

Energetic costs of digestion in Australian crocodiles

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Abstract. We measured standard metabolic rate (SMR) and the metabolic response to feeding in the Australian crocodiles, *Crocodylus porosus* and *C. johnsoni*. Both species exhibit a response that is characterised by rapidly increasing metabolism that peaks within 24 h of feeding, a postfeeding metabolic peak (peak \dot{V}_{O_2}) of 1.4–2.0 times SMR, and a return to baseline metabolism within 3–4 days after feeding. Postfeeding metabolism does not significantly differ between species, and crocodiles fed intact meals have higher total digestive costs (specific dynamic action; SDA) than those fed homogenised meals. Across a more than 100-fold range of body size (0.190 to 25.96 kg body mass), SMR, peak \dot{V}_{O_2} , and SDA all scale with body mass to an exponent of 0.85. Hatchling (≤ 1 year old) *C. porosus* have unexpectedly high rates of resting metabolism, and this likely reflects the substantial energetic demands that accompany the rapid growth of young crocodylians.

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Introduction

For many species, the energetic costs associated with digestion can be considerable. Recent reviews have shown that the energy used in digesting a meal, relative to the total energy value of the meal, averages around 7% in humans, 10% in birds and mammals and >20% in amphibians and reptiles (McCue 2006; Secor 2009). Digestive costs arise from many factors, including the energy expended in the upregulation of digestive organs and biochemical systems following feeding, from the mechanical and chemical breakdown of food items, and from the process of nutrient absorption and protein synthesis (see reviews of Andrade *et al.* 2005; McCue 2006; Secor 2009). Proximate differences in digestive costs have been attributed to variation in meal size, meal type, body size, and body temperature (Secor 2009) while ecological and evolutionary factors such as foraging mode, local adaptation, and phylogenetic differences among taxa remain less explored (Secor and Nagy 1994; Secor and Diamond 2000).

Digestive costs are important from an energy balance perspective in that energy used to digest meals cannot be used for maintenance of body systems, growth, reproduction, or other important activities. The metabolic response to feeding can therefore be a significant component of the energy budget of many species (McCue and Lillywhite 2002; Zaidan and Beaupre 2003; Secor 2009), and by understanding the influence of digestion on

energy allocation, we may better understand animal nutrition and the role of diet in animal function.

Here we investigate factors that influence postfeeding metabolism and digestive costs in the Australian crocodiles, *Crocodylus porosus* and *C. johnsoni*. Although somewhat different ecologically (Webb and Manolis 1989), both species are opportunistic predators that feed on a wide variety of arthropods, fish, and small vertebrates (Taylor 1979; Webb *et al.* 1982). Occasionally, large prey can be taken by adults (Tucker *et al.* 1996), but crocodiles in general tend to rely on small prey items relative to their body size, and likely feed as frequently as opportunity allows. We compare the energetic costs of digestion between the species and examine the influences of meal type and body size on metabolic responses to feeding.

Materials and methods

We first compared differences between species using yearling *C. porosus* ($n = 5$) and yearling *C. johnsoni* ($n = 4$) from a captive population (Wildlife Management International, Darwin, Northern Territory). Metabolic responses were assessed from crocodiles that were fed a meal of homogenised chicken by gavage (Country Cuisine Chicken Pet Loaf, Hills Pet Cuisine, Mt Barker, South Australia), equivalent to 3% of body mass. Preliminary feeding trials and previously published data (Garnett 1988) suggested that meals equivalent to 3% of body mass

were sufficient to fill the stomach of juveniles without regurgitation.

Second, we investigated the effects of meal composition on postfeeding metabolism by comparing *C. porosus* fed the homogenised chicken with a second group of similar-sized *C. porosus* ($n = 4$) fed whole chicken necks (3% of body mass). Crocodiles were fed chicken necks using 30-cm feeding tongs to push the food into the opening of the oesophagus behind the palatal valve. The food bolus was pushed down the oesophagus and into the stomach by inserting a gavage tube and by massaging the outside of the throat. Lastly, we investigated the allometric effects of body size on postfeeding metabolism by measuring individuals from four size classes of *C. porosus* fed the homogenised meal ($n = 5$ per size class; size class means = 0.235, 1.24, 6.63, and 21.70 kg; range = 0.190–25.96 kg).

