingestion, dismembering the prey, etc.), and this, in turn, might affect feeding performance in lizards (Loop, 1974; De Queiroz and De Queiroz, 1987; Diaz and Carrascal, 1993; O'Connell and Formanowicz, 1998). For example, the Gilbert's skink, *Eumeces gilberti*, handled and ingested soft-bodied prey faster than hard-bodied prey, and for hard-bodied prey, headfirst ingestion was more rapid than tail-first ingestion (De Queiroz and De Queiroz, 1987). Given the correlation between Vo_{2HI} and T_{HI}, it is possible that aerobic metabolism will also vary with either behavior and/or prey type. For a similar prey type, individuals of *C. ocellatus* that dismembered their prey showed a higher number of bites and a higher T_{HI} than those that ate prey whole (De Queiroz et al., 1987). However, no effect of these behaviors or of tail-first ingestion on Vo_{2HI} was found. Vo_{2HI} for *C. ocellatus* and *E. inexpectatus* feeding crickets of three different species were highly correlated with number of bites (Andrews et al., 1987). In this study, data where the lizards ingested tail-first were omitted and, although some individuals dismembered their prey, the data were pooled for analysis. Grimmond et al. (1994) quantified Vo_2 for *C. ocellatus* handling and ingesting soft, medium and hard-bodied prey and found no effect of prey type on the duration of prey handling and ingestion. Despite the lack of correlation between time and prey type, *C. ocellatus* feeding on hard-bodied prey showed a twofold increase in Vo_{2HI}, when compared to medium and soft-bodied prey. However, in this study, Vo_{2HI} included measurements following ingestion (oxygen debt — see Section 3.1). Thus, from the above examples, it seems that behavior is a potential confounding effect, although disentangling cause and effect from such data is, at present, not possible.

3.4. Thermal effects

Temperature exerts a pervasive effect on the metabolic rate of lizards, and this effect may, in turn, constrain the behavioral capacity of these animals (Bennett, 1983). The only study that directly test for the effects of temperature on Vo_{2HI} and T_{HI} and time was done by De Queiroz et al. (1987) on the skink *C. ocellatus* (Table 2). They verified that, between 25°C and 35°C, handling time decreases with increasing temperature (see Table 3), but the differences were not statistically significant. They claimed that these results was probably due to a small sample size, since other studies with larger sample sizes found that handling time significantly decreased with increased temperature (Avery et al., 1982; Avery and Mynott, 1990). Moreover, an inverse effect of temperature on T_{HI} is predicted from the thermal dependence of muscle function; increased temperature increases muscle shortening and rate of muscle-tension development in lizards (Marsh and Bennett, 1985).

Vo_{2HI} for *C. ocellatus* increased with temperature between 25°C and 30°C, then remained unchanged (De Queiroz et al., 1987; see Table 2). As temperature increases so does aerobic metabolism and, above a certain body temperature, the animal will get close to its maximum capacity to deliver oxygen to the tissues, so that any need for further energy must be supplied by anaerobic metabolism. This may explain the independence of Vo_{2HI}, if only anaerobic input increases with temperature. This may be true for intense activities (Gatten, 1985), although it seems that for sustainable activities, anaerobic input is also temperature independent (Bennett, 1978, 1982). Thus, at the present, the reasons why Vo_{2HI} is temperature independent is unclear and future studies are in need to clarify this issue. Nonetheless, if this pattern holds for all species listed in

Table 2
Values for resting oxygen consumption (Vo_{2res}, ml O_2 h^{-1}), maximum oxygen consumption (Vo_{2max}, ml O_2 h^{-1}), aerobic scope (AS: $Vo_{2max} - Vo_{2rest}$; ml O_2 h^{-1}) and aerobic fractional scope for feeding (AFS), calculated as the net Vo_2 during handling and ingestion divided by AS, for *Chalcides ocellatus* and *Eumeces inexpectatus*[a]

	Vo_{2res}	Vo_{2max}	AS	AFS			
				2.5	5	7	10
Chalcides occelatus[b] (mean mass = 11.1 g)	1.35	10.94	9.6	0.17	0.19	0.21	
Eumeces inexpectatus[b] (mean mass = 11.1 g)	2.33	15.08	12.7	0.15	0.17	0.2	0.28
Small *Chalcides occelatus*[c] (mean mass = 5.1 g)	0.86	6.14	5.28	0.39	0.42	0.54	
Large *Chalcides occelatus*[c] (mean mass = 7.6 g)	11.1	8.49	7.38	0.26	0.45	0.53	0.63

[a] AFS calculated for relative prey mass ranging from 2.5 to 10% of the lizard body mass. See text for further details.
[b] Data based on Andrews et al. (1987).
[c] Data based on Pough and Andrews (1985a). Values for Vo_{2res} and Vo_{2max} based on allometric equations provided by Pough and Andrews (1984).

Table 1, then variations in Vo_{2HI} and T_{HI} would not be confounded by thermal effects, as all studies were conducted between 28°C and 35°C.

