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Effects of meal size, meal type, and body temperature on the specific dynamic action of anurans

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Abstract Specific dynamic action (SDA), the increase in metabolism stemming from meal digestion and assimilation, varies as a function of meal size, meal type, and body temperature. To test predictions of these three determinants of SDA, we quantified and compared the SDA responses of nine species of anurans, *Bombina orientalis*, *Bufo cognatus*, *Ceratophrys ornata*, *Dyscophus antongilli*, *Hyla cinerea*, *Kassina maculata*, *Kassina senegalensis*, *Pyxicephalus adspersus*, and *Rana catesbeiana* subjected to meal size, meal type, and body temperature treatments. Over a three to seven-fold increase in meal size, anurans experienced predicted increases in postprandial rates of oxygen consumption ($\dot{V}O_2$), the duration of elevated $\dot{V}O_2$, and SDA. Meal type had a significant influence on the SDA response, as the digestion and assimilation of hard-bodied, chitinous crickets, mealworms, and superworms required 76% more energy than the digestion and assimilation of soft-bodied earthworms, waxworms, and neonate rodents. Body temperature largely effected the shape of the postprandial metabolic profile; peak $\dot{V}O_2$ increased and the duration of the response decreased with an increase in body temperature. Variation in body temperature did not significantly alter SDA for four species, whereas both *H. cinerea* and *R. catesbeiana* experienced significant increases in SDA with body temperature. For 13 or 15 species of anurans ranging in mass from 2.4 to 270 g, SMR, postprandial peak $\dot{V}O_2$, and SDA scaled with body mass (log–log) with mass exponents of 0.79, 0.93, and 1.05, respectively.

Keywords Amphibians · Anurans · Digestion · Metabolism · Specific dynamic action

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Introduction

Specific dynamic action (SDA) is the metabolic phenomenon resulting from the digestion and assimilation of a meal. Quantitatively, SDA represents the accumulated energy expended on pre- and postabsorptive activities, including gastrointestinal smooth muscle contraction, the production of digestive acids and enzymes, nutrient absorption, and the synthesis of structure, metabolites, and waste products from absorbed nutrients (Brody 1945; Kleiber 1975). These activities are responsible for increasing metabolic rates above fasting and resting levels by as little as 50% for humans to as much as 4,300% for Burmese pythons (Westerterp-Plantenga et al. 1992; Secor and Diamond 1997a). Generally among invertebrates and vertebrates, metabolic rates increase with feeding by an order of two to five-fold, with the most notable increases (>10-fold) observed for amphibian and reptile species that feed infrequently on large meals (Bradley et al. 2003; Campbell et al. 2000; Janes and Chappell 1995; Jobling 1981; Secor and Diamond 2000; Secor 2005; Sigsgaard et al. 2003).

Independent of interspecific variation in postprandial metabolism that may reflect differences in feeding habits, intraspecific variation in the magnitude and

duration of the SDA response is attributed to differences in meal characteristics and environmental conditions. For both ectotherms and endotherms, investigators have explored the effects of meal size, meal type, and body temperature on SDA. Observed in these studies is that larger meals generate larger SDA responses (Carefoot 1990a; Janes and Chappell 1995; Jobling 1981; Secor and Diamond 1997a). Independent of meal size, SDA responses have been found to vary among different meal types as a function of meal composition and structure (Hailey 1998; Secor and Faulkner 2002; Secor and Boehm 2006). With a change in body temperature for ectotherms, observed are shifts in pre- and postprandial metabolic rates and the duration of the metabolic response (Secor and Faulkner 2002; Zaidan and Beaupre 2003).

Concluded from these studies is that the profile of postprandial metabolism and the magnitude of SDA are both a function of the intensity and rate of digestive performance (Hailey 1998; Secor 2003; Secor and Boehm 2006; Toledo et al. 2003). Any meal trait (i.e., size or structure) that increases the workload of digestion will predictably result in a larger and more prolonged metabolic response. Likewise, any feature that alters the rate of digestion (i.e., body temperature) will influence the duration of the response. Whereas we can make broad generalizations on the determinants of SDA based on the diversity of species yet studied (isopods to humans), a more refined approach would allow us to better test proposed hypotheses regarding the effects of these determinants on SDA. Such an approach would benefit by reducing the influence of potential large-scale phylogenetic effects, while still maintaining some degree of species diversity. We therefore designed this study to explore the effects of meal size, meal type, and body temperature on the SDA responses of anurans.

We used nine species of anurans representing seven families to test three hypotheses of SDA response. First, we hypothesized that the magnitude of the SDA response will increase with meal size. We predicted that the effort to digest and assimilate larger meals will be reflected in higher peaks in postprandial metabolism, longer durations of the metabolic response, and greater overall SDA's. We addressed this hypothesis by feeding species a range of different size meals while controlling for meal type and body temperature. Our second hypothesis was that SDA will vary with meal type as a function of meal structure. Predicted is that meals possessing a hard exoskeleton will require more effort to digest than soft-bodied meals, and thus generate larger SDA responses. Therefore, we fed anurans meals differing in structure while controlling for meal size and body temperature. Third, we tested the hypothesis that body temperature will influence the profile of postprandial metabolism, but not SDA. Whereas a change in body temperature is expected to alter pre and postprandial metabolic rates and duration of the metabolic response, it should not affect SDA given the assumption that the same amount of accumulated effort would be used to digest and assimilate any particular meal regardless of temperature and rate of digestion. We assessed body temperature effects by feeding anurans cricket meals 10% of body mass and maintaining them at three different temperatures. In addition, we took advantage of this multi-species study to compare SDA responses among species and to explore interspecific relationships between body mass and metabolic variables.

Materials and methods

Anurans and their maintenance

In this study, we used the following nine species of anurans; fire-bellied toad, *Bombina orientalis* (Bombinatoridae), Great Plains toad, *Bufo cognatus* (Bufonidae), South American horned frog, *Ceratophrys ornata* (Leptodactylidae), tomato frog, *Dyscophus antongilli* (Microhylidae), green tree frog, *Hyla cinerea* (Hylidae), red-legged kassina, *Kassina maculata* (Hyperoliidae), bubbling kassina, *Kassina senegalensis* (Hyperoliidae), African bullfrog, *Pyxicephalus adspersus* (Ranidae), and American bullfrog, *Rana catesbeiana* (Ranidae). The distribution of these species encompasses tropical, subtropical, and temperate regions of the world. *B. cognatus*, *H. cinerea*, and *R. catesbeiana* inhabit portions of eastern and central North America; *C. ornata* exists in southern South America; *K. maculata*, *K. senegalensis*, and *P. adspersus* range through areas of sub-Saharan Africa; *D. antongilli* inhabits Madagascar; and *B. orientalis* occurs in northwest Asia (Obst et al. 1984). Body mass of anurans used in this study ranged from a mean (± 1 SE) of 4.19 ± 0.30 g for *B. orientalis* to 228 ± 19 g for *R. catesbeiana*.

All anurans were purchased commercially and maintained individually or in small groups in either glass aquariums (80 l) or plastic storage containers (12–60 l) at 25–28°C under a photoperiod of 14L:10D. We fed *C. ornata* and *P. adspersus* neonate rats weekly and fed all other anurans live crickets every other day. Prior to metabolic measurements, individuals were fasted for 2–3 weeks to ensure that their digestive

tracts had emptied and all digestive activities had ceased. At all times during the study, individuals had access to water.

Measurements of gas exchange

We quantified pre- and postprandial metabolism of anurans from rates of gas exchange, oxygen consumption ($\dot{V}O_2$) and carbon dioxide production ($\dot{V}CO_2$), measured using closed-system respirometry as described by Vleck (1987) and Secor and Faulkner (2002). Anurans were placed individually into opaque respirometry chambers (0.5–3.5 l) and maintained at a target temperature within an environmental chamber. Each respirometry chamber was fitted with an incurrent and excurrent air port, each attached to a three-way stopcock. With the exception of sampling periods, air was continuously pumped into chambers through the incurrent air port. We maintained a small amount of water in each respirometry chamber to prevent anurans from desiccating due to constant air flow.

For each measurement of gas exchange, we withdrew a 20-ml air sample from the excurrent air port, and closed both ports to seal the chamber. One-half to an hour later, the excurrent air port was opened and a second 20-ml air sample was withdrawn. Air samples were pumped (125 ml min^{-1}) through a column of water absorbent (Drierite; W. A. Hammond Drierite Co., Xenia, OH, USA) and CO_2 absorbent (Ascarite II; Thomas Scientific, Swedesboro, NJ, USA) into an O_2 analyzer (S-3A/II; AEI Technologies, Pittsburgh, PA, USA) and through a column of water absorbent into a CO_2 analyzer (CD-3A; AEI Technologies, Pittsburgh, PA, USA). We calculated whole-animal (ml h^{-1}) rates of $\dot{V}O_2$ and $\dot{V}CO_2$ corrected for standard pressure and temperature, using a modification of equation 9 presented in Vleck (1987).

We began each metabolic trial by measuring each individual's standard metabolic rate (SMR). From fasted individuals, we measured rates of gas exchanges twice a day (~0800 and 2000 h) for 3–4 days. We assigned for each individual its SMR as the lowest $\dot{V}O_2$ and accompanied $\dot{V}CO_2$ measured over those days. Following SMR measurements, anurans were removed from respirometry chambers and fed one of the selected meal types weighing a targeted percentage of individual body mass. Following feeding, anurans were returned to their respirometry chambers and measurements of gas exchange were resumed at 12-h intervals (~0800 and 2000 h) for 3 day and at 1-day intervals (~800) thereafter for 3–7 more days.

Experimental procedures

We used all species, with the exception of *K. maculata*, to investigate the effects of meal size on SDA. Individuals of *B. orientalis*, *B. cognatus*, *D. antongilli*, *K. senegalensis*, and *R. catesbeiana* were fed cricket (*Acheta domesticus*) meals equaling 2.5, 5, 7.5, and 10% of their body mass , *H. cinerea* were fed cricket meals equaling 5, 10, and 15% of their body mass, and *C. ornata* and *P. adspersus* were fed neonate rat (*Rattus norvegicus*) meals equaling 5, 15, 25, and 35% (*C. ornata* only) of their body mass. Because anurans will commonly store water in their urinary bladders (thus inflating their body mass), we manually emptied their bladders by inserting a small glass rod into their cloaca and gently squeezing their abdominal region. Each individual was then weighed and the target meal mass was determined. We conducted these metabolic measurements at a constant 30°C.

We explored the effects of meal type on SDA for *B. orientalis*, *D. antongilli*, *H. cinerea*, *K. maculata*, and *R. catesbeiana* by feeding individuals three or four of the following food types; crickets, mealworms (larva *Tenebrio molitor*), superworms (larva *Zophobas morio*), redworms (*Eisenia fetida*), waxworms (larva *Galleria mellonella*), neonate mice (*Mus musculus*), and neonate rats. Meal sizes were held constant at 10% of anuran body mass and measurements were undertaken at 30°C.

We assessed the effects of body temperature by comparing the SDA responses of anurans digesting cricket meals equal in mass to 10% of their body mass and maintained at temperatures of 20, 25, and 30°C. For this comparison, we used *B. orientalis*, *B. cognatus*, *D. antongilli*, *H. cinerea*, *K. maculata*, and *R. catesbeiana*. Anurans were acclimated to each temperature for five days prior to feeding.