Animal housing

Crocodiles were housed in communal outdoor raising pens and were fasted for 3–4 days before initiating experiments to ensure that they had become postabsorptive. Individuals were weighed and placed into opaque PVC respirometry chambers (similar to those used by Grigg 1978) that were size-matched to different body sizes (chambers 250–400 mm diameter; 30–200 L). Chambers were filled approximately half full with water, and maintained at 30°C by submersed 100-W aquarium heaters connected to temperature controllers (ViaAqua). Partially filling the chambers allowed crocodiles the choice to be completely submerged beneath the water, but also allowed sufficient room to raise the entire head above water to breathe. The addition of water within chambers also reduced the headspace of air within the chambers, increasing the temporal sensitivity of the respirometry system (Frappell *et al.* 1989). Water was changed every 36–48 h to avoid accumulation of waste products, and each chamber was fitted with a drain system that allowed chamber water to be renewed without having to physically handle animals. Metabolism was measured for three days before feeding and continued for eight days after feeding. Crocodiles were then returned to communal raising pens. All housing procedures and experimental protocols were approved by the Charles Darwin University Animal Ethics Committee (project reference no. A09015).

Respirometry

We quantified pre- and postprandial metabolism by measuring rates of oxygen consumption (\dot{V}_{O_2}) using flow-through respirometry (Withers 2001; Lighton 2008). For each respirometry chamber, a laboratory air pump (Reciprotor) pushed dried room air (~28°C) through a mass flow controller (McMillan Flow Products 80D) and then through the chamber. Airflow was adjusted to allow a maximum of 1% reduction in O_2 within the chamber, compared with room air. A continuous subsample of excurrent chamber air was drawn through a drying column (Drierite™) and passed through O_2 and CO_2 analysers (Fox Box; Sable Systems International). We used a solenoid multiplexing system to sequentially measure four crocodiles in each trial, sampling each for 45 min with a 15-min baseline (drawn from a chamber not containing a crocodile, but half filled with water) interspersed between samples. Crocodiles were each sampled

during six periods per day, and we used the most level (lowest sum of absolute differences from the interval mean) 15 min of each 45-min sample period to calculate rates of gas exchange.

We calculated \dot{V}_{O_2} using the equations of Withers (1977) implemented in LabAnalyst (Warthog Systems) and then converted \dot{V}_{O_2} to energy equivalent units assuming a factor of 19.5 J mL⁻¹ O_2 consumed (Gessaman and Nagy 1988). Energetic values of the meals were calculated using total meal mass and the mass-specific nutritional information provided by the manufacturers (chicken necks = 9.46 kJ g⁻¹ wet mass; homogenised chicken = 9.50 kJ g⁻¹ wet mass). Values were cross-checked against values published by the USDA National Nutrient Database for Standard Reference (<http://www.nal.usda.gov>).

For each individual, we quantified the following variables as described by McCue (2006) and Secor (2009): SMR (standard metabolic rate), the lowest measurement of \dot{V}_{O_2} during the three-day prefeeding (fasting) period; peak \dot{V}_{O_2} , the highest recorded \dot{V}_{O_2} following feeding; factorial scope of peak \dot{V}_{O_2} , calculated as the peak \dot{V}_{O_2} divided by SMR; duration of elevated metabolic rate, measured as the time from feeding when \dot{V}_{O_2} was no longer significantly greater than SMR (determined from *post hoc* pairwise comparisons); SDA, the total energy expended above SMR during the duration of significantly elevated \dot{V}_{O_2} ; and SDA coefficient, SDA quantified as a percentage of the energetic value of the meal.

Statistical analyses

We used repeated-measures ANOVA to determine whether feeding state (before or after feeding) significantly affected \dot{V}_{O_2} (mL h⁻¹) and followed each ANOVA with *post hoc* comparisons (Tukey–Kramer HSD) to determine whether \dot{V}_{O_2} differed significantly among successive sampling days. We tested for differences in body mass between groups using ANOVA, and compared rates of whole-animal metabolism using analysis of covariance (ANCOVA) with body mass as a covariate (Packard and Boardman 1999; Hayes 2001). We assessed the effects of body size on postfeeding metabolism using least-squares regression to determine how SMR and peak \dot{V}_{O_2} scale with body mass. Data were log-transformed before analysis in order to meet the assumptions for parametric testing and to linearise scaling relationships.