3.5. Aerobic fractional scope and anaerobic metabolism

The increase in Vo_{2HI}, as a fraction of the aerobic scope (the difference between maximum Vo_2 and the standard metabolic rate), is termed the aerobic fractional scope for feeding (Bennett, 1978, 1982). This measurement can give information about whether aerobic metabolism during prey handling and ingestion approaches the limits that the physiological machinery is able to support. Some results for this parameter are presented in Table 2. In general, large prey is associated with a large aerobic fractional scope for feeding. There is a marked difference between studies for a given species (*C. ocellatus*) and it seems that none of the factors expressed in the above sections can explain this discrepancy. Comparison between small and large *C. ocellatus* re-

vealed the same aerobic fractional scope for feeding, even though they differ considerably in their aerobic scope. The same pattern applies when the fractional scope for feeding of *E. inexpectatus* is compared with the similar-sized *C. ocellatus*. It should be remembered, however, that *C. ocellatus* needs to increase its Vo_{2HI} well above the increase observed for *E. inexpectatus* to handle and ingest the same relative prey mass (see Section 3.2). The low resting Vo_2 of *C. ocellatus* translates into a lower maximum Vo_2 and aerobic scope than *E. inexpectatus*. Thus, it seems that aerobic metabolism of *C. ocellatus* during prey handling and ingestion more closely approaches the maximum capacity of its cardio-respiratory system as compared to *E. inexpectatus*. If the anaerobic threshold is a relatively constant percentage of the aerobic capacity (Taigen and Beuchat, 1984), then *C. ocellatus* will use more anaerobically derived energy than *E. inexpectatus* to eat prey with the same relative mass, despite the fact that these two species do not differ in their aerobic fractional scopes for feeding. This

Table 3
Thermal dependence of prey-handling costs for *Chalcides ocellatus* (mean mass = 11.78 g) feeding on a prey with relative masses of 5%[a]

Variables	25°C	30°C	35°C	Q_{10}
Handling time (min)	8.9 ± 4.9	8.7 ± 2.79	6.5 ± 3.9	0.73
Net aerobic cost during handling (ml O_2 g^{-1})	0.03 ± 0.02	0.05 ± 0.02	0.05 ± 0.04	1.67
Fractional cost during handling	0.36 ± 0.13	0.41 ± 0.11	0.43 ± 0.2	1.19

[a] Values presented as mean ± S.D. Q_{10} calculated on the basis of mean values. Fractional costs refer to aerobic fractional costs of feeding and was calculated in the same way as presented in Table 2 (modified from De Queiroz et al., 1987).

conclusion seems to be reinforced by the fact that *E. inexpectatus* did not show a pronounced oxygen debt after ingestion (Andrews et al., 1987), suggesting that lactate accumulation, if any, was negligible.

Even though aerobic fractional scope for feeding does not overcome the capacity of the physiological system to deliver oxygen, all the studies that quantified whole body lactate concentrations reported increases in this variable above pre-feeding levels. Rates of lactate production increased during prey handling and ingestion by *A. carolinensis* (Preest, 1994). However, unlike $V_{O_{2HI}}$, lactate accumulation was dependent on prey mass and time and was not correlated with the head size dimorphism found in this species. In the lizard *S. lateralis*, for the maximum relative prey mass eaten (15%), whole body lactate levels did not differ from pre-feeding values and were only half of the concentrations obtained during intense activity (Preest, 1991). For *C. ocellatus*, lactate concentrations after handling and ingesting large prey (10% of the lizard body mass) increased fourfold, with an average net increase of 0.174 mg g^{-1} Pough and Andrews, 1985a). This value is far above those reported for *S. lateralis* feeding on the same relative prey mass (Preest, 1991). Even in natural conditions, anaerobiosis seems to be common during a feeding bout. In fact, lactate concentrations in free-ranging *Sceloporus virgatus* emerging from nocturnal retreats averaged 0.229 mg g^{-1}. However, just after feeding on preys with a relative mass of 4%, lactate concentrations rose to 0.415 mg g^{-1}, corresponding to a net increase in lactate concentration of 0.186 mg g^{-1} (Pough and Andrews, 1985b).

Despite the increase in lactate concentration, the relative contribution of anaerobic metabolism to ATP production during prey handling and ingestion is minor. The relative contribution of aerobic and anaerobic metabolism during prey handling and ingestion was calculated for the lizard *S. lateralis* (Preest, 1991). For small-sized prey (5%) total ATP production was from glycolysis. For medium (10%) and large-sized (15%) prey the anaerobic metabolism contributed to 8% and 4%, respectively, of the total ATP produced. On the other hand, anaerobiosis contributed 43% of the total ATP required during intense activity. Similar results were presented for *C. ocellatus* by Pough and Andrews (1985a). These results suggest that anaerobic metabolism can be activated

during prey handling and ingestion, but its magnitude might be associated with individual variation in the anaerobic thresholds of muscles involved in this activity. Also, as is the case with other sustainable activities performed by lizards (Bennett, 1983), its relative contribution to the overall energy production is negligible

3.6. Costs of prey handling and ingestion

The net costs of prey handling and ingestion can be expressed as a percentage of the net energy assimilated from the prey. Alternatively, the profitability can be calculated as the net energy gain per time spent handling and ingesting a given prey. Below we present both calculations for the lizards *C. ocellatus* and *E. inexpectatus* (Fig. 3 — based on data from Andrews et al., 1987). For the calculations, we used the same assumptions of Pough and Andrews (1985a). When only the aerobic energy output during prey handling and ingestion is considered, the ratio between net costs and the net meal energy increases faster with prey mass for *C. ocellatus* than for *E. inexpectatus* (Fig. 3a). However, even for the largest prey eaten, the net cost is less than 0.2% of the net energy content of the prey for both species. For calculations by other authors, where total V_{O_2} (including the oxygen debt) and the energy from anaerobic metabolism were included, the costs of prey handling and ingestion still is a negligible part of the net energy assimilated from the prey, with average values of 1% for the largest prey eaten (Pough and Andrews, 1985a; Preest, 1991; Grimmond et al., 1994). Thus, on the basis of a simple cost−benefit analysis a lizard should eat all potential prey items, with the maximum prey size probably being set by morphological limitations and time constraints (see below).

