Specific Dynamic Action of Ambystomatid Salamanders and the Effects of Meal Size, Meal Type, and Body Temperature

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Accepted 11/1/2005; Electronically Published 6/21/2006

ABSTRACT

The past decade has witnessed a dramatic increase in studies of amphibian and reptile specific dynamic action (SDA). These studies have demonstrated that SDA, the summed energy expended on meal digestion and assimilation, is affected significantly by meal size, meal type, and body size and to some extent by body temperature. While much of this attention has been directed at anuran and reptile SDA, we investigated the effects of meal size, meal type, and body temperature on the postprandial metabolic responses and the SDA of the tiger salamander (*Ambystoma tigrinum tigrinum*). We also compared the SDA responses among six species of *Ambystoma* salamanders representing the breadth of *Ambystoma* phylogeny. Postprandial peaks in $\dot{V}O_2$ and $\dot{V}CO_2$, duration of elevated metabolism, and SDA of tiger salamanders increased with the size of cricket meals (2.5%–12.5% of body mass). For *A. tigrinum*, as for other ectotherms, a doubling of meal size results in an approximate doubling of SDA, a function of equal increases in peak $\dot{V}O_2$ and duration. For nine meal types of equivalent size (5% of body mass), the digestion of hard-bodied prey (crickets, superworms, mealworms, beetles) generated larger SDA responses than the digestion of soft-bodied prey (redworms, beetle larvae). Body temperature affected the profile of postprandial metabolism, increasing the peak and shortening the duration of the profile as body temperature increased. SDA was equivalent among three body temperatures (20°, 25°, and 30°C) but decreased significantly at 15°C. Comparatively, the postprandial metabolic responses and SDA of *Ambystoma jeffersonianum*, *Ambystoma maculatum*, *Ambystoma opacum*, *Ambystoma talpoideum*, *Ambystoma texanum*, and the conspecific *Ambystoma tigrinum mavortium* digesting cricket meals that were 5% of their body mass were similar (independent of body mass) to those of *A. t. tigrinum*. Among the six species, standard metabolic rate, peak postprandial $\dot{V}O_2$, and SDA scaled with body mass with mass exponents of 0.72, 0.78, and 1.05, respectively.

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Physiological and Biochemical Zoology 79(4):720–735. 2006. 1522-2152/2006/7904-5078$15.00

Introduction

Specific dynamic action (SDA) represents the summed energy expended on meal ingestion, digestion, and assimilation (Brody 1945; Kleiber 1975). Among endotherms, SDA contributes modestly to an individual's daily energy expenditure, largely because it seldom generates more than a 50% increase in metabolic rate, and such increases are relatively brief (Costa and Kooyman 1984; Hawkins et al. 1997; Campbell et al. 2000). In contrast, meal digestion induces much larger metabolic responses for amphibians and reptiles, increasing metabolic rates by factors of four to 44 (Coulson and Hernandez 1979; Secor and Diamond 1997; Secor and Phillips 1997; Powell et al. 1999; Secor 2001). In addition to the large magnitude of their postprandial metabolic response, metabolic rates of digesting amphibians and reptiles will remain elevated for up to 2 wk (Secor and Diamond 1997; Secor 2005). Hence, SDA can contribute significantly to an ectotherm's energy budget, being responsible for as much as 43% of its daily energy expenditure in the field, measured with doubly labeled water (Secor and Nagy 1994; Peterson et al. 1998).

For 60 yr following the pioneering studies of Francis Benedict (1932), interest in the postprandial metabolic responses of amphibians and reptiles was limited to approximately a dozen published studies. In contrast, the past decade has witnessed a dramatic increase in attention to amphibian and reptile SDA, with more than three dozen studies published. These studies, in addition to illustrating the breadth of metabolic responses experienced by amphibians and reptiles during digestion, have experimentally demonstrated the effects on SDA of meal size (Andrade et al. 1997; Secor and Diamond 1997; Powell et al. 1999), meal type (Secor and Phillips 1997; Hailey 1998; Pan et al. 2005), body temperature (Toledo et al. 2003; Wang et al. 2003), body size (Secor and Diamond 1997), experimental feeding frequency (Overgaard et al. 2002), and natural feeding frequency (Secor and Diamond 2000). For two species, several determinants of SDA have been simultaneously examined: meal size, meal type, body temperature, and body size for the marine toad (*Bufo marinus*) and meal size, body size, body temperature,

and fasting duration for the timber rattlesnake (*Crotalus horridus*; Secor and Faulkner 2002; Zaidan and Beaupre 2003). While the majority of these SDA studies have been on reptiles, the attention to amphibian SDA has been directed largely at anurans (Wang et al. 1995; Powell et al. 1999; Sievert and Bailey 2000; Secor and Faulkner 2002), with relatively little known regarding the SDA responses of salamanders (Feder et al. 1984; Secor 2001).

To enhance our understanding of salamander SDA and to investigate the determinants of salamander SDA, we undertook an experimental and comparative study on the SDA responses of ambystomatid salamanders. Our first objective was to explore the effects of meal size on the SDA responses of the salamander *Ambystoma tigrinum*. We hypothesized that, as previously observed, the magnitude of the SDA response would increase with meal size (Secor and Diamond 1997; Secor and Faulkner 2002). Our second objective was to assess the impact of meal type on the SDA responses of *A. tigrinum*. For this component of the study, we hypothesized that meals more difficult to digest would incur a larger SDA. Our third objective was to address the impact of body temperature on *A. tigrinum* SDA. Whereas body temperature influences the profile of the postprandial metabolic response, it remains controversial whether body temperature significantly affects the overall cost of digestion (Secor and Faulkner 2002; Toledo et al. 2003; Wang et al. 2003). Our fourth objective was to compare the SDA responses among seven taxa of ambystomatid salamanders and to explore the potential role of body size on their SDA.

Material and Methods

Salamanders and Their Maintenance

Ambystomatid salamanders are generally stout bodied with short, rounded heads and conspicuous costal grooves, and as adults they range in total length from 8 cm for *Ambystoma opacum* to 35 cm for *Ambystoma tigrinum* (Petranka 1998). The 30 extant species of ambystomatid salamanders are distributed throughout most of North America and southward into central Mexico (Petranka 1998). They all feed on a variety of invertebrates, with the largest species, *A. tigrinum*, known to also consume small fishes, amphibians, reptiles, and mammals in the wild (Petranka 1998).

We assess the effects of meal size, meal type, and body temperature on SDA using eight *A. tigrinum* that were wild-caught in Wisconsin (*Ambystoma tigrinum tigrinum*) and purchased commercially (Charles Sullivan, Nashville, TN). Body mass of these salamanders averaged (± 1 SE) 28.4 ± 2.1 g at the start of the study and increased to 34.4 ± 2.6 g by the end of the study. Our intraspecific and interspecific comparison of SDA was undertaken using individuals of *A. tigrinum* captured in Texas (*A. tigrinum mavortium*) and of five other *Ambystoma* species, *A. jeffersonianum*, *A. maculatum*, *A. opacum*, *A. talpoideum*, and *A. texanum*. These species represent the four distinct clades of *Ambystoma* phylogeny (Shaffer et al. 1991; Jones et al. 1993). *Ambystoma jeffersonianum* (unisexual population) and *A. texanum* were collected in Wabash County and Huntington County, Indiana, *A. maculatum* were collected in Wilson County, Tennessee, and *A. opacum* and *A. talpoideum* were collected in Aiken County, South Carolina.

We housed salamanders in large plastic storage boxes (60 L) with a 5-cm-deep layer of loose soil and several pieces of bark for cover. Salamanders were maintained at 24°–27°C under a photoperiod of 14L : 10D and fed a diet of crickets at 3-d intervals. Before metabolic trials, we fasted individuals for up to 2 wk to ensure that their guts were emptied and that all digestive activities had ceased. Animal care and experimentation were conducted under the approval of the University of Alabama Institutional Animal Care and Use Committee.

Measurements of Gas Exchange

We quantified metabolic rates of salamanders as rates of 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). Individual salamanders were placed within a respirometry chamber (0.5–0.7 L) and maintained at a target temperature within an environmental chamber (model DS54SD; Powers Scientific, Pipersville, PA). Each respirometry chamber was fitted with an incurrent and excurrent air port, each attached to a three-way stopcock. Between measurements, air was pumped into the chambers through the incurrent air port. A small amount of water was placed in each chamber to prevent salamanders from desiccating as a result of constant air flow. For each metabolic measurement, a 20-mL air sample was withdrawn from the excurrent air port, and both incurrent and excurrent ports were then closed to seal the chamber. One-half to 1 h later, the excurrent air port was opened and a second 20-mL air sample was withdrawn. A portion of each air sample was pumped (125 mL min^{-1}) through a column of water absorbent (Drierite; W. A. Hammond, Xenia, OH) and CO_2 absorbent (Ascarite II; Thomas Scientific, Swedesboro, NJ) into an O_2 analyzer (S-3A/II; AEI, Pittsburgh, PA). The remaining air sample was pumped through a column of water absorbent into a CO_2 analyzer (CD-3A; AEI). We calculated whole-animal (mL h^{-1}) and mass-specific (mL g^{-1} h^{-1}) rates of gas exchange corrected for standard pressure and temperature using a modification of equation (9) of a study by Vleck (1987).

Each metabolic trial began with the measurements of gas exchange of fasted salamanders twice a day (~0800 and 2000 hours) for 3 d. For each salamander, we assigned for its SMR the lowest $\dot{V}O_2$ and accompanying $\dot{V}CO_2$ measured over those 3 d. After SMR measurements, salamanders were fed one of the selected meal types weighing a targeted percentage of individual body mass. Salamanders were then returned to their respirometry chambers, and measurements of gas exchange were resumed at

12-h intervals (~0800 and ~2000 hours) for 3 d and thereafter at 1-d intervals (~0800) for an additional 3–7 d.