Quantifying the SDA response

For each metabolic trial, we quantified the following seven variables: SMR (lowest measured $\dot{V}O_2$ prior to feeding), peak $\dot{V}O_2$ (highest recorded $\dot{V}O_2$ following feeding), factorial scope of peak $\dot{V}O_2$ (calculated as peak $\dot{V}O_2$ divided by SMR), respiratory exchanged ratio (RER, $\dot{V}CO_2/\dot{V}O_2$ calculated at peak $\dot{V}O_2$,) duration (time from feeding that $\dot{V}O_2$ was no longer significantly greater than SMR), SDA (the total energy expended above SMR over the duration of significantly elevated $\dot{V}O_2$, quantified as kJ and kJ kg^{-1}), and SDA coefficient (SDA quantified as a percentage of the energy content of the meal). We quantified SDA (kJ) by

summing the extra O_2 consumed above SMR during the duration of the significant metabolic response and multiplying that value by 18.3 J ml^{-1} of O_2 consumed, assuming the catabolism of a diet that is 70% protein, 25% fat, and 5% carbohydrate, and an RQ of 0.75 (Gessaman and Nagy 1988).

We calculated the energy content of each meal by multiplying meal wet mass by its energy equivalent (kJ g^{-1} wet mass) determined by bomb calorimetry. Samples of each meal were weighed (wet mass), dried to constant mass at 60°C, reweighed (dry mass), ground to a fine powder, and pressed into cylindrical pellets. Fifteen pellets of each meal type were ignited in a bomb calorimeter (model 1266; Parr Instrument Co., Moline, IL, USA) to determine energy content (kJ g^{-1}). For each meal, wet mass energy equivalent was determined as the product of dry-mass energy content (from bomb calorimetry) and the meal's dry mass percentage. For each meal type, we assigned the following wet-mass energy equivalent: small crickets, 5.67 ± 0.13 kJ g^{-1}; large crickets, 8.18 ± 0.10 kJ g^{-1}; mealworms, 9.97 ± 0.14 kJ g^{-1}; superworm, 10.80 ± 0.10 kJ g^{-1}; redworms, 4.13 ± 0.09 kJ g^{-1}; waxworms, 9.88 ± 0.19 kJ g^{-1}; neonate mice, 4.51 ± 0.18 kJ g^{-1}; and neonate rats, 5.05 ± 0.07 kJ g^{-1}.

Statistical analysis

For each SDA trial, we used repeated-measures design ANOVA to test for significant effects of time (before and after feeding) on $\dot{V}O_2$, $\dot{V}CO_2$, and RER. Each ANOVA was accompanied by a post hoc pairwise mean comparison (Tukey–Kramer procedure) to identify significant differences in $\dot{V}O_2$, $\dot{V}CO_2$, and RER between sampling times and when $\dot{V}O_2$ did not differ from SMR. To test for significant effects of meal size, meal type, body temperature, and taxon on metabolic variables we used ANOVA for measures of body mass, scope of peak $\dot{V}O_2$, RER, SDA (kJ kg^{-1}), and SDA coefficient, and ANCOVA (body mass as a covariate) for measures of SMR, peak $\dot{V}O_2$, and SDA (kJ). Likewise these ANOVA and ANCOVA were accompanied by pairwise mean comparisons to identify significant differences between treatments and taxa. We used least-squares regression analysis to demonstrate the relationship between meal energy and SDA, and between body mass and metabolic variables among species. We report the results of ANOVA and ANCOVA in terms of their P values, and provide P values of selected significant pairwise mean comparisons. We designate the level of statistical significance as $P < 0.05$ and report mean values as means ± 1 SE.

Results

Meal size effects

In the meal-size experiment, only *P. adspersus* differed significantly ($P = 0.0055$) in body mass among treatments (Table 1). For each species, SMR did not significantly differ among the three or four meal-size trials (Table 1). Each species, regardless of meal size, experienced significant (P's < 0.0001) variation in $\dot{V}O_2$ and $\dot{V}CO_2$ among pre- and postfeeding sampling periods. The metabolic profile of each trial was characterized by a rapid increase in $\dot{V}O_2$ and $\dot{V}CO_2$ that peaked 1–2 days postfeeding and declined more slowly thereafter (Figs. 1, 2). For each species, meal size had a significant (P's < 0.048) effect on peak $\dot{V}O_2$ (Table 1). From their smallest to largest meals, peak $\dot{V}O_2$ increased for each species by an average of 117 ± 31%. Likewise, the scope of peak $\dot{V}O_2$ (peak $\dot{V}O_2$/SMR) varied significantly (P's < 0.022) among meal sizes for each species (Table 1). We found for these anurans that a three and five-fold increase in meal size generated on average a 95 ± 38 and 318 ± 97% increase, respectively, in the scope of peak $\dot{V}O_2$ (Fig. 3). When calculated at peak $\dot{V}O_2$, RER ranged between 0.67 and 0.74, and for each species did not significantly differ among meal-size treatments (Table 1). With an increase in meal size, there was a corresponding increase in the duration for which postprandial metabolism was significantly elevated above SMR (Fig. 3). For smaller meals (2.5 and 5% of body mass), gas exchange rates remained significantly elevated for 2–3 days, whereas for larger meals (10% or larger of body mass), $\dot{V}O_2$ and $\dot{V}CO_2$ were elevated for 4–8 days (Table 1).

As a product of higher peak $\dot{V}O_2$ and a longer duration of the metabolic response, larger meals generated greater SDA's (Fig. 3). For each species, meal size had a significant (P's < 0.002) impact on SDA (kJ or kJ kg^{-1}), as SDA increased fairly linearly with meal size (Table 1). We found that with a doubling of meal size, SDA of these eight species increased on average by 132 ± 18%. The SDA coefficient, the relative percent of ingested energy equivalent to SDA, also varied significantly (P's < 0.006) among meal sizes for *C. ornata*, *D. antongilli*, *H. cinerea*, and *P. adspersus* (Table 1). For these four species, SDA coefficients increased by an average of 94 ± 17% from the smallest to the largest size meals.

Table 1 Body mass, SMR, and six variables of the metabolic response to feeding on different size meals (percentage of body mass) for eight species of anurans at 30°C

Variable	Meal size (% of body mass)							
	2.5%	5%	7.5 %	10%	15%	25%	35%	*P*
Bombina orientalis (n = 6)								
Body mass (g)	4.03 ± 0.20	4.12 ± 0.36	3.45 ± 0.35	4.53 ± 0.31				0.165
SMR (ml O_2 h^{-1})	0.54 ± 0.05	0.55 ± 0.03	0.41 ± 0.04	0.54 ± 0.03				0.146
Peak $\dot{V}O_2$ (ml h^{-1})	1.32 ± 0.16^{a}	1.57 ± 0.08^{a,b}	1.26 ± 0.11^{a}	1.94 ± 0.19^{b}				0.048
Scope (Peak $\dot{V}O_2$/SMR)	2.43 ± 0.27^{a}	2.87 ± 0.11^{a,b}	3.04 ± 0.17^{a,b}	3.64 ± 0.33^{b}				0.010
RER ($\dot{V}CO_2/\dot{V}O_2$)	0.68 ± 0.03	0.73 ± 0.03	0.74 ± 0.01	0.74 ± 0.01				0.082
Duration (day)	2	3	4	5				
SDA (kJ)	0.40 ± 0.07^{a}	0.72 ± 0.06^{a}	0.70 ± 0.03^{a}	1.17 ± 0.18^{b}				0.0008
SDA (kJ kg^{-1})	97.5 ± 12.7^{a}	179 ± 16^{a,b}	215 ± 27^{b}	258 ± 36^{b}				0.0013
SDA coefficient (%)	66.6 ± 8.9	62.4 ± 5.0	50.8 ± 6.6	45.3 ± 6.3				0.134
Bufo cognatus (n = 8)								
Body mass (g)	65.2 ± 8.7	75.2 ± 9.1	64.0 ± 7.7	76.3 ± 9.0				0.642
SMR (ml O_2 h^{-1})	2.76 ± 0.42	3.20 ± 0.40	2.65 ± 0.28	3.26 ± 0.37				0.932
Peak $\dot{V}O_2$ (mL h^{-1})	8.35 ± 1.11^{a}	12.6 ± 1.4^{b}	12.1 ± 1.4^{b}	16.7 ± 1.9^{c}				0.0001
Scope (peak $\dot{V}O_2$/SMR)	3.27 ± 0.37^{a}	4.02 ± 0.14^{a,b}	4.57 ± 0.25^{b,c}	5.13 ± 0.30^{c}				0.0004
RER ($\dot{V}O_2/\dot{V}O_2$)	0.68 ± 0.01	0.68 ± 0.02	0.67 ± 0.01	0.68 ± 0.01				0.841
Duration (days)	2	3	4	5				
SDA (kJ)	2.17 ± 0.34^{a}	4.91 ± 0.57^{b}	7.13 ± 1.00^{b}	12.2 ± 1.7^{c}				<0.0001
SDA (kJ kg^{-1})	37.2 ± 6.8^{a}	66.3 ± 2.8^{b}	111 ± 9^{c}	157 ± 10^{d}				<0.0001
SDA coefficient (%)	18.3 ± 3.3	16.2 ± 0.7	18.2 ± 1.5	19.2 ± 1.2				0.744
Ceratophrys ornata (n = 6)								
Body mass (g)		110 ± 26			110 ± 8	101 ± 6	109 ± 8	0.950
SMR (ml O_2 h^{-1})		4.30 ± 0.56			4.67 ± 0.39	4.22 ± 0.43	4.34 ± 0.25	0.856
Peak $\dot{V}O_2$ (mL h^{-1})		17.2 ± 4.1^{a}			40.7 ± 4.9^{b}	55.3 ± 5.6^{c}	63.3 ± 3.8^{c}	<0.0001
Scope (peak $\dot{V}O_2$/SMR)		3.76 ± 0.58^{a}			8.70 ± 0.70^{b}	13.2 ± 0.7^{c}	14.6 ± 0.4^{c}	<0.0001
Duration (day)		2			4	5	8	
SDA (kJ)		6.23 ± 1.69^{a}			28.0 ± 3.8^{b}	46.8 ± 4.5^{c}	78.9 ± 6.4^{d}	<0.0001
SDA (kJ kg^{-1})		52.7 ± 4.0^{a}			249 ± 19^{b}	461 ± 24^{c}	726 ± 32^{d}	<0.0001
SDA coefficient (%)		17.6 ± 1.4^{a}			27.8 ± 2.1^{b}	30.9 ± 1.6^{b,c}	34.7 ± 1.5^{c}	<0.0001
Dyscophus antongilli (n = 5)								
Body mass (g)	41.8 ± 3.3	44.7 ± 3.2	43.9 ± 3.2	39.8 ± 3.3				0.737
SMR (ml O_2 h^{-1})	1.58 ± 0.11	1.55 ± 0.18	1.61 ± 0.13	1.64 ± 0.22				0.245
Peak $\dot{V}O_2$ (ml h^{-1})	3.20 ± 0.30^{a}	3.96 ± 0.26^{a}	6.45 ± 0.59^{b}	7.49 ± 0.55^{b}				<0.0001
Scope (peak $\dot{V}O_2$/SMR)	2.09 ± 0.32^{a}	2.62 ± 0.15^{a}	4.01 ± 0.17^{b}	4.71 ± 0.24^{b}				<0.0001
RER ($\dot{V}O_2/\dot{V}O_2$)	0.74 ± 0.01	0.67 ± 0.01	0.70 ± 0.03	0.68 ± 0.04				0.317
Duration (day)	2	3	4	6				
SDA (kJ)	0.74 ± 0.08^{a}	1.84 ± 0.06^{b}	4.38 ± 0.39^{c}	5.57 ± 0.35^{d}				<0.0001
SDA (kJ kg^{-1})	18.5 ± 2.9^{a}	42.6 ± 4.4^{b}	99.9 ± 5.3^{c}	142 ± 5^{d}				<0.0001
SDA coefficient (%)	9.03 ± 1.44^{a}	10.4 ± 1.0^{a}	16.3 ± 0.9^{b}	17.3 ± 0.6^{b}				<0.0001
Hyla cinerea (n = 8)								
Body mass (g)		8.87 ± 0.81		8.83 ± 1.2	8.56 ± 0.56			0.963
SMR (ml O_2 h^{-1})		0.91 ± 0.09		0.88 ± 0.09	0.91 ± 0.11			0.751
Peak $\dot{V}O_2$ (ml h^{-1})		2.16 ± 0.22^{a}		2.73 ± 0.30^{b}	3.55 ± 0.24^{c}			<0.0001
Scope (peak $\dot{V}O_2$/SMR)		2.40 ± 0.10^{a}		3.09 ± 0.10^{b}	4.09 ± 0.28^{c}			<0.0001
RER ($\dot{V}O_2/\dot{V}O_2$)		0.67 ± 0.01		0.72 ± 0.02	0.67 ± 0.01			0.182
Duration (day)		2		4	5			
SDA (kJ)		0.60 ± 0.09^{a}		1.69 ± 0.21^{b}	2.47 ± 0.21^{c}			<0.0001
SDA (kJ kg^{-1})		66.4 ± 4.7^{a}		195 ± 11^{b}	297 ± 30^{c}			<0.0001
SDA coefficient (%)		23.5 ± 1.5^{a}		34.4 ± 1.9^{b}	34.4 ± 3.4^{b}			0.0054
Kassina senegalensis (n = 6)								
Body mass (g)	4.59 ± 0.44	4.11 ± 0.23	5.13 ± 0.53	5.67 ± 0.36				0.054
SMR (ml O_2 h^{-1})	0.55 ± 0.05	0.50 ± 0.06	0.65 ± 0.07	0.70 ± 0.06				0.935
Peak $\dot{V}O_2$ (ml h^{-1})	1.42 ± 0.13^{a}	1.50 ± 0.17^{a}	2.29 ± 0.22^{b}	3.08 ± 0.29^{c}				0.0009
Scope (peak $\dot{V}O_2$/SMR)	2.62 ± 0.13^{a}	3.04 ± 0.17^{ab}	3.60 ± 0.20^{b}	4.40 ± 0.19^{c}				<0.0001
RER ($\dot{V}O_2/\dot{V}O_2$)	0.72 ± 0.03	0.71 ± 0.01	0.73 ± 0.01	0.73 ± 0.01				0.829

