Effects of Meal Size, Meal Type, Body Temperature, and Body Size on the Specific Dynamic Action of the Marine Toad, *Bufo marinus*

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ABSTRACT

Specific dynamic action (SDA), the accumulated energy expended on all physiological processes associated with meal digestion, is strongly influenced by features of both the meal and the organism. We assessed the effects of meal size, meal type, body temperature, and body size on the postprandial metabolic response and calculated SDA of the marine toad, *Bufo marinus*. Peak postprandial rates of O_2 consumption ($\dot{V}O_2$) and CO_2 production ($\dot{V}CO_2$) and SDA increased with meal size (5%–20% of body mass). Postprandial metabolism was impacted by meal type; the digestion of hard-bodied superworms (*Zophobas* larva) and crickets was more costly than the digestion of soft-bodied earthworms and juvenile rats. An increase in body temperature (from 20° to 35°C) altered the postprandial metabolic profile, decreasing its duration and increasing its magnitude, but did not effect SDA, with the cost of meal digestion remaining constant across body temperatures. Allometric mass exponents were 0.69 for standard metabolic rate, 0.85 for peak postprandial $\dot{V}O_2$, and 1.02 for SDA; therefore, the factorial scope of peak postprandial $\dot{V}O_2$ increased with body mass. The mass of nutritive organs (stomach, liver, intestines, and kidneys) accounted for 38% and 20% of the variation in peak postprandial $\dot{V}O_2$ and SDA, respectively. Toads forced to exercise experienced 25-fold increases in $\dot{V}O_2$, much greater than the 5.5-fold increase experience during digestion. Controlling for meal size, meal type, and body temperature, the specific dynamic responses of *B. marinus* are similar to those of the congeneric *Bufo alvarius*, *Bufo boreas*, *Bufo terrestris*, and *Bufo woodhouseii*.

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Introduction

A physiological response to feeding is an increase in metabolic rate, a phenomenon commonly referred to as specific dynamic action (SDA). In its entirety, SDA represents the accumulated energy expended on the ingestion, digestion, absorption, and assimilation of a meal (Brody 1945; Kleiber 1975). Contributing to SDA are the associated costs of gut motility; production and secretion of acids and enzymes; nutrient transport; and the consequential synthesis of proteins, glycogen, lipids, and excretory products (Webster 1983; Blaxter 1989). These postfeeding responses collectively generate increases in metabolic rates above basal rates ranging from 50% for humans to 100%–800% for invertebrates, fishes, amphibians, reptiles, birds, and other mammals and to as high as 4,400% for the Burmese python (Jobling 1981; Diamond et al. 1985; Westerterp-Plantenga et al. 1992; Janes and Chappell 1995; Secor and Diamond 1997*a*; Secor 2001).

Historic interest in SDA has included its variation with respect to meal composition (Boorsook 1936; Forbes and Swift 1944; Karst et al. 1984), its impact on growth and obesity (Kaplan and Leveille 1976; Vahl 1984), its contribution to thermoregulation (Kleiber 1975; Costa and Kooyman 1984), and its application to quantifying the cost of growth (Brown and Cameron 1991; Wieser 1994). Recent inquires have found SDA to contribute heavily to an animal's energy budget (Secor and Nagy 1994; Peterson et al. 1998), to vary with respect to feeding and digestive strategies (Secor 2001), and to possess rates of oxygen consumption ($\dot{V}O_2$) that exceed maximal oxygen consumption rates ($\dot{V}O_2$max) experienced during locomotion (Andrade et al. 1997; Secor and Diamond 1997*a*; Secor et al. 2000). These findings indicate that SDA may have important ramifications on life-history traits, may be adaptively linked to feeding ecologies and digestive physiology, and may provide a new model to study maximum capacities of tissue aerobic performance independent of exercise. Studies across invertebrate and vertebrate taxa have shown the profile of the SDA response (typically presented as $\dot{V}O_2$ as a function of time postfeeding) and its overall magnitude (quantified in terms of energy) to be influenced by meal, environmental, and/or organismal variables. Acknowledged determinants of the SDA response include meal size (Janes and Chappell 1995; Secor and Diamond 1997*a*), meal type (Secor and Phillips 1997; Hailey 1998), body temperature (Soofiani and Hawkins 1982; Whiteley et al. 2001), and body size (Carefoot 1990*a*; Secor and Diamond 1997*a*).

Given that most studies have focused on the effects of only

Table 1: Body mass, standard metabolic rate (SMR), and six variables of the metabolic response to feeding on four different size rodent meals for the toad *Bufo marinus* at 30°C

	Meal Size (% of Body Size)					
Variables	5	10	15	20	*F*	*P*
n	8	8	8	4	…	…
Body mass (g)	127 ± 12	124 ± 13	126 ± 11	110 ± 12	.25	.859
SMR (mL O_2 h^{-1})	6.20 ± .56	6.31 ± .58	6.14 ± .59	4.79 ± 1.25	.97	.424
SMR (mL O_2 g^{-1} h^{-1})	.053 ± .002	.051 ± .002	.050 ± .004	.044 ± .003	1.36	.279
Peak $\dot{V}o_2$ (mL h^{-1})	19.4 ± 2.5	22.4 ± 3.1	30.8 ± 3.7	30.7 ± 7.2	8.68	.0005
Peak $\dot{V}o_2$ (mL g^{-1} h^{-1})	.152 ± .010	.178 ± .014	.251 ± .022	.283 ± .025	10.6	.0001
Scope (peak $\dot{V}o_2$/SMR)	2.9 ± .2	3.5 ± .2	5.1 ± .4	6.4 ± .4	19.6	<.0001
RER ($\dot{V}co_2/\dot{V}o_2$)	.76 ± .01	.72 ± .01	.75 ± .01	.74 ± .01	2.60	.075
Duration (d)	2	5	5	6	…	…
SDA (kJ)	6.76 ± .90	17.3 ± 3.2	30.9 ± 3.6	40.3 ± 3.4	42.5	<.0001
SDA (kJ kg^{-1})	54 ± 4	132 ± 15	246 ± 20	365 ± 11	67.0	<.0001
SDA coefficient (%)	13.0 ± .9	16.5 ± 1.9	20.5 ± 1.7	22.8 ± .7	7.05	.0015

Note. RER = respiratory exchange ratio; SDA = specific dynamic action. Values are presented as mean ± 1 SE. *F* and *P* values result from ANOVA 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 (percentage ingested energy) and from ANCOVA (body mass as the covariate) for SMR (mL O_2 h^{-1}), peak $\dot{V}o_2$ (mL h^{-1}), and SDA (kJ). RER presented in this table represents the mean of individual RER calculated at peak $\dot{V}o_2$.

one or two determinants of SDA, we examined the impacts of meal size, meal type, body temperature, and body size on the SDA of the marine toad, *Bufo marinus*. In addition, we assessed the relative metabolic demands of digestion for *B. marinus* by comparing its peak postfeeding rates of gas exchange with those maximally experienced during activity. Acknowledging the value of a comparative approach to evaluating physiological variables, we made lateral comparisons of postfeeding metabolic responses of *B. marinus* with those of four other toad species: *Bufo alverius*, *Bufo boreas*, *Bufo terrestris*, and *Bufo woodhouseii*. We selected *B. marinus* as the focal animal of this study because it possesses a varied diet, spans as much as a 5,000-fold range in body mass, and is one of only a few anurans for which SDA has been previously documented (Oliver 1949; Wang et al. 1995; Secor 2001). The objectives of our study were to document and compare the profile, time course, and magnitude of *B. marinus* postfeeding metabolic responses among four meal sizes, four natural diets, and four body temperatures; identify the allometric relationships of body mass with standard metabolic rate (SMR), peak postprandial $\dot{V}o_2$, SDA, and organ masses; examine rates of gas exchange during exercise; and compare postfeeding metabolic responses of *B. marinus* with those of four other species of toads.