Experimental Procedures

We explored the individual effects of meal size, meal type, and body temperature on the SDA response of *A. tigrinum* using the following three experimental procedures. To assess effects of meal size, we fed salamanders adult cricket meals equaling 2.5%, 5%, 7.5%, 10%, and 12.5% of their body mass, and measurements were undertaken at 25°C. To investigate the effects of meal type, we fed salamanders one of the following nine meals: adult crickets (*Acheta domesticus*), mealworms (larva *Tenebrio molitor*), mealworm beetles (adult *T. molitor*), superworms (larva *Zophobas morio*), redworms (*Eisenia fetida*), beetle larvae (Scarabaeidae), golden shiners (*Notemigonus crysoleucas*), juvenile spotted salamanders (*A. maculatum*), and neonate mice (*Mus musculus*). The mass of each meal was held at 5% of salamander body mass, with measurements conducted at 25°C. Body-temperature effects were addressed by comparing the SDA response of salamanders digesting adult cricket meals equaling 5% of their body mass and maintained at temperatures of 15°, 20°, 25°, and 30°C. Before these metabolic measurements, salamanders were acclimated to each temperature for 2 d. The same eight individual *A. tigrinum* were used in all of these experiments, with the exception that only four of these individuals were used to measure the SDA response to the mealworm beetle and beetle larva meals. Our comparison of the SDA response among *A. t. tigrinum*, *A. t. mavortium*, and the other five species of *Ambystoma* was undertaken by comparing the metabolic responses of salamanders digesting cricket meals equaling 5% of their body mass and maintained at 25°C.

For each metabolic trial, we quantified the following seven variables: SMR (lowest measured $\dot{V}O_2$ before feeding), peak $\dot{V}O_2$ (highest recorded $\dot{V}O_2$ after feeding), factorial scope of peak $\dot{V}O_2$ (calculated as peak $\dot{V}O_2$ divided by SMR), respiratory exchange ratio (RER; $\dot{V}CO_2/\dot{V}O_2$ calculated at peak $\dot{V}O_2$), duration (time from feeding until $\dot{V}O_2$ was no longer significantly greater than SMR), SDA (total energy expended above SMR over the duration of significantly elevated $\dot{V}O_2$, quantified as kJ and kJ g^{-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 per milliliter of O_2 consumed, assuming the catabolism of a diet that is 70% protein, 25% fat, and 5% carbohydrate and a respiratory quotient of 0.75 (Gessaman and Nagy 1988).

The energy content of each meal was calculated by multiplying its 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. Five to 15 pellets of each meal type were ignited in a bomb calorimeter (model 1266; Parr Instruments, Moline, IL) 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. We present the energy equivalent of each meal in Table 1.

Table 1: Wet mass, dry mass, percentage dry mass, and energy content of nine different meal types fed to *Ambystoma tigrinum* in order to assess the effects of meal type on their SDA responses

Meal Type	Wet Mass (g)	Dry Mass (g)	Percentage Dry Mass	Energy of Dry Mass (kJ g^{-1})	Energy of Wet Mass (kJ g^{-1})
Adult crickets (*Acheta domesticus*)	.483 ± .008 (50)	.158 ± .003	32.54 ± .33	25.08 ± .18	8.18 ± .10
Subadult crickets (*A. domesticus*)	.352 ± .004 (50)	.103 ± .002	29.17 ± .31	26.26 ± .25	7.67 ± .13
Juvenile crickets *(A. domesticus*)	.148 ± .003 (100)	.033 ± .001	22.39 ± .18	25.15 ± .39	5.67 ± .13
Mealworms (*Tenebrio molitor*)	.130 ± .003 (50)	.046 ± .001	35.71 ± .32	27.97 ± .37	9.97 ± .14
Mealworm beetles (*T. molitor*)	.087 ± .003 (50)	.032 ± .001	36.70 ± .41	25.29 ± .43	9.26 ± .26
Superworms (*Zophobas morio*)	.623 ± .012 (50)	.243 ± .005	39.09 ± .41	27.71 ± .26	10.80 ± .10
Beetle larvae (Scarabaeidae)	2.55 ± .10 (15)	.491 ± .033	19.07 ± .67	19.10 ± .56	3.69 ± .26
Redworms (*Eisenia fetida*)	.404 ± .015 (100)	.074 ± .003	18.20 ± .19	22.60 ± .06	4.13 ± .09
Golden shiners (*Notemigonus crysoleucas*)	1.92 ± .08 (15)	.47 ± .02	24.23 ± .37	23.26 ± .25	5.65 ± .10
Spotted salamanders (*Ambystoma maculatum*)	1.08 ± .09 (3)	.21 ± .02	19.20 ± .34	20.23 ± .30	3.88 ± .06
Neonate mice (*Mus musculus*)	1.97 ± .38 (14)	.38 ± .01	19.24 ± .40	23.32 ± .11	4.51 ± .18

Note. The number in parentheses under wet mass represents the sample size of individuals weighed to determine mean wet mass, dry mass, and percentage dry mass. For all meal types except spotted salamanders, dried specimens were divided into five separate groups, then ground and pressed into pellets (0.04–0.17 g). From each set, three pellets were bombed, and the measured energy content of 15 samples was used to calculate energy equivalent per gram dry and wet mass. For spotted salamanders, the available dry specimens were combined, ground, and formed into three pellets, which were bombed to calculate energy equivalent per gram dry and wet mass.

Table 2: Body mass, meal size, SMR, and six variables of the metabolic response to feeding for five different-sized adult cricket meals fed to the tiger salamander *Ambystoma tigrinum tigrinum* at 25°C

	Meal Size (Percentage of Body Mass)						
Variable	2.5%	5%	7.5%	10%	12.5%	*F*	*P*
Body mass (g)	31.6 ± 2.0	30.1 ± 2.2	29.1 ± 2.1	33.1 ± 2.6	30.8 ± 2.5	.44	.777
Meal size (g)	.79 ± .05^{A}	1.51 ± .11^{B}	2.18 ± .16^{C}	3.32 ± .26^{D}	3.85 ± .32^{E}	21	<.0001
Meal size (% of body mass)	2.49 ± .01^{A}	5.03 ± .01^{B}	7.50 ± .02^{C}	10.04 ± .02^{D}	12.49 ± .04^{E}	23,471	<.0001
SMR (mL O_2 h^{-1})	1.21 ± .07	1.11 ± .08	1.11 ± .08	1.20 ± .08	1.09 ± .08	.58	.680
SMR (mL O_2 g^{-1} h^{-1})	.039 ± .002	.037 ± .002	.039 ± .002	.037 ± .002	.036 ± .001	.57	.689
SMR (mL CO_2 h^{-1})	.773 ± .047	.778 ± .055	.779 ± .062	.867 ± .057	.691 ± .052	1.55	.211
SMR (mL CO_2 g^{-1} h^{-1})	.027 ± .002	.026 ± .002	.027 ± .002	.026 ± .001	.023 ± .001	.88	.484
Peak $\dot{V}O_2$ (mL h^{-1})	2.75 ± .23^{A}	3.02 ± .24^{A}	4.04 ± .30^{B}	4.88 ± .32^{C}	4.58 ± .32^{BC}	29.5	<.0001
Peak $\dot{V}O_2$ (mL g^{-1} h^{-1})	.088 ± .006^{A}	.101 ± .003^{A}	.139 ± .002^{B}	.150 ± .008^{B}	.150 ± .005^{B}	30.6	<.0001
Scope (peak $\dot{V}O_2$/SMR)	2.28 ± .13^{A}	2.72 ± .10^{A}	3.67 ± .18^{B}	4.11 ± .18^{B}	4.27 ± .23^{B}	26.9	<.0001
RER ($\dot{V}CO_2/\dot{V}O_2$)	.707 ± .014	.706 ± .17	.733 ± .15	.701 ± .014	.714 ± .011	.78	.546
Duration (d)	3	5	6	6	7	…	…
SDA (kJ)	1.32 ± .16^{A}	2.08 ± .23^{A}	3.54 ± .28^{B}	5.45 ± .54^{C}	5.71 ± .47^{C}	56.2	<.0001
SDA (kJ kg^{-1})	42.0 ± 4.7^{A}	68.3 ± 3.3^{A}	122 ± 6^{B}	166 ± 14^{C}	186 ± 6^{C}	66.4	<.0001
SDA coefficient (%)	20.5 ± 2.2	16.6 ± .8	19.9 ± 1.0	20.2 ± 1.6	18.2 ± .6	1.45	.237

Note. Variables are defined in the text. Values are presented as mean ± 1 SE. For all meal-size treatments, $n = 8$. Values of F and P result from ANOVAs for SMR (mL O_2 g^{-1} h^{-1}), SMR (mL CO_2 g^{-1} h^{-1}), peak $\dot{V}O_2$ (mL g^{-1} h^{-1}), scope, RER, SDA (kJ kg^{-1}), and SDA coefficient and from ANCOVAs (body mass as the covariate) for SMR (mL O_2 h^{-1}), SMR (mL CO_2 h^{-1}), peak $\dot{V}O_2$ (mL h^{-1}), and SDA (kJ). Values for RER presented in this table represent means of individual RER calculated at peak $\dot{V}O_2$. Different superscript letters denote significant ($P < 0.05$) differences between means among the five meal sizes as determined from post hoc pairwise comparisons (Tukey HSD test).

Statistical Analysis

For each SDA trial, we used repeated-measures ANOVAs to test for significant effects of time (before and after feeding) on $\dot{V}O_2$ and $\dot{V}CO_2$ (as mL h^{-1} and mL g^{-1} h^{-1}) and on RER. Each ANOVA was followed with a post hoc pairwise mean comparison (Tukey-Kramer procedure) to identify significant changes in gas exchange and RER between sampling time points and the time at which $\dot{V}O_2$ did not differ from SMR. We used ANOVA for mass-specific measures and ANCOVA (body mass as a covariate) for whole-animal measures to test for significant effects of meal size, meal type, body temperature, and taxon on metabolic variables. These ANOVAs and ANCOVAs were also followed by pairwise mean comparisons to identify significant differences in metabolic variables between treatments and taxa. Since we used the same eight individual salamanders across treatments (treatment measurements may have been more than a year apart), we simultaneously analyzed the data using repeated-measures ANOVAs. Results from the two sets of ANOVAs were very similar and thus lead to the same conclusions regarding the significance of treatment effects. We used least squares regression analysis to demonstrate the relationship between meal energy and SDA and the interspecific relationship between body mass and SMR, peak $\dot{V}O_2$, and SDA (kJ). For the latter set of analyses, we log transformed metabolic data and body mass before analysis to linearize relationships. Because of the significant variation in body mass among the seven *Ambystoma* taxa, we recalculated whole-animal measures of SMR ($\dot{V}O_2$), peak $\dot{V}O_2$, and SDA for each salamander, assuming a body mass of 14 g (approximate average mass of all salamanders in this comparison). Values were recalculated using allometric equations that we developed from measurements of SMR, peak $\dot{V}O_2$, and SDA of all salamanders. From these equations, we assumed mass exponents of 0.72, 0.78, and 1.05, respectively. We report the results of ANOVAs and ANCOVAs 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 mean ± 1 SE.