Table 1 continued

Variable	Meal size (% of body mass)							
	2.5%	5%	7.5 %	10%	15%	25%	35%	*P*
Duration (day)	2	2	4	5				
SDA (kJ)	0.41 ± 0.04[a]	0.55 ± 0.07[a]	1.39 ± 0.12[b]	1.74 ± 0.28[b]				0.0001
SDA (kJ kg^{-1})	92.3 ± 11.4[a]	137 ± 23[a]	285 ± 37[b]	297 ± 36[b]				<0.0001
SDA coefficient (%)	63.6 ± 7.5	47.8 ± 7.9	67.7 ± 8.7	52.5 ± 6.3				0.334
Pyxicephalus adspersus (n = 6)								
Body mass (g)		130 ± 27[a]			230 ± 13[b]	210 ± 16[b]		0.0055
SMR (ml O_2 h^{-1})		3.29 ± 0.70			6.08 ± 0.49	5.60 ± 0.28		0.650
Peak $\dot{V}O_2$ (ml h^{-1})		13.3 ± 3.8[a]			57.9 ± 6.9[b]	68.5 ± 8.3[b]		0.0077
Scope (peak $\dot{V}O_2$/SMR)		3.76 ± 0.33[a]			9.57 ± 0.88[b]	12.1 ± 1.0[b]		<0.0001
Duration (day)		2			5	6		
SDA (kJ)		4.61 ± 1.44[a]			53.0 ± 4.5[b]	78.0 ± 5.9[c]		<0.0001
SDA (kJ kg^{-1})		33.1 ± 3.8[a]			232 ± 18[b]	384 ± 18[c]		<0.0001
SDA coefficient (%)		11.0 ± 1.2[a]			26.1 ± 2.0[b]	25.0 ± 1.5[b]		<0.0001
Rana catesbeiana (n = 6)								
Body mass (g)	173 ± 43	158 ± 25	152 ± 25	161 ± 27				0.278
SMR (ml O_2 h^{-1})	7.04 ± 1.61	7.11 ± 0.82	6.51 ± 0.84	6.86 ± 0.80				0.370
Peak $\dot{V}O_2$ (ml h^{-1})	18.6 ± 4.9[a]	21.4 ± 2.2[ab]	22.2 ± 4.1[ab]	26.7 ± 4.5[b]				0.0050
Scope (peak $\dot{V}O_2$/SMR)	2.61 ± 0.15[a]	3.04 ± 0.14[ab]	3.34 ± 0.19[ab]	3.83 ± 0.35[b]				0.022
RER ($\dot{V}O_2/\dot{V}O_2$)	0.72 ± 0.01	0.71 ± 0.01	0.71 ± 0.01	0.72 ± 0.02				0.714
Duration (day)	2	2.5	3	4				
SDA (kJ)	5.89 ± 2.30[a]	9.26 ± 1.28[a,b]	13.6 ± 3.6[b]	21.8 ± 4.0[c]				<0.0001
SDA (kJ kg^{-1})	31.8 ± 5.1[a]	59.4 ± 2.4[a,b]	84.5 ± 6.8[b]	136 ± 15[c]				<0.0001
SDA coefficient (%)	15.5 ± 2.5	14.5 ± 0.6	13.8 ± 1.1	16.6 ± 1.8				0.054

Bombina orientalis, *B. cognatus*, *D. antongilli*, *H. cinerea*, *K. senegalensis*, and *R. catesbeiana* were fed crickets, whereas *C. ornata* and *P. adspersus* were fed neonate rats

Note Variables are defined in the text. Values are presented as mean ± 1 SE. *P* values result from ANOVA for body mass, scope, RER, SDA (kJ kg^{-1}), and SDA coefficient, and from ANCOVA (body mass as the covariate) for SMR, peak $\dot{V}O_2$, and SDA (kJ). RER presented in this table represent the mean of individual RER calculated at peak $\dot{V}O_2$. For variables with significant *P* values, superscript letters that differ denote significant ($P < 0.05$) differences between means among meal sizes as determined from post-hoc pairwise comparisons (Tukey HSD test)

Meal type effects

For each of the five species that we assessed meal-type effects on SDA responses, there were no significant differences among meal-type trials in body mass, SMR, or RER (Table 2). As demonstrated in the meal-size study, anurans responded to each meal type with a relatively rapid increase in gas exchange that peaked 1–2 days after feeding, followed by a slower decline (Fig. 4). Significant variation (P's < 0.045) in peak $\dot{V}O_2$ among meal-type trials was observed for *B. orientalis*, *B. antongilli*, *H. cinerea*, and *K. maculata*, but not for *R. catesbeiana* (Table 2). Three of the former four species experienced significant (P's < 0.01) meal-type variation in the scope of peak $\dot{V}O_2$ (Table 2). Hard-bodied cricket, mealworm, and superworm meals generated larger peaks in gas exchange, and thus greater scopes, compared to the soft-bodied redworm and waxworm meals (Table 2). Among meals, the duration of significantly elevated rates of gas exchange ranged from 2.5 to 7 days (Table 2). There was a trend among these five species for gas exchange rates to remain significantly elevated for longer durations during the digestion of mealworm or superworm meals (5–7 days) compared to redworm, waxworm, or neonate rodent meals (2.5–5 days) (Table 2).

The most notable effect of meal type was on SDA, which varied significantly (P's < 0.003) among meal types for all five species. The digestion of redworms, waxworms, or neonate rodents generated the lowest set of SDA's (133.5 ± 5.5 kJ kg^{-1}), cricket meals produced intermediate SDA's (185.8 ± 10.9 kJ kg^{-1}), whereas mealworm and superworm meals gave rise to the largest SDA's (274.4 ± 20.0 kJ kg^{-1}). The SDA coefficient likewise varied significantly among meal types for each species with the exception of *R. catesbeiana* (Table 2). For *B. orientalis*, *D. antongilli*, and *K. maculata*, the waxworm meals produced significantly smaller SDA coefficients compared to other meals, while for *H. cinerea* the superworm meal generated a significantly lower coefficient (Table 2). Across species and meal type, SDA increased linearly as function of

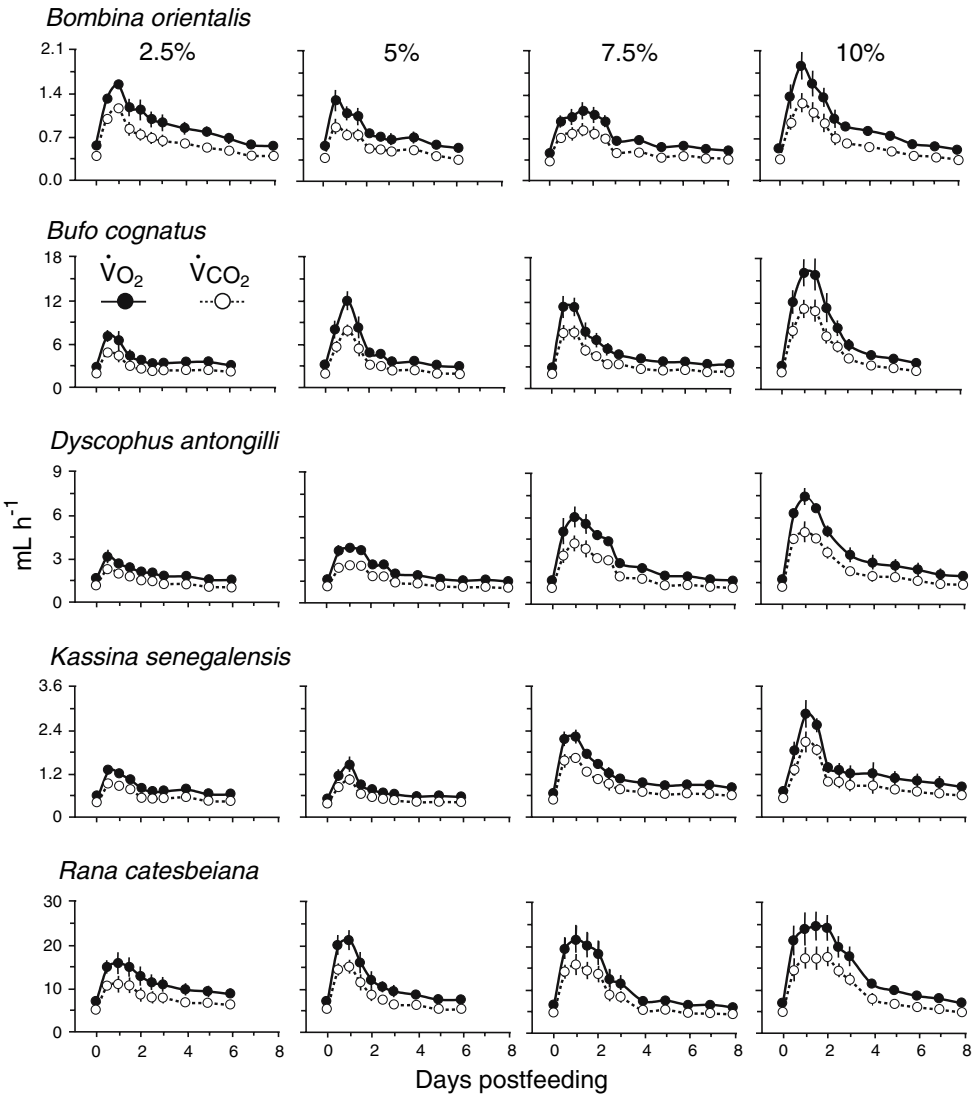

Fig. 1 Mean $\dot{V}O_2$ and $\dot{V}CO_2$ (ml h^{-1}) at 30°C of *Bombina orientalis*, *Bufo cognatus, Dyscophus antongilli*, *Kassina senegalensis*, and *Rana catesbeiana* prior to (day 0) and up to 8 d following the ingestion of cricket meals equaling 2.5, 5, 7.5, and 10% of anuran body mass. For each trial, n = 5–8. Note for each species the increase in magnitude and the longer duration of postprandial metabolic rates with an increase in meal size. For this and subsequent figures, error bars represent ±1 SE and are omitted if the SE is smaller than the symbol for the mean value

meal energy with a slope (0.193 ± 0.004) that represents an overall average SDA coefficient of 19.3% (Fig. 5).