What are the costs of prey handling and ingestion compared to the costs of the other phases of a feeding bout? Whilst costs of prey searching might be negligible for a sit-and-wait predator, they can substantially increase energy expenditure above resting levels for widely-searching lizards (Andrews, 1984). Also, costs of digestion can increase metabolic rate several fold above resting levels in lizards (e.g. Beaupre et al., 1993; Secor and Phillips, 1997). Thus, it seems that prey handling and ingestion are the least expensive activities of a feeding bout, at least for sit-and-wait
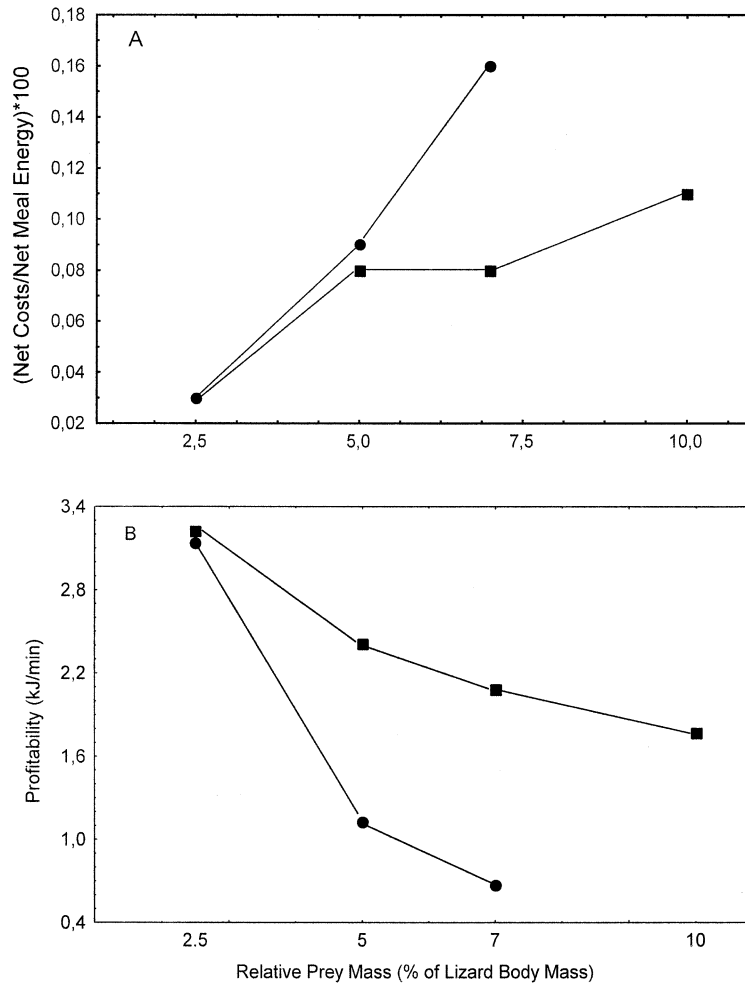
Fig. 3. Cost–benefit analysis showing the relationship between the net costs for prey handling and ingestion/net meal energy (a), and profitability (b), as a function of relative prey mass, for the skinks *Chalcides ocellatus* (●) and *Eumeces inexpectatus* (■). Profitability (e/t) defined as the energy gain (kJ) per time spent feeding (min) (after Andrews et al., 1987).

lizards (see Fig. 3). However, a detailed analysis of the relative contribution of all feeding stages to the overall energy budget devoted to feeding will be required to fully resolve this question. Also, this analysis must consider the combined effects of factors such as temperature, prey selectivity, and prey type on the relative contribution of each feeding phase to the total energy expenditure during a feeding bout.

Another way to analyze the energetic costs of feeding is by quantifying profitability. Profitability (e/t), defined as the energy gain (e in kJ) per time spent feeding (t in minutes) is a key variable in optimal foraging models, and it has been used to predict prey selection for a wide variety of animals (Stephens and Krebs, 1986). For the

lizards *C. ocellatus* and *E. inexpectatus*, e/t decreases with increased prey size and, for any given relative prey size, it was higher for *E. inexpectatus* (Fig. 3b). The decrease in the e/t curve is due to the fact that, for both species, time increases faster with prey mass than net energy assimilated (Pough and Andrews, 1985a). Furthermore, due to morphological constraints, time increases faster for *C. ocellatus* (see Section 3.2), so e/t values, for a given relative prey mass, are smaller than for *E. inexpectatus*. For a given prey type, e/t for the lacertid lizard *Psammodromus algirus* (with the term e calculated from the mass of the prey) does not vary with prey mass, probably because handling time for this species increases at a slower pace with prey mass (Diaz and Carrascal, 1993).

The costs of prey handling and ingestion for lizards are trivial when compared with the energy content of the prey, and inclusion of the cost of prey pursuit probably would not change this picture, at least for sit-and-wait foragers. In this condition, the shape of e/t curve is mainly determined by time and by the gross energy content of the prey (Pough and Andrews, 1985a), so that a lizard can either maximize gross energy intake or minimize time spent feeding. Andrews et al. (1987) suggested that the best strategy for a lizard with a energy conservative life-style such as *C. ocellatus* would be to capture the same amount of small prey as *E. inexpectatus* would do with large prey, and this hypothesis seems to be partially supported by the e/t curve modeled for these two species (Fig. 3B). Moreover, the e/t curve probably follows the same pattern for sexually dimorphic *A. carolinensis* (Preest, 1994), so that females would behave in a similar way to *C. ocellatus*. However, the precise strategy employed may vary seasonally as a function of factors such as prey abundance, prey size distribution, prey selectivity (use vs. availability), prey type and predation risks (Pough and Andrews, 1985a; Diaz and Carrascal, 1993). Thus, e/t alone can be of little use to predict prey selection by lizards (Diaz and Carrascal, 1993; Stamps et al., 1997), or by any other organism with low energy requirements (see examples with snakes below).