Results

Effects of Meal Size

Among the five meal-size treatments, there was no significant difference in salamander body mass or in SMR (Table 2). Regardless of meal size, $\dot{V}O_2$ and $\dot{V}CO_2$ (quantified as mL h^{-1} or mL g^{-1} h^{-1}) differed significantly (all $P < 0.0001$) among sampling periods, increasing ($P < 0.0002$) within 12 h postfeeding (Fig. 1). Peak rates of gas exchange were reached at 1–2.5 d postfeeding, with the time to the peak increasing with meal size (Fig. 1). Postprandial peaks in $\dot{V}O_2$ and $\dot{V}CO_2$ increased with meal size (Table 2); peaks attained during the digesting of the meals 7.5%, 10%, and 12.5% of body mass were significantly (all $P <$ 0.0011) greater than those peaks occurring during the digestion

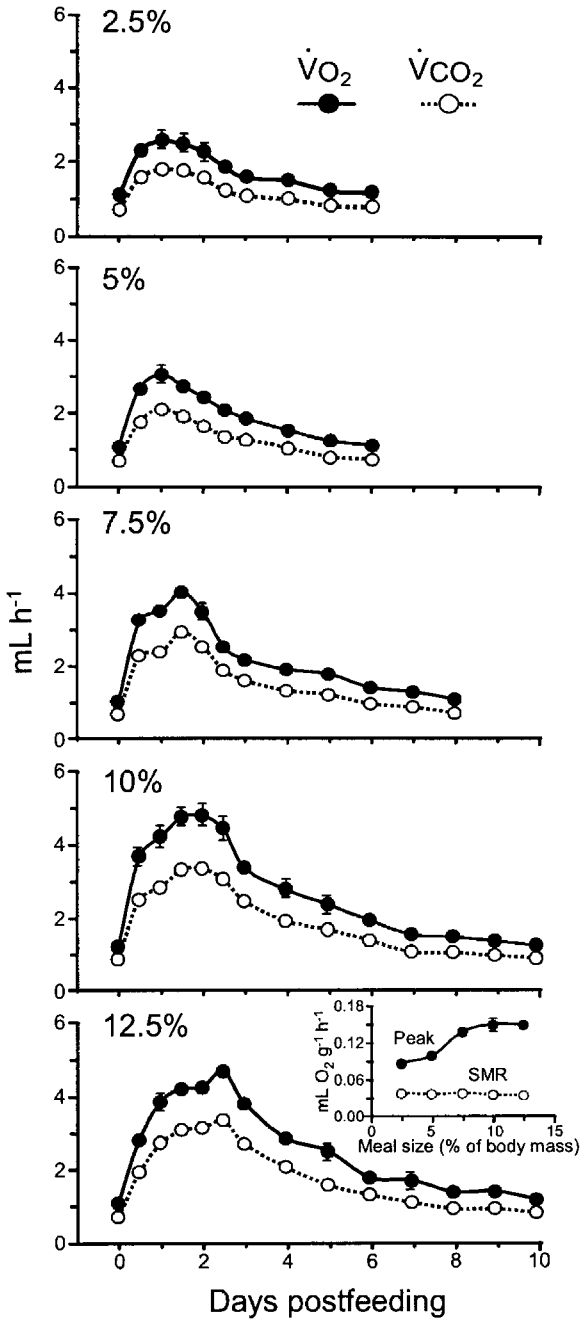

Figure 1. Mean $\dot{V}O_2$ and $\dot{V}CO_2$ (mL h^{-1}) at 25°C of tiger salamanders (*Ambystoma tigrinum tigrinum*) before (day 0) and up to 10 d after the ingestion of cricket meals equaling 2.5%, 5%, 7.5%, 10%, and 12.5% of salamander body mass. For all meal trials, $n = 8$. The insert in the last panel illustrates the lack of any effect of meal-size treatment on SMR and the increase in peak $\dot{V}O_2$ with meal size. For tiger salamanders, an increase in meal size generated larger magnitudes and longer durations of postprandial metabolic rates. Error bars represent ±1 SE and are omitted if the SE is smaller than the symbol for the mean value.

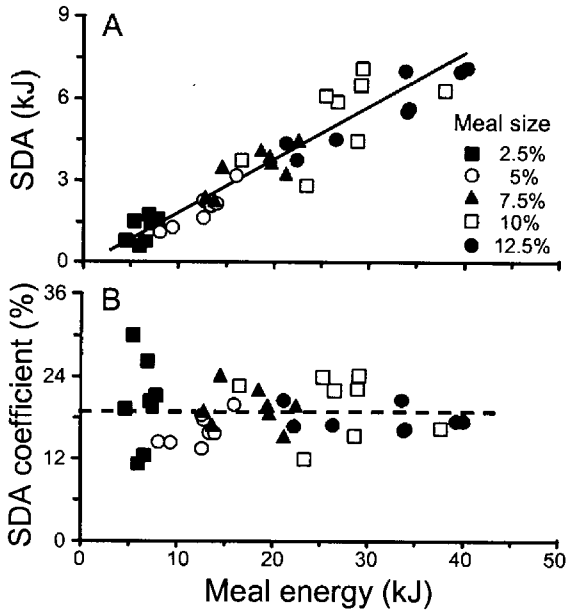

Figure 2. SDA plotted against meal energy for eight tiger salamanders (*Ambystoma tigrinum tigrinum*) digesting each of five meal sizes (*A*) and the SDA coefficients of those meals plotted against meal energy (*B*). The dashed horizontal line in *B* represents the mean SDA coefficient of 19.1%. SDA increases predictably with meal energy, whereas SDA coefficient remains stable.

of the meals 2.5% and 5% of body mass. Likewise, there was a significant effect of meal size on the factorial scope of gas exchange; the scope of $\dot{V}O_2$ (peak $\dot{V}O_2$/SMR) increased from 2.27 ± 0.13 for the 2.5% meals to 4.27 ± 0.23 for the 12.5% meals (Table 2). Salamander RER ($\dot{V}CO_2/\dot{V}O_2$) differed significantly ($P < 0.0005$) among sampling periods for the 7.5% and 12.5% meal-size trials but did not differ among the five meal-size trials when quantified at peak $\dot{V}O_2$ (Table 2). The duration of significantly elevated postprandial metabolism ranged from 3 d for the 2.5% meals to 7 d for the 12.5% meals. As a function of the increase in the metabolic response and duration of that response, the increase in relative meal size, and thus meal energy, generated a corresponding increase in SDA (Fig. 2*A*). The SDA resulting from the 7.5% meals was significantly greater than that from the 2.5% and 5% meals and significantly less than that from the 10% and 12.5% meals (Table 2). With a fivefold increase in meal size (from 2.5% to 12.5% of body mass), SDA increased by a factor of 4.3. The relationship between meal energy and SDA was linear, the slope representing the SDA coefficient (Fig. 2*A*). For the five meal sizes, the SDA coefficient did not significantly vary, averaging 19.1% (Fig. 2*B*; Table 2).

Effects of Meal Type

Among the nine meal-type treatments, there was no significant difference in salamander body mass or in SMR (Table 3). The

Table 3: Body mass, meal size, SMR, and six variables of the metabolic response to feeding for nine different meal types equaling 5% of body mass for the salamander *Ambystoma tigrinum tigrinum* at 25°C