Material and Methods

Animals and Their Maintenance

Bufo marinus ranged historically from extreme southern Texas, through Central America, to central Brazil (Zug and Zug 1979). Beginning in the mid-1800s, *B. marinus* was deliberately introduced into many tropical and subtropical regions as a biological control agent for agricultural insect pests, and henceforth became well established in Australia, Pacific and Caribbean islands, and southern Florida (Easteal 1981). *Bufo marinus*, one of the largest toad species in the world, reaching a body mass of over 1 kg, feeds on a diverse diet of plant material, insects, other invertebrates, and small amphibians, reptiles, birds, and mammals (Oliver 1949; Rabor 1952; Krakauer 1968; Jaeger 1976; Zug and Zug 1979). The 55 *B. marinus* used in this study were collected from Dade County in southern Florida and ranged in mass from 2.4 to 265 g. In addition, we studied postprandial metabolic responses of eight *Bufo alvarius* (mean body mass = 161 ± 10 g) collected in central Arizona, five *Bufo boreas* (78.6 ± 10.0 g) collected in southern California, eight *Bufo terrestris* (19.3 ± 1.1 g) collected in central Florida, and eight *Bufo woodhouseii* (23.2 ± 2.1 g) collected in northern Mississippi.

We housed the toads in 60-L plastic storage boxes (three to five toads per box) at 24°–27°C under a photoperiod of 14L : 10D. Containers were elevated at one end such that the water within each container covered half of its floor, allowing toads access to both water and a dry surface. We fed toads crickets, earthworms, or catfood once every 3 d. Before metabolic trials, toads were fasted for a minimum of 10 d to ensure that they had become postabsorptive. We measured body mass of toads following the emptying of their bladder, either voluntarily by the toads or by inserting a smooth glass tube into the cloaca and gently applying pressure to the toad's body. Housing and experiments were conducted with the approval of the University of Mississippi Institutional Animal Care and Use Committee (protocol 99-011).

Measurements of Gas Exchange

We measured $\dot{V}O_2$ and rates of carbon dioxide production ($\dot{V}CO_2$) of toads using closed-system respirometry as described by Vleck (1987) and Secor and Diamond (1997*a*). Toads were placed individually into respirometry chambers (0.7–3 L) and maintained within an environmental chamber at a prescribed target temperature (±0.5°C). Respirometry chambers were constructed with an incurrent and excurrent air port, each attached to a three-way stopcock. We placed a small amount of water into each chamber during metabolic trials to prevent desiccation. For each sampling period, we withdrew a 20-mL sample of air from each chamber, sealed the chamber (closing the incurrent and excurrent stopcocks), and withdrew a second 20-mL gas sample 0.5–1 h later from the reopened excurrent air port. Air samples were pumped (125 mL min^{-1}) through a column of water absorbent (Drierite) into a CO_2 analyzer (CD-3A, AEI Technologies, Pittsburgh, Pa.) and then through a column of Drierite and CO_2 absorbent (Ascarite) and into an O_2 analyzer (S-3A/II, AEI Technologies). We calculated whole-animal (mL h^{-1}) and mass-specific (mL g^{-1} h^{-1}) rates of gas exchange corrected for standard temperature and pressure by equation (9) of Vleck (1987).

We began each metabolic trial by measuring gas exchange rates of fasted toads twice a day for 3 d. We assigned the lowest measure of $\dot{V}O_2$ (and concurrent $\dot{V}CO_2$) from each toad over those 3 d as its SMR (coefficient of variation of fasting measurements averaged 12.7% ± 0.8% for $\dot{V}O_2$ and 11.2% ± 0.7% for $\dot{V}CO_2$). Following SMR measurements, toads were removed from the respirometry chambers and were fed one of the four test meals weighing a predetermined percentage of the toad's body mass. Immediately after feeding, toads were returned to their respirometry chambers, and rates of gas exchange were measured at 12-h intervals (at 0800 and 2000 hours) for up to 3 d and thereafter at 1-d intervals (at 0800 hours) for 2–7 more days. The only exception to this protocol were measurements taken at 6-h intervals for the first day during the trial at 35°C.

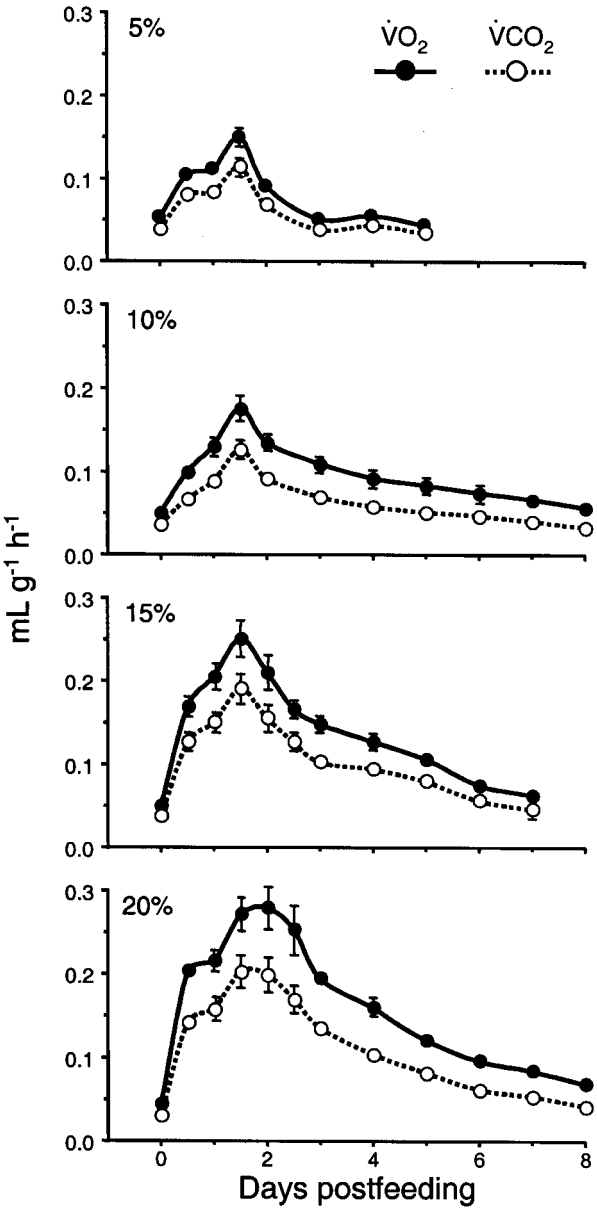

Figure 1. Mean $\dot{V}O_2$ and $\dot{V}CO_2$ (mL g^{-1} h^{-1}) at 30°C of marine toads (*Bufo marinus*) before (day 0) and up to 8 d following the ingestion of rodent meals equaling 5%, 10%, 15%, or 20% of toad body mass; $n = 8$ for 5%, 10%, and 15% meal-size trials, and $n = 4$ for the 20% meal-size trial. Note the increase in the magnitude and duration of the postfeeding metabolic response with increasing meal size. Error bars are ±1 SE and are omitted if the SE is smaller than the symbol for mean value.

Experimental Procedures

We investigated the individual effects of meal size, meal type, body temperature, and body size on the postfeeding metabolic response of toads following four protocols. Effects of meal size were assessed from toads that had consumed, either voluntarily or by force-feeding, juvenile rat (*Rattus norvegicus*) meals weighing 5%, 10%, 15%, or 20% of the toads' body mass and were maintained at 30°C during metabolic measures. Meal-type effects were evaluated by feeding toads one of the following four meals: earthworms (*Lumbricus*), superworms (*Zophobas* larva), crickets (*Acheta domesticus*), or juvenile rats. Meal size was held at 10% of body mass, and toads were maintained at 30°C. Effects of body temperature were investigated at four temperatures: 20°, 25°, 30°, and 35°C. Toads were acclimated to each temperature for 2 d before SMR measurements. Following measurements of SMR, toads were fed juvenile rat meals weighing 10% of the toad's body mass and returned to their

Table 2: Body mass, standard metabolic rate (SMR), and six variables of the metabolic response to feeding on four different meal types equaling 10% of body mass for the toad *Bufo marinus* at 30°C