Pough and Andrews (1985a) suggested that the energy source employed during feeding might be more useful than quantification of the total costs in predicting prey selection (see also Preest, 1991). For example, use of anaerobic metabolism entails costs that extended beyond a single feeding event; extensive lactate accumulation may lead to fatigue and, hence, may impair subsequent activity (Bennett, 1978, 1982). Within this context, it has been suggested that the largest prey a lizard will consume is that which will not require a substantial accumulation of lactate and potentially impair further activity (Pough and Andrews, 1985a). Although, at least for short-term activities, anaerobic metabolism is not associated with impairment of the oxygen delivery system (Bennett, 1978), this hypothesis assumes that the physiological capacity of a lizard will be responsible, in part, for prey selection. Large prey will take longer to be handled and ingested, increasing metabolic rate. Thus, everything being equal, a lizard with a system more capable of delivering oxygen at high rates for extended periods of time might be able to consume larger prey without having to use substantial amount of anaerobic metabolism. Albeit attractive, this hypothesis has yet to be empirically examined against other possible, but not mutually exclusive, hypotheses about what factors determine prey size selection in lizards.

4. Snakes

The evolution of an elongate, legless body form is a distinctive characteristic of snakes and influences all aspects of their biology (Greene, 1997). One of the corollaries of such body form is related to food acquisition: how to acquire an adequate supply of energy through a transversal section (mouth) that becomes increasingly smaller in relation to the size of an elongate body (Gans, 1961, 1983)? The way snakes solved this problem was the main driving force for the impressive adaptive radiation exhibited by these reptiles (Greene, 1983, 1997). In this regard, the feeding biology of snakes has been extensively examined from an ecological, morphological, and ecological perspective (Cundall, 1987; Arnold, 1993; Greene, 1997). From a physiological perspective, however, studies on the feeding biology largely reflect studies on the physiology of digestion (Secor, 2001). To our knowledge, only four studies have directly addressed the physiological correlates of prey handling and ingestion by these reptiles (see Table 1), and none of then provides a complete picture on the subject.

Notwithstanding such problems, in this section we will attempt to summarize the available information, using a somewhat similar protocol as adopted for lizards. We will rely heavily on data for two species to highlight some of our points. The crotaline *Crotalus durissus* and the boid *Boa constrictor amarali* were subject of studies where aerobic costs of prey handling and ingestion (measured as oxygen consumption — $V_{O_{2HI}}$) and time (T_{HI}) were measured as functions of prey size (Cruz-Neto et al., 1999; Canjani et al., unpublished data). These two species represent the extremes of snake adaptations associated with prey handling and ingestion (constriction vs. venom inoculation — Greene, 1997). Data from two other studies (Feder and Arnold, 1982; Stinner and Ely, 1993) will be used to clarify points related to the use of anaerobic metabolism and the

cardio-respiratory adjustments during prey handling and ingestion. Data on Vo_{2HI} was calculated as for lizards, but expressed as $mlO_2.g^{-1}$. Also data on Vo_{2HI} was separately calculated for handling (Vo_{2H}) and ingestion (Vo_{2I}) for *B. constrictor*, and as a single measure for *C. durissus* (see below). Expression of aerobic metabolism in a mass-specific basis was done to minimize the effects of body mass, since there was a 13-fold difference in this parameter between *B. constrictor* (mean mass: 638 g) and *C. durissus* (mean mass: 50 g). Due to this difference, prey mass eaten by both species during the experiments did not overlap, so we expressed prey mass in a relative basis (% of snake body mass) for comparisons. As we shall see, however, the use of relative prey size probably was a potential confounding effect in our interpretations.

4.1. Aerobic metabolism

4.1.1. Prey handling

One of the consequences of the different feeding strategies displayed by *B. constrictor* and *C. durrisus* is that the Vo_{2H} and T_H is virtually negligible for the latter species. Crotaline snakes relied on a parenteral venom injection to subdue their prey (Greene, 1997). Strike and venom injection are very high-speed behaviors, so that the energy necessary to support these behaviors probably will be meet solely by anaerobic metabolism. In fact, it is well know that reptiles rely on anaerobic metabolism to supply energy for very short and intense activities (Bennett, 1978, 1982). Cruz-Neto et al. (1999) reported data for only aerobic metabolism during ingestion in *C. durissus*. All their experimental snakes used parenteral venom injection for prey handling and, given these considerations, no attempt was made to measure aerobic metabolism during prey subjugation, which, nonetheless, can assumed to be negligible. Thus in this case, Vo_{2HI} is, in fact, only equated to oxygen consumption during ingestion (Vo_{2I}).

Boid snakes, on the other hand, use constriction for prey handling and this behavior is associated with a intense muscular activity that can lasts for extended periods of time (Willard, 1977; Greene and Burghardt, 1978; Moon, 2000). Also, there is a significant effect of prey size on T_H and V_{O_2H}, for *B. c. amarali* constricting prey ranging from 5 to 40% of their own body mass (see Fig.

4a,b). T_H and Vo_{2H} increase with prey size almost linearly between 5 and 20%, but as relative prey mass increases from 20 to 40%, there is a plateau in both T_H and Vo_{2H} (Canjani et al., unpublished data; see Fig. 4a,b). When the aerobic metabolism during prey handling is compared with the aerobic metabolism during ingestion (Vo_{2I} — see Section 4.1.2), Vo_{2H} is responsible for up to 78% of the total oxygen consumed (Vo_{2HI}). Thus, the pattern of variation in Vo_{2HI} seems to be determined by the pattern observed for Vo_{2H}. However, the contribution of Vo_{2H} to Vo_{2HI} dropped to 50% when relative prey mass is increased to 40% (Fig. 5a). This difference in the relative contribution of Vo_{2I} and Vo_{2H} to Vo_{2HI} as relative prey mass increases is due to the fact that Vo_{2H} remains stable at large prey size.