Body temperature effects

Of the six species used to assess the effects of body temperature on SDA response, only *R. catesbeiana* differed significantly (P = 0.04) in body mass among temperature treatments (Table 3). All six species exhibited significant (P's < 0.0001) body temperature effects on SMR as SMR differed significantly (P's < 0.05) between each trial temperature for each species (Table 3). Likewise, peak $\dot{V}O_2$ differed significantly (P's < 0.023) among temperature treatments for all species, increasing with a rise in body temperature (Table 3). The factorial increase in metabolic rate (Q_{10}) with a 10°C increase in body temperature (20–30°C) averaged among the six species 1.99 ± 0.10 and 2.34 ± 0.28, respectively, for SMR and peak $\dot{V}O_2$. With fairly matched increases in SMR and peak $\dot{V}O_2$ with body temperature, the scope of peak $\dot{V}O_2$ remained relatively stable across temperature treatments, only differing (P < 0.0001) for *R. catesbeiana* (Table 3). Body temperature had an observable effect on the shape of the postprandial metabolic profile (Fig. 6). With an increase in body temperature, peak $\dot{V}O_2$ was reached sooner and there was a more rapid return to prefeeding rates. Across species, increasing body temperature from 20 to 30°C generally shortened the duration of the postprandial metabolic response by one-third (Table 3). We observed no effects of body temperature on RER when quantified at peak $\dot{V}O_2$ for any of the six species (Table 3).

The effect of body temperature on SDA was mixed among species. Whereas *B. orientalis*, *B. cognatus, D.*

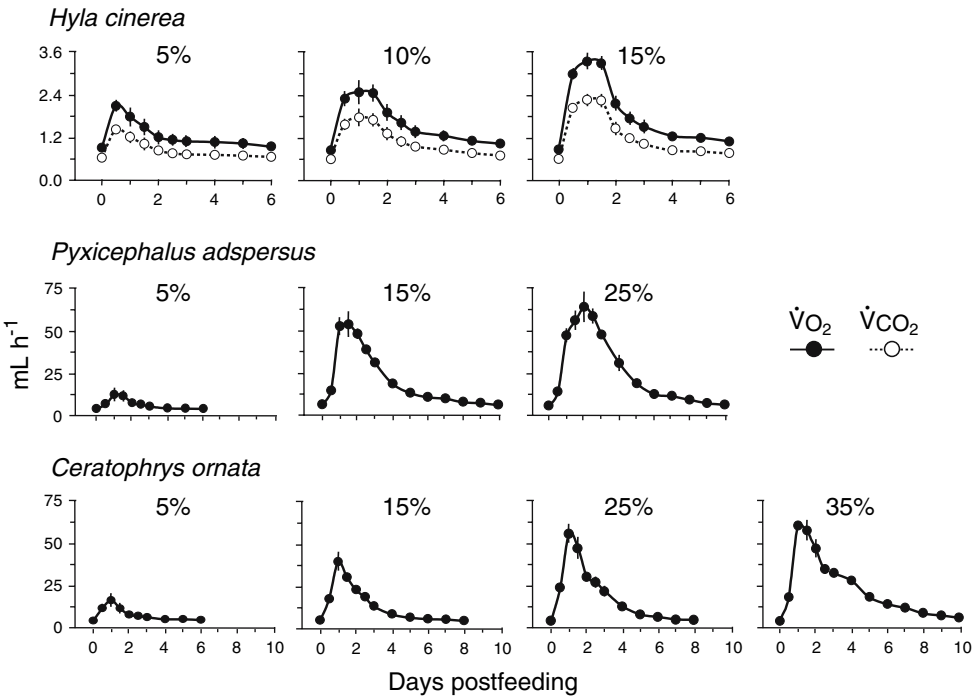

Fig. 2 Mean $\dot{V}O_2$ and $\dot{V}CO_2$ (ml h^{-1}) at 30°C prior to (day 0) and up to 10 day following the digestion of cricket meals equaling 5, 10, and 15% of body mass for *Hyla cinerea*, and following the digestion of neonatal rat meals equaling 5, 15, 25, and 35% (*C. ornata* only) of body mass for *Pyxicephalus adspersus* and *Ceratophrys ornata*. For each trial, n = 5–6. Note as for the previous figure the increase in height and duration of the postprandial metabolic profile with larger meals

antongilli, and *K. maculata* exhibited no significant variation in SDA or the SDA coefficient among temperature trials, both *H. cinerea* and *R. catesbeiana* experienced significant (P's < 0.0006) differences in SDA among temperature treatments (Table 3). For *H. cinerea* at 30°C and *R. catesbeiana* at 25°C, SDA was significantly (P's < 0.006) greater (by 51 and 33%, respectively) than at 20°C. Body temperature likewise had significant (P's < 0.0004) effects on the SDA coefficient for these two species as coefficients increased (P's < 0.003) by an average of 54% from 20 to 30°C (Table 3).

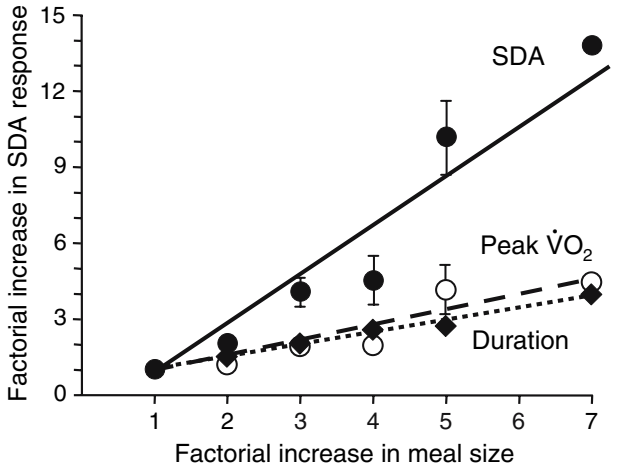

Fig. 3 Mean factorial increase in response duration (◆), peak $\dot{V}O_2$ (◯) and SDA (●) plotted against the factorial increase in meal size relative to the smallest meal (2.5 or 5% of body mass) consumed. Mean factorial increases in SDA response were generated from the eight species used to investigate meal size effects. Note that with each factorial increase in meal size, response duration, peak $\dot{V}O_2$, and SDA likewise increased

Interspecific comparisons and relationships

To compare interspecifically the variables of the SDA response, we used species data generated from feeding trials of cricket meals 10% of body mass at 30°C. These parameters thus eliminated *C. ornata* and *P. adspersus* from analysis. Body mass and SMR varied significantly (P's < 0.034) among the seven species of this comparison. For each of these variables, means for *B. orientalis*, *H. cinerea*, *K. maculata*, and *K. senegalensis* were significantly less than those for *D. antongilli*, which were less than those for *B. cognatus*, and which were less than those for *R. catesbeiana*. Postprandial peak $\dot{V}O_2$, RER, and SDA (kJ) did not statistically differ among the seven anuran species (ANCOVA with body mass the covariate for peak $\dot{V}O_2$ and SDA), whereas both the scope of peak $\dot{V}O_2$ and the SDA coefficient did vary (P's < 0.0001) interspecifically. We found *B. cognatus*, *D. antongilli*, *K. senegalensis*, and *R. catesbeiana* to experience significantly greater scopes than either *B. orientalis* and *H. cinerea*. Among the seven species there was a 3.2-fold range in the SDA coefficient with *B. orientalis* and *K. senegalensis* possessing significantly higher coefficients than *B. cognatus*, *D. antongilli*, and *R. catesbeiana*.

Table 2 Body mass, SMR, and six variables of the metabolic response to feeding on different types of meals for five species of anurans at 30 °C. All meals weighed approximately 10% of individual's body mass