	Meal Type					
Variables	Earthworm	Superworm[a]	Cricket	Rodent	*F*	*P*
n	8	8	8	8	…	…
Body mass (g)	121 ± 8	116 ± 8	115 ± 11	124 ± 13	.18	.911
SMR (mL O_2 h^{-1})	6.03 ± .43	5.89 ± .53	5.54 ± .39	6.31 ± .58	.29	.831
SMR (mL O_2 g^{-1} h^{-1})	.050 ± .003	.051 ± .003	.051 ± .002	.051 ± .002	.01	.999
Peak $\dot{V}O_2$ (mL h^{-1})	24.8 ± 1.7	24.4 ± 1.9	28.8 ± 2.7	22.4 ± 3.1	5.52	.004
Peak $\dot{V}O_2$ (mL g^{-1} h^{-1})	.206 ± .006	.212 ± .009	.264 ± .015	.178 ± .014	9.40	.0002
Scope (peak $\dot{V}O_2$/SMR)	4.2 ± .3	4.2 ± .2	5.3 ± .4	3.5 ± .2	6.18	.0023
RER ($\dot{V}CO_2/\dot{V}O_2$)	.71 ± .02	.69 ± .01	.70 ± .02	.72 ± .01	.97	.419
Duration (d)	4	7	4	5	…	…
SDA (kJ)	14.2 ± 2.0	28.6 ± 2.3	23.2 ± 2.3	17.3 ± 3.2	21.0	<.0001
SDA (kJ kg^{-1})	116 ± 12	249 ± 18	202 ± 8	132 ± 15	20.9	<.0001
SDA coefficient (%)	36.9 ± 3.7	21.1 ± 1.5	25.2 ± 1.0	16.5 ± 1.9	15.1	<.0001

Note. RER = respiratory exchange ratio; SDA = specific dynamic action. Values are presented as mean ± 1 SE. *F* and *P* values result from ANOVA 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 (percentage ingested energy) and from ANCOVA (body mass as the covariate) for SMR (mL O_2 h^{-1}), peak $\dot{V}O_2$ (mL h^{-1}), and SDA (kJ). RER presented in this table represents the mean of individual RER calculated at peak $\dot{V}O_2$.

[a] *Zophobas* larva.

chambers for the continued measure of postprandial metabolism at the target temperature. Sample size for each meal size, meal type, and body temperature trial was eight toads, with the exception of four toads used in the 20% meal-size trial.

We evaluated body size effects on SMR, peak $\dot{V}O_2$ during digestion, and SDA at 30°C using 37 toads ranging in mass from 2.4 to 265 g that had consumed (voluntarily or force-fed) juvenile rat meals equaling 10% of body mass. In addition, we dissected 54 toads (2.4–265 g) to determine the allometric relationships of the wet and dry masses of the heart, lungs, liver, stomach, small intestine, large intestine, and kidneys. Organs were weighed immediately after their removal from the animal (wet mass), dried to a constant mass at 60°C, and reweighed (dry mass).

To evaluate the relative metabolic demand experienced by toads during digestion, we compared peak postfeeding metabolic rates with those experienced during exercise. We measured $\dot{V}O_2$ and $\dot{V}CO_2$ of 11 toads (108 ± 9 g, range 65–175 g) forced to exercise at 30°C following the procedure of Hillman and Withers (1979). Toads were placed individual in 3.3-L cylindrical respirometry chambers, and rates of gas exchange measured over a 3-min period while the chambers were manually rotated, keeping the toads in constant motion as they attempted to right themselves.

We compared postfeeding metabolic responses of *B. marinus* with those of *B. alvarius* that has consumed juvenile rat meals weighing 5% or 15% of body mass and with *B. boreas*, *B. terrestris*, and *B. woodhouseii* that had consumed cricket meals weighing 10% of body mass. Metabolic trials with *B. alvarius*, *B. boreas*, *B. terrestris*, and *B. woodhousei* were all conducted at 30°C.

For each SDA trial, we quantified the following seven variables as described and illustrated by Secor and Diamond (1997*a*): SMR, the lowest measure of $\dot{V}O_2$ during fasting; peak $\dot{V}O_2$, the 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 exchange ratio (RER), $\dot{V}CO_2$ divided by $\dot{V}O_2$; duration, time from feeding when $\dot{V}O_2$ was no longer significantly greater than SMR (determined from post hoc pairwise mean comparisons explained in Statistical Analysis); SDA, the total energy expended above SMR during 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 calculated SDA (kJ) from the extra O_2 consumed above SMR during the period of significantly elevated $\dot{V}O_2$ assuming 19.8 J of energy expended per milliliter of O_2 consumed (Gessaman and Nagy 1988). We calculated the energy of each meal by multiplying meal wet mass by the energy equivalent of that meal (kJ g^{-1} wet mass) determined by bomb calorimetry. Samples of each meal type were weighed (wet mass), dried, reweighed (dry mass), ground to a fine powder, and pressed into pellets. Three to five pellets of each meal type were ignited in a bomb calorimeter (model 1261, Parr, Moline, Ill.) to determine energy content. For each sample, we determined wet-mass energy equivalent as a product of dry-mass energy equivalent (determined by bomb calorimetry) and the sample's percentage dry mass. Energy equivalent of earthworms, crickets,

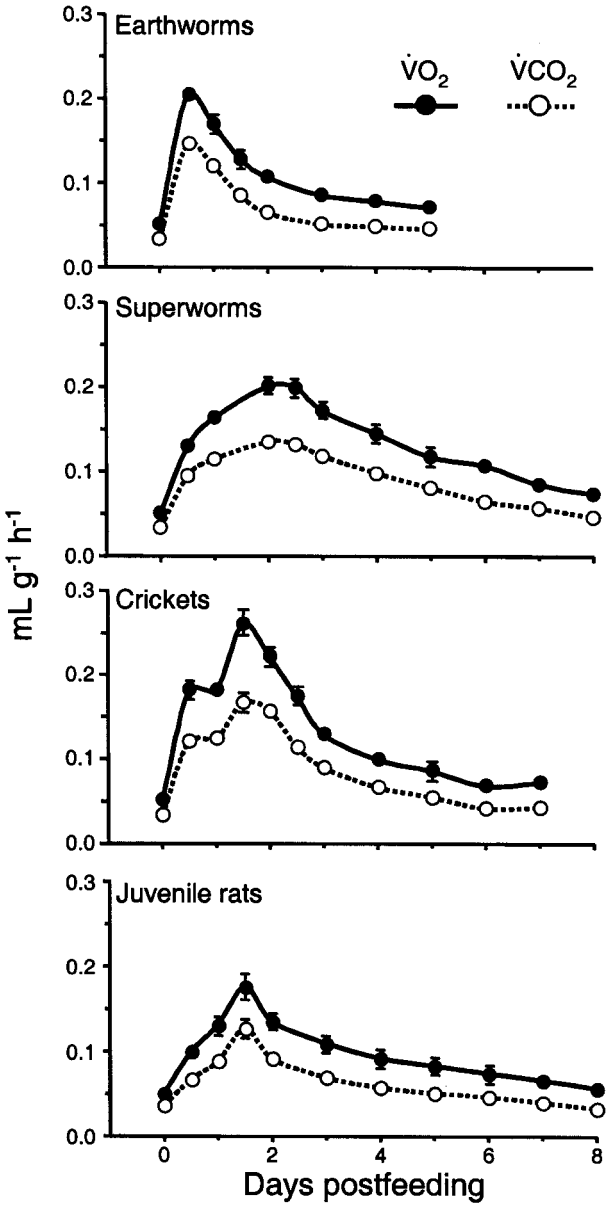

Figure 2. Mean $\dot{V}o_2$ and $\dot{V}co_2$ (mL g^{-1} h^{-1}) at 30°C of marine toads (*Bufo marinus*) before (day 0) and up to 8 d following the ingestion of earthworms, superworms (*Zophobas* larva), crickets, or juvenile rat meals equaling 10% of the toad's body mass; $n = 8$ for all four meal-type trials. Note the distinct differences in postfeeding metabolic profiles among the four meal types. Error bars are ±1 SE and are omitted if the SE is smaller than the symbol for mean value.

juvenile rats, and superworms were 3.2, 8.0, 8.0, and 11.8 kJ g^{-1} wet mass, respectively.

Statistical Analysis

For each SDA trial, we used a repeated-measure design ANOVA to determine whether time (before and after feeding) significantly affected $\dot{V}o_2$ and $\dot{V}co_2$ (either as mL h^{-1} or mL g^{-1} h^{-1}) and RER. We followed each ANOVA with post hoc pairwise mean comparisons (Tukey-Kramer procedure) to determine whether gas exchange rates differed significantly between sampling times. We tested for differences in body mass and metabolic measures among meal sizes, meal types, body temperatures, and toad species, using ANOVA for body mass and mass-specific measures and ANCOVA (body mass entered as a covariate) for whole-animal measures. We likewise employed pairwise mean comparisons to identify whether there were significant differences in measured variables between meal sizes, meal types, body temperatures, and species.

To assess body-size effects, we used least squares regression analysis to determine how SMR, peak $\dot{V}o_2$, scope of peak $\dot{V}o_2$, SDA, SDA coefficient, exercise $\dot{V}o_2$, and the wet and dry masses of each measured organ scaled with body mass. Metabolic data (except for scope of peak $\dot{V}o_2$ and SDA coefficient), body mass, and organ masses were $\log_{10}$ transformed before analysis to linearize relationships and meet the assumptions of variance homoscedasticity (Zar 1974). We assessed possible mass-independent relationships between organ masses and between metabolic measures (SMR, peak $\dot{V}o_2$, and SDA) and organ masses by converting organ masses and metabolic data to mass residuals from double-logarithmic regressions (organ mass or metabolic measure plotted against body mass). Sets of residuals were subjected to correlation analyses to determine the extent of their association. We report the results of ANOVA, ANCOVA, and correlation and regression analyses in terms of their F, r or r^2, and P values and note the P values of significant pairwise mean comparisons. We designate the level of statistical significance as $P < 0.05$ and report mean values as means ± 1 SE.

Results

Effects of Meal Size

Neither body mass nor SMR differed significantly among or between meal-size treatments (Table 1). Both $\dot{V}o_2$ and $\dot{V}co_2$ (quantified either as mL h^{-1} or mL g^{-1} h^{-1}) differed significantly (F values = 23.8–52.7; all P values < 0.0001) among sampling times for each of the four meal sizes (Fig. 1). For each meal size, $\dot{V}o_2$ and $\dot{V}co_2$ increased significantly within 12 h after feeding and peaked either at 1.5 or 2 d postfeeding. Peak $\dot{V}o_2$, as well as its factorial scope over SMR, increased with meal size; each 5% increase in meal size generated an average 23% increase in peak $\dot{V}o_2$. RER ($\dot{V}co_2/\dot{V}o_2$) varied significantly (P values < 0.009) with time during the digestion of the 10% and 20% size meals but did not differ among meal sizes when quantified at peak $\dot{V}o_2$. The duration of elevated rates increased with meal size from 2 d for the 5% meals to 6 d for the 20% meals. Increasing meal size resulted in a corresponding increase in SDA, quantified as kJ or kJ kg^{-1}, and the SDA coefficient. Toads digesting a meal 20% of body mass expended more than

six times the energy than while digesting a meal 5% of body mass.

Effects of Meal Type

Body mass and SMR did not vary significantly among the four meal-type treatments (Table 2). For each meal type, $\dot{V}O_2$ and $\dot{V}CO_2$ differed significantly (F values = 23.8–86.1; all P values < 0.0001) among sampling times, as toads experienced significant (P values < 0.012) increases in $\dot{V}O_2$ and $\dot{V}CO_2$ within 12 h of feeding (Fig. 2). Peak rates of gas exchange occurred at 0.5, 1.5, 1.5, and 2 d postfeeding for toads digesting the earthworm, cricket, rodent, and superworm meals, respectively. Peak postprandial $\dot{V}O_2$ and its factorial scope significantly varied among meal types, being greater during the digestion of crickets than during the digestion of rodents. For each meal, RER differed significantly (F values = 3.73–6.24; P values < 0.0025) among pre- and postfeeding samples. Meal type did not significantly affect RER when quantified at peak $\dot{V}O_2$. Duration of the SDA response was 4 d for the earthworm and cricket meals, extending to 7 d for the superworm meals. Meal type significantly affected SDA, as the digestion of superworms was twice as costly as the digestion of earthworms. However, the SDA coefficient of earthworm meals was more than twice that of the rodent meals.

Effects of Body Temperature

Body mass did not differ among the four body temperature treatment groups, whereas SMR increased significantly (F = 33.6; P < 0.0001) with body temperature (Table 3). For each temperature treatment, $\dot{V}O_2$ and $\dot{V}CO_2$ varied significantly (F values = 13.2–63.3; P values < 0.0001) among sampling times, increasing (P values < 0.012) above SMR within 12 h after feeding (Fig. 3). As body temperature increased, peak $\dot{V}O_2$ and RER (quantified at peak $\dot{V}O_2$) increased, the factorial scope of peak $\dot{V}O_2$ did not change, and the duration of the elevated metabolic response decreased. Over the range of body temperatures investigated (20°–35°C), the Q_{10} of SMR and peak $\dot{V}O_2$ equaled 2.58 and 2.92, respectively. SDA, quantified as kJ or kJ kg^{-1}, and the SDA coefficient did not significantly differ among or between body temperature trials.

Effects of Body Size

Over a 100-fold range in body mass, SMR (mL O_2 h^{-1}) of *Bufo marinus* scaled with a mass exponent of 0.68 ± 0.02, with body mass accounting for 97.7% of the variation in SMR (Fig. 4*A*; Table 4). Peak $\dot{V}O_2$ (mL O_2 h^{-1}) during digestion scaled with a mass exponent of 0.85 ± 0.03 significantly (t = 5.64; P < 0.001) greater than the scaling exponent of SMR (Fig. 4*A*; Table 4). Because peak postprandial $\dot{V}O_2$ increased more steeply than SMR with body mass, the scope of peak $\dot{V}O_2$ (peak $\dot{V}O_2$/SMR) increased with body mass; larger toads possessed greater factorial scopes of peak $\dot{V}O_2$ than did smaller toads.

SDA, calculated as energy expended (kJ), scaled with a mass exponent of 1.02 ± 0.04, which is significantly (P values < 0.001) greater than the scaling exponent of either SMR or peak $\dot{V}O_2$ (Fig. 4*B*; Table 4). Residuals of SDA (kJ) correlated (r = 0.505; P = 0.005) with residuals of peak $\dot{V}O_2$; toads possessing

Table 3: Body mass, standard metabolic rate (SMR), and six variables of the metabolic response to feeding on rodent meals equaling 10% of body mass at four body temperatures for the toad *Bufo marinus*

	Body Temperature					
Variables	20°C	25°C	30°C	35°C	*F*	*P*
n	8	8	8	8	…	…
Body mass (g)	123 ± 13	121 ± 5	124 ± 13	124 ± 10	.02	.997
SMR (mL O_2 h^{-1})	2.21 ± .20	4.32 ± .32	6.31 ± .58	8.91 ± 1.08	33.6	<.0001
SMR (mL O_2 g^{-1} h^{-1})	.018 ± .001	.036 ± .002	.051 ± .002	.071 ± .004	63.4	<.0001
Peak $\dot{V}O_2$ (mL h^{-1})	8.4 ± .9	15.4 ± .9	22.4 ± 3.1	36.4 ± 3.9	35.0	<.0001
Peak $\dot{V}O_2$ (mL g^{-1} h^{-1})	.068 ± .002	.128 ± .007	.178 ± .014	.298 ± .024	45.4	<.0001
Scope (peak $\dot{V}O_2$/SMR)	3.8 ± .2	3.7 ± .3	3.5 ± .2	4.2 ± .3	1.32	.289
RER ($\dot{V}CO_2/\dot{V}O_2$)	.63 ± 0 .02	.65 ± .01	.71 ± .01	.72 ± .01	13.1	<.0001
Duration (d)	9	7	5	2.5	…	…
SDA (kJ)	15.4 ± 1.9	18.6 ± 1.5	17.3 ± 3.2	16.1 ± 1.3	1.07	.379
SDA (kJ kg^{-1})	125 ± 7	155 ± 12	132 ± 15	133 ± 10	1.28	.300
SDA coefficient (%)	15.6 ± .9	19.4 ± 1.5	16.5 ± 1.9	16.6 ± 1.2	1.32	.287

Note. RER = respiratory exchange ratio; SDA = specific dynamic action. Values are presented as mean ± 1 SE. F and P values result from ANOVA 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 (percentage ingested energy) and from ANCOVA (body mass as the covariate) for SMR (mL O_2 h^{-1}), peak $\dot{V}O_2$ (mL h^{-1}), and SDA (kJ). RER presented in this table represents the mean of individual RER calculated at peak $\dot{V}O_2$.

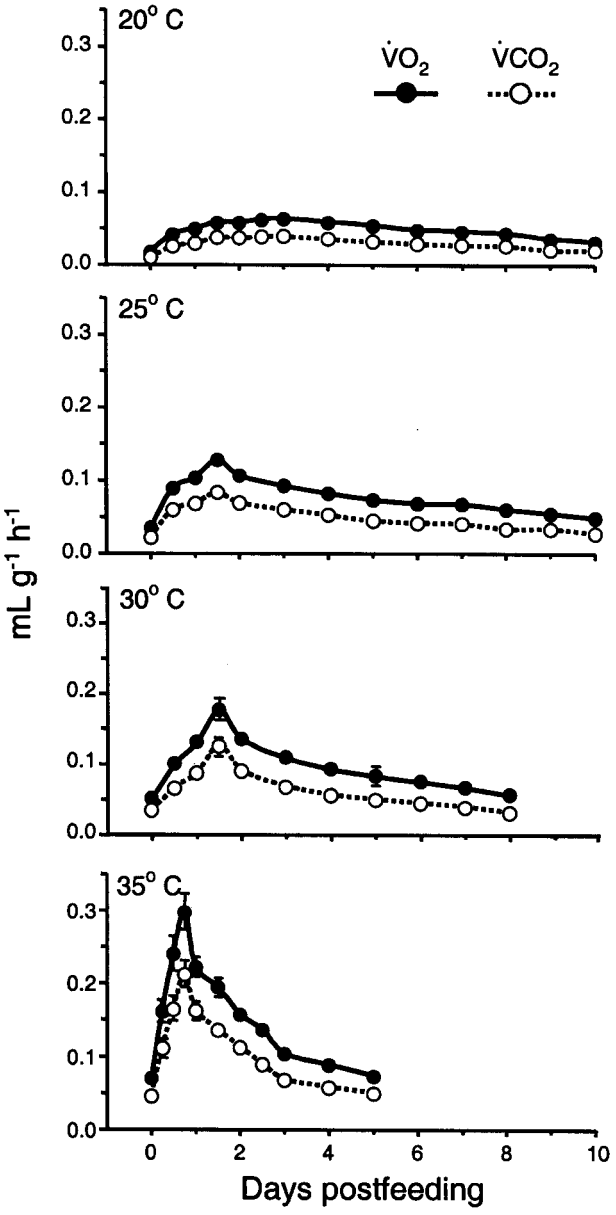

Figure 3. Mean $\dot{V}o_2$ and $\dot{V}co_2$ (mL g^{-1} h^{-1}) of marine toads (*Bufo marinus*) before (day 0) and up to 10 d following the ingestion of rodent meals equaling 10% of body mass and maintained at body temperatures of 20°, 25°, 30°, or 35°C; $n = 8$ for all four temperature trials. Note the postfeeding metabolic profile becoming more elevated and shorter with increasing body temperature. Error bars are ±1 SE and are omitted if the SE is smaller than the symbol for mean value.

higher-than-predicted peak $\dot{V}o_2$ tended to possess higher-than-predicted SDA. SDA coefficient did not vary with body mass and averaged 21.0% ± 1.1% (Fig. 4*C*; Table 4).

Exercise Metabolism

Toads elevated their $\dot{V}o_2$ and $\dot{V}co_2$ while attempting to right themselves during the exercise trials. The maximum recorded $\dot{V}o_2$ and $\dot{V}co_2$ for each of the 11 toads averaged 1.21 ± 0.07 and 1.05 ± 0.05 mL g^{-1} h^{-1}, respectively, representing respective 25-fold and 31-fold increases over SMR and 4.7-fold and 5.9-fold increases over peak postprandial rates (Fig. 5). Exercise $\dot{V}o_2$ scaled with body mass with a mass exponent of 1.17, significantly greater than the scaling exponents of SMR ($t = 2.78$; $P < 0.01$) and peak $\dot{V}o_2$ ($t = 2.68$; $P < 0.02$), but not different from that of SDA (Table 4). RER during exercise (0.88 ± 0.02) was significantly (P values < 0.002) greater than that observed during SMR (0.67 ± 0.02) or at peak $\dot{V}o_2$ (0.67 ± 0.02) during the digestion of rodent meals equaling 10% of body mass.

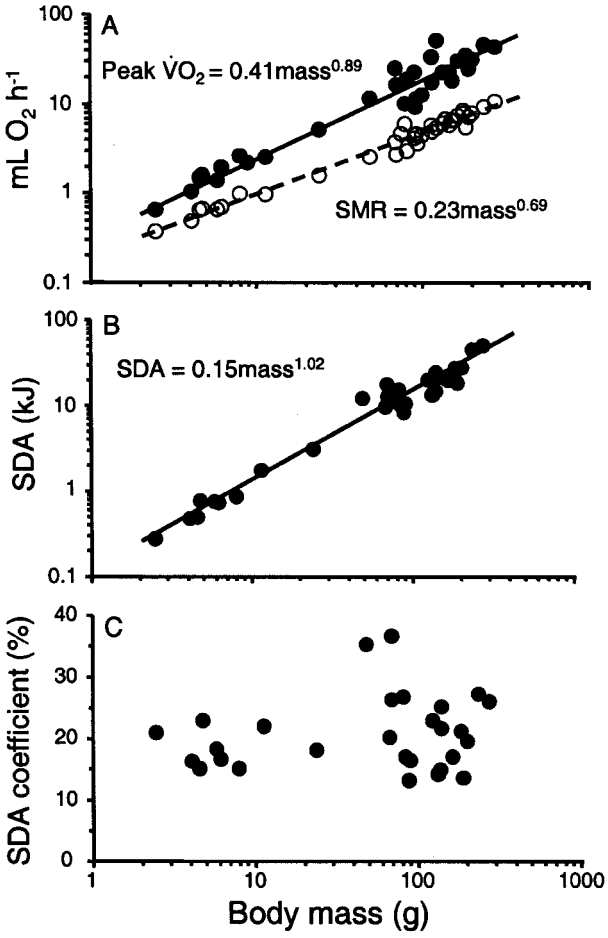

Figure 4. Allometric scaling of standard metabolic rate (SMR) and peak $\dot{V}o_2$ (*A*), specific dynamic action (SDA) quantified in kJ (*B*), and the SDA coefficient (*C*) for 29–37 *Bufo marinus* ranging in body mass from 2.4 to 265 g. Body mass, SMR, peak $\dot{V}o_2$, and SDA (kJ) were $\log_{10}$ transformed before generating allometric equations.

Table 4: Parameters of allometric regressions of standard metabolic rate (SMR), metabolic response to the ingestion of rodent meals equaling 10% of body mass, and exercise metabolism for the toad *Bufo marinus* at 30°C

Dependent Variable	*n*	Mass Coefficient	Mass Exponent	r^2	*F*	*P*
SMR (mL O_2 h^{-1})	37	.23 ± .01	.69 ± .02	.977	1,482	<.0001
Peak $\dot{V}O_2$ (mL h^{-1})	29	.41 ± .02	.85 ± .03	.975	1,073	<.0001
Scope (peak $\dot{V}O_2$/SMR)	29	1.38 ± .37	1.45 ± .21	.643	48.6	<.0001
SDA (kJ)	29	.15 ± .01	1.02 ± .04	.970	871	<.0001
SDA coefficient (%)	29	18.7 ± 3.2	1.37 ± 1.80	.021	.58	.451
Exercise $\dot{V}O_2$ (mL h^{-1})	11	.55 ± .41	1.17 ± .20	.787	33.4	.0003

Note. SDA = specific dynamic action. We $\log_{10}$ transformed body mass, SMR, peak $\dot{V}O_2$, and SDA (kJ), but neither scope nor SDA coefficient, before regression analyses. SMR, peak $\dot{V}O_2$, SDA (kJ), and exercise $\dot{V}O_2$ can be predicted using the equation variable = a(mass)^b, where a is the mass coefficient and b is the mass exponent. Both scope and SDA coefficient can be predicted using the equation variable = b(log mass) + a.

Allometry of Organ Masses and Relationships with Metabolism

Logged wet and dry masses of the lungs, heart, liver, stomach, small intestine, large intestine, and kidneys scale with logged body mass, with mass exponents ranging from 0.72 to 1.09 (Table 5). The combined wet mass of nutritive organs (stomach, liver, small intestine, large intestine, and kidneys) scaled allometrically with a mass exponent of 0.92 ± 0.02. Mass residuals were significantly correlated (r values = 0.299–0.581; P values < 0.03) between the heart and liver and the kidneys and between the stomach and small intestine. We found no correlations between organ wet and dry mass residuals and the residuals of SMR. Significant correlations (r values = 0.447–0.502; P values < 0.043) did exist between residuals of peak $\dot{V}O_2$ and residuals of liver and stomach wet masses and between residuals of SDA and residuals of stomach wet and small intestinal wet and dry masses. Residuals of peak $\dot{V}O_2$ ($r = 0.617$; $P = 0.003$) and SDA ($r = 0.451$; $P = 0.040$) were also correlated with residuals of the combined nutritive organs wet mass (Fig. 6).

Postfeeding Metabolic Response of Bufo alvarius, Bufo boreas, Bufo terrestris, *and* Bufo woodhouseii

Bufo alvarius responded to the ingestion of rodent meals weighing 5% or 15% of toads' body mass with significant (P values < 0.0001) increases in $\dot{V}O_2$ within 12 h after feeding (Fig. 7). For these two size meals, $\dot{V}O_2$ peaked at 1 and 2 d postfeeding at 0.113 ± 0.012 and 0.206 ± 0.006 mL g^{-1} h^{-1}, respectively, with individual peak $\dot{V}O_2$ averaging 3.6- and 6.5-fold of SMR (0.034 ± 0.001 mL O_2 g^{-1} h^{-1}). The duration of the postprandial metabolic response was 3 and 6 d for the 5% and 15% size meals, respectively. SDA averaged 10.4 ± 1.0 kJ and 37.6 ± 2.5 kJ, and the SDA coefficient averaged 15.3% ± 0.7% and 19.5% ± 0.6%, respectively, for the 5% and 15% meals (Table 6).

Bufo boreas experienced significant ($P < 0.001$) increases in $\dot{V}O_2$ within 12 h following the ingestion of cricket meals equaling 10% of the toad's body mass (Fig. 7). $\dot{V}O_2$ peaked at 1.5 d postfeeding at 0.282 ± 0.026 mL g^{-1} h^{-1}, averaging 3.3 times SMR (0.090 ± 0.007 mL O_2 g^{-1} h^{-1}). This toad's elevated response lasted 3 d and culminated in an SDA of 12.7 ± 1.7 kJ, representing an SDA coefficient of 20.2% ± 1.3% (Table 6). Cricket meals induced a 2.4-fold increase ($P < 0.0002$) in $\dot{V}O_2$ within 12 h after feeding for *B. terrestris* (Fig. 7). *Bufo terrestris* postprandial $\dot{V}O_2$ peaked at 1.5 d postfeeding at 0.311 ± 0.019 mL g^{-1} h^{-1}, 2.8 times SMR (0.111 ± 0.004 mL O_2 g^{-1} h^{-1}). The SDA response of *B. terrestris* lasted 3 d at a cost of 3.05 ± 0.14 kJ, generating an SDA coefficient of 20.2% ± 1.2% (Table 6). *Bufo woodhouseii* similarly responded to the 10% cricket meals; $\dot{V}O_2$ increased significantly ($P < 0.0001$) within 12 h and peaked at 1 d at 0.287 ± 0.006 mL g^{-1} h^{-1}, 2.7 times SMR (0.108 ± 0.005 mL O_2 g^{-1} h^{-1}). The duration of elevated $\dot{V}O_2$ for *B. woodhouseii* was 3 d and accounted for

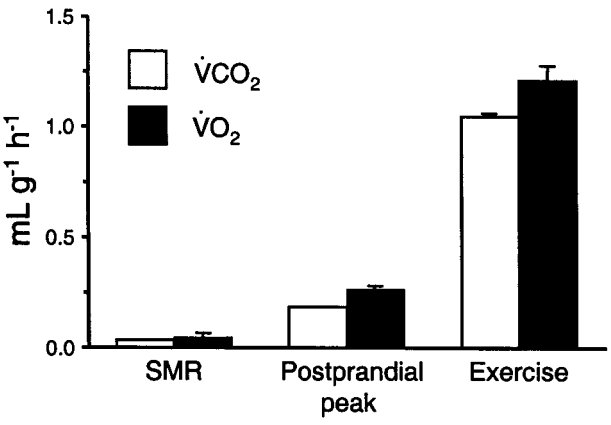

Figure 5. Mean standard metabolic rate (SMR) and peak postprandial and exercise gas exchange rates ($\dot{V}O_2$ and $\dot{V}CO_2$) of 11 *Bufo marinus*. Note that peak postprandial rates of gas exchange average 5.5 times SMR, whereas during exercise, $\dot{V}O_2$ and $\dot{V}CO_2$ have increased by a factor of 25- and 31-fold over SMR, respectively.

Table 5: Parameters of allometric regressions of wet and dry organ masses of the toad *Bufo marinus*

Organ	*n*	Mass Coefficient	Mass Exponent	r^2	*F*	*P*
Lung wet mass	54	.0093 ± .0002	1.01 ± .02	.982	2,864	<.0001
Lung dry mass	54	.0012 ± .0001	1.04 ± .02	.983	3,124	<.0001
Heart wet mass	54	.0058 ± .0002	1.02 ± .02	.971	1,774	<.0001
Heart dry mass	54	.0007 ± .0001	1.09 ± .04	.948	957	<.0001
Liver wet mass	54	.0161 ± .0005	1.06 ± .02	.979	2,420	<.0001
Liver dry mass	54	.0040 ± .0002	1.04 ± .03	.956	1,127	<.0001
Stomach wet mass	54	.0392 ± .0012	.81 ± .02	.961	1,276	<.0001
Stomach dry mass	54	.0080 ± .0003	.75 ± .03	.941	837	<.0001
Small intestine wet mass	44	.0200 ± .0007	.82 ± .02	.964	1,115	<.0001
Small intestine dry mass	40	.0046 ± .0003	.72 ± .04	.914	403	<.0001
Large intestine wet mass	44	.0046 ± .0002	1.02 ± .03	.961	1,044	<.0001
Large intestine dry mass	44	.0010 ± .0001	.93 ± .03	.955	889	<.0001
Kidney wet mass	54	.0083 ± .0004	.97 ± .04	.932	715	<.0001
Kidney dry mass	54	.0013 ± .0001	.98 ± .04	.924	636	<.0001
Nutritive organs wet mass	44	.0848 ± .0020	.92 ± .02	.987	3,312	<.0001
Nutritive organs dry mass	40	.0183 ± .0005	.87 ± .02	.981	1,953	<.0001

Note. We $\log_{10}$ transformed body mass and organ mass data before regression analyses. Organ mass can be predicted using the equation variable $= a(\text{mass})^b$, where *a* is the mass coefficient and *b* is the mass exponent. Nutritive organs include stomach, liver, small intestine, large intestine, and kidneys.

an SDA of 3.31 ± 0.50 kJ and an SDA coefficient of 17.5% ± 1.2% (Table 6).

With a common meal type (rodents) and meal sizes (5% and 15% of body mass) and no significant differences in body mass, we made lateral comparisons between *B. marinus* and *B. alvarius*. Although *B. alvarius* had a significantly (ANCOVA, $P = 0.007$) lower SMR than *B. marinus*, all postprandial metabolic measurements (peak $\dot{V}O_2$, scope, and SDA) did not differ between the two species for either the 5% or 15% size meals. We made similar lateral comparisons among *B. marinus*, *B. boreas*, *B. terrestris*, and *B. woodhouseii* that had consumed cricket meals equaling 10% of body mass. Body mass differed significantly ($F = 43.9$; $P < 0.0001$) among the four species; *B. marinus* averaged six times heavier than *B. terrestris*. SMR (mL h^{-1}), scope of peak $\dot{V}O_2$, and SDA (kJ) varied significantly (*P* values < 0.041) among the four species, whereas peak postprandial $\dot{V}O_2$ (mL h^{-1}), SDA quantified as kJ kg^{-1}, and the SDA coefficient did not significantly differ among species.

Discussion

Bufo marinus exhibits the classic metabolic response to feeding; a rapid increase in gas exchange rates reaching peaks at 1–2 d postfeeding, followed by a slower decline to prefeeding levels. A similar postprandial metabolic profile has been documented for many species, ranging from isopods to humans (Carefoot 1990*b*; Segal et al. 1987). For *B. marinus*, as throughout the animal kingdom, the parameters of SDA are influenced by meal size, meal type, body temperature, and body size. The effect of each of these variables on the postfeeding metabolic response will be discussed, and we conclude by commenting on the evaluation of SDA from a comparative perspective.

Effects of Meal Size, Meal Type, and Body Temperature

A universal phenomena of SDA is that larger meals, either as absolute mass or relative to body mass, generate greater magnitudes of postfeeding responses. Peak $\dot{V}O_2$, the duration of the metabolic response, and overall SDA increase as a function of meal size for invertebrates, fishes, amphibians, reptiles, birds, and mammals (Jobling 1981; LeBlanc and Diamond 1986; Carefoot 1990*a*; Janes and Chappell 1995; Secor and Diamond 1997*a*; Powell et al. 1999). We found *B. marinus* peak $\dot{V}O_2$, scope of peak $\dot{V}O_2$, and SDA (kJ) to increase steadily with each increase in meal size. Whereas peak $\dot{V}O_2$ may plateau with increasing meal size for some fishes (Jobling and Davies 1980), a linear increase in peak $\dot{V}O_2$ with meal size appears to be more common (Soofiani and Hawkins 1982; Andrade et al. 1997; Secor and Diamond 1997*a*; Powell et al. 1999). *Bufo marinus* exhibited the characteristic linear relationship between meal energy and SDA (kJ), as previously documented for the turtle *Kinixys spekii* and the lizard *Varanus albigularis* (Secor and Phillips 1997; Hailey 1998). Combining all rodent-meal trials, *B. marinus* SDA (kJ) can be described by the equation, SDA (kJ) = 0.22(kJ ingested) − 2.44 ($r^2 = 0.84$; $P < 0.0001$; Fig. 8). For *B. marinus*, the largest meal, 20% of body mass, appeared to be the largest that toads were physically capable of consuming

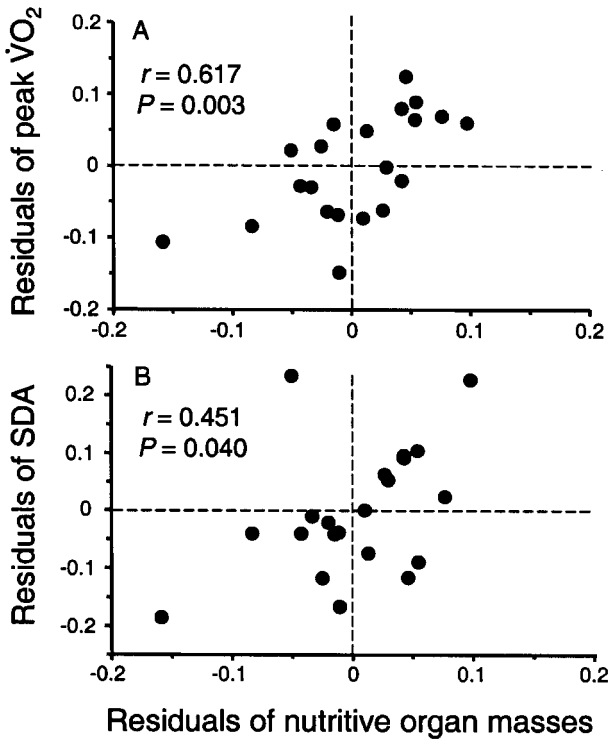

Figure 6. Residuals of individual variation in peak $\dot{V}O_2$ (*A*) and specific dynamic action (SDA) quantified in kJ (*B*) resulting from the digestion of rodent meals equaling 10% of body mass plotted against residuals of individual variation in the combined wet mass of nutritive organs for *Bufo marinus* ($n = 21$). Residuals were obtained from $\log_{10}$-$\log_{10}$ regressions of peak $\dot{V}O_2$, SDA, or combined organ masses on body mass, thereby correcting for effects of body mass. Note that the residuals of peak $\dot{V}O_2$ and SDA are significantly correlated with the residuals of nutritive organ masses.

(several toads regurgitated this meal). Therefore, it is unlikely that $\dot{V}O_2$ would plateau because meal size could not be further increased. SDA quantified, as a percentage of meal energy, the SDA coefficient, also increased with meal size, as observed for several fish species and the snake *Python molurus* (Soofiani and Hawkins 1982; Chakraborty et al. 1992; Secor and Diamond 1997*a*). In contrast, meal size had no significant influence on this measure of SDA for several other fish species, the frog *Ceratophrys cranwelli*, and the snake *Crotalus durissus* (Tandler and Beamish 1980; Ross et al. 1992; Andrade et al. 1997; Powell et al. 1999). One possible explanation for the disproportionately greater cost of digesting larger meals is the added recruitment of intestinal nutrient transporters (and other cellular activities) with larger meals, as observed for *P. molurus* (Secor and Diamond 1997*b*).

Meal composition (relative content of protein, carbohydrates, and fats) has well-established effects on the SDA response (Rubner 1902; Lusk 1931; Forbes and Swift 1944). Studies, largely with fishes and humans, have shown that increasing protein content of a meal invokes a greater peak $\dot{V}O_2$, longer duration of the metabolic response, and an elevated SDA (Jobling and Davies 1980; Nair et al. 1983; Ross et al. 1992). Whereas many of these studies used artificial diets, we assessed the effects of different natural diets, varying in mass-specific energy con-

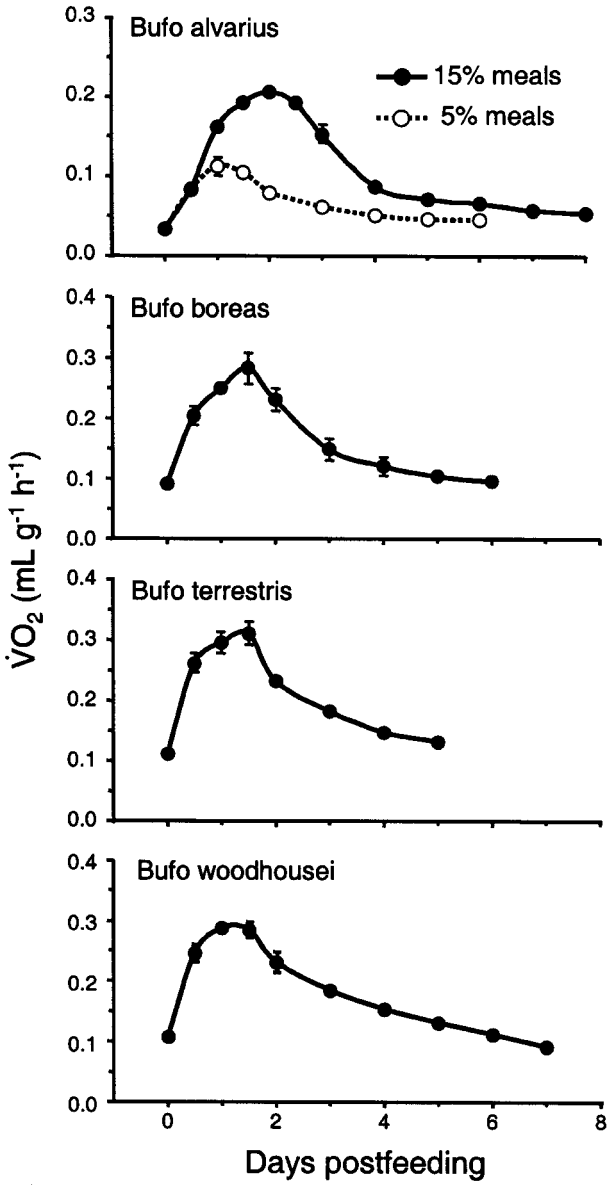

Figure 7. Profiles of the postfeeding metabolic response ($\dot{V}O_2$ as mL g^{-1} h^{-1}) of the toads *Bufo alvarius*, *Bufo boreas*, *Bufo terrestris*, and *Bufo woodhouseii*. *Bufo alvarius* ($n = 8$) consumed rodent meals equaling 5% and 15% of body mass, whereas *B. boreas* ($n = 5$), *B. terrestris* ($n = 8$), and *B. woodhouseii* ($n = 8$) consumed cricket meals equaling 10% of body mass. Error bars are ± 1 SE and are omitted if the SE is smaller than the symbol for mean value.

Table 6: Body mass and temperature, meal type and size (percentage of body mass), factorial scope of postfeeding $\dot{V}O_2$ (peak $\dot{V}O_2$/standard metabolic rate), specific dynamic action (SDA), and SDA coefficient for five species of toads (*Bufo*) and six other anuran species

Species	Body Mass (g)	Body Temperature (°C)	Meal Type	Meal Size (%)	Scope	SDA (kJ)	SDA (kJ kg^{-1})	SDA Coefficient (%)	Source
Bufo alvarius	163	30	Rodent	5	3.6	10.4	65	15.3	This study
B. alvarius	161	30	Rodent	15	6.5	37.6	235	19.5	This study
Bufo boreas	78.6	30	Cricket	10	3.3	12.7	161	20.2	This study
Bufo marinus	127	30	Rodent	5	2.9	6.76	54	13.0	This study
B. marinus	126	30	Rodent	15	5.1	30.9	246	20.5	This study
B. marinus	115	30	Cricket	10	5.3	23.2	202	25.2	This study
B. marinus	293	24	Peptone[a]	.3	1.0	4.14[b]	14.1[b]	23.0[b]	Wang et al. 1995
Bufo terrestris	19.3	30	Cricket	10	2.9	3.05	161	20.2	This study
Bufo woodhouseii	23.2	30	Cricket	10	2.8	3.31	139	17.5	This study
B. woodhouseii	82	23	Cricket/ mealworm	5	1.7				Sievert and Bailey 2000
Hyla cadaverina	3.4	30	Cricket	10	2.8	.2	63	9.9	Secor 2001
Hyla regilla	2.4	30	Cricket	10	2.6	.2	64	9.8	Secor 2001
Ceratophrys cranwelli	19.3	20	Rodent	~15[b]	2.5[b]	2.29	119[b]	9.0	Powell et al. 1999
C. cranwelli	13.1	25	Rodent	~20[b]	3.2[b]	2.63	201[b]	11.5	Powell et al. 1999
C. cranwelli	23.2	30	Rodent	~15[b]	4.0[b]	3.89	168[b]	12.1	Powell et al. 1999
Ceratophrys ornata	149	30	Rodent	15	8.7	38.8	254	21.1	Secor 2001
Pyxicephalus adspersus	225	30	Rodent	15	8.0	59.9	266	22.2	Secor 2001
Rana catesbeiana	296	30	Rodent	15	4.6	59.8	202	16.8	Secor 2001
R. catesbeiana	445	22	Rodent	10	2.9[b]				Busk et al. 2000

[a] Peptone consists of a commercial mixture of free amino acids and peptides (Sigma, St. Louis, Mo.).
[b] Listed values were estimated from figures and tables presented in the source article.

tent and structure, on toad SDA. Intuitively, the cost of digesting a meal could be a function of the difficulty of mechanically and chemically breaking down that meal. Predictably, meals entering the stomach intact and/or possessing a strong structure (e.g., chitinous exoskeleton) would require more enzymes, acids, and mechanical churning than fragmented and/or soft-bodied meals before passing into the small intestine. With meal size held constant, the higher cost of digesting crickets or superworms for *B. marinus* may reflect a greater effort by the stomach to break down intact meals possessing a chitinous exoskeleton. In contrast, soft-bodied earthworms and rodents (usually cut to achieve a specific targeted meal size) were digested at a lower cost. Similarly, the digestion of chitinous millipedes was more costly than the digestion of either leaves or fungi for the turtle *K. spekii* (Hailey 1998). The monitor lizard *V. albigularis* exhibited greater metabolic responses following the ingestion of intact rodents than after the ingestion of shelled hard-boiled eggs (Secor and Phillips 1997).

Body temperature impacts the profile of the postprandial metabolic response, having its largest influence on SMR, peak $\dot{V}O_2$, and duration. An increase in body temperature generates corresponding increases in SMR and peak $\dot{V}O_2$ and a decrease in the duration of the response for invertebrates, fishes, amphibians, and reptiles (Soofiani and Hawkins 1982; Bear 1992; Kalarani and Davies 1994; Powell et al. 1999). As illustrated in Figure 3, the metabolic profile at 20°C is flat and prolonged, but it becomes more elevated and shorter with each 5°C increase in body temperature. The decreased duration of the metabolic response with increasing body temperature is likely attributed to a corresponding increase in the rate of digestion. For the green treefrog, *Hyla cinerea*, a 10°C increase in body temperature (25°–35°C) increases the rate of digestion by 43% (Freed 1980). For *B. marinus* starting at 20°C, each 5°C increase in body temperature shortens the duration of the postprandial metabolic response by 2 d.

In spite of the temperature effects on several metabolic measures, SDA, quantified as kJ or kJ kg^{-1}, and the SDA coefficient were not significantly altered by temperature (Table 3). Likewise, body temperature did not significantly influence SDA for either the fish *Pleuronectes platessa* or the frog *C. cranwelli* (Jobling and Davies 1980; Powell et al. 1999). These findings indicate that, irrespective of body temperature and, therefore, the speed of digestion, digestion of a given meal requires a fixed amount of energy. At a lower body temperature, the same total amount of acid and enzyme secretion, motility, absorption, and assimilation seems to occur, but at a slower pace. Understand-

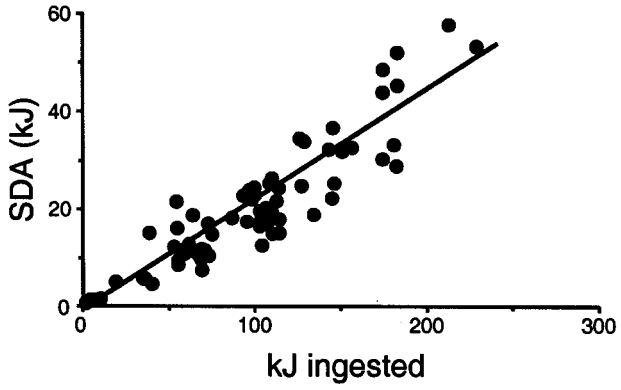

Figure 8. Specific dynamic action (SDA; kJ) plotted against ingested energy (kJ) for all rodent-meal trials of *Bufo marinus* in this study. SDA can be explained as a function of ingested energy by the equation SDA (kJ) = 0.22(kJ ingested) − 2.44.

ably, digestion can only precede within a species-specific range of body temperatures; above that temperature range the animal becomes thermally stressed, whereas below the mechanisms of digestion occur too slowly to allow adequate processing of the meal. For the tropical *B. marinus*, digestive performance may become compromised at temperatures of 15° and 40°C (outside the experimental range of this study).

Allometry of Fasting and Digestive Metabolism

For 14 species of anurans at 30°C (from Table 12.1 of Gatten et al. 1992), the interspecific mass exponent for resting metabolic rate is 0.68 (95% CI = 0.58–0.78), a value almost identical to the intraspecific mass exponent of 0.69 for *B. marinus* SMR. Allometric scaling exponents of peak $\dot{V}O_2$ include 0.90 for *P. molurus* (Secor and Diamond 1997*a*) and 0.89 for seven python species (Thompson and Withers 1999), neither of which differ significantly from that of 0.85 for *B. marinus*. For anurans, elevated rates of metabolism are more commonly studied during locomotion or calling. For the toads *B. alvarius*, *B. boreas*, *B. cognatus*, and *B. retiformis*, intraspecific allometric mass exponents of maximal rates of oxygen consumption ($\dot{V}O_2$max) during strenuous exercise ranged from 0.75 to 0.90 (Hillman and Withers 1979); for 17 species of anurans, $\dot{V}O