	Meal Type										
Variable	Adult Crickets	Mealworms	Mealworm Beetles	Superworms	Redworms	Beetle Larvae	Golden Shiners	Spotted Salamanders	Neonate Mice	*F*	*P*
n	8	8	4	8	8	4	8	8	8		
Body mass (g)	30.1 ± 2.2	34.4 ± 2.6	37.6 ± 2.8	31.8 ± 2.3	33.5 ± 2.5	38.0 ± 2.7	37.2 ± 2.9	39.2 ± 2.9	33.2 ± 2.3	1.42	.211
Meal size (g)	1.51 ± .11	1.73 ± .13	1.89 ± .14	1.60 ± .11	1.68 ± .13	1.89 ± .14	1.86 ± .15	1.96 ± .14	1.66 ± .12	.90	.526
Meal size (% of body mass)	5.03 ± .01	5.01 ± .02	5.01 ± .01	5.02 ± .01	5.03 ± .03	4.98 ± .02	4.99 ± .01	5.00 ± .01	5.01 ± .01	.85	.558
SMR (mL O_2 h^{-1})	1.11 ± .08	1.07 ± .08	1.14 ± .11	1.18 ± .08	1.01 ± .06	1.11 ± .07	1.21 ± .14	1.21 ± .07	1.17 ± .08	.98	.460
SMR (mL O_2 g^{-1} h^{-1})	.037 ± .002	.032 ± .002	.030 ± .003	.037 ± .002	.035 ± .002	.029 ± .002	.033 ± .003	.032 ± .002	.035 ± .001	1.98	.066
SMR (mL CO_2 h^{-1})	.778 ± .055	.778 ± .061	.829 ± .084	.809 ± .058	.683 ± .045	.801 ± .042	.882 ± .097	.821 ± .039	.832 ± .052	.69	.694
SMR (mL CO_2 g^{-1} h^{-1})	.026 ± .002	.023 ± .001	.022 ± .002	.026 ± .001	.024 ± .001	.021 ± .001	.024 ± .002	.021 ± .001	.025 ± .001	1.42	.209
Peak $\dot{V}o_2$ (mL h^{-1})	3.02 ± .24	3.15 ± .14	3.09 ± .42	3.25 ± 2.8	2.65 ± .32	2.56 ± .17	3.23 ± .28	3.05 ± .26	3.27 ± .35	1.16	.341
Peak $\dot{V}o_2$ (mL g^{-1} h^{-1})	.101 ± .003^{AB}	.094 ± .006^{AB}	.080 ± .006^{AB}	.103 ± .008^{B}	.091 ± .009^{AB}	.068 ± .006^{A}	.088 ± .007^{AB}	.078 ± .004^{AB}	.100 ± .009^{AB}	2.32	.032
Scope (peak $\dot{V}o_2$/SMR)	2.72 ± .10	3.01 ± .18	2.68 ± .23	2.77 ± .20	2.64 ± .29	2.31 ± .12	2.81 ± .29	2.50 ± .12	2.81 ± .24	.71	.683
RER ($\dot{V}co_2$/$\dot{V}o_2$)	.706 ± .017	.722 ± .015	.752 ± .008	.664 ± .007	.686 ± .027	.707 ± .035	.751 ± .014	.696 ± .027	.712 ± .019	1.93	.074
Duration (d)	5	6	5	6	4	4	3	3	4	…	…
SDA (kJ)	2.08 ± .23^{AB}	3.50 ± .24^{C}	2.65 ± 0.28^{ABC}	2.77 ± .39^{BC}	1.54 ± .32^{A}	1.50 ± .05^{A}	1.55 ± .17^{A}	1.42 ± .15^{A}	2.04 ± .22^{AB}	9.32	<.0001
SDA (kJ kg^{-1})	68.3 ± 3.3^{BC}	104.5 ± 8.0^{D}	69.8 ± 5.3^{BC}	87.0 ± 9.8^{CD}	48.9 ± 10.8^{AB}	40.0 ± 2.1^{AB}	42.6 ± 4.9^{AB}	35.7 ± 1.8^{A}	62.3 ± 5.8^{ABC}	10.8	<.0001
SDA coefficient (%)	16.6 ± .8^{A}	20.9 ± 1.6^{AB}	15.0 ± 1.1^{A}	16.1 ± 1.8^{A}	23.5 ± 5.1^{AB}	21.7 ± 1.1^{AB}	15.1 ± 1.7^{A}	18.4 ± .9^{AB}	27.7 ± 2.6^{B}	3.04	.007

Note. Variables are defined in the text. Values are presented as mean ± 1 SE. Values of *F* and *P* result from ANOVAs for SMR (mL O_2 g^{-1} h^{-1}), peak $\dot{V}o_2$ (mL g^{-1} h^{-1}), scope, RER, SDA (kJ kg^{-1}), and SDA coefficient and from ANCOVAs (body mass as the covariate) for SMR (mL O_2 h^{-1}), peak $\dot{V}o_2$ (mL h^{-1}), and SDA (kJ). Values of RER presented in this table represent means of individual RER calculated at peak $\dot{V}o_2$. Different superscript letters denote significant ($P < 0.05$) differences between means among the nine meal types as determined from post hoc pairwise comparisons (Tukey HSD test).

digestion of each of the nine different meals generated a significant response in gas exchange (all $P < 0.0001$); $\dot{V}O_2$ and $\dot{V}CO_2$ increased (all $P < 0.003$) within 12 h after feeding (Fig. 3). Postprandial peaks in $\dot{V}O_2$ (mL h^{-1}) were reached between 12 and 36 h postfeeding and did not differ among the nine meal types (Fig. 3; Table 3). The factorial scope of peak $\dot{V}O_2$ ranged from 2.31 ± 0.12 for beetle larvae to 3.01 ± 0.18 for mealworms and also did not differ among the meal types (Table 3). The duration of the significant postprandial metabolic response ranged from 3 d for the golden shiner and salamander meals to 6 d for the mealworm and superworm meals (Table 3). This variation in duration of the metabolic response is partly responsible for the significant difference in SDA among meals (Table 3). The digestion of the mealworm meals (3.50 ± 0.24 kJ) was more than twice as costly as the digestion of the salamander meals (1.42 ± 0.15 kJ). SDA coefficient varied ($P = 0.002$) among different meals, ranging from 15.0% ± 1.1% for the mealworm beetle meals to 27.7% ± 2.6% for the neonate mouse meals. The costs relative to meal energy of digesting redworms and neonate mice were significantly greater than those of digesting mealworm beetles and superworms (Table 3).

Effects of Body Temperature

Among the four body-temperature treatments, there was no significant difference in salamander body mass. Standard metabolic rate did vary significantly ($P < 0.0001$) among treatments, increasing significantly ($P < 0.04$) with each 5°C increase in body temperature (Table 4). Between 15° and 30°C, the Q_{10} of salamander SMR was 2.02. At each body temperature, salamander $\dot{V}O_2$ and $\dot{V}CO_2$ varied significantly ($P < 0.0001$) among sampling times, increasing ($P < 0.0002$) within 12 h after feeding (Fig. 4). The most notable difference among these postprandial metabolic profiles is that with an increase in body temperature, the profiles become more elevated and shorter (Fig. 4). Peak rates of gas exchange, attained at 1 d postfeeding, differed ($P < 0.0001$) among temperature treatments, increasing with each increase in body temperature (between 15° and 30°C, the Q_{10} was 2.70; Table 4). Although both SMR and postprandial peaks in gas exchange increased with body temperature, there was still a significant ($P < 0.001$) difference among temperature treatments in the scope of peak rates. At 15°C the scope was significantly ($P < 0.005$) less than that at the other three temperatures (Table 4). RER, which did vary significantly

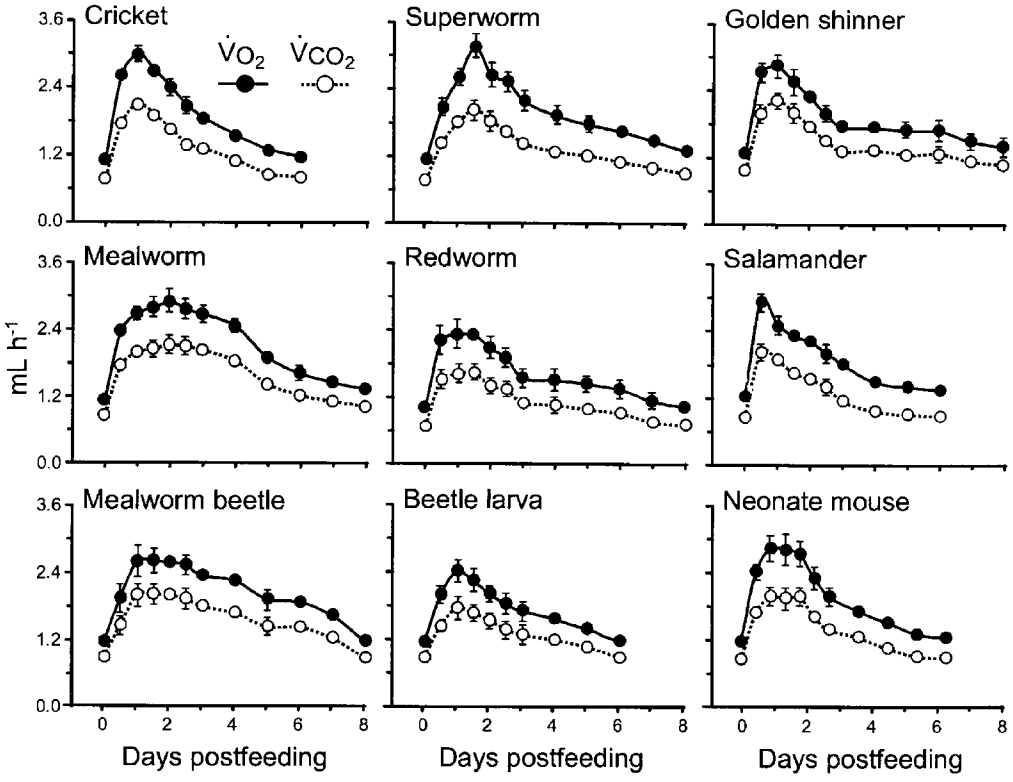

Figure 3. Mean $\dot{V}O_2$ and $\dot{V}CO_2$ (mL h^{-1}) at 25°C of tiger salamanders (*Ambystoma tigrinum tigrinum*) before (day 0) and up to 8 d after the ingestion of nine meal types equaling 5% of salamander body mass. For all meal trials, $n = 8$, with the exception of the mealworm beetle and beetle larva meals, for which $n = 4$. Note that hard-bodied cricket and superworm meals resulted in larger peak $\dot{V}O_2$ than soft-bodied redworm and beetle larva meals. Error bars represent ±1 SE and are omitted if the SE is smaller than the symbol for the mean value.