Results

Species

Body mass, SMR, and all measures of postfeeding metabolism did not significantly differ between juvenile *C. porosus* and juvenile *C. johnsoni* (Table 1). However, for both species, \dot{V}_{O_2} differed significantly between pre- and postfeeding periods ($F = 13.4$ and 7.8, $P < 0.01$ for *C. porosus* and *C. johnsoni*, respectively). For both species, metabolic rates peaked within 24 h after feeding, remained elevated for 48–72 h, and became statistically indistinguishable from prefeeding levels by the third day after feeding (Fig. 1).

Meal type

In *C. porosus*, there was a significant difference in postfeeding metabolism between individuals fed a meal of homogenised

Table 1. Metabolism and responses to feeding in Australian crocodiles

Comparison of body mass, standard metabolic rate (SMR), and postfeeding metabolic measures of oxygen consumption (\dot{V}_{O_2}); peak oxygen consumption, scope of peak, duration of increased metabolism, specific dynamic action (SDA), and coefficient of SDA in response to feeding in juvenile Australian crocodiles (values are mean \pm s.e.m.)

Variable	<i>C. johnsoni</i>	<i>C. porosus</i>	<i>C. porosus</i>	Species		Meal type	
	homog. chicken	homog. chicken	chicken necks	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
<i>N</i>	4	5	4				
Body mass (kg)	0.93 \pm 0.13	1.24 \pm 0.30	1.32 \pm 0.09	3.68	0.10	0.24	>0.50
SMR (mL O ₂ h ⁻¹)	38.03 \pm 4.43	53.06 \pm 6.85	74.21 \pm 8.94	0.13	>0.50	5.75	0.06
Peak \dot{V}_{O_2} (mL O ₂ h ⁻¹)	50.75 \pm 5.58	83.16 \pm 11.01	141.47 \pm 19.76	1.88	0.21	8.05	0.03
Scope (peak \dot{V}_{O_2} /SMR)	1.36 \pm 0.15	1.58 \pm 0.11	2.01 \pm 0.46	1.31	0.29	1.07	0.34
Duration (days)	3	3	4				
SDA (kJ)	8.10 \pm 2.65	19.26 \pm 4.61	55.48 \pm 12.53	3.13	0.12	9.64	0.02
SDA coefficient (%)	3.08 \pm 1.08	5.86 \pm 1.68	14.95 \pm 3.50	3.64	0.10	8.34	0.02

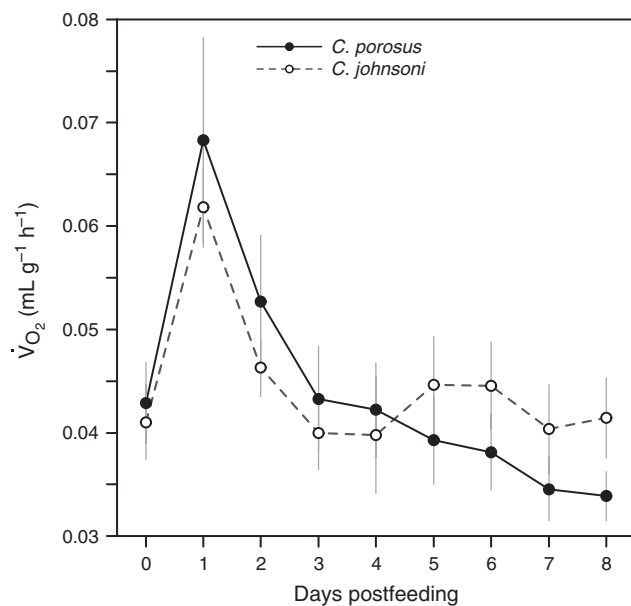


Fig. 1. Metabolic responses to feeding in the Australian crocodiles *Crocodylus porosus* and *C. johnsoni*. Symbols are means \pm 1 s.e.m. For both species, \dot{V}_{O_2} was significantly elevated above baseline levels following feeding, but the species did not differ in postfeeding metabolic peak (peak \dot{V}_{O_2}) or in total energetic costs of digestion (specific dynamic action, SDA).

chicken and those fed chicken necks. Peak \dot{V}_{O_2} (mL h⁻¹) following feeding was greater in the group fed chicken necks ($F_{1,7} = 8.05$, $P = 0.03$) (Fig. 2), and metabolism was significantly elevated for one day longer (Table 1). Total energetic costs to digest the meal, SDA (kJ) and SDA coefficient (%), were more than double in *C. porosus* fed chicken necks than those fed the homogenised chicken (Table 1).