4.1.2. Prey ingestion

For *C. durissus*, both Vo_{2I} and time increased with prey size, albeit in an different fashion (Fig. 4a,b). Vo_{2I} increased sharply as relative prey mass increased from 10 to 30%, and then, between 30 and 50%, Vo_{2I} increase occurred in a slower pace (Cruz-Neto et al., 1999; see Fig. 4a). Ingestion time, on the other hand, increased in an approximately linear way with relative prey mass (except between relative prey mass of 10 and 20% — Fig. 4b). For *B. c. amarali*, Vo_{2I} also increased with increase relative prey mass (Fig. 4a). For this boid snake, Vo_{2I} increased linearly between prey with a relative mass of 5 and 10%, then tended to plateau as relative prey mass increase to 20%. However, as relative prey mass double (from 20 to 40%), V_{O_2I} increased linearly again. Ingestion time showed a somewhat similar pattern as Vo_{2I}, with prey of relative mass of 10 and 20% requiring the same amount of time to be ingested.

Although patterns of variation in Vo_{2I} and time with relative prey mass seems to be similar for *C. durissus* and *B. c. amarali*, the absolute values for each of these parameters, for a given relative prey mass, differs widely. *Crotalus durissus* ingesting a relative prey mass of 10% needed 3 min and consumed 0.04 ml O_2 g^{-1}, whilst *B. c. amarali* took approximately 10 min and consumed 1.06 ml O_2 g^{-1} to ingest a prey item with the same relative mass (Fig. 4a,b). As relative prey mass increased, this difference tended to be more pronounced, so that, for the largest relative prey mass eaten, *C. durissus* took approximately 12 min and consumed 1.86 ml O_2 g^{-1}, while *B. c.*
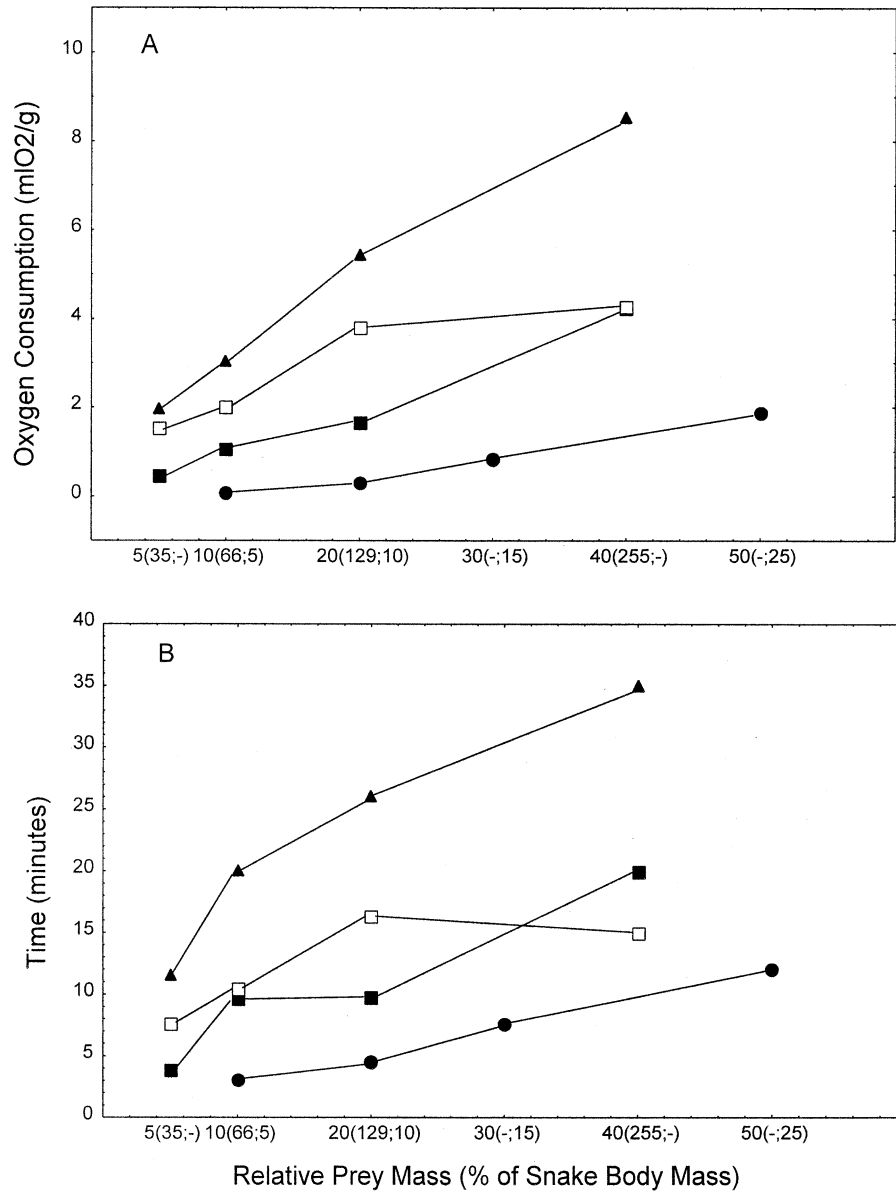
Fig. 4. Variations in oxygen consumption (a) and time (b), as a function of relative prey mass for the snakes *Crotalus durissus* and *Boa constrictor*. Values for *C. durissus* include only the ingestion phase (●), whilst for *B. constrictor* they includes the constriction (handling, □) and ingestion phases (■), as well as the sum of both values (▲). Number in parenthesis on the *x*-axis denotes the equivalent absolute prey mass for *B. constrictor* and *C. durissus*, respectively. See text for further details (after Cruz-Neto et al., 1999; Canjani et al., unpublished data).

amarali took 20 min and consumed 4.24 ml O_2 g^{-1} (Fig. 5a,b). At first, we suggested that such difference might be due, in part, to the difference in cranial morphology associated with feeding. Crotaline snakes, such as *C. durissus*, possess the most remarkable modifications in cranial morphology and kinematics among snakes (Cundall, 1983, 1987), so that gape size in these snakes

allows the ingestion of a given prey size at less cost than for other snakes (Greene, 1983, 1997).