Table 4: Body mass, meal size, SMR, and six variables of the metabolic response to feeding on cricket meals equaling 5% of body mass for four body temperatures in the salamander *Ambystoma tigrinum tigrinum*

	Body Temperature					
Variable	15°C	20°C	25°C	30°C	*F*	*P*
Body mass (g)	34.3 ± 2.5	34.0 ± 2.9	30.1 ± 2.2	33.3 ± 2.1	.90	.453
Meal size (g)	1.71 ± .12	1.71 ± .14	1.51 ± .11	1.66 ± .11	2.50	.081
Meal size (% of body mass)	4.98 ± .01	5.03 ± .03	5.03 ± .01	4.99 ± .01	2.64	.069
SMR (mL O_2 h^{-1})	.62 ± .04^A	.91 ± .14^B	1.11 ± .08^B	1.86 ± .17^C	71.3	<.0001
SMR (mL O_2 g^{-1} h^{-1})	.018 ± .001^A	.027 ± .002^B	.037 ± .002^C	.055 ± .002^D	123	<.0001
SMR (mL CO_2 h^{-1})	.435 ± .024^A	.646 ± .097^B	.778 ± .055^C	1.281 ± .123^D	49.7	<.0001
SMR (mL CO_2 g^{-1} h^{-1})	.013 ± .001^A	.019 ± .002^B	.026 ± .002^C	.038 ± .002^D	77.5	<.0001
Peak $\dot{V}o_2$ (mL h^{-1})	1.28 ± .07^A	2.79 ± .78^B	3.02 ± .24^B	5.12 ± .43^C	58.5	<.0001
Peak $\dot{V}o_2$ (mL g^{-1} h^{-1})	.038 ± .001^A	.070 ± .009^B	.101 ± .003^C	.154 ± .008^D	115	<.0001
Scope (peak $\dot{V}o_2$ /SMR)	2.06 ± .05^A	2.64 ± .28^B	2.72 ± .10^B	2.80 ± .16^B	9.27	.0002
RER ($\dot{V}co_2/\dot{V}o_2$)	.708 ± .012	.702 ± .059	.706 ± .017	.731 ± .08	.75	.529
Duration (d)	7	6	5	3	…	…
SDA (kJ)	1.13 ± .08^A	2.30 ± .32^B	2.08 ± .23^B	2.28 ± .17^B	10.5	<.0001
SDA (kJ kg^{-1})	33.0 ± .9^A	66.9 ± 8.6^B	68.3 ± 3.3^B	69.3 ± 5.0^B	10.9	<.0001
SDA coefficient (%)	8.09 ± .22^A	16.3 ± 2.1^B	16.6 ± .8^B	17.0 ± 1.2^B	11.1	<.0001

Note. Variables are defined in the text. Values are presented as mean ± 1 SE. For all body-temperature treatments, $n = 8$. Values of *F* and *P* result from ANOVAs for SMR (mL O_2 g^{-1} h^{-1}), peak $\dot{V}o_2$ (mL g^{-1} h^{-1}), scope, RER, SDA (kJ kg^{-1}), and SDA coefficient and from ANCOVAs (body mass as the covariate) for SMR (mL O_2 h^{-1}), peak $\dot{V}o_2$ (mL h^{-1}), and SDA (kJ). Values of RER presented in this table represent means of individual RER calculated at peak $\dot{V}o_2$. Different superscript letters denote significant ($P < 0.05$) differences between means among the four body temperatures as determined from post hoc pairwise comparisons (Tukey HSD test).

($P = 0.04$) among sampling times for the 30°C trial, did not differ among temperature treatments when quantified at peak $\dot{V}o_2$. SDA, quantified as kilojoules or kilojoules per kilogram, and the SDA coefficient differed significantly ($P < 0.0001$) among temperature treatments because of the significantly lower SDA experienced at 15°C (Table 4).

Metabolic Response of Ambystoma *Salamanders*

Body mass varied among the two subspecies of *Ambystoma tigrinum* and the five other *Ambystoma* species, ranging from 3.41 ± 0.34 g for *Ambystoma opacum* to 30.1 ± 2.2 g for *A. tigrinum* (Table 5). SMR differed significantly ($P < 0.002$) among the seven taxa; *A. opacum* possessed significantly higher mass-specific $\dot{V}o_2$ than all other species and a higher adjusted $\dot{V}o_2$ (mL h^{-1}) than *Ambystoma tigrinum mavortium*, *Ambystoma maculatum*, *Ambystoma talpoideum*, and *Ambystoma texanum* (Table 5). Interspecifically, SMR (mL O_2 h^{-1}) scaled among the six species (*Ambystoma tigrinum tigrinum* data was used to represent *A. tigrinum*) with a mass exponent of 0.72 ± 0.09, with body mass accounting for 92.9% of the variation in SMR (Fig. 5). The ingestion of the cricket meals produced significant metabolic responses for all species (among sampling periods, all $P < 0.0001$), inducing significant increases in gas exchange within 12 h of feeding (Fig. 6). We found gas exchange rates to peak at 24 h postfeeding for *A. maculatum*, *A. opacum*, *A. talpoideum*, and *A. texanum* and at 36 h for *A. t. mavortium* and *Ambystoma jeffersonianum* (Fig. 6). Postprandial peaks in $\dot{V}o_2$, quantified as mass specific, varied significantly ($P < 0.0001$) among the seven taxa of salamanders, whereas whole-animal peak measures did not differ (Table 5). For the six species, peak postprandial $\dot{V}o_2$ (mL h^{-1}) scaled with a mass exponent of 0.78 ± 0.06; body mass was responsible for 97.1% of the variation in peak rates (Fig. 5). The factorial scope of the postprandial peak did differ among the salamanders; the scopes of *A. t. mavortium* (3.42 ± 0.24) and *A. texanum* (3.40 ± 0.23) were significantly greater than those of *A. opacum* (2.27 ± 0.35; Table 5). Only *A. t. mavortium* experienced significant ($P = 0.023$) variation in RER among sampling periods, while among the seven taxa, RER at peak $\dot{V}o_2$ varied ($P = 0.006$), with *A. t. mavortium* possessing higher RER than either *A. t. tigrinum* or *A. opacum*. The duration of the SDA response ranged from 3 to 5 d and was positively correlated ($r = 0.87$, $P = 0.01$) with body mass (Table 5). SDA (kJ or kJ g^{-1}) did not differ among the seven taxa, and when adjusted to a body mass of 14 g, it varied by only 9% (Table 5). For the six species, SDA (kJ) scaled with a mass exponent of 1.05 ± 0.06, significantly ($P < 0.05$) greater than the scaling exponent for either SMR or peak $\dot{V}o_2$ (Fig. 5).

Discussion

The postprandial metabolic response of *Ambystoma tigrinum* and the other ambystomatid salamanders is characterized by a

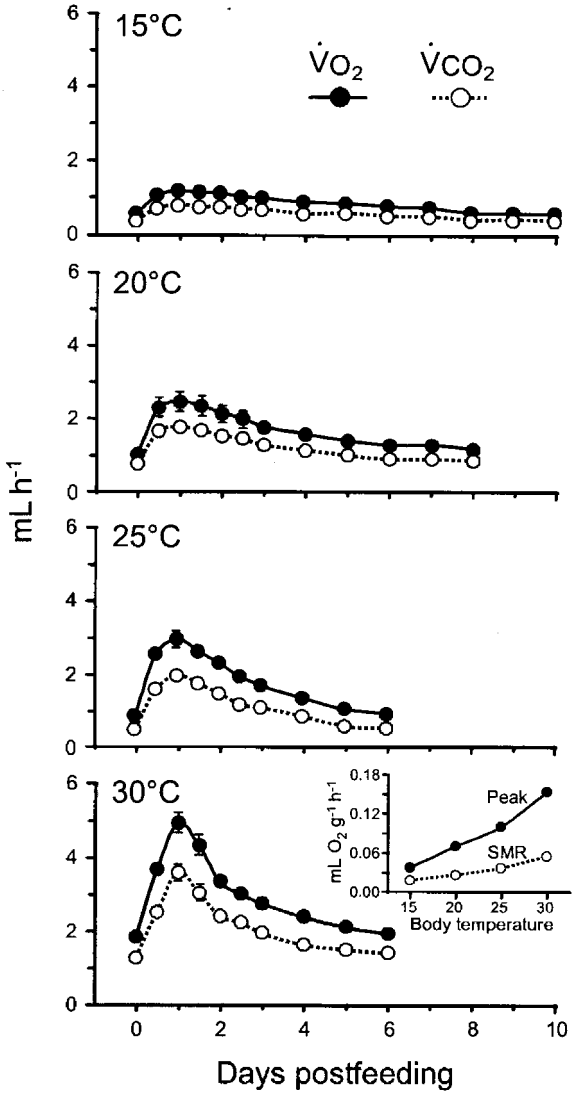

Figure 4. Mean $\dot{V}O_2$ and $\dot{V}CO_2$ (mL h^{-1}) of tiger salamanders (*Ambystoma tigrinum tigrinum*) before (day 0) and up to 10 d after the ingestion of cricket meals equaling 5% of salamander body mass at body temperatures of 15°, 20°, 25°, and 30°C. For all temperature trials, $n = 8$. The inset in the last panel illustrates the temperature-dependent increase in SMR and peak $\dot{V}O_2$. With an increase in body temperature, the SDA response of tiger salamanders becomes more elevated and shorter. Error bars represent ± 1 SE and are omitted if the SE is smaller than the symbol for the mean value.

rapid increase in metabolic rate that peaks 24–48 h after feeding, followed by a slower decline in metabolism that returns to prefeeding levels a few days later. As previously demonstrated for other ectotherms, the profile of the postprandial metabolic response of this salamander is affected by meal size, meal type, and body temperature. As quantified from their postprandial metabolic profile, SDA of *A. tigrinum* varies predictably with digestive effort, increasing with meal size and with meals that are more difficult to digest. In the following discussion, we will draw attention to (1) the impact of meal size, meal type, and body temperature on salamander SDA; (2) the application and hazards of quantifying SDA as a percentage of meal energy; and (3) the interspecific variation in SDA among *Ambystoma* salamanders.

Determinants of SDA

Larger meals predictably induce larger metabolic responses, simply as a function of the increased time and effort needed for their digestion and assimilation. Hence, when meal size is experimentally increased while other determinants of SDA (meal type, body temperature, and body size) are controlled for, there is a corresponding elevation in the metabolic response, observed as both a further increase in peak $\dot{V}O_2$ and a longer duration of elevated metabolism (Andrade et al. 1997; Secor and Diamond 1997; Secor and Faulkner 2002; Toledo et al. 2003). Together, the increase of these two variables (peak $\dot{V}O_2$ and duration) results in an overall increase in SDA. Over a fivefold range in meal size (2.5%–12.5% of body mass), *A. tigrinum* exhibited predictable increases in peak $\dot{V}O_2$ and response duration that produced a 4.4-fold range in SDA. We calculated that with each doubling of meal size, *A. tigrinum* experiences on average a 28% increase in peak $\dot{V}O_2$, a 43% increase in duration, and a 94% increase in SDA (Table 6). For *Bufo marinus* and five snake species, the doubling of meal size generates similar, though slightly larger, increases in peak $\dot{V}O_2$, duration, and SDA (Table 6). Among these seven species, the response coefficient (Q_{2x}; magnitude of response with a doubling of demand) of SDA averaged 2.18 ± 0.08, indicating that with a doubling of meal size, and thus digestive demand, SDA increases by a factor of 2.18 (Table 6). The mean response coefficients of 1.45 and 1.53 for peak $\dot{V}O_2$ and duration, respectively, demonstrate that the approximate doubling of SDA with a doubling of meal size is largely a shared function of equal relative increases in peak $\dot{V}O_2$ and duration (Table 6).