Scaling with body size

C. porosus measured across more than a 100-fold range of body mass (0.19–25.96 kg) had SMR and postfeeding peak \dot{V}_{O_2} that each scaled with a mass exponent of 0.85 ± 0.03 s.e.m. ($F_{1,18} = 691.4$, $P < 0.001$, and $F_{1,18} = 671.5$, $P < 0.001$, respectively) (Fig. 3a). Body mass accounted for 97.4% of the

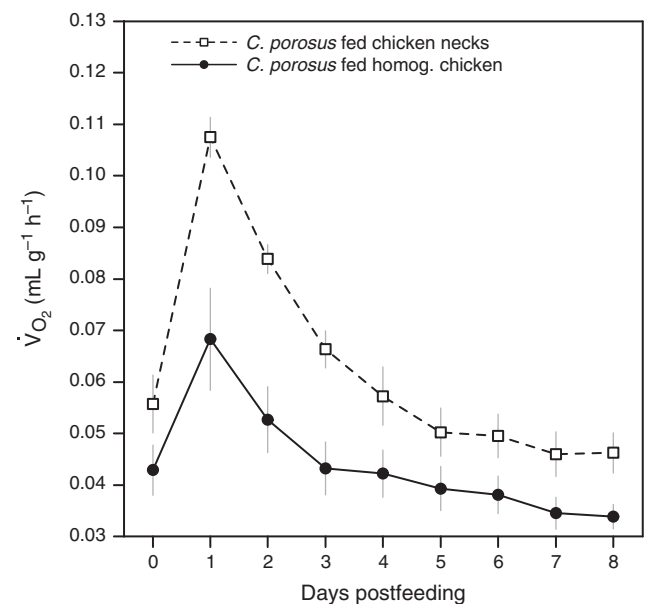


Fig. 2. Metabolic response to feeding in *C. porosus* fed chicken necks versus those fed homogenised chicken. Symbols are means \pm 1 s.e.m. Crocodiles fed chicken necks had a higher postfeeding metabolic peak (peak \dot{V}_{O_2}), longer duration of elevated metabolism, and higher total energetic costs of digestion (specific dynamic action, SDA).

variation in metabolism in both cases. SDA (kJ) scaled with body mass to an exponent of 0.85 ± 0.06 s.e.m. ($F_{1,18} = 193.2$, $P < 0.001$) (Fig. 3b).

Discussion

Regardless of species (*C. porosus* and *C. johnsoni*), meal type (homogenised chicken and chicken necks), or body size (190 g to 25.96 kg), juvenile Australian crocodiles exhibited a similar physiological response to feeding. The response is characterised by rapidly increasing metabolism, peaking within 24 h of feeding, a postfeeding peak in metabolism averaging 1.4–2.0 times SMR, and a return to baseline metabolism within 3–4 days after feeding. This general pattern is similar to that of many other episodically feeding reptiles (see review by Secor 2009), and also similar to

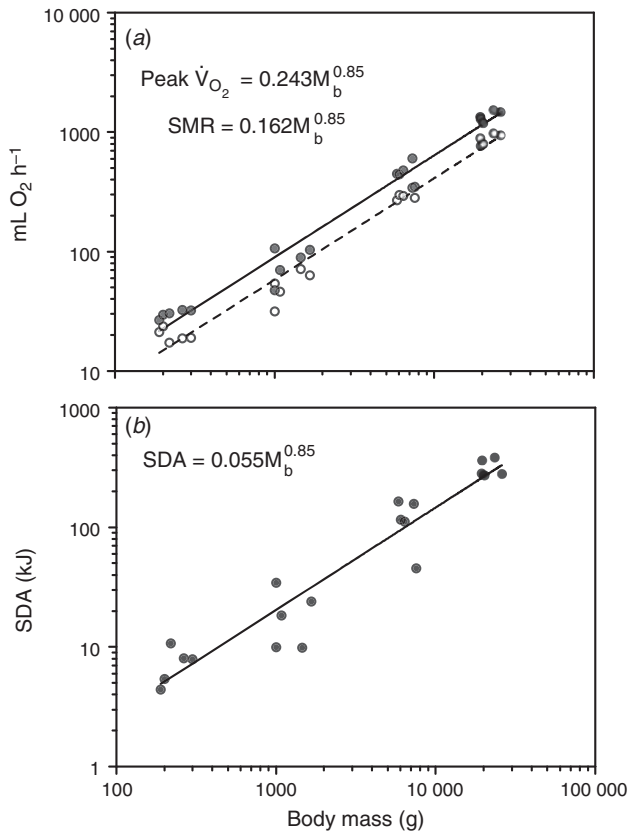


Fig. 3. (a) Allometric scaling of standard metabolic rate (SMR) and postfeeding metabolic peak (peak \dot{V}_{O_2}) with body mass (M_b) for *C. porosus*; (b) allometric scaling of total energetic costs of digestion (specific dynamic action, SDA) with body mass for *C. porosus*.