Even if this hypothesis is correct, we should acknowledge some potential confounding factors. For example, *B. c. amarali* is much larger than *C. durissus* (Greene, 1997), and it has been suggested that the intensity of selection on characters determining ingestion capacity is lower in larger
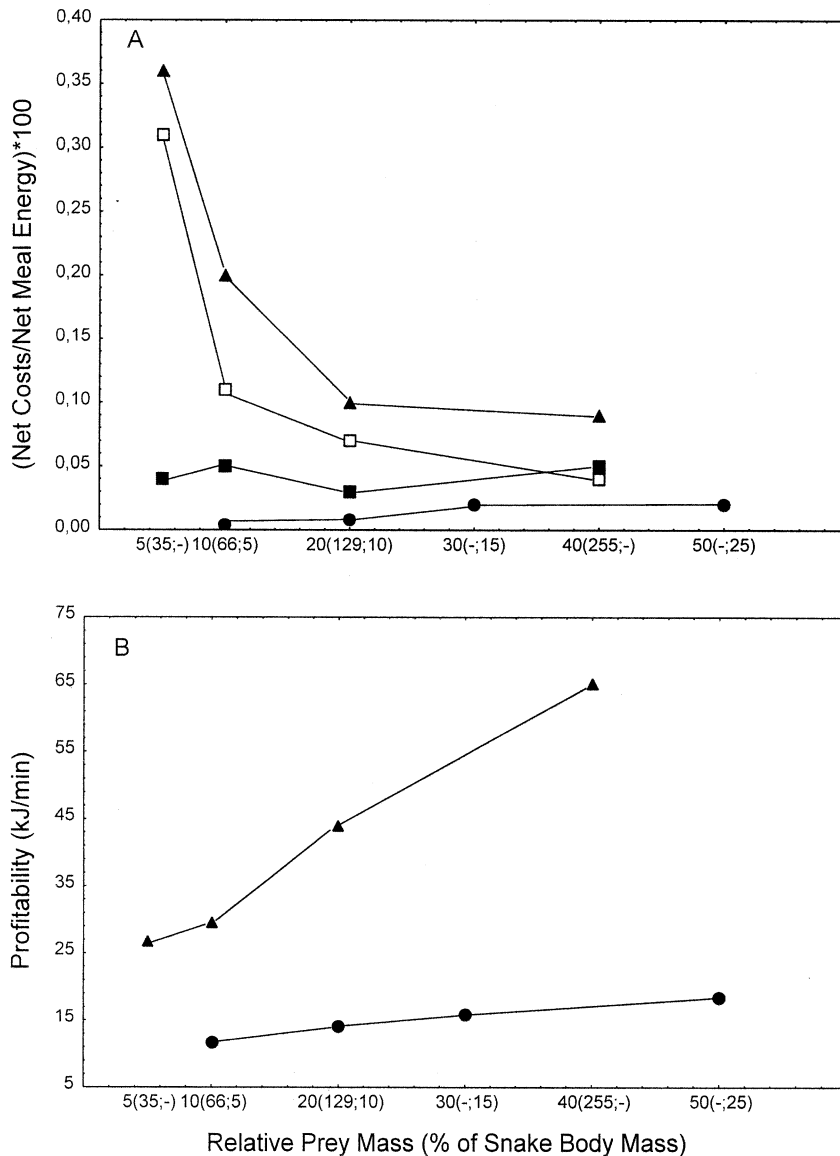
Fig. 5. Cost−benefit analysis showing the relationship between the ratio of net costs for prey handling and ingestion/net meal energy (a), and profitability (b), as a function of relative prey mass, for the snakes *C. durissus* and *B. constrictor*. See Fig. 4 for symbols (after Cruz-Neto et al., 1999; Canjani et al., unpublished data).

species (Forsman, 1996). Thus, even if there was no difference in cranial morphology and kinematics between these two species, *B. c. amarali* would still have a lower ingestion ability than *C. durissus*. A more serious confounding effect is the difference in body mass between *C. durissus* and *B. c. amarali*. Although we expressed values for aerobic metabolism and prey mass as ratios, this seldom abolishes allometric effects (Packard and Boardman, 1999). Concerning aerobic metabolism this problem can not be solved with the available

data. Assuming that we minimize as much as possible the allometric effects of snake body mass, the limitation of expressing prey mass as a ratio still exists. Ingestion of a prey item weighing 25 g must present different problems than ingesting a prey item with 250 g, even though both prey could represent the same relative value with respect to the snake mass. This potential problem was noted in an intraspecific study of prey handling ability in the python *Morelia spilota* (Shine, 1991). Although larger pythons ingested a given-sized prey

more quickly than did smaller snakes, smaller pythons were quicker than larger ones when ingesting prey with a relative mass of 20%. Given the possibility that this observation holds for interspecific comparisons, and given the correlation between T_I and Vo_{2I}, it is feasible that much of the difference observed between *C. durissus* and *B. c. amarali* might reflect differences in the absolute size of the prey taken. Since there was no overlap between the absolute prey mass eaten by *C. durissus* and *B. c. amarali*, this confounding effect cannot be assessed with the available data. In the future, it will be worth examining aerobic metabolism in snakes with the same mass, but with marked differences in cranial morphology and kinematics.