Variable	Meal type							
	Cricket	Mealworm	Superworm	Redworm	Waxworm	Neonate mice	Neonate rats	*P*
Bombina orientalis ($n = 6$)								
Body mass (g)	4.53 ± 0.31	3.73 ± 0.39		4.49 ± 0.78	5.43 ± 0.85			0.330
SMR (ml O_2 h^{-1})	0.54 ± 0.03	0.49 ± 0.04		0.64 ± 0.08	0.65 ± 0.10			0.068
Peak $\dot{V}O_2$ (ml h^{-1})	1.94 ± 0.19	1.59 ± 0.22		1.79 ± 0.29	1.56 ± 0.19			0.045
Scope (peak $\dot{V}O_2$/SMR)	3.64 ± 0.33^{c}	$3.24 \pm 0.32^{b,c}$		$2.78 \pm 0.15^{a,b}$	2.44 ± 0.17^{a}			0.0093
RER ($\dot{V}CO_2/\dot{V}O_2$)	0.74 ± 0.01	0.68 ± 0.02		0.68 ± 0.02	0.63 ± 0.04			0.931
Duration (day)	5	6		5	5			
SDA (kJ)	$1.17 \pm 0.18^{a,b}$	1.54 ± 0.21^{b}		0.83 ± 0.19^{a}	0.65 ± 0.08^{a}			0.0009
SDA (kJ kg^{-1})	258 ± 36^{a}	424 ± 54^{b}		177 ± 16^{a}	129 ± 20^{a}			<0.0001
SDA coefficient (%)	45.3 ± 6.3^{b}	42.7 ± 5.5^{b}		42.7 ± 3.8^{b}	13.0 ± 2.0^{a}			0.0002
Dyscophus antongilli ($n = 5$)								
Body mass (g)	39.8 ± 3.3		40.6 ± 2.8		42.0 ± 3.7	40.9 ± 2.9		0.969
SMR (ml O_2 h^{-1})	1.64 ± 0.22		1.68 ± 0.13		1.68 ± 0.16	1.58 ± 0.10		0.755
Peak $\dot{V}O_2$ (ml h^{-1})	7.49 ± 0.55^{b}		$6.05 \pm 0.54^{a,b}$		5.42 ± 0.87^{a}	$6.07 \pm 0.60^{a,b}$		0.0064
Scope (peak $\dot{V}O_2$/SMR)	4.71 ± 0.24^{b}		3.55 ± 0.13^{a}		3.17 ± 0.28^{a}	$3.84 \pm 0.27^{a,b}$		0.0017
RER ($\dot{V}CO_2/\dot{V}O_2$)	0.68 ± 0.04		0.68 ± 0.01		0.68 ± 0.01	0.67 ± 0.01		0.988
Duration (day)	6		7		5	4		
SDA (kJ)	5.57 ± 0.35^{ab}		7.02 ± 0.93^{b}		4.99 ± 0.97^{a}	4.15 ± 0.36^{a}		0.0026
SDA (kJ kg^{-1})	142 ± 5^{ab}		161 ± 12^{b}		116 ± 14^{a}	101 ± 5^{a}		0.0019
SDA coefficient (%)	17.3 ± 0.6^{b}		14.9 ± 1.1^{ab}		11.7 ± 1.1^{a}	22.5 ± 1.2^{c}		0.0001
Hyla cinerea ($n = 8$)								
Body mass (g)	8.83 ± 1.2		10.0 ± 0.9	9.36 ± 0.80				0.678
SMR (ml O_2 h^{-1})	0.88 ± 0.09		1.04 ± 0.08	0.97 ± 0.07				0.167
Peak $\dot{V}O_2$ (ml h^{-1})	2.73 ± 0.30^{a}		3.82 ± 0.42^{b}	2.99 ± 0.20^{a}				0.039
Scope (peak $\dot{V}O_2$/SMR)	3.09 ± 0.10		3.68 ± 0.31	3.11 ± 0.12				0.078
RER ($\dot{V}CO_2/\dot{V}O_2$)	0.72 ± 0.02		0.70 ± 0.01	0.72 ± 0.01				0.097
Duration (day)	4		5	3				
SDA (kJ)	1.69 ± 0.21^{a}		2.31 ± 0.25^{b}	1.43 ± 0.10^{a}				0.0027
SDA (kJ kg^{-1})	195 ± 11^{ab}		233 ± 20^{b}	157 ± 12^{a}				0.0071
SDA coefficient (%)	34.4 ± 1.9^{b}		21.7 ± 2.0^{a}	37.8 ± 2.9^{b}				0.0002
Kassina maculata ($n = 6$)								
Body mass (g)	5.85 ± 0.76	7.67 ± 1.22		8.33 ± 1.09	6.92 ± 1.04			0.409
SMR (ml O_2 h^{-1})	0.51 ± 0.07	0.63 ± 0.10		0.73 ± 0.11	0.63 ± 010			0.454
Peak $\dot{V}O_2$ (ml h^{-1})	2.04 ± 0.17^{a}	3.11 ± 0.51^{b}		2.41 ± 0.35^{a}	2.00 ± 0.31^{a}			0.0003
Scope (peak $\dot{V}O_2$/SMR)	$4.09 \pm 0.19^{b,c}$	4.89 ± 0.28^{c}		$3.32 \pm 0.21^{a,b}$	3.20 ± 0.10^{a}			<0.0001
RER ($\dot{V}CO_2/\dot{V}O_2$)	0.69 ± 0.04	0.68 ± 0.01		0.71 ± 0.02	0.69 ± 0.01			0.769
Duration (day)	3	5		2.5	3			
SDA (kJ)	0.93 ± 0.10^{a}	2.53 ± 0.40^{b}		1.03 ± 0.11^{a}	1.00 ± 0.14^{a}			<0.0001
SDA (kJ kg^{-1})	163 ± 13^{a}	317 ± 15^{b}		125 ± 5^{a}	149 ± 8^{a}			<0.0001
SDA coefficient (%)	28.7 ± 2.3^{b}	31.7 ± 1.4^{b}		30.4 ± 1.1^{b}	15.0 ± 0.8^{a}			<0.0001
Rana catesbeiana ($n = 6$)								
Body mass (g)	270 ± 19		269 ± 18				283 ± 17	0.837
SMR (ml O_2 h^{-1})	12.4 ± 1.8		12.1 ± 0.6				11.9 ± 1.0	0.633
Peak $\dot{V}O_2$ (ml h^{-1})	51.8 ± 6.8		46.5 ± 1.8				43.6 ± 3.4	0.128
Scope (peak $\dot{V}O_2$/SMR)	4.25 ± 0.13		3.90 ± 0.24				3.71 ± 0.19	0.196
RER ($\dot{V}CO_2/\dot{V}O_2$)	0.69 ± 0.03		0.71 ± 0.01				0.69 ± 0.02	0.374
Duration (day)	4		6				4	
SDA (kJ)	40.2 ± 24.0^{b}		57.7 ± 5.6^{c}				28.0 ± 1.7^{a}	<0.0001
SDA (kJ kg^{-1})	148 ± 7^{b}		216 ± 17^{c}				99.4 ± 3.4^{a}	<0.0001
SDA coefficient (%)	18.6 ± 0.9		20.0 ± 1.6				19.7 ± 0.7	0.508

Note Variables are defined in the text. Values are presented as mean ± 1 SE. *P* values result from ANOVA for body mass, scope, RER, SDA (kJ kg^{-1}), and SDA coefficient, and from ANCOVA (body mass as the covariate) for SMR, peak $\dot{V}O_2$, and SDA (kJ). RER presented in this table represent the mean of individual RER calculated at peak $\dot{V}O_2$. For variables with significant *P* values, superscript letters that differ denote significant ($P < 0.05$) differences between means among meal types as determined from post-hoc pairwise comparisons (Tukey HSD test)

When plotted against body mass, SMR for all nine species of this study scaled ($\log_{10} - \log_{10}$) with a mass exponent of 0.69 ± 0.05 (r^2 = 0.96). For the seven species that consumed the 10% size cricket meals, peak $\dot{V}O_2$ and SDA scaled with mass exponents of 0.77 ± 0.06 (r^2 = 0.97) and 0.86 ± 0.05 (r^2 = 0.98), respectively. For this sample of anurans, none of the mass exponents differed significantly from each other.

Discussion

The nine anuran species of this study share with all organisms studied to date the physiological phenomena of a postprandial increase in metabolic rate, known as the SDA of the meal. This metabolic response represents the accumulated energy being expended as the meal is being broken down in the stomach, transported through the GI tract, hydrolyzed and absorbed by the small intestine, and assimilated. For each individual anuran of this study, we can imagine the energy-consuming tasks of digestion, including the production and secretion of pepsinogen and HCl in the stomach, the peristaltic contraction of enteric smooth muscle, the production and operation of intestinal membrane-bound hydrolases and nutrient transporters, and the channeling of absorbed nutrients into either catabolic or anabolic pathways. While each of these tasks will undoubtedly be shared by all feeding events, differences in the intensity and duration of these processes will undoubtedly underlie the variation in the SDA response. By focusing on one group of organisms (anurans) to address three hypotheses of SDA, we have shown that by altering the workload (changing meal size and type) or rate (changing body temperature) of digestion there are corresponding shifts in the

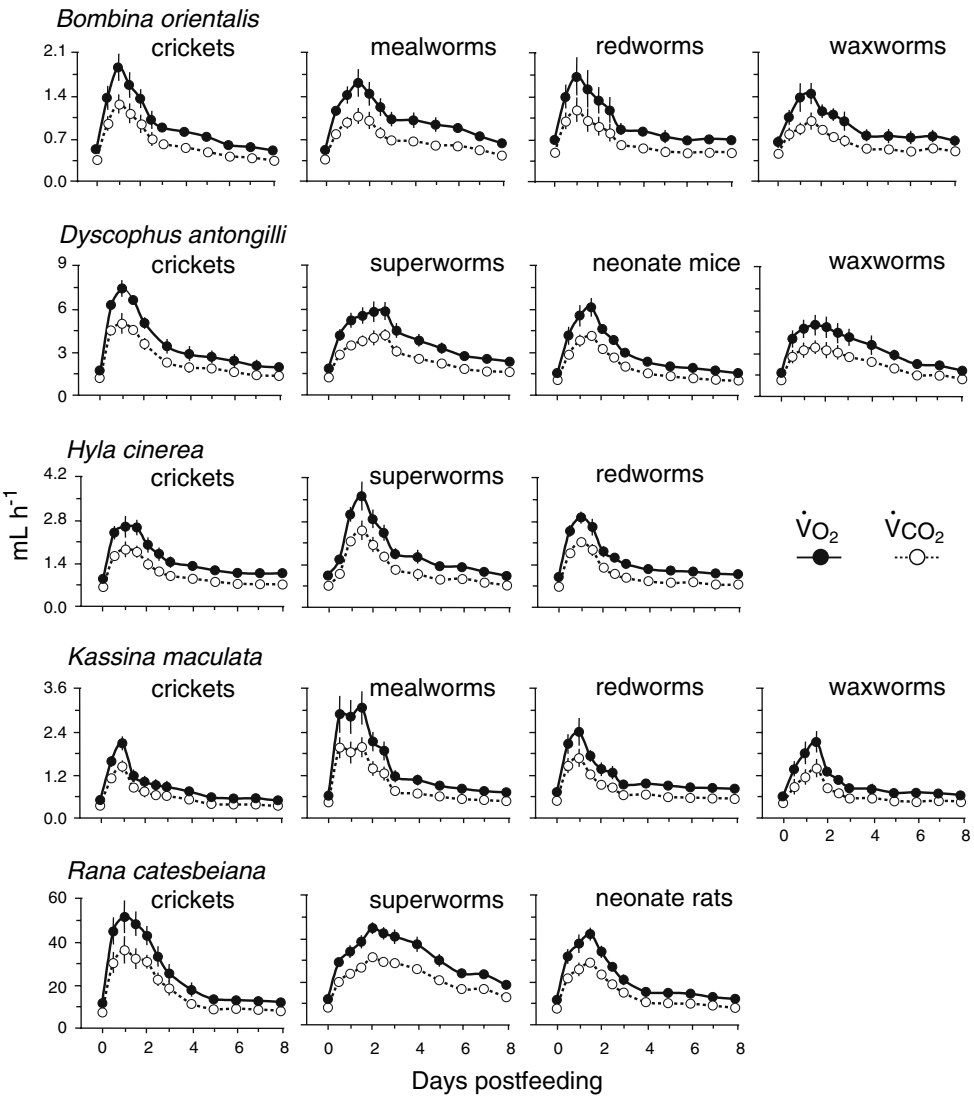

Fig. 4 Mean $\dot{V}O_2$ and $\dot{V}O_2$ (mL h^{-1}) at 30°C of *Bombina orientalis*, *Dyscophus antongilli*, *Hyla cinerea*, *Kassina maculata*, and *Rana catesbeiana* prior to (day 0) and up to 8 day following the ingestion of six different meal types equaling 10% of anuran body mass. For each trial, n = 5–6. Note that hard-bodied cricket, mealworm, and superworm meals typically generated higher peak $\dot{V}O_2$ compared to soft-bodied redworm, neonate rodent, and waxworm meals

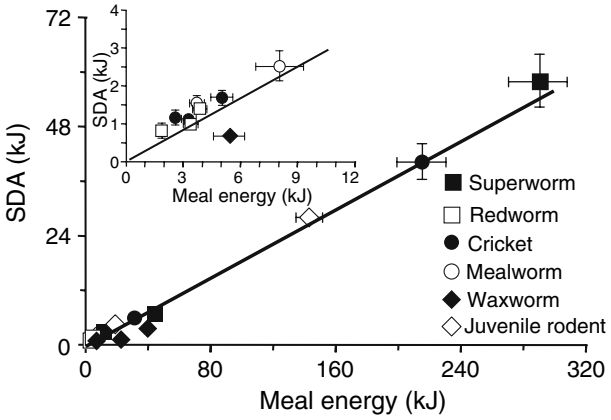

Fig. 5 Specific dynamic action (*SDA*) plotted against meal energy for six different meal types, each equaling 10% of anuran body mass, being digested at 30°C by *Bombina orientalis*, *Dyscophus antongilli*, *Hyla cinerea*, *Kassina maculata*, and *Rana catesbeiana*. Not all meal types were digested by each anuran species. The insert serves to better illustrate the data close to junction of the *X* and *Y* axis. The *solid line* represents the mean SDA coefficient for all meal types of 19.3%

temporal profile and magnitude of the SDA response. In the following, we will discuss each of these determinants of SDA and include the findings of other studies to comment further on interspecific patterns of SDA within anurans.

