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Effects of prey type on specific dynamic action, growth, and mass conversion efficiencies in the horned frog, *Ceratophrys cranwelli*

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Abstract

To be most energetically profitable, predators should ingest prey with the maximal nutritional benefit while minimizing the cost of processing. Therefore, when determining the quality of prey items, both the cost of processing and nutritional content must be considered. Specific dynamic action (SDA), the increase in metabolic rate associated with feeding in animals, is a significant processing cost that represents the total cost of digestion and assimilation of nutrients from prey. We examined the effects of an invertebrate diet (earthworms) and a vertebrate diet (newborn mice) on mass conversion efficiencies, growth, and SDA in the Chacoan horned frog, *Ceratophrys cranwelli*. We found the earthworm diet to be significantly lower in lipid, protein, and energy content when compared to the diet of newborn mice. Growth and mass conversion efficiencies were significantly higher in frogs fed newborn mice. However, mean SDA did not differ between frogs fed the two diets, a finding that contradicts many studies that indicate SDA increases with the protein content of the meal. Together, our results indicate that future studies evaluating the effect of meal type on bioenergetics of herpetofauna are warranted and may provide significant insight into the underlying factors driving SDA.

Keywords: Amphibian; *Ceratophrys cranwelli*; Diet; Mass conversion efficiency; Oxygen consumption; Prey type; Specific dynamic action

1. Introduction

For amphibians, as well as for many other animals, the rapid attainment of adult body size provides considerable advantages, such as reaching sexual maturity and the avoidance of gape-limited predators, and thus juveniles commonly allocate a large percentage of their ingested energy to growth (Pough, 1980; Pedersen, 1997). For example, juvenile Western toads (*Bufo boreas*) not only partition large amounts of energy into growth, but also adopt a thermoregulation strategy to maximize growth rates and reach adult size quickly (Lillywhite et al., 1973). Female marbled salamanders (*Ambystoma opacum*) fed higher energy diets achieved larger body sizes, and consequently achieved greater reproductive success (Scott and Fore, 1995). Several studies have demonstrated that amphibians can have high mass conversion efficiencies, the production of predator body mass relative to ingested prey mass, particularly when compared to endothermic birds and mammals (Pough, 1980; Claussen and Layne, 1983).

Before an animal can allocate ingested energy to growth, it must first meet maintenance costs related to daily functions and metabolism (Angilletta, 2001). The maintenance costs associated with food processing are referred to as Specific Dynamic Action (SDA). Specific dynamic action can be equivalent to 10–30% of energy from an ingested meal and can therefore have a significant impact on

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the amount of net assimilated energy that is available for growth (Krieger, 1978; Jobling, 1981; Secor, 2001). Physiological processes that contribute to SDA include gastrointestinal motility, production of digestive enzymes and nitrogenous wastes, protein catabolism and synthesis, and intestinal nutrient transport (Jobling, 1981; Hailey, 1998; Secor, 2003; McCue et al., 2005). Numerous factors can affect the magnitude of SDA in animals. These factors include, but are not limited to, temperature (Powell et al., 1999; Toledo et al., 2003), meal size (Andrade et al., 1997; McCue and Lillywhite, 2002), body size (Secor and Faulkner, 2002), and foraging strategy (reviewed by Secor, 2001). Studies have also indicated that meal type and composition, particularly protein content, can affect SDA (Coulson and Hernandez, 1979; Jobling, 1981; Secor and Phillips, 1997; Hailey, 1998; Secor and Faulkner, 2002; McCue et al., 2005). However, the importance of prey type has only begun to be examined in amphibians. Meal type was recently shown to significantly affect SDA in a study on the marine toad, *Bufo marinus,* using four different diets (Secor and Faulkner, 2002).

After maintenance costs have been met in juvenile animals, the remaining net assimilated energy is available for production of new tissue. Hence, variation in the magnitude of SDA due to prey type could influence the net energy remaining from a meal for production. For example, assuming constant assimilation efficiency, if the cost of digestion (i.e., SDA) is equivalent between two prey types, then the prey type with the highest energy content will provide the greatest amount of energy for other energetic demands (e.g., growth). However, if SDA differs according to prey type, then the prey that generates the smallest SDA response relative to its energy content will yield the greater energetic benefits. Thus, variations in the relationship between SDA and nutritional content of prey can influence growth, which can in turn impact survivorship, reproductive success, and ultimately fitness (Brodmann et al., 1997; Rosen and Trites, 2000; Babu, 2001).

Chacoan horned frogs (*Ceratophrys cranwelli*) are ambush predators from Argentina and Uruguay that generally exhibit low resting metabolic rates (Duellman and Lizana, 1994; Powell et al., 1999; Bartlett and Bartlett, 2000). Diets of *C. cranwelli* have not been documented in the field; however, other members of this genus feed on a variety of food items including ants, orthopterans, spiders, earthworms, other anurans, and mice (Murphy, 1976; Duellman and Lizana, 1994). Although the number of vertebrates consumed in a study on *C. cornuta* was proportionally smaller than other prey types, vertebrates constituted a larger portion of prey biomass than invertebrates (Duellman and Lizana, 1994). As observed in other infrequently feeding ambush predators (Secor, 2001), *C. cranwelli* exhibits a large increase in metabolic rate following feeding (SDA; Powell et al., 1999).

In this study, we examined the effects of prey type on bioenergetics in *C. cranwelli*. We first measured the nutritional quality of an invertebrate prey (earthworms) and a vertebrate prey (newborn mice). Then we examined the effects of prey type on SDA, mass conversion efficiency, and growth and used those data to evaluate the energy costs and benefits of processing different quality prey items. We predicted that the mouse diet would have higher lipid, protein, and energy content than the worm diet and would result in higher growth rates and mass conversion efficiencies in *Ceratophrys*. Because protein content of the meal is commonly linked to the SDA response in predators (Coulson and Hernandez, 1979; Jobling, 1981; Hailey, 1998), we also predicted that ingesting the higher protein vertebrate diet would result in a greater SDA response than the lower protein invertebrate diet, but not to a degree such that the SDA response would overwhelm the energy benefit of the vertebrate diet. By measuring energetic responses of frogs fed two diets, we sought to reveal the energy tradeoffs that likely occur when an organism ingests prey of differing nutritional quality.

2. Materials and methods

2.1. Animals

Twenty-four newly metamorphosed Chacoan horned frogs were purchased from Finn's Aquatics, Inc., (Atlanta, GA) for our study. We used eight frogs to examine the effects of prey type on SDA and the remaining sixteen individuals to examine the effects of prey type on growth and mass conversion efficiency. Frogs were housed individually in 12×12 cm plastic containers (Ziploc) with moistened paper towels as a substrate at 25 °C and with a 12 : 12 photoperiod in an environmental chamber. For two weeks before the beginning of the experiments, frogs were fed crickets (*Acheta domesticus*) twice a week. During the experiments, frogs were fed an intact portion of either previously frozen newborn mice (*Mus musculus*) or live earthworms (*Lumbricus terrestris*) cut to equal 10% of their body mass. Only heads were removed from mice to generate appropriate meal sizes. Nutritional analyses were conducted on both intact and headless mice and showed that there was no difference in proximate composition ($P > 0.16$ for lipid, protein, and energy content).

2.2. Nutritional analysis

Composite dietary samples ($n = 4$ per prey type) were analyzed as follows. Approximately 50 g (wet mass) of earthworms ($n = 52–59$ individuals/sample) and newborn mice ($n = 21–26$ individuals/sample) were homogenized and lyophilized to a constant dry mass before being shipped to the University of Georgia's Poultry Science Research Laboratory for analysis. Lipid and protein content of composite samples was determined using petroleum ether extraction and the Kjeldahl combustion technique, respec-

tively. Energy content of composite prey samples was determined using an adiabatic bomb calorimeter (Parr Instrument Co., Moline IL, USA). All dietary values are reported on a wet mass basis because differences in water content existed between prey (mean water content = 72.57% ± 0.37 SE for newborn mice and 85.17% ± 0.19 SE for earthworms) and prey rations were determined based upon the wet mass of the prey. The nutritional content (energy content and percent composition of lipid and protein) of the two diets was compared using single-factor ANOVAs. We performed a sequential Bonferroni adjustment to maintain an experiment-wide error rate of $\alpha = 0.05$. Newborn mice had a higher mean percent lipid content (9.32% ± 0.52 SE vs. 1.76% ± 0.08 SE; $F = 206.93$, $df = 7$, $P < 0.001$), mean percent protein content (13.13% ± 0.31 SE vs. 8.97% ± 0.15 SE; $F = 149.68$, $df = 7$, $P < 0.001$), and mean energy content (7.16 kJ/g ± 0.17 SE vs. 3.21 kJ/g ± 0.04 SE; $F = 504.19$, $df = 7$, $P < 0.001$) than earthworms, respectively.

2.3. SDA experiment

We quantified the metabolic rates of *C. cranwelli* from oxygen consumption rates (VO_2). Eight frogs were fasted for ten days prior to the first resting metabolic rate (RMR) measurements to ensure that all frogs were postabsorptive. We placed each frog into a one-liter Erlenmeyer flask within a darkened environmental chamber maintained at 25 °C. Each flask contained 25 mL of distilled water so that frogs remained hydrated throughout respiratory measurements. Each sealed flask was connected to an individual channel of an indirect, closed circuit respirometer system (Micro Oxymax, Columbus Instruments, Columbus, OH) interfaced to a desktop computer. Chamber volumes and leaks were measured and checked by the Micro Oxymax software. One empty flask contained a medical battery (Procell medical battery, Bethesda, MD) with a known VO_2 to serve as a control for each trial. The system recorded the VO_2 of each frog every 60–80 minutes over a two day period. At every sample interval, samples of air from each frog's chamber were passed over Drierite and VO_2 was determined by the respirometer. The O_2 sensors were purged with outside air passed over a column containing Drierite after each measurement. All measurements were corrected for standard temperature, pressure, and CO_2 by the Micro Oxymax software.

Following RMR measurements, frogs were removed from their respiratory chambers and fed for SDA measurements using methods similar to those of Hopkins et al. (2004). Frogs were arbitrarily selected to be fed either earthworms or newborn mice equaling 10% of their body mass. Frogs were then returned to their respective respirometry chambers and VO_2 was monitored every 60–80 minutes for 5 days. Postprandial VO_2 returned to RMR in all frogs within 5 days (see Results). Frog mass was recorded to the nearest 0.1 mg before and after each trial.

After the 5-day SDA trial, frogs were removed from their respiratory chambers and returned to their respective 12×12 cm holding containers. Once frogs were again ten days postabsorptive, we collected a second set of RMR measurements for each frog. Following RMR measurements, the diet of each frog was reversed (compared to the first SDA trial) and SDA measurements were repeated as described above.

2.4. Growth experiment

To examine the effects of prey type on change in mass and mass conversion efficiencies, sixteen frogs were arbitrarily assigned to one of two experimental groups and fed either earthworms or newborn mice. Frogs received rations of their respective diets equaling 10% of their body mass three times a week for six weeks. Prior to growth trials, the mean mass of frogs in the earthworm and newborn mouse dietary treatments was statistically similar (6.88 g ± 0.33 SE and 5.67 g ± 0.56 SE, respectively; $P = 0.08$). One frog receiving the earthworm diet died early in the experiment due to unknown causes, and was omitted from the study. Once a week, frogs were fasted for 72 h prior to being weighed to the nearest 0.01 g. Two frogs on the mouse diet repeatedly retained feces for more than 72 h, which inflated their body mass and resulted in inaccurate mass conversion calculations. These two individuals were omitted from all data analyses.

2.5. Data analysis

Activity occurring during respirometry measurements elevates VO_2 above the resting or post-feeding rate. These periods of activity were obvious due to abrupt spikes in VO_2. A number of techniques have been used to remove these outliers from estimates of baseline metabolic rate, including the mean of a truncated data set (e.g., mean of lowest 30–50% of data; Hopkins et al., 1999; Litzgus and Hopkins, 2003) and use of a single ranked value (e.g., lowest quartile value; Dorcas et al., 2004; Hopkins et al., 2004; Roe et al., 2004). In each of these cases, the method of estimation was based upon the activity level of the study species and the frequency of respiratory measurements. To calculate RMR of *C. cranwelli* we used the mean of the lowest 50% of measurements collected for each frog (Rowe et al., 1998; Hopkins et al., 1999), because visual inspection of the data revealed that this technique reliably removed activity outliers from RMR measures (Fig. 1). The estimated RMR from the mean of the lower 50% of the measurements was then used as a baseline value from which elevations in metabolism during digestion (i.e., SDA) could be evaluated.

Respirometry data collected during the SDA trials were analyzed as follows. Oxygen consumption values obtained during SDA trials can be assumed to represent RMR plus the additional metabolic cost of digestion and random

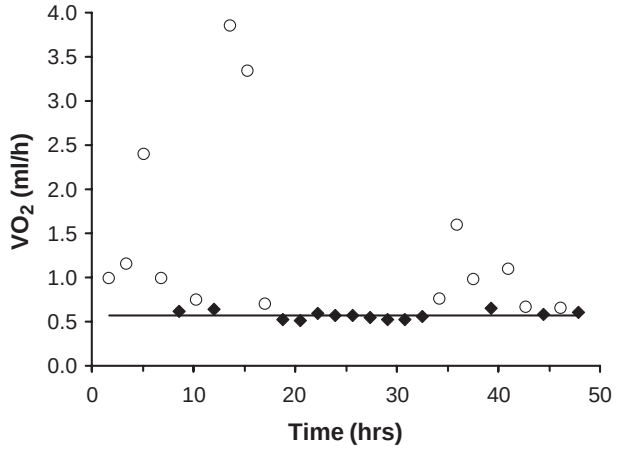

Fig. 1. Graphic representation of our method of estimating RMR for one frog. ♦=points considered to represent baseline RMR. ○=upper 50% of points, which were removed. The solid line is the RMR for the frog calculated as the mean of the lower 50% of the data points.

increases in VO_2 due to some activity occurring during measurements (Jobling, 1981; Andrade et al., 1997). Spikes in VO_2 caused by periods of activity were obvious from plots of oxygen consumption over time and were deleted following the procedures of Janes and Chappell (1995) (Fig. 2).

Total SDA values were determined by plotting the VO_2 curve and integrating the area under the curve above RMR (Jobling, 1981). We used a curve-fitting program (TableCurve, ver. 2.12, Jandell Scientific) to fit an equation to the VO_2 data collected after ingestion. We selected curves with high R^2 values (>0.7) and the simplest possible standard polynomial equation. We determined that all frogs had clearly returned to RMR levels before 100 h (range=42.0–89.8 h). We integrated each curve from time zero (i.e., the time of feeding) to the 100th hour and subtracted the integral of RMR from the total integral to

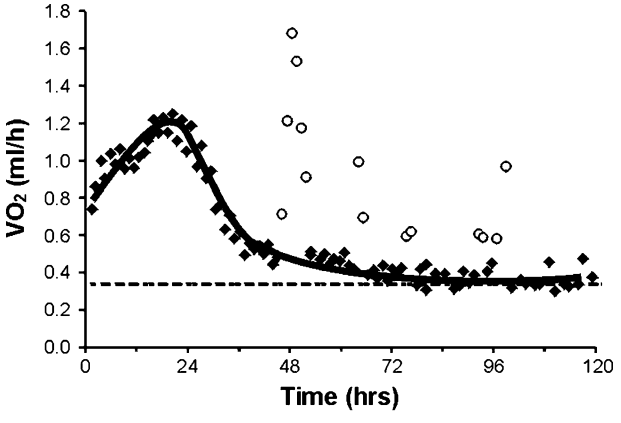

Fig. 2. Graphic representation of our method of estimating SDA after ingestion of prey for one frog. ♦=points considered part of the metabolic response after prey ingestion. ○=points removed as outliers due to activity. The dotted line is RMR and the solid line is the best-fit curve. The area between the RMR line and the best-fit curve to 100 h represents the total SDA.

Table 1
Comparison of the metabolic response after ingestion between a high and low quality diet (newborn mice and earthworms, respectively) in *C. cranwelli*

Variable	Meal type	
	Newborn mouse	Earthworm
Frog mass (g)	8.42±0.74	8.55±0.75
RMR (mL O_2 h^{-1})	0.37±0.004	0.41±0.003
SDA (mL O_2)	43.40±4.47	44.60±3.64
SDA (kJ)	0.87±0.09	0.90±0.07
Factorial increase	4.16±0.36	4.35±0.33
Peak VO_2 (mL O_2 h^{-1})	1.45±0.005	1.72±0.003
Time of peak (h)	19.77±1.68	16.43±1.32
Duration above RMR (h)	65.53±4.08	68.86±5.10

None of these variables were significantly affected by diet (ANCOVA, $P>0.20$ in all cases; Table 2). Sample size=8, meal size=10% of body mass, and temperature=25 °C for both diets. Values are reported as means± 1 SE.

generate a single SDA value (mL O_2) for each frog after each meal. Peak VO_2 values were determined at the maximum height of the curve. The duration of SDA was calculated based on the time when oxygen consumption first returned to within 90% of resting levels. The SDA value was converted from mL O_2 to kJ using the conversion factor 1 liter O_2=20.083 kJ (Schmidt-Nielsen, 1997). The overall SDA value, RMR, factorial increase, peak VO_2, time of peak VO_2, and the duration of SDA were all compared statistically using a repeated measures analysis of covariance with mass as a covariate (SAS, Proc Mixed; Zaidan and Beaupre, 2003).

Mass conversion efficiency was calculated for each frog by dividing the total change in body mass by the total mass of food ingested over the course of the study (Pough, 1980).

Table 2
Results of repeated measures analysis of covariance (mass as a covariate) comparing frogs fed two diets (newborn mice and earthworms)

Variable	Effect	*F* value	*P*
RMR (mL O_2 h^{-1})	Mass	139.37	**<0.001**
	Diet	2.21	0.20
	Mass × Diet	1.86	0.23
SDA (mL O_2)	Mass	18.53	**0.007**
	Diet	0.01	0.92
	Mass × Diet	0.02	0.90
Peak VO_2 (mL O_2 h^{-1})	Mass	98.85	**<0.001**
	Diet	0.30	0.61
	Mass × Diet	0.04	0.85
Factorial increase	Mass	19.70	**0.006**
	Diet	0.90	0.39
	Mass × Diet	1.07	0.35
Time of peak (h)	Mass	0.10	0.77
	Diet	0.01	0.93
	Mass × Diet	0.00	0.96
Duration above RMR (h)	Mass	0.01	0.93
	Diet	0.21	0.67
	Mass × Diet	0.25	0.64

The mixed procedure was performed using SAS. Sample size=8 for both diets for all variables.

Conversion efficiencies were arcsin square-root transformed and compared between dietary treatments using a single-factor ANOVA. The weekly body mass of each individual was $\log_{10}$ transformed and compared between dietary treatments using repeated-measures ANOVA.

3. Results

Variables related to pre-and post-prandial respiration are listed in Table 1. None of these variables (SDA, RMR, peak VO_2, factorial increase, time of peak, or duration above RMR) were significantly affected by diet nor was the interaction between diet and mass significant (ANCOVA, $P>0.20$ for all comparisons; Table 2). Frog mass significantly affected all of the dependent variables ($P<0.008$) except those relating to time (duration of SDA and time to reach peak VO_2, $P>0.70$).

Mass conversion efficiency and growth of frogs differed depending on the diet they were fed. The average mass conversion efficiency of the frogs fed mice was significantly greater than those fed earthworms (77.3%± 3.3 SE vs. 38.2%±9.7 SE, newborn mouse and earthworm diet respectively; $F=8.44$, $df=12$, $P=0.014$). Diet also had a significant effect on change in body mass, but the effect was dependent on time (repeated-measures ANOVA; diet, $F_{1,11}=0.45$, $P=0.51$; time, $F_{6,66}=89.34$, $P<0.001$; time * diet, $F_{6,66}=11.23$, $P=0.002$). Frogs fed newborn mice increased their mass exponentially, with some of the frogs weighing four times their initial mass at the end of the six-week experiment. In contrast, frogs fed earthworms gained less mass and their growth curves were linear (Fig. 3).

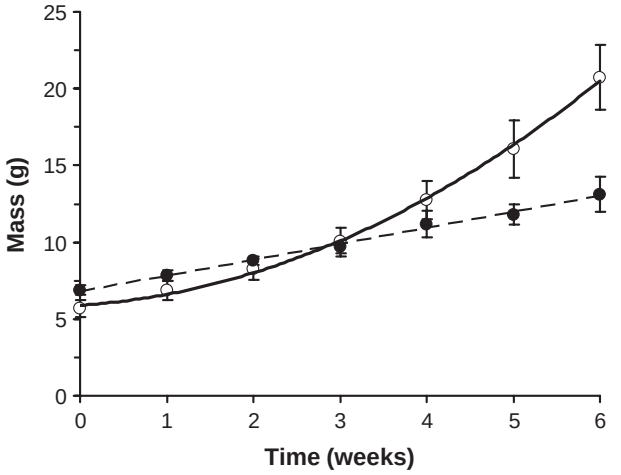

Fig. 3. Growth curves over six weeks of Chacoan horned frogs (*C. cranwelli*) fed 10% of their body mass in either newborn mice or earthworms three times per week. ○=weekly mass of frogs on the newborn mice diet, with a solid line indicating the growth curve. ●=weekly mass of frogs on the earthworm diet, with a dashed line indicating the growth curve. Means are ±1 SE and $n=6$ and 7 for the newborn mice diet and earthworm diets, respectively.

4. Discussion

Nutritional analysis revealed that frogs maintained on a diet of newborn mice received significantly more energy, lipid, and protein compared to frogs that ingested a diet of earthworms. As expected based on the nutritional analysis, mass conversion efficiency and growth were significantly higher in frogs ingesting newborn mice compared to those ingesting earthworms. These findings support other studies that indicate amphibian growth rates are not only affected by the amount of food ingested (Smith, 1976; Scott and Fore, 1995), but also by the type of prey consumed (Modzelewaski and Culley, 1974; Claussen and Layne, 1983). Diets high in protein are associated with rapid growth, especially in juvenile animals (Avery et al., 1993). However, our findings relating to digestive metabolism contradicted our predictions; despite significant differences in nutrient composition of the meals, the metabolic costs incurred by frogs processing the different diets (as shown by SDA) were similar.

Patterns of SDA have been documented in a wide variety of reptiles but have not been well established in amphibians. Overall, we observed increases in post-prandial metabolism that fall within the range of patterns described in previous studies of *Ceratophrys* and other amphibians that use ambush predatory strategies (Powell et al., 1999; Secor, 2001). Our factorial increase in post-feeding oxygen consumption (overall mean=4.26) is comparable to both the two to five-fold increases observed in a previous study of *C. cranwelli* (Powell et al., 1999) and the three to five-fold increases documented in a recent study of *Bufo marinus* (Secor and Faulkner, 2002). The response of *C. cranwelli* in this study was smaller than the eightfold increase in post-prandial metabolism observed by Secor (2001) in *C. ornata* and *Pyxicephalus adspersus*, possibly due to differences in meal size, temperature, and body size between studies. However, the SDA responses of the frogs in our study and in these previous studies are higher than the one to two-fold increases seen in frequently feeding anuran species (Wang et al., 1995; Sievert and Bailey, 2000).

Previous research has suggested that the protein content of a meal is a primary determinant of the magnitude of SDA (Coulson and Hernandez, 1979; Jobling, 1981). In particular, research on SDA and diet in fish has identified protein as a major factor (e.g., Brown and Cameron, 1991; Chakraborty et al., 1992; Ross et al., 1992). However, in our study SDA did not differ between frogs fed earthworms and newborn mice despite the fact that newborn mice contained 46% more protein than earthworms. Thus, our results suggest that protein content is not the sole factor influencing the magnitude of SDA in *C. cranwelli*.

The similarity in SDA between frogs fed the two diets may be due to several factors. One possibility is that differences in protein composition (i.e., the types of protein) exist between the prey types that could result in different processing costs per unit protein. McCue et al. (2005) found

that the chemical composition of a meal greatly affects SDA. Meals of animal tissue containing more complex proteins resulted in higher SDA responses than meals of simple proteins in Burmese pythons (*Python molurus*), suggesting protein complexity as an important contributor to SDA. Another factor that may be involved is the physical composition of prey, rather than nutritional composition. Secor and Faulkner (2002) also found no significant difference between the SDA of frogs digesting rodents and earthworms, but SDA was much higher in frogs digesting prey with chitinous exoskeletons (crickets or superworms). They proposed that higher SDA in frogs fed prey with chitinous exoskeletons reflects larger mechanical and chemical breakdown costs. Although neither of our diets were chitinous, the physical composition of earthworms and mice is clearly different and may complicate comparisons based on chemical composition alone. Additional studies that address the effect of prey composition on SDA will provide insight into the bioenergetic consequences of ingesting different prey types.

Despite a similarity in SDA, frogs on the higher quality diet exhibited higher mass conversion efficiencies and growth than frogs on the lower quality diet. High conversion efficiencies have been documented within many amphibian groups (Pough, 1980; Larson, 1992). The conversion efficiency documented for the earthworm-fed frogs in our study (38%) falls within the conversion efficiencies reported for Bufonids fed a variety of invertebrate diets. For example, *Bufo terrestris* and *B. fowleri* had mass conversion efficiencies of 36% and 24% (respectively) when fed crickets (*Acheta domestica*; Smith, 1976; Claussen and Layne, 1983). Mass conversion efficiencies of *B. fowleri* fed a cabbage looper diet (*Trichoplusia ni*) and mealworm diet (*Tenebrio molitor*) were 15% and 60%, respectively (Claussen and Layne, 1983). In contrast, the mass conversion efficiency of our mouse-fed frogs (77%) was higher than most efficiencies reported in other amphibians (above references and Pough, 1980), likely due to the high nutritional content of the newborn mice.

Optimal foraging theory predicts that animals should select diets with the highest possible energy content if all other factors are equal (Seale, 1987). Amphibians, especially those that are ambush predators, are generally not selective in their food intake and prey availability is usually the most important factor affecting their diet composition (Smith, 1976; Larson, 1992). Field studies of other members of the South American litter anurans indicate that their diet includes a broad range of prey types (Toft, 1981; Duellman and Lizana, 1994). However, a field study of *C. cornuta* in Peru, suggests that vertebrate prey is a particularly important component of the diet of *Ceratophrys* in the wild (Duellman and Lizana, 1994). Although representing a small percentage of prey items (3%), vertebrates constituted a significantly larger portion of the overall prey biomass than all other taxa combined (53%), with 34% of vertebrate prey being mice (Duellman and Lizana, 1994). Together with our results, this suggests that occasional vertebrate captures are an important component of the wild diet of *Ceratophrys* due to their high nutritional content and prey biomass.

Our findings on SDA, growth, and mass conversion efficiency suggest that prey type should be considered a critical factor in future studies of digestive physiology. Despite the long-held contention that protein content drives SDA, our results suggest that other factors, such as the type of protein digested or mechanical break down costs, should be considered. Future studies that determine the underlying factors driving SDA will ultimately be important for constructing more comprehensive energy budgets for organisms feeding on multiple prey types.

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