4.2. Aerobic fractional scope and anaerobic metabolism

For *C. durissus*, aerobic factorial scope for ingesting relative prey masses of 10, 20, 30 and 50% represents approximately 36, 55, 77 and 93% of the maximal aerobic scope (Cruz-Neto et al., 1999). Similar data are not available for *B. c. amarali*. Assuming that the anaerobic threshold is a relatively constant percentage of the maximum aerobic capacity (Taigen and Beuchat, 1984), we expected that rates of lactate production would increase with relative prey mass for *C. durissus*, a pattern also reported for lizards. Unfortunately, no data are available on rates of lactate production during prey handling and ingestion for *C. durissus* to test this hypothesis. Garter snakes (*Thamnophis elegans*), preying upon salamanders (*Plethodon jordani*), showed substantial increases in whole body lactate when compared to resting levels (Feder and Arnold, 1982). In a typical 14.4-min event, a 16.6-g snake ingesting a 2.2-g salamander (Feder and Arnold, 1982), the maximal increase in lactate level was 0.56 mg g^{-1}. This value represented an increase of 260% above resting levels and is higher than any other value measured for lizards during prey handling and ingestion. When compared to the average maximal anaerobic scope of different species of snakes (Bennett, 1982), *T. elegans* seems to be using as much as 30% of the maximal anaerobic scope in handling and ingesting a prey item with a relative mass of approximately 14%. Also, indirect calculations showed that the amount of ATP generated by the anaerobic metabolism may be as much as

26% of the total energy necessary for feeding by *T. elegans* (Arnold, 1993). This single study suggested, contrary to what was observed for lizards, that anaerobiosis might be an important component of the total energy devoted to prey handling and ingestion in snakes. Clearly more studies with rates of aerobic and anaerobic metabolism being measured in a single species as a function of relative prey mass will be needed to clarify the metabolic pathways and their relative contribution during prey handling and ingestion in snakes.

4.3. Energetic costs of prey handling and ingestion

The net costs of prey handling and ingestion, expressed as a function of the net meal energy content, is shown in Fig. 5a for *C. durissus* and *B. constrictor* (see Cruz-Neto et al., 1999 for the assumptions involved in these calculations). As far as ingestion alone is concerned, *C. durissus* showed a lower cost than *B. constrictor*. For both species, contrary to what was observed for lizards, these costs are less than 0.05% of the net energy content of the prey and seem to be independent of relative prey mass. For *B. constrictor*, the cost of prey handling was higher than the cost for ingestion and decreased as relative prey mass increased. Thus, the total cost for this species is determined by the costs of handling, and was less than 0.5% of the net energy content of the prey. For *B. constrictor*, the total cost for handling and ingesting increase slower than the net energy content of the prey. These calculations were underestimated as they did not include the costs of prey searching, the energy derived from anaerobic metabolism and the cost of the oxygen debt. Arnold (1993) included all these cost (except for prey searching) and calculated that the cost for *T. elegans* feeding on a prey item with a relative mass of 14% would be approximately 1% of the energy content of the prey. As reported for lizards, if this cost−benefit analysis alone were responsible for prey selection, snakes should eat all potential prey, with the maximum prey size probably being set by a combination of morphological limitations (gape size) and prey size distribution (Shine, 1991; Forsman, 1996).

Data on the cost of searching for prey are not available for *C. durissus* and *B. constrictor*. However, the cost of digestion for snakes can be substantial. For *C. durissus*, it has been calculated that the costs of digestion, for prey item with a

relative mass ranging from 10 to 50%, varied from 12 to 18% of the ingested assimilated energy (Andrade et al., 1997). Although no data are available for *B. constrictor*, information on the boid *Python molurus* suggested that the cost of digestion might be even higher than that reported for *C. durissus* (Secor, 2001). Therefore, as was shown for lizards, among the phases of feeding (searching, handling, ingestion and digestion), the costs of prey handling and ingestion in snakes seem to represent the least energy demanding activity.

Profitabilities (*e/t*) for *C. durissus* and *B. constrictor* are shown in Fig. 5b. Contrary to what was observed for lizards, *e/t* showed a marked increase with relative prey mass for *B. constrictor*, from 26.8 kJ/min for a prey with a relative mass of 5% to 65.1 kJ/min for a prey with a relative mass of 40%. For *C. durissus*, *e/t* also increased with relative prey mass, but less sharply. For prey with relative mass of 10%, *e/t* was 11.8 kJ/min, increasing to 18.5 kJ/min for prey with a relative mass of 50%. In our example, the increase in *e/t* with prey mass could be due to the fact that time for prey handling and ingestion increased slower with prey mass than did the net energy content of the prey, and this pattern seems to be more pronounced for *B. constrictor* (see Shine, 1991). This fact, and the fact that for any given relative prey mass, the energy content of the prey will be higher for *B. constrictor*, could be used to explain the higher *e/t* for this species when compared to *C. durissus*. Although the pattern of *e/t* reported here suggests that 'big is better', *e/t* alone cannot be a good predictor of prey size selection in snakes. Models that have been advanced to explain prey size selection in snakes (Shine, 1991; Arnold, 1993; Forsman, 1996) suggested that, besides *e/t*, other factors, such as prey size distribution, predation risk, prey type, and morphology (gape size) may interact in a complex way to determine the observed patterns of prey-size–snake-size relationships.

4.4. Physiological constraints on prey handling and ingestion

As hitherto discussed, for snakes the use of anaerobic metabolism probably is more acute than for lizards. Since there is no difference in patterns of metabolic recovery between lizards and snakes (Gleeson, 1991), then the high rates of lactate accumulation in snakes would entail more costs in terms of fatigue. Moreover, as some snake species ingest relatively larger prey than lizards, the locomotory ability of snakes is reduced after feeding (Garland and Arnold, 1983), further impairing activities.