Meal size effect on SDA

The effect of meal size on SDA is well established among invertebrates and vertebrates, all exhibiting an increase in the SDA response with an increase in meal size (Carefoot 1990a; Janes and Chappell 1995; Jobling 1981; Secor and Faulkner 2002). The anurans of this study likewise responded with increases in peak $\dot{V}O_2$, longer duration of significantly elevated metabolism, and greater SDA as meal size increased. Given that meal type and body temperature were controlled for in this experiment, the observed increase in postprandial metabolism is largely due to the added work load of digesting and assimilating larger meals. The increase in expenditure reflects the required increases in tissue performance (i.e. HCl production, enzyme activity, nutrient transport, etc.) and time to digest larger meals. While meal size is a well known determinant of SDA, less known is the extent that meal size and thus digestive load are matched to digestive and assimilation costs (SDA).

Theoretically, we would expect that a doubling of meal size would take twice the effort for digestion and assimilation and thus generate twice the SDA. In this study, we found that with a doubling of meal size, anurans responded by increasing SDA on average by 2.32-fold. Instead of a predicted two-fold increase, these anurans appear to expend more energy per gram of food with the larger meals, observed in this study by the significantly greater SDA coefficients for larger meals for four of the anuran species. Hypothetically, the GI tract of these anurans responded to the larger meals by further upregulating function; as observed previously for the Burmese python, *Python molurus* (Secor and Diamond 1997b). For seven other species of amphibians and reptiles, the factorial increase in a SDA responses with a doubling of meal size, referred to as the response coefficient (Q_{2x}), averaged 2.18 for SDA (Secor and Boehm 2006). For the eight anurans of this study and the seven species reviewed in Secor and Boehm (2006), the Q_{2x} of SDA (averaging 2.25) is in part a product of the Q_{2x} of peak $\dot{V}O_2$ and the Q_{2x} of duration which averaged 1.47 and 1.60, respectively. Thus with larger meals, the increase in peak metabolic rates and the increase in duration of the metabolic response contributes fairly equally to the quantified increase in SDA (see Fig. 3).

Postprandial peak $\dot{V}O_2$ has been found to plateau with larger meal sizes for fishes, amphibians, and reptiles (Jobling and Davies 1980; Roe et al. 2004; Secor and Boehm 2006). This observation lead researchers to suggest that cellular metabolism may be reaching its maximum rate during the digestion of large meals (Jobling and Davies 1980). In this study, none of the eight anurans exhibited any leveling of peak $\dot{V}O_2$ with meal size. For each species, peak $\dot{V}O_2$ progressively increased from the smallest to the largest size meals. Over the range of meal sizes tested, it is unlikely that these anurans would approach their maximum $\dot{V}O_2$ ($\dot{V}O_2$max). When exercising at 30°C, other species of similar-size anurans experience $\dot{V}O_2$ that are two to seven times greater than the largest $\dot{V}O_2$ we recorded during digestion (Gatten et al. 1992). We therefore suspect that anurans of this study possess the capacity to increase aerobic performance beyond that recorded during the digestion of the largest meals used in this study.

Having said that, could these anurans still consume even larger meals and therefore experience peak $\dot{V}O_2$ that approaches their $\dot{V}O_2$max? The largest meals we have been able to feed to species of *Bufo* and *Hyla* were equivalent to 20% of their body mass and to *C. ornata*, 35% of body mass. Therefore, we predict that the largest possible meal for *B. orientalis*, *B. cognatus, D. antongilli*, *H. cinerea*, *K. senegalensis*, and *R. catesbeiana* is 25% of their body mass, and for *C. ornata* and *P. adspersus*, 40% of body mass. Based on the extent that peak $\dot{V}O_2$ increased over the tested meal

Table 3 Body mass, SMR, and six variables of the metabolic response to feeding on cricket meals 10% of body mass at three different body temperatures for six species of anurans

Variable	Body temperature			
	20°C	25°C	30°C	*P*
Bombina orientalis (n = 6)				
Body mass (g)	3.63 ± 0.39	3.79 ± 0.21	4.53 ± 0.31	0.117
SMR (ml O_2 h^{-1})	0.26 ± 0.03[a]	0.34 ± 0.01[b]	0.54 ± 0.03[c]	<0.0001
Peak $\dot{V}O_2$ (ml h^{-1})	1.09 ± 0.13[a]	1.22 ± 0.15[b]	1.94 ± 0.19[c]	0.023
Scope (peak $\dot{V}O_2$/SMR)	4.11 ± 0.14	3.62 ± 0.40	3.64 ± 0.33	0.486
RER ($\dot{V}CO_2/\dot{V}O_2$)	0.70 ± 0.02	0.71 ± 0.03	0.74 ± 0.01	0.633
Duration (day)	6	5	5	
SDA (kJ)	0.72 ± 0.11	0.80 ± 0.14	1.17 ± 0.18	0.546
SDA (kJ kg^{-1})	195 ± 17	212 ± 39	258 ± 36	0.424
SDA coefficient (%)	34.2 ± 3.1	37.5 ± 6.9	45.3 ± 6.3	0.426
Bufo cognatus (n = 8)				
Body mass (g)	63.8 ± 7.3	67.5 ± 8.2	76.3 ± 9.0	0.550
SMR (ml O_2 h^{-1})	1.29 ± 0.16[a]	1.93 ± 0.25[b]	3.26 ± 0.37[c]	<0.0001
Peak $\dot{V}O_2$ (ml h^{-1})	7.14 ± 0.79[a]	10.2 ± 1.0[b]	16.7 ± 1.9[c]	<0.0001
Scope (peak $\dot{V}O_2$/SMR)	5.62 ± 0.18	5.55 ± 0.52	5.13 ± 0.30	0.590
RER ($\dot{V}CO_2/\dot{V}O_2$)	0.71 ± 0.02	0.68 ± 0.01	0.68 ± 0.01	0.367
Duration (day)	9	5	5	
SDA (kJ)	11.6 ± 1.5	8.87 ± 0.81	12.2 ± 1.7	0.101
SDA (kJ kg^{-1})	182 ± 10	137 ± 8	157 ± 10	0.098
SDA coefficient (%)	22.2 ± 1.2	17.2 ± 1.0	19.2 ± 1.2	0.100
Dyscophus antongilli (n = 5)				
Body mass (g)	41.6 ± 4.0	40.7 ± 3.7	39.8 ± 3.3	0.942
SMR (ml O_2 h^{-1})	0.75 ± 0.07[a]	1.13 ± 0.09[b]	1.64 ± 0.22[c]	<0.0001
Peak $\dot{V}O_2$ (ml h^{-1})	3.17 ± 0.26[a]	4.88 ± 0.48[b]	7.49 ± 0.55[c]	<0.0001
Scope (peak $\dot{V}O_2$/SMR)	4.23 ± 0.17	4.28 ± 0.18	4.71 ± 0.24	0.246
RER ($\dot{V}CO_2/\dot{V}O_2$)	0.70 ± 0.01	0.70 ± 0.01	0.68 ± 0.04	0.646
Duration (day)	9	7	5	
SDA (kJ)	5.12 ± 0.43	5.25 ± 0.57	5.57 ± 0.35	0.084
SDA (kJ kg^{-1})	124 ± 2	128 ± 7	142 ± 5	0.076
SDA coefficient (%)	15.1 ± 0.2	15.6 ± 0.8	17.3 ± 0.6	0.071
Hyla cinerea (n = 8)				
Body mass (g)	9.13 ± 0.96	9.15 ± 1.25	8.83 ± 1.2	0.976
SMR (ml O_2 h^{-1})	0.48 ± 0.05[a]	0.65 ± 0.08[b]	0.88 ± 0.09[c]	<0.0001
Peak $\dot{V}O_2$ (ml h^{-1})	1.33 ± 0.21[a]	1.68 ± 0.20[b]	2.73 ± 0.30[c]	<0.0001
Scope (peak $\dot{V}O_2$/SMR)	2.67 ± 0.19	2.60 ± 0.14	3.09 ± 0.10	0.058
RER ($\dot{V}CO_2/\dot{V}O_2$)	0.66 ± 0.01	0.70 ± 0.01	0.72 ± 0.02	0.160
Duration (day)	6	5	4	
SDA (kJ)	1.12 ± 0.14[a]	1.21 ± 0.21[a]	1.69 ± 0.21[b]	<0.0001
SDA (kJ kg^{-1})	121 ± 8[a]	126 ± 11[a]	195 ± 11[b]	<0.0001
SDA coefficient (%)	21.4 ± 1.3[a]	22.1 ± 1.9[a]	34.4 ± 1.9[b]	<0.0001
Kassina maculata (n = 6)				
Body mass (g)	5.80 ± 0.74	5.67 ± 0.74	5.85 ± 0.76	0.985
SMR (ml O_2 h^{-1})	0.28 ± 0.04[a]	0.37 ± 0.05[b]	0.51 ± 0.07[c]	<0.0001
Peak $\dot{V}O_2$ (mL h^{-1})	1.19 ± 0.14[a]	1.54 ± 0.25[a]	2.04 ± 0.17[b]	<0.0001
Scope (peak $\dot{V}O_2$/SMR)	4.32 ± 0.20	4.08 ± 0.19	4.09 ± 0.19	0.632
RER ($\dot{V}CO_2/\dot{V}O_2$)	0.71 ± 0.01	0.73 ± 0.02	0.69 ± 0.04	0.528
Duration (day)	5	4	3	
SDA (kJ)	0.80 ± 0.07[a]	0.86 ± 0.15[a,b]	0.93 ± 0.10	0.164
SDA (kJ kg^{-1})	136 ± 9[a]	148 ± 8[a,b]	163 ± 13[b]	0.204
SDA coefficient (%)	23.7 ± 1.4[a]	26.1 ± 1.4[a,b]	28.7 ± 2.3[b]	0.190
Rana catesbeiana (n = 6)				
Body mass (g)	323 ± 13	292 ± 5	270 ± 19	0.040
SMR (ml O_2 h^{-1})	6.89 ± 0.41[a]	8.65 ± 0.43[b]	12.4 ± 1.8[c]	0.0001
Peak $\dot{V}O_2$ (ml h^{-1})	23.3 ± 1.3[a]	37.3 ± 1.8[b]	51.8 ± 6.8[c]	<0.0001
Scope (peak $\dot{V}O_2$/SMR)	3.40 ± 0.11[a]	4.32 ± 0.08[b]	4.25 ± 0.13[b]	<0.0001
RER ($\dot{V}CO_2/\dot{V}O_2$)	0.69 ± 0.01	0.69 ± 0.01	0.69 ± 0.03	0.997

Table 3 continued

Variable	Body temperature			
	20°C	25°C	30°C	*P*
Duration (day)	8	6	4	
SDA (kJ)	33.6 ± 2.0[a]	44.8 ± 4.2[b]	40.2 ± 4.0[a,b]	0.0005
SDA (kJ kg^{-1})	104 ± 4[a]	154 ± 12[b]	148 ± 7[b]	0.0005
SDA coefficient (%)	12.7 ± 0.4[a]	18.8 ± 1.5[b]	18.6 ± 0.9[b]	0.0004

Variables are defined in the text. Values are presented as mean ± 1 SE. *P* values result from ANOVA for body mass, scope, RER, SDA (kJ kg^{-1}), and SDA coefficient, and from ANCOVA (body mass as the covariate) for SMR, peak $\dot{V}O_2$, and SDA (kJ). RER presented in this table represent the mean of individual RER calculated at peak $\dot{V}O_2$. For variables with significant *P* values, superscript letters that differ denote significant ($P < 0.05$) differences between means among body temperatures as determined from post-hoc pairwise comparisons (Tukey HSD test)

sizes (Fig. 3), we calculated that at these maximum meal sizes (25 and 40%), peak $\dot{V}O_2$ would increase an additional 50%. These predicted maximum peaks in postprandial $\dot{V}O_2$ are still shy (by 57%) of expected $\dot{V}O_2$max. Hence, it is unlikely that anurans would ever approach their maximum metabolic performance during digestion.