The relationship between meal size (or meal energy) and peak $\dot{V}O_2$ and SDA has been found to be both linear and nonlinear (Secor and Diamond 1997; Toledo et al. 2003; Roe et al. 2004). For *A. tigrinum*, peak $\dot{V}O_2$ appears to plateau with larger meals (Fig. 1), while SDA remains linear across meal sizes (Fig. 2*A*), two trends that have also been observed for the snake *Lamprophis fuliginosus* (Roe et al. 2004). In considering the dependency of the SDA response on meal size, it would be pertinent to ask whether the profile of these relationships (linear or nonlinear) is dependent on the range of meal sizes tested. Consider that animals vary in the size of meals (relative to their body mass) that they can ingest. Whereas some snakes are able to ingest prey that exceed their own body mass, meal sizes for anurans are more likely to peak at 20%–25% of their body mass, and for salamanders the range of meal sizes is relatively less (possibly up to 15% of body mass). Thus, over the full

Table 5: Body mass, meal size, SMR, and six variables of the metabolic response to feeding on cricket meals equaling 5% of body mass at 25°C for two populations of *Ambystoma tigrinum* and five other species of *Ambystoma*

	Ambystoma Species								
Variable	*A. tigrinum tigrinum*	*A. tigrinum mavortium*	*A. jeffersonianum*	*A. maculatum*	*A. opacum*	*A. talpoideum*	*A. texanum*	*F*	*P*
n	8	8	6	8	8	4	8	…	…
Body mass (g)	30.1 ± 2.2^{F}	14.4 ± .8^{D}	10.9 ± .3^{C}	17.9 ± 1.1^{E}	3.41 ± .34^{A}	5.75 ± .25^{AB}	8.22 ± .44^{BC}	57.7	<.0001
Meal type (cricket size)	Adult	Subadult	Juvenile	Subadult	Juvenile	Juvenile	Juvenile	…	…
Meal size (g)	1.51 ± .11	.72 ± .04	.54 ± .02	.90 ± .05	.17 ± .02	.29 ± .01	.41 ± .02	1.25	.305
Meal size (% of body mass)	5.03 ± .01	4.99 ± .01	5.00 ± .04	5.01 ± .02	5.03 ± .03	4.98 ± .03	4.93 ± .07	1.42	.230
SMR (mL O_2 h^{-1})	1.11 ± .08^{D}	.506 ± .033^{B}	.559 ± .029^{BC}	.636 ± .032^{C}	.248 ± .020^{A}	.261 ± .012^{A}	.369 ± .021^{A}	4.33	.002
SMR (mL O_2 h^{-1}) corrected to 14 g	.644 ± .028^{B}	.497 ± .023^{A}	.669 ± .023^{B}	.534 ± .026^{A}	.689 ± .061^{B}	.495 ± .017^{A}	.544 ± .032^{A}	7.74	<.0001
SMR (mL O_2 g^{-1} h^{-1})	.037 ± .002^{A}	.035 ± .002^{A}	.051 ± .001^{B}	.036 ± .002^{A}	.074 ± .007^{C}	.045 ± .002^{AB}	.045 ± .003^{AB}	22.5	<.0001
SMR (mL CO_2 h^{-1})	.778 ± .055	.373 ± .020	…	.439 ± .020	.169 ± .017	.195 ± .009	…	2.21	.093
SMR (mL CO_2 g^{-1} h^{-1})	.026 ± .002^{A}	.026 ± .001^{A}	…	.025 ± .001^{A}	.050 ± .005^{B}	.034 ± .001^{A}	…	17.9	<.0001
Peak $\dot{V}o_2$ (mL h^{-1})	3.02 ± .24	1.67 ± .20	1.41 ± .04	1.81 ± .11	.537 ± .060	.736 ± .043	1.25 ± .11	1.46	.216
Peak $\dot{V}o_2$ (mL h^{-1}) corrected to 14 g	1.66 ± .06	1.61 ± .15	1.72 ± .03	1.50 ± .08	1.64 ± .17	1.48 ± .09	1.88 ± .10	1.68	.151
Peak $\dot{V}o_2$ (mL g^{-1} h^{-1})	.101 ± .003^{A}	.115 ± .010^{A}	.130 ± .002^{AB}	.102 ± .006^{A}	.160 ± .017^{B}	.129 ± .008^{AB}	.151 ± .006^{B}	7.95	<.0001
Scope (peak $\dot{V}o_2$/SMR)	2.72 ± .10^{AB}	3.24 ± .24^{B}	2.54 ± .09^{AB}	2.85 ± .11^{AB}	2.27 ± .35^{A}	2.85 ± .21^{AB}	3.40 ± .23^{B}	3.61	.006
RER ($\dot{V}co_2/\dot{V}o_2$)	.706 ± .017^{AB}	.771 ± .011^{C}	…	.662 ± .010^{A}	.720 ± .019^{BC}	.726 ± .016^{BC}	…	8.92	<.0001
Duration (d)	5	3	4	4	3	3	3	…	…
SDA (kJ)	2.08 ± .23	.857 ± .082	.744 ± .037	1.15 ± .09	.226 ± .050	.315 ± .030	.467 ± .075	.95	.474
SDA (kJ) corrected to 14 g	1.02 ± .01	1.07 ± .04	1.00 ± .01	1.04 ± .02	.99 ± .04	1.08 ± .03	1.08 ± .03	1.53	.195
SDA (kJ kg^{-1})	68.3 ± 3.3	60.0 ± 5.4	68.6 ± 3.2	64.0 ± 3.7	68.8 ± 15.9	55.1 ± 5.8	55.4 ± 6.4	.86	.531
SDA coefficient (%)	16.6 ± .8^{AB}	15.7 ± 1.4^{A}	24.2 ± 1.2^{B}	16.6 ± 1.0^{AB}	23.4 ± 5.3^{AB}	19.5 ± 2.0^{AB}	19.6 ± 2.6^{AB}	2.55	.035

Note. Variables are defined in the text. Values are presented as mean ± 1 SE. Values of *F* and *P* result from ANOVAs for SMR (mL O_2 g^{-1} h^{-1}), peak $\dot{V}o_2$ (mL g^{-1} h^{-1}), scope, RER, SDA (kJ kg^{-1}), and SDA coefficient and from ANCOVAs (body mass as the covariate) for SMR (mL O_2 h^{-1}), peak $\dot{V}o_2$ (mL h^{-1}), and SDA (kJ). Values of RER presented in this table represent means of individual RER calculated at peak $\dot{V}o_2$. Different superscript letters denote significant ($P < 0.05$) differences between means among the seven taxa as determined from post hoc pairwise comparisons (Tukey HSD test).

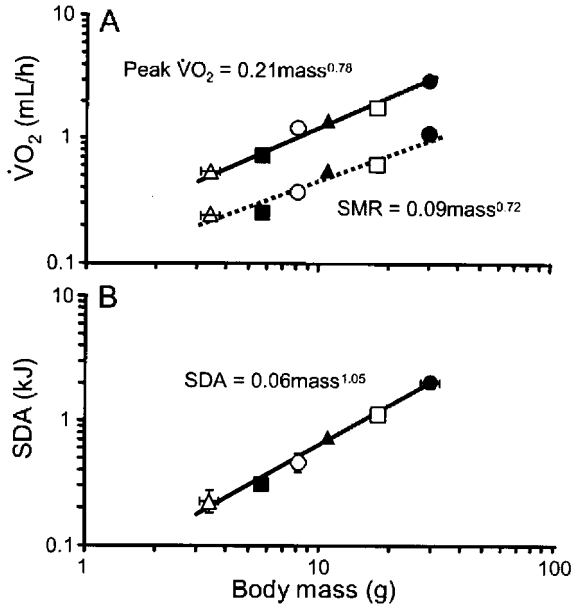

Figure 5. Allometric scaling of SMR and peak $\dot{V}o_2$ (*A*) and specific dynamic action (*B*) for six species of *Ambystoma* salamanders: *A. tigrinum* (*filled circles*), *A. maculatum* (*open squares*), *A. jeffersonianum* (*filled triangles*), *A. texanum* (*open circles*), *A. talpoideum* (*filled squares*), and *A. opacum* (*open triangles*). Body mass, SMR, $\dot{V}o_2$, and SDA were log transformed before generating allometric equations. Error bars represent ± 1 SE and are omitted if the SE is smaller than the symbol for the mean value.

range of possible prey sizes, is the relationship between SDA and meal size constant, or does it differ between smaller and larger relative meal sizes? For *A. tigrinum*, *B. marinus*, and *Python molurus*, peak $\dot{V}o_2$, duration, and SDA have been quantified over approximately the full range of meal sizes that these species can potentially consume (Secor and Diamond 1997; Secor and Faulkner 2002; this study). For these three species, SDA continues to increase linearly across the range of meal sizes, whereas peak $\dot{V}o_2$ for *A. tigrinum* and duration for *B. marinus* and *P. molurus* increase linearly with the smaller meal sizes and then begin to plateau with the larger meals. Therefore, studies that quantify SDA from submaximum sets of meal sizes should be able to extrapolate a predicted SDA resulting from larger possible meals. In undertaking such an exercise, however, it might be important to maintain a constant body size, given the potential allometric relationship between SDA and body mass (Beaupre 2005). We do advise caution in the linear extrapolation of peak $\dot{V}o_2$ and response duration for larger meal sizes, considering the prevalence of their curvilinear relationships with meal size.