Constriction is an activity with high energy demand and it may be that, beyond some relative prey mass, the O_2 transport system of *B. constrictor* is not able to sustain the increasing costs of prey handling (see plateau in Fig. 5a). In these cases, it is plausible that the extra energy necessary for constriction might come from the anaerobic metabolism, with the attendant consequences already discussed. Also, limitations of the cardiovascular system might also be significant. The colubrid snake, *Coluber constrictor*, feeding on prey with a relative mass of 5–10%, showed a threefold increase in heart rate and a fourfold increase in systemic arterial blood pressure above resting levels (Stinner and Ely, 1993). The abrupt cardiovascular change associated with handling and ingestion showed three marked phases: the first two were associated with handling (constriction), and were characterized by a rapid increase in heart rate (peak value of 99 beats/min), and arterial blood pressure (peak value of 99 mmHg), lasting for 6–15 min (Stinner and Ely, 1993). After handling, and with the onset of ingestion, heart rate and arterial blood pressure dropped to prefeeding levels (Stinner and Ely, 1993). Recently, Moon (2000) showed that muscle activity and force exertion during constriction by gopher (*Pituophis melanoleucus*) and king (*Lampropeltis getula*) snakes followed a somewhat similar pattern as described for the cardiovascular changes hitherto discussed. Taken together, these data suggested that, even when feeding on relatively small prey, constriction requires substantial adjustment in the cardiovascular systems to match the attendant energy need of an increase in muscle activity. It is possible, thus, that the constriction of larger prey might place a demand in terms of oxygen supply that can not be accommodated by further adjustments of the cardiovascular system.

It has been suggested that the development of a nonvascular portion of the lung in snakes (air sacs) was due to non-respiratory constraints, particularly in response to feeding (McDonald, 1959; Milsom, 1989). If this is true, then the O_2 stores presented in air sacs could ameliorate the effects

of a blocked airway. Given this consideration, it seems that, for *C. durissus* and *B. constrictor* the O_2 stores present in the air sacs are enough to accommodate the increase demand for O_2. For rattlesnakes, this feature could ameliorate the limitations of the oxygen delivery systems typical of viperid snakes (Lillywhite and Smits, 1992). Therefore, the limited data set presently available seems to indicate that there is no physiological (cardio-respiratory) limitation for prey ingestion. However, this hypothesis needs further studies to be confirmed.

The above results suggest that, besides morphological (gape size) limitations, the low capacity of the cardio-respiratory systems of snakes counteract to some extent the morphological and behavioral adaptations associated with the ingestion of large prey. However, the effects of these cardio-respiratory constraints seem to be more pronounced during handling in constricting snakes, as this limitation during ingestion is probably ameliorated by the presence of air sacs. Clearly, further studies are needed to fully address this problem but, nevertheless, we suggest that physiology must be taken into account in models that attempt to analyze patterns in prey size selection.

5. Summary

Lizards and snakes showed similar patterns in the variation in aerobic metabolism during prey handling and ingestion relative to prey mass, but direct comparisons of the absolute magnitude of these rates is hampered by the fundamental kinematics differences in feeding mechanism between these two groups (Gans, 1961). The total ATP synthesis during prey handling and ingestion in lizards came almost exclusively from oxidative pathways. For snakes, no single study measured rates of anaerobic and aerobic metabolism in the same individual, but indirect evidence suggests that glycolytic pathways may also be important. For lizards, rates of aerobic metabolism during prey handling and ingestion also varied as a function of morphological specializations (fossorial vs. non-fossorial habits), prey type and behavior. The only data available on the effects of temperature on aerobic metabolism showed no thermal effects at relatively high temperatures. No comparable data are available for snakes concerning these

effects on rates of aerobic and anaerobic metabolism, so filling these gaps will be a fruitful avenue for future investigations [but see Moon (2000) for some information on effects of prey behavior and muscle activity during constriction in snakes]. For snakes, rates of aerobic metabolism during prey handling seem to be linked to the two major strategies employed for subduing prey. Snakes that rely on venom injection probably have negligible increments in aerobic metabolism, and may rely solely on anaerobic metabolism. This suggestion, however, has not yet been empirically verified. On the other hand, constricting snakes show elevated rates of aerobic metabolism and, in fact, constriction seems to be responsible for up to 78% of the total oxygen consumed during a feeding bout. This pattern seems to be directly related to muscle force exerted during constriction (Moon, 2000), and we suggest that the amount of energy supplied might be limited by the cardio-respiratory system (see below). During ingestion, snakes with the most specialized cranial morphology seem to have lower rates of aerobic metabolism. However, this correlation is confounded by differences in body mass between the only two snakes studied. Further studies on the physiological and energetic correlates of prey handling and ingestion in snakes should focus on the relative and absolute contribution of aerobic and anaerobic metabolism for ATP production, and how this varies with factors such as prey mass, prey shape, and temperature. These studies must be done in species with varying degrees of morphological and ecological specializations for feeding.

The net costs of prey handling and ingestion for lizards and snakes, when compared to the net assimilated energy of the prey, seem to be negligible. In fact, among the four phases of a feeding bout, prey handling and ingestion are the least expensive in energetic terms. Similar results were obtained for fishes (Stein et al., 1984; Sanderson and Cech, 1992) and shore crabs (Rovero et al., 2000). However, given the possible effects of prey type and behavior on the costs, either measured by energy or time, this suggestion may be valid only for a specific prey type (see also Pough and Andrews, 1985a). Moreover, speculations on the extent to which energetic considerations alone might be used to predict patterns of prey size selection proved unfruitful. It seems that energetic analysis would be more fruitful if combined

with information on some ecological parameters such as prey size distribution and availability, in order to determine patterns of prey size selection.

We also showed indirect evidence that, besides morphological and ecological constraints, the capacity of the cardio-respiratory systems may also constrain handling in constricting snakes. This physiologically-based limitation is not apparent during ingestion, but detailed studies are await to confirm this observation. For lizards, this consideration is inconclusive and it was based solely on the deleterious consequences of the extensive use of anaerobic metabolism. For snakes, however, the peculiar morphology of their respiratory systems, plus some scant data on cardiovascular adjustments during feeding, suggest that the limitations of the cardio-respiratory system, at least for handling in constricting species, together with morphological and ecological factors, could also be an important factor in explaining some of the observed patterns of prey size-snake size relationships.

Acknowledgements

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