Meal type effects on SDA

In addressing the impact of meal type or composition on the SDA response, it is debated whether the meal should be standardized to mass or energy (McCue et al. 2005; Secor 2003). We elected to standardize to relative meal size (10% of body mass) because of the strong effect of meal size on SDA. For example, if we were to maintain constant meal energy, our redworm meals would have to be 2.6 times the mass of the superworm meals. By standardizing relative meal size, we were able to assess specifically the impact of meal structure on SDA. We categorized the structure of each meal as either hard-bodied (possessing a chitinous exoskeleton) or soft-bodied (lacking an exoskeleton and possibly an endoskeleton). Hard-bodied meals included crickets, mealworms, and superworms, whereas soft-bodied meals included redworms, waxworms, and neonate mice and rats.

Among the five anurans studied, it was clear that SDA responses differed between hard and soft-bodied meals. On average, hard-bodied meals resulted in a 20% increase in peak $\dot{V}O_2$, a 40% increase in the duration of elevated $\dot{V}O_2$, and a 76% increase in SDA compared to soft-bodied meals. Similarly for the tiger salamander, *Ambystoma tigrium*, the same hard-bodied food items generated a 10% increase in peak $\dot{V}O_2$, a 42% increase in duration, and a 71% increase in SDA compared to the digestion of soft-bodied redworms, beetle larva, and neonate mice (Secor and Boehm 2006). Similar patterns in the magnitude of the SDA response with respect to meal type have been observed for other amphibians and reptiles. The SDA of marine toads, *Bufo marinus*, generated from digesting cricket or superworm meals was 64% greater than their SDA resulting from the digestion of earthworms or neonate rodents (Secor and Faulkner 2002). For two soft-bodied meals, neonate mice and earthworms, there was no significant difference in the peak, duration, and magnitude of the generated SDA response for the frog *Ceratophrys cranwelli* (Grayson et al. 2005). Hailey (1998) noted for the turtle, *Kinixys spekii*, that the digestion of chitinous millipedes was four times more costly (per gram of food) than the digestion of fungi.

We attribute these meal type effects to the differential work load necessary to breakdown and assimilate meals of different structural integrity and composition. We suggest that additional energy and time are necessary to break through the chitinous exoskeleton of crickets, mealworms, and superworms compared to the softer, more digestible outer layers of redworms, waxworms, and neonatal rodents. For the turtle, *K. spekii*, a millipede meal took twice as long to pass through the stomach and small intestine compared to a meal of fungi (Hailey 1998).

In addition to the meal's physical structure, its composition, in particular its relative protein content, can also effect the SDA response. Studies using artificial diets have demonstrated that as relative protein content is increased in the diet there is a corresponding increase in SDA (Carefoot 1990b; Jobling and Davies 1980; Ross et al. 1992). Proposed is that diets high in protein generate more postabsorptive protein synthesis and experience greater deamination of excess amino acids, both of which elevate SDA (Brown and Cameron 1991; LeGrow and Beamish 1986). In contrast, a study using natural diets failed to observe a relationship between meal protein content and SDA response for the amphibian *C. cranwelli* (Grayson et al. 2005). In

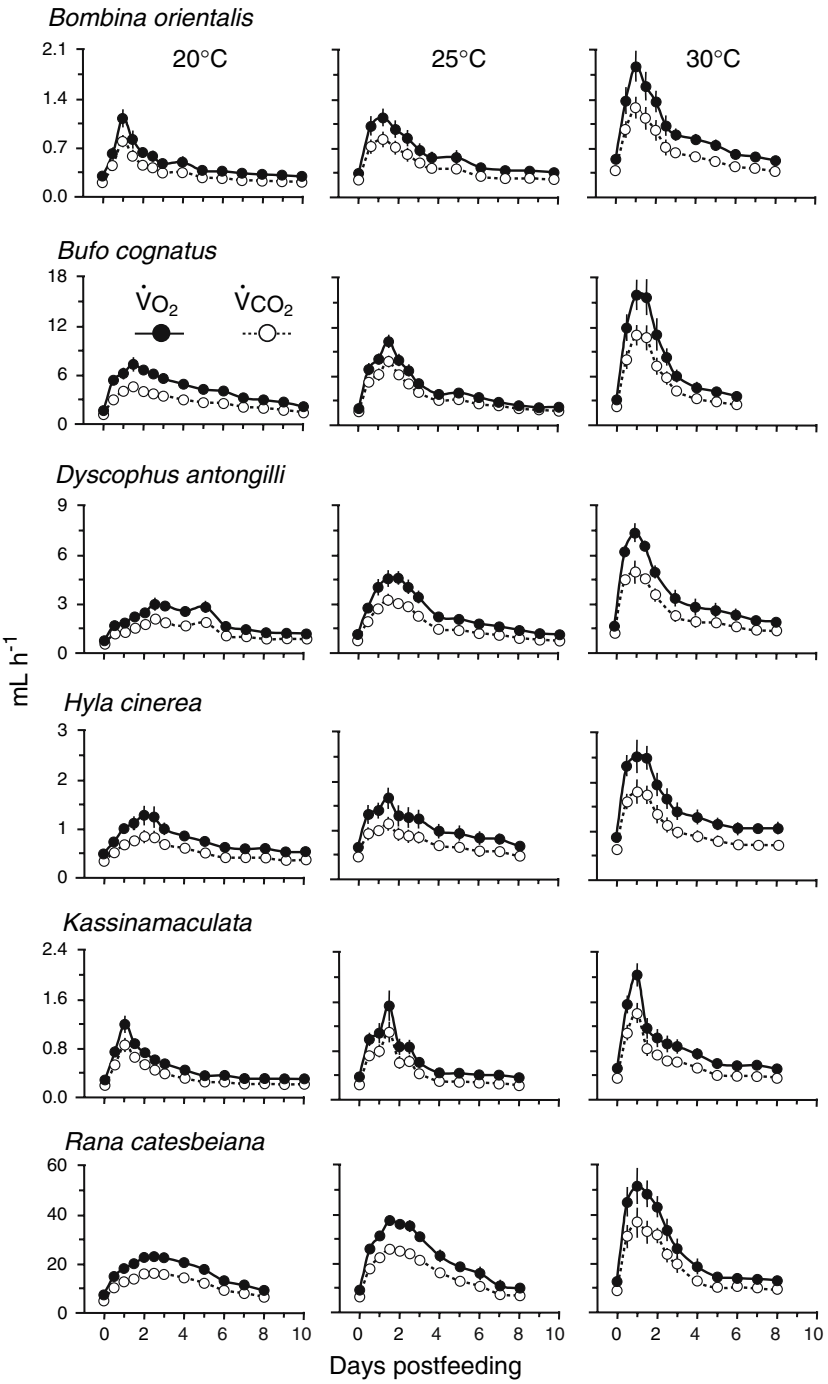

Fig. 6 Mean $\dot{V}O_2$ and $\dot{V}CO_2$ (mL h^{-1}) of *Bombina orientalis*, *Bufo cognatus*, *Dyscophus antongilli*, *Hyla cinerea*, *Kassina maculata*, and *Rana catesbeiana* prior to (day 0) and up to 10 days following the ingestion of cricket meals equaling 10% of anuran body mass at body temperatures of 20, 25, and 30°C. For each trial, $n = 6$–8 per temperature trial. Note that with an increase in body temperature, the SDA profile becomes more elevated and shorter

a previous study (Secor and Boehm 2006), we estimated protein contents of the same meals used in the current study and found no significant relationship between meal protein content and SDA for the amphibian *A. tigrinum*. A similar analysis revealed no relationship between protein content and SDA for the five anurans species studied here (data not shown). Whereas the effects of relative protein content on SDA is evident for more easily digested artificial diets, its effects may be masked by the variation in effort expended to breakdown and absorb natural diets that comparatively have greater preabsorptive costs.

Although SDA coefficient varied consistently among meal types, this not always due to differences in meal structure and toughness. Consider that SDA coefficient is a function of both the effort to digest the meal, a product of meal structure, and meal energy, a product of its energy density (remember that meals in

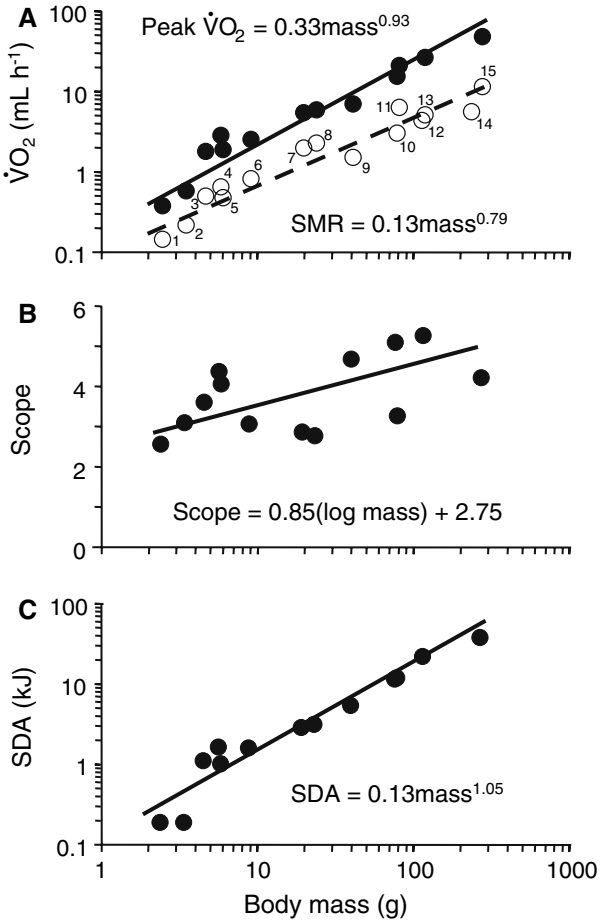

Fig. 7 Log SMR (**a**), log postprandial peak $\dot{V}O_2$ (A), scope of peak $\dot{V}O_2$ (**b**), and log SDA (**c**) of 13–15 species of anurans plotted against log body mass. Species used to generate plots are identified in the first panel as *1 Pseudacris regilla*, *2 Psuedacris cadaverina*, *3 Bombina orientalis*, *4 Kassina senegalensis*, *5 Kassina maculata*, *6 Hyla cinerea*, *7 Bufo terrestris*, *8 Bufo woodhousei*, *9 Dyscophus antongilli*, *10 Bufo cognatus*, *11 Bufo boreas*, *12 Ceratophrys ornata*, *13 Bufo marinus*, *14 Pyxicephalus adspersus*, and *15 Rana catesbeiana*. Postprandial peak $\dot{V}O_2$, scope of peak $\dot{V}O_2$, and SDA data originated from trials where anurans consumed cricket meals equaling 10% of body mass at 30°C (thereby excluding *C. ornata* and *P. adspersus*). Body mass, SMR, peak $\dot{V}O_2$, and SDA were $\log_{10}$ transformed prior to generating interspecific allometric equations. Data are from Secor (2001), Secor and Faulkner (2002), and this study