It is becoming increasingly more evident that the type of natural meals (Hailey 1998; Secor and Faulkner 2002) and the composition of artificial meals (Secor 2003; McCue et al. 2005) significantly affect the SDA response. For any natural food item, the time and effort required for its digestion and absorption reflect its structural integrity, a function of tissue density and toughness. For *P. molurus*, a large component of SDA is attributed to the cost of gastric breakdown, and as the structural integrity of a meal is decreased, so is the cost of gastric digestion and SDA (Secor 2003). Thus, the more mechanical (peristalsis) and chemical (acid and enzyme production) effort required for gastric digestion, the greater the postprandial peak $\dot{V}o_2$, duration of response, and thus SDA. Among the nine different meals that we fed to *A. tigrinum*, we expected a priori differences in the SDA response, given predicted differences in the difficulty of the meals' digestion. Dividing prey into the categories of soft-bodied prey (red worms, beetle larvae, golden shiners, spotted salamanders, and neonate mice) and hard-bodied prey with chitinous exoskeletons (crickets, mealworms, mealworm beetles, and superworms), we predicted that the latter prey items would take more effort to digest than the former items and would thus generate larger responses. We found this to be generally true; collectively, the hard-bodied prey items elicited a 12% greater peak $\dot{V}o_2$, a 50% increase in duration in the metabolic response, and an 80% greater SDA than the soft-bodied meals (Table 3). Likewise, for *B. marinus*, the digestion of crickets and superworms resulted in, on average, 24%, 22%, and 82% greater peak $\dot{V}o_2$, duration of response, and SDA, respectively, than the digestion of earthworms and neonatal rats (Secor and Faulkner 2002). Hailey (1998) found for the turtle *Kinixys spekii* that the digestion of chitinous millipedes was more costly then the digestion of either kale leaves or commercially grown mushrooms.

Secondary to meal structure and the cost of gastric breakdown, meal protein content can also affect SDA. Increasing the relative protein content of meals results in higher peak $\dot{V}o_2$, longer duration of the metabolic response, and greater SDA (Jobling and Davies 1980; Ross et al. 1992; McCue et al. 2005). To evaluate the potential contribution of protein content to *A. tigrinum* SDA, we estimated protein content of each meal by assuming that meal dry mass is 4% ash, 5% carbohydrates, and the remaining 91% split between protein and fat. For each meal, we used dry-mass energy content (Table 1) and the energy content of carbohydrates (17.1 kJ g^{-1}), protein (17.6 kJ g^{-1}), and fat (38.9 kJ g^{-1}) to calculate relative protein content. Our estimate of relative dry-mass protein content, similar to those published for several of the food items (Douglas et al. 1994; Bernard and Allen 1997*a*, 1997*b*; Schairer et al. 1998), ranged from 40.1% for superworms to 79.4% for beetle larvae. Protein content of meals, calculated from meal dry mass and relative protein mass, ranged from 0.194 g for neonate mice to 0.367 for beetle larvae and was found not to correlate ($P > 0.56$) with either peak $\dot{V}o_2$ or SDA (Fig. 7).

As expected, rates of gas exchange for *A. tigrinum* increased with body temperature. Both SMR and peak $\dot{V}o_2$ displayed predicted Q_{10} effects, increasing by factors of between two and three for each 10°C increase in body temperature. The most

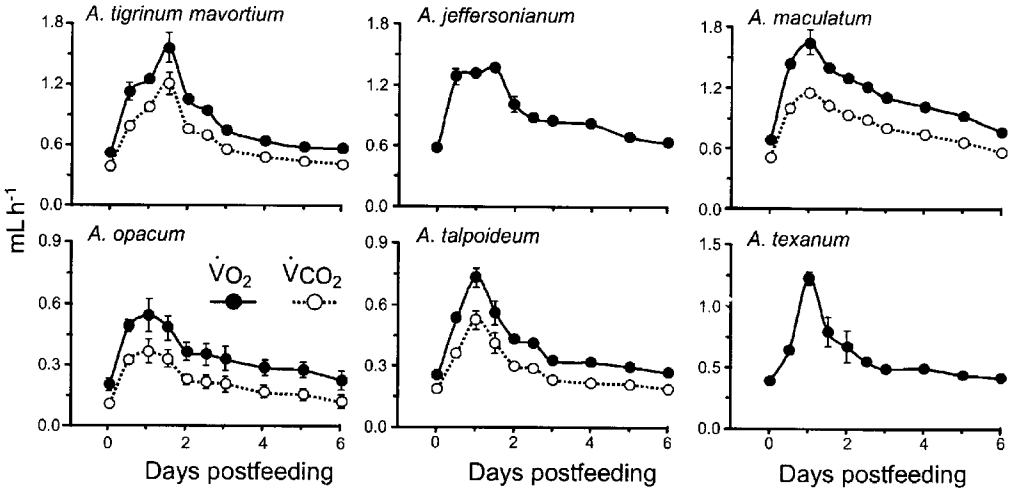

Figure 6. Mean $\dot{V}O_2$ and $\dot{V}CO_2$ (mL h^{-1}) of six species of *Ambystoma* salamanders before (day 0) and up to 6 d after the ingestion of cricket meals equaling 5% of salamander body mass at 25°C. For all species, $n = 8$, with the exception of *Ambystoma jeffersonianum*, for which $n = 6$, and *Ambystoma talpoideum*, for which $n = 4$. Error bars represent ± 1 SE and are omitted if the SE is smaller than the symbol for the mean value.

distinct effect that body temperature has on the SDA response of this salamander is on the profile of its postprandial metabolic rates. At 15°C, the profile is flat and long, becoming more elevated and shortening with each 5°C increase in body temperature. Similar response of the SDA profile has also been observed for *Boa constrictor*, *B. marinus*, and *P. molurus*, which reflects the fact that with an increase in body temperature, the processes of digestion occurs more rapidly, and digestion is completed sooner (Secor and Faulkner 2002; Toledo et al. 2003; Wang et al. 2003). For both amphibians and reptiles, an increase in body temperature increases the rate of digestion and decreases gut passage time (Freed 1980; Bedford and Christian 2000; McConnachie and Alexander 2004).

With noted effects on the postprandial metabolic profile, is it possible that temperature also affects SDA, the overall cost of digestion? One prediction is that regardless of body temperature and the duration of digestion, the amount of digestive and assimilated effort (SDA) would remain the same, given that meal size, meal type, and digestive efficiency are held constant. Hence, SDA, quantified from the area under the metabolic profile, would not vary with temperature. An alternative prediction is that temperature has differential effects on digestive and assimilative functions, whereby at a particular temperature or range of temperatures, there is a disproportionally greater or lesser amount of energy expended on digestion.

Whereas Secor and Faulkner (2002) and Wang et al. (2003) did not observe a significant temperature effect on SDA, thereby supporting the first hypothesis, we found a significant decrease in SDA when salamanders were digesting at the lowest temperature (15°C). In this study, a low body temperature generated not only a lower overall rate of metabolism but also an additional depression of the metabolic expenditures of tissues involved in digestion. In contrast, the snake *B. constrictor* experienced significantly greater SDA at a lower body temperature (25°C) than at a higher body temperature (30°C) over a range of meal sizes (Toledo et al. 2003).

Applications and Pitfalls of the SDA Coefficient

A frequently employed exercise in SDA studies is to express SDA as a percentage of meal energy (or metabolizable meal energy), the SDA coefficient (see Beaupre 2005 for a chronology of this variable). One rationale for presenting SDA coefficients is to facilitate intraspecific and interspecific comparisons of SDA independent of body and meal size. This approach has been very popular in fish SDA studies, especially to evaluate the energy conversion efficiencies of different diets (LeGrow and Beamish 1986; Ross et al. 1992). In a study on eight species of snakes of different sizes digesting rodent meals of similar energy densities and equaling 25% of snake body mass, SDA coefficients revealed a significantly lower cost of digestion relative to meal energy for frequently feeding species than for infrequently feeding species (Secor and Diamond 2000).

An intraspecific evaluation of SDA coefficients over a range of meal sizes may identify an optimal meal size (or range of meal sizes) that generates a lower SDA coefficient. A proposed optimization model of SDA would be characterized by lower SDA coefficients for more frequently consumed meal sizes and higher coefficients for meal sizes smaller or larger than those normally consumed. Mechanistic explanations for such an optimization profile could include the possibility that there is a set cost to gut upregulation regardless of meal size and that

Table 6: Body mass range, meal type, meal sizes, and response coefficient (Q_{2x}) of peak $\dot{V}O_2$, duration, and SDA for seven species of amphibians and reptiles for which SDA responses were measured during the digestion of three or more different-sized meals

Species	Body Mass (g)	Meal Type	Meal Sizes (% of Body Mass)	Response Coefficient (Q_{2x})			Source
				Peak $\dot{V}O_2$	Duration	SDA	
Tiger salamander (*Ambystoma tigrinum*)	29–33	Cricket	2.5, 5, 7.5, 10, 12.5	1.28 ± .16	1.43 ± .16	1.94 ± .25	This study
Marine toad (*Bufo marinus*)	110–127	Rodent	5, 10, 15, 20	1.46 ± .19	1.70 ± .44	2.54 ± .09	Secor and Faulkner 2002
African house snake (*Lamprophis fuliginosus*)	16.3–17.1	Rodent	10, 20, 30	1.35 ± .10	…	2.22 ± .13	Roe et al. 2004
Timber rattlesnake (*Crotalus cerastes*)	87–718	Rodent	10, 30, 50	1.62 ± .29	1.50 ± .28	2.12 ± .17	Zaidan and Beaupre 2003
South American rattlesnake (*Crotalus durissus*)	42–93	Rodent	10, 20, 30, 50	1.43 ± .10	1.59 ± .21	2.35 ± .24	Andrade et al. 1997
Boa constrictor (*Boa constrictor*)	114–204	Rodent	5, 10, 20, 40	1.39 ± .15	1.57 ± .22	2.14 ± .37	Toledo et al. 2003
Burmese python (*Python molurus*)	640–790	Rodent	5, 15, 25, 35, 45, 55, 65, 75, 100	1.62 ± .04	1.41 ± .08	1.95 ± .18	Secor and Diamond 1997

Note. Response coefficients are presented as mean ± 1 SE determined by calculating for each species a response coefficient between each consecutive pair of meal sizes. The coefficient represents the factorial increase in a parameter with a doubling of meal size.

small meals must incur that cost even though they impart a modest demand on the gut. At the other end of the profile, much larger meals generate a disproportionately larger metabolic expenditure because of systemic further upregulation of all tissues and possible stress-induced increase (from such a large meal) in metabolism. Any indication of an optimal meal size could be observed from a plot of SDA coefficient versus meal size, given that meal type, body temperature, and body size are held constant. In studies that controlled for meal type, body temperature, and body size, SDA coefficients varied significantly with meal size for *P. molurus* and *B. marinus*, with smaller meals generating lower coefficients (Secor and Diamond 1997; Secor and Faulkner 2002). However, meal size had no significant impact on the SDA coefficients of *A. tigrinum* and the snakes *B. constrictor*, *Crotalus durissus*, and *L. fuliginosus* (Andrade et al. 1997; Toledo et al. 2003; Roe et al. 2004; this study). Whereas an optimal meal size is an attractive hypothesis, it is not apparent from these collective studies that a particular meal size would be selected to minimize SDA. It should be noted that energetically, especially for infrequently feeding organisms, the optimal meal size is the largest meal size that can be obtained, thereby providing the maximum amount of assimilated energy.

The pitfalls in the application of SDA coefficient reside in its potential allometric expression and its use in comparisons made among different meal types. The former objective to the SDA coefficient is described in detail by Beaupre (2005). In brief, the predictive use of the SDA coefficient assumes isometric scaling between SDA and meal energy. Therefore, if SDA scales allometrically with meal energy, then predictions based on a preidentified coefficient will potentially be in error. In this study for *A. tigrinum*, as well as for *B. marinus* and *P. molurus* in other studies, SDA was found to scale isometrically with meal energy (Secor and Diamond 1997; Secor and Faulkner 2002).

The latter objective stems from the significant impact of meal type on SDA coefficient, given that the coefficient's denominator, SDA, reflects the cost of meal digestion and assimilation, and its numerator reflects the energy of the meal. If we control for meal size, a meal type more difficult to digest will generate a larger SDA, and a meal more dense in energy will thereby contain more energy. Therefore, because each meal type differs in energy content and required digestive effort, it is problematic to compare SDA coefficients among different meals. This is demonstrated in Table 3, where SDA coefficients vary from 15.0% for mealworm beetles to 27.7% for neonatal mice. Since the two meals do not differ in SDA, the significant difference

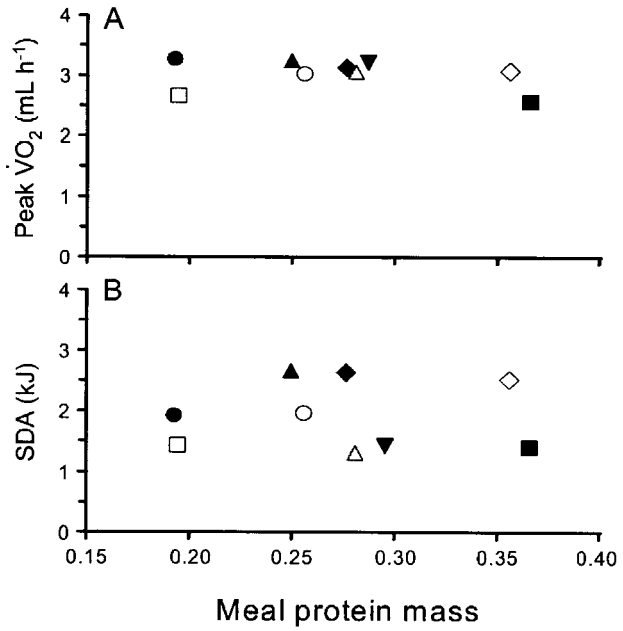

Figure 7. Peak $\dot{V}o_2$ (*A*) and SDA (*B*) plotted against calculated protein mass of the neonate mouse (*filled circles*), redworm (*open squares*), superworm (*filled triangles*), cricket (*open circles*), mealworm (*filled diamonds*), spotted salamander (*open triangles*), golden shiner (*inverted triangles*), mealworm beetle (*open diamonds*), and beetle larva (*filled squares*) meals consumed by *Ambystoma tigrinum tigrinum*. Meal protein mass was calculated as the product of estimated relative protein dry-mass content and meal dry mass. Among these nine meals there was no detectable relationship between SDA response and meal protein mass.

in SDA coefficients reflects the higher energy density of the mealworm beetles (9.26 ± 0.26 kJ g^{-1} wet mass) and the lower energy density of the neonatal mice (4.51 ± 0.18 kJ g^{-1} wet mass). Likewise, SDA differed between the superworm and spotted salamander meals, but SDA coefficients did not, a function of the higher energy content of superworms (10.80 ± 0.10 kJ g^{-1} wet mass) compared with spotted salamanders (3.88 ± 0.06 kJ g^{-1} wet mass). Therefore, we also advise caution in any proposal of a functional or adaptive significance of SDA coefficients generated from different meal types.

Ambystoma *Pre- and Postprandial Metabolism*

The body mass allometry of SMR for the six *Ambystoma* species of this study did not differ in either slope or *y*-intercept from an allometric equation developed from 61 salamander species whose SMRs were similarly measured at 25°C (Table 12.2 of Gatten et al. 1992). Elevated rates of metabolism have been measured in salamanders induced to exercise, and in several species of *Ambystoma* moving on a treadmill at 21°C, $\dot{V}o_2$ increased to as much as 0.410 mL g^{-1} h^{-1} (Full et al. 1988). Such metabolic rates are notably higher than those that we observed during digestion; the maximum recorded individual $\dot{V}o_2$ (0.132–0.174 mL g^{-1} h^{-1}) occurred during the digestion of the two largest cricket meals. Likewise, the toad *B. marinus* experienced a 25-fold increase in $\dot{V}o_2$ during forced exercise and a more modest 6.4-fold maximum increase during meal digestion (Secor and Faulkner 2002). In matching of elevated rates of metabolism between digestion and exercise, the scaling exponent of peak $\dot{V}o_2$ during digestion (0.78 ± 0.06) for the six *Ambystoma* did not differ from that determined during exercise (0.72 ± 0.16) for 11 salamander species, although the *y*-intercept was significantly greater for the exercise data set (Gatten et al. 1992). The other studies that have evaluated the allometry of postprandial peak $\dot{V}o_2$ have found mass exponents to be generally higher: 0.85 ± 0.03 for *B. marinus*, 0.85 ± 0.03 for 40 anuran species, 0.89 ± 0.15 for seven python species, and 0.90 ± 0.03 for *P. molurus* (Secor and Diamond 1997; Thompson and Withers 1999; Secor and Faulkner 2002; Wooten and Secor 2004). Ascertaining whether peak $\dot{V}o_2$ scales interspecifically with a higher exponent for salamanders will require studies of SDA for a broader range of salamander taxa. The few studies that have explored the allometry of SDA have found scaling exponents not to differ from 1.0. Intraspecific exponents of 1.01 ± 0.02 and 1.02 ± 0.04 were identified for *P. molurus* and *B. marinus*, respectively, while exponents of 1.04 ± 0.05 and 1.05 ± 0.06 were observed for 40 species of anurans and the six *Ambystoma* species of this study, respectively (Secor and Diamond 1997; Secor and Faulkner 2002; Wooten and Secor 2004). The generality of a linear relationship between body mass and SDA derived from a common meal type and relative size will be decided by future studies.

The general lack of any distinct differences in SDA response among the studied *Ambystoma* taxa may simply reflect the similarities in their ecology. The species of this study all inhabit bottomland and upland deciduous forests, breed from late fall to early spring (depending on latitude), and feed on a wide array of invertebrates (Petranka 1998). Even the larger *A. tigrinum*, which inhabits a wider range of habitats and whose diet includes small vertebrates, exhibited metabolic responses (independent of body size) similar to those of the smaller, more habitat-specific species. Reproductively unique among the six species are the triploid unisexual *Ambystoma jeffersonianum* (hybrid origin between *A. jeffersonianum* and *Ambystoma laterale*) and *Ambystoma opacum*, one of only two *Ambystoma* species that mate and oviposit on land (Petranka 1998). Again, neither of these two species possessed any distinct differences in pre- and postprandial metabolic responses compared with the other species.

The primary goal of this article is to introduce the SDA responses of salamanders and to demonstrate how meal size, meal type, and body temperature affect the SDA of one salamander species. We hope that this study will encourage others to further explore salamander SDA. While our findings were largely predictable based on previous studies of ectotherm SDA, salamanders may still exhibit unique adaptive responses of their

SDA. Consider the potential challenge of continuous bouts of elevated gas exchange stemming from meal digestion for plethodontid salamanders, which lack lungs and therefore must rely exclusively on cutaneous respiration. Exercise studies have revealed that plethodontid salamanders possess a reduced capacity for maximum aerobic metabolism compared to lunged salamanders (Full et al. 1988). The limitation of their cutaneous diffusion may restrict the size of meals that they can consume, or these salamanders may possess the capacity to upregulate respiratory performance early in digestion by capillary recruitment and increased blood flow (Malvin 1988). Similarly, aquatic salamanders are thought to possess diffusion limitations of their gills and skin for gas exchange (Boutilier et al. 1992). A neotenic tiger salamander during the digestion of a large meal may respond by actively moving its gills, increasing blood flow through gill filaments, and making more frequent trips to the surface to ventilate its lungs. Comparatively, larger postprandial metabolic responses have been observed in amphibians and reptiles that naturally experience long episodes of fasting between infrequent meals (Secor and Diamond 2000; Secor 2005). Among salamanders, fasts exceeding a year have been reported for *Amphiuma*, *Proteus*, and *Siren* (Gunter 1968; Gehlbach et al. 1973; Hervant et al. 2001). Hence, these salamanders may similarly experience a lower fasting metabolic rate and larger magnitudes of SDA than more frequently feeding species.

Acknowledgments

We thank Brian Ott, Katie Stubblefield, and Jessica Wooten for their assistance with metabolic measurements and Michael Finkler and William Hopkins for kindly providing *A. jeffersonianum*, *A. opacum*, *A. talpoideum*, and *A. texanum*. This work was undertaken with support from the National Science Foundation (IOB-0446139) and the University of Alabama Department of Biological Sciences.

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