feeding responses of other juvenile crocodylians. Other crocodylians have peak postfeeding metabolism ranging from 1.6 times prefeeding values in *Caiman crocodylus* (mean body mass = 1.68 kg) (Gatten 1980) to 4.1 times prefeeding levels in *Alligator mississippiensis* (mean body mass = 0.70 kg; meal = 10% of body mass) (Coulson and Hernandez 1983). Postfeeding metabolism remained elevated for 5–10 days following feeding in *A. mississippiensis* (mean body mass = 0.70 kg; meal = 5–10% of body mass) (Coulson and Hernandez 1979, 1983) and for 6–9 days in *Caiman latirostris* (mean body mass = 1.68 kg; meal = 11.5% of body mass) (Starck *et al.* 2007).

However, metabolic responses to feeding in Australian crocodiles are somewhat modest when compared with other large reptiles. Some of the highest rates of postfeeding metabolism have been observed in large-bodied pythons and varanid lizards, where postfeeding metabolic increases of 10–15 times SMR are common (Secor and Phillips 1997; Secor and Diamond 2000; Bedford and Christian 2001). These dramatic increases in metabolism may lead to high digestive costs, as nearly one-quarter of the energy value of a meal is used to fuel the digestive process (Secor and Phillips 1997; Ott and Secor 2007; Secor 2008).

The postfeeding metabolic differences between crocodiles and other large reptiles are probably due primarily to differences

in meal size. Large pythons may commonly consume meals equal to a quarter of their body mass (Bedford and Christian 2000, 2001), but also may occasionally eat very large prey that is equal to, or more than, their body mass (Pope 1961; Shine *et al.* 1998). Crocodiles likely never consume such large meals, and stomach capacity in crocodiles is proportionately far less than that of other large reptiles. Juvenile *C. porosus* fed homogenised chicken in this study had stomach capacity ~3% of body mass, but previous studies using whole foods suggest that stomach capacity could be as high as ~14% of body mass (Davenport *et al.* 1990). Thus, estimates of postfeeding metabolism could potentially be larger if crocodiles were to consume larger meals.

Field observations of *C. porosus* support the link between diet, metabolic costs of digestion, and energy allocation. Webb *et al.* (1991) report conversion efficiency (wet mass prey converted to wet mass crocodile) of wild juvenile *C. porosus* to be 82.4%, with individuals consuming a food equivalent of ~4% of body mass per week. Captive juveniles that were given large meals at frequent intervals required nearly four times as much food to achieve similar growth rates as wild juveniles (Webb *et al.* 1991), and thus conversion efficiencies were much lower when the stomach was repeatedly filled to capacity. The metabolic response to feeding and the associated energy demands of digestion in crocodiles may, in part, explain this disparity.

Application of digestive costs to crocodile production

The inefficiency with which captive crocodiles digest food and use energy is of particular concern to the crocodile farming industry (Webb *et al.* 1987). Fresh meat is the main diet used in crocodile, alligator, and caiman farms around the world, despite the high costs associated with transport and storage. Alternative diets have been used with mixed success. A simple vegetable-based pellet diet has been used successfully with alligators in North America (Kercheval and Little 1990; Staton *et al.* 1992), but has yet to be successfully applied in Australian crocodiles (Van Barneveld *et al.* 2004; Peucker and Jack 2006).

Our data support the possibility that a simpler processed food diet, such as a pelleted food made from homogenised animal tissues, may contribute to more efficient commercial production of crocodiles. The energetic costs of digestion in *C. porosus* (SDA) were much lower when fed homogenised chicken than when fed intact chicken necks (Table 1; Fig. 2). This difference stems from two sources: crocodiles had both significantly higher postfeeding peaks in metabolism (peak \dot{V}_{O_2}) and maintained postfeeding metabolic increases for up to 24 h longer when fed chicken necks. The energetic costs to mechanically and chemically break down whole tissue and bone are predictably larger than those in which food must only be digested chemically before absorption (Boback *et al.* 2007). Lower digestive costs in simple versus whole-animal meals have also been shown in carnivorous lizards consuming whole rodents versus those consuming simpler egg meals (Secor and Phillips 1997; Christel *et al.* 2007), and thus meal composition undoubtedly plays an important role in the metabolic response to feeding in reptiles (Hailey 1998; McCue *et al.* 2005).

Scaling of metabolic responses to feeding

Both SMR and postfeeding peak \dot{V}_{O_2} scaled with body mass to an exponent of 0.85 (Fig. 3a). The intercepts of the relationships

differ, but the slopes do not, suggesting that the metabolic peak following feeding in *C. porosus* is proportionally similar across the range of body sizes we measured (0.190–25.96 kg). The allometric scaling exponent of 0.85 for peak \dot{V}_{O_2} of digesting *C. porosus* is similar to those observed in other species measured over a wide range of body sizes, including 0.90 for *Python molurus* (Secor and Diamond 1997) and 0.89 for seven python species analysed by Thompson and Withers (1999). Much work remains to be done on allometric scaling of the metabolic responses to feeding, but because few species range much more than a single order of magnitude in body size throughout life, few studies have been able to investigate SDA across more than two orders of magnitude, as we have done.

An interesting, but unplanned discovery is the considerably higher rates of resting metabolism in hatchling *C. porosus* (≤ 1 year old) relative to larger (older) juveniles. On a mass-specific basis, hatchlings (mean body size = 0.235 kg, 493 mm total length) have mean SMR that is 106% higher than older juvenile conspecifics (range = 96–117%) (Fig. 4). Part of this difference may be attributed to the allometric scaling relationship between body size and metabolism, and when excluding hatchlings, the relationship between body mass (range = 0.820–25.96 kg) and SMR shifts from a scaling exponent of 0.85 to the isometric relationship

$$\text{SMR} = 0.00017 M_b^{1.0}.$$

Future work that examines allometric scaling of hatchling metabolism in relation to older, but similar-sized conspecifics is needed to fully understand the magnitude of elevated metabolism in very young crocodiles.

Rapid increases in body size and energy demands for fueling rapid tissue synthesis may partially explain high metabolism in

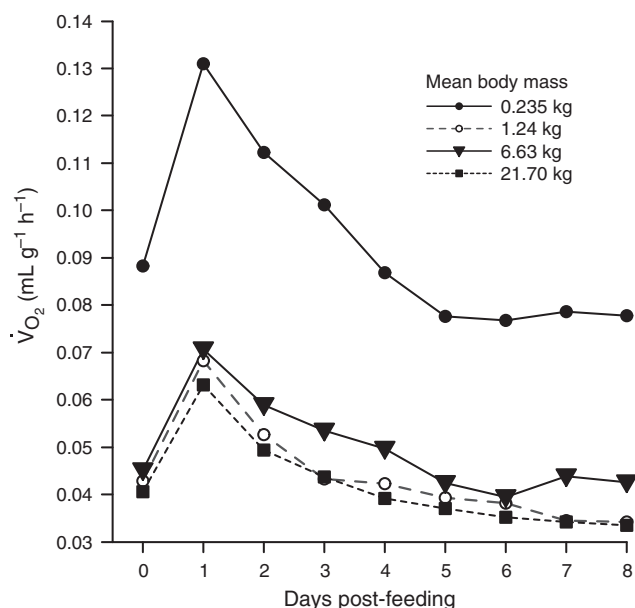


Fig. 4. Differences in metabolic responses to feeding among four size classes of juvenile *C. porosus*. Hatchlings (mean mass = 235 g) have higher than expected rates of metabolism, likely reflecting the high energetic demands of rapid growth.

hatchlings (Thompson and Withers 1998; Nagy 2000; Beaupre and Zaidan 2001). In the field, juvenile *C. porosus* (< 0.5 m total length) gain up to 2.9 g day^{-1} in body mass (Webb *et al.* 1991; Sah and Stuebing 1996), which allows them to rapidly reach a minimum threshold body size in which they are no longer prey for mesopredators such as wading birds and snakes, or larger crocodiles. Thus, the interplay between digestion and metabolism is likely important in influencing survivorship, as well as growth, in juvenile crocodiles.

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