this experiment were of equivalent size). Meals in this experiment vary in the cost of digestion and assimilation and range in energy density from 4.13 kJ g^{-1} wet mass for redworms to 10.80 kJ g^{-1} wet mass for superworms. A low energy meal that is difficult to digest will result in a higher SDA coefficient compared to an easily digestible meal of high energy. For example in our study, the SDA coefficients of the small cricket meals (5.67 kJ g^{-1} wet mass) were 3.5 and 1.9 times those of the waxworm meals (9.88 kJ g^{-1} wet mass), respectively, for *B. orientalis* and *K. maculata*. Significant variation in the SDA coefficient due to combined differences in meal toughness and energy density has also been noted *for A. tigrinum* (Secor and Boehm 2006). In that study, mealworm beetles and neonatal mice produced similar SDA, whereas their SDA coefficients differed by almost 100% because the beetles were more energy dense (9.26 kJ g^{-1} wet mass) compared to the neonate mice (4.51 kJ g^{-1} wet mass). Given how meal structure and energy density can dictate the SDA coefficient and the assumptions which underly this coefficient, researchers should be cautious in proposing any functional or adaptive significance of the SDA coefficients when they are calculated from different meal types (Beaupre 2005; Secor and Boehm 2006).

Effects of body temperature on SDA

Independent of meal size and type, a shift in body temperature changes the position and shape of the profile of pre- and postfeeding $\dot{V}O_2$ and $\dot{V}CO_2$. From 20 to 30°C, both SMR and peak $\dot{V}O_2$ of each species increased as expected with Q_{10} values ranging from 1.42 to 2.57. These Q_{10} values are within the span of Q_{10}'s reported for anuran SMR and $\dot{V}O_2$max (reviewed in Gatten et al. 1992). The temperature-induced increase in peak $\dot{V}O_2$ kept pace with the increase in SMR, thus the factorial scope of peak $\dot{V}O_2$ seldom varied significantly with body temperature. The one exception was for *R. catesbeiana* which experienced larger scopes at 25°C and 30°C compared to 20°C.

Whereas body temperature had little effect on the magnitude of peak $\dot{V}O_2$ relative to SMR, increasing body temperature resulted in the peak being reached sooner after feeding. At 20°C, peak $\dot{V}O_2$ occurred on average 48 h postfeeding, whereas at 30°C peaks were usually reached 24 h after feeding. Similarly for *P. molurus*, postprandial peak $\dot{V}O_2$ occurred much sooner at higher body temperatures (0.9 day at 35°C) than at lower body temperatures (3 days at 25°C; Wang et al. 2003). Following the peak in $\dot{V}O_2$, body temperature continued to influence the metabolic profile, decreasing the remaining duration of the response by 33% with a 10°C increase in body temperature. Thus, from 20 to 30°C, the full duration of the SDA response for these anurans decreased on average by 2.5 days. In three studies that also controlled for meal size and type, an increase in body temperature by 5, 15, and 15°C for the rattlesnake *Crotalus horridus*, the toad *B. marinus*, and the salamander *A. tigrinum* reduced the duration of the SDA response by 22, 72,

and 57%, respectively (Secor and Boehm 2006; Secor and Faulkner 2002; Zaidan and Beaupre 2003). The shortening of the SDA response with higher body temperature reflects the temperature-dependent increase in digestive and passage rates (Stevenson et al. 1985; McConnachie and Alexander 2004). For *H. cinerea*, a rise in body temperature from 25 to 35°C increased the rate of digestion by 43% (Freed 1980). In the present study, a 10°C increase in body temperature (from 20 to 30°C) for *H. cinerea* reduced the duration of their SDA response by 33%.

Whereas our first prediction on body temperature effects (body temperature will influence the position and shape of the postprandial metabolic profile) proved accurate, our second prediction met mixed results. We hypothesized that if meal size and type are standardized, SDA will not vary with body temperature. This hypothesis was based on the assumption that for any given meal there was a fixed amount of energy used for its digestion and assimilation, and that body temperature only affected the rate of digestion. This hypothesis is supported by the lack of any significant variation in SDA among tested body temperatures for the anurans *C. cranwelli* and *B. marinus*, and the snake *P. molurus* (Powell et al. 1999; Secor and Faulkner 2002; Wang et al. 2003). Likewise for four of our studied species (*B. orientalis*, *B. cognatus*, *D. antongilli*, and *K maculata*), SDA did not vary significantly among body temperature treatments. In contrast, two other species of this study exhibited significant variation in SDA with body temperature, each experiencing an increase in SDA with temperature. The significant increase in SDA with body temperature occurred between 20 and 25°C for *R. catesbeiana*, and between 25 and 30°C for *H. cinerea*. Similarly, *A. tigrinum* experienced a significant increase in SDA, independent of meal size and type, from 15 to 20°C with no additional change in SDA at 25 and 30°C (Secor and Boehm 2006).

While the lack of temperature effects on SDA can be explained by the assumption that there is a set cost to digest a particular meal and that temperature only influences the rate of digestion, we propose one possible explanation for the increase in SDA with body temperature. At higher body temperatures, digestion and passage rates increase, thereby the intestine receives a greater volume of food per unit time. Faced with an increase demand, the gut upregulates intestinal and pancreatic performance, but at an additional cost (thus a greater SDA). As previously discovered for *P. molurus*, an increase in demand on small intestinal performance resulted in the further increase in nutrient uptake rates (Secor and Diamond 1997b).

Interspecific relationships of SDA for anurans

Spanning seven families and over a 100-fold range in body mass, the nine species of this study combined with those species of other studies provide the opportunity to explore interspecific relationships of SDA among anurans. In the present study, the observed interspecific variation in SMR can largely be explained by the variation in body mass. Differences in the scope of peak $\dot{V}O_2$ may best be explained by the comparatively low SMR of *B. cognatus* and *D. antongilli* that resulted in the highest set of calculated scope. The significant variation in the SDA coefficient is due in part because *B. orientalis* and *K. senegalensis* consumed smaller size crickets (0.148 ± 0.003 g) which were less energy dense (5.67 kJ g^{-1}) than the large crickets (0.483 ± 0.008 g, 8.18 kJ g^{-1}) fed to *B. cognatus*, *D. antongilli*, and *R. catesbeiana*. With similar SDA's (relative to mass), less meal energy resulted in larger SDA coefficents for *B. orientalis* and *K. senegalensis*.

To expand our analysis of interspecific relationships between body mass and SDA variables for anurans, we included data from Secor (2001) and Secor and Faulkner (2002). For SMR, we combined data from all nine species of this study and from six species presented in Secor (2001) and Secor and Faulkner (2002). For postprandial variables, we used from these three studies data generated from anurans digesting cricket meals equaling 10% of body mass at 30°C. For 15 species of anurans ranging in body mass from 2.4 to 270 g, SMR scaled with body mass ($\log_{10} - \log_{10}$ regression) with a mass exponent of 0.79 ± 0.06 (r^2 = 0.93) (Fig. 7a). For the same set of anurans (with the exception of *C. ornata* and *P. adspersus*), peak $\dot{V}O_2$ and SDA scaled with body mass with mass exponents of 0.93 ± 0.07 (r^2 = 0.94) and 1.05 ± 0.08 (r^2 = 0.93), respectively (Fig. 7a, c). Given the differences in the scaling exponents of SMR and peak $\dot{V}O_2$, we found the scope of peak $\dot{V}O_2$ to increase significantly (P = 0.038) with body mass (Fig. 7b).

Body size effects on SDA variables has previously been investigated both intra- and interspecifically. Over respective 110- and 120-fold ranges in body mass, peak $\dot{V}O_2$ scaled with mass exponents of 0.85 ± 0.03 and 0.90 ± 0.03, respectively, for *B. marinus* and *P. molurus* (Secor and Faulkner 2002; Secor and Diamond 1997a). For six species of ambystomatid salamanders, peak $\dot{V}O_2$ scaled interspecifically with an exponent of 0.78 ± 0.06 (Secor and Boehm 2006). As observed interspecifically for anurans, the scope of peak $\dot{V}O_2$ increased with body mass for both *B. marinus* and *P. molurus* (Secor and Faulkner 2002; Secor and Diamond 1997a). Interestingly, the scaling exponents of SDA are

quite similar among intra- and interspecific data sets. Intraspecifically, SDA scale with body mass with exponents of 1.02 ± 0.04 and 1.01 ± 0.02, respectively, for *B. marinus* and *P. molurus*, and interspecifically with exponents of 1.05 ± 0.06 and 1.05 ± 0.08 for ambystomatid salamanders and anurans (Secor and Boehm 2006; Secor and Faulkner 2002; Secor and Diamond 1997a; this study). Whereas the body mass scaling of peak $\dot{V}O_2$ is variable within and among taxa (range of 0.78–0.94), the scaling mass exponents of SDA appear to vary little intra- or interspecifically.

Outlook

The goal of this study was to test three hypotheses of the determinants of the SDA response which we achieved by investigating the postprandial metabolic responses of nine anuran species representing seven families. These species provided a modest degree of phylogenetic diversity and variation in body size. We have shown for anurans, as others have for other taxa, that the SDA response is influenced by meal size, meal type, and body temperature. Given the potential variation in SDA and that SDA can contribute substantially to an individual's daily energy expenditure (Peterson et al. 1998; Secor and Nagy 1994), it would be worth asking whether particular meal sizes and types, as well as body temperatures during digestion, may be selected for in order to reduce the energy lost to SDA and therefore increase net energy gain? This question could be explored by comparing the tradeoffs between energy expended and gained for each determinant of SDA. While selection pressure might favor the meal size with the lowest SDA coefficient, this may be in conflict with the advantage of consuming the largest possible meal in order to gain the most absolute energy. The selection of meal type may stem from a tradeoff between choosing more easily digestible meals that generate a lower SDA but are of low energy and selecting more difficult to digest meals (higher SDA) that are more energy rich. For species in which SDA increases with body temperature, body temperature selection may represent a balance between the advantages of a lower cost per gain at lower temperatures and the advantage of higher passage rates and more frequent feeding, and thus more overall energy intake, at higher body temperatures. Experimental laboratory studies may shed light on possible selective behaviors involved in feeding and digesting that are founded in maximizing energy gain from a meal by reducing SDA. Whereas such selective traits can be rationalized from theories of optimal foraging (Schoener 1971), in the wild they may be masked or outweighed by a combination of ecological variables, including the relative abundance and ease of capture of prey species, prey composition, predation risks, available temperatures, competition, and the predator's own foraging tactics (Grayson et al. 2005). Although largely considered the metabolic consequence of meal digestion and assimilation, SDA may alternatively be viewed as the interaction between the selective pressures to reduce the cost of digestion and the choices and risks available in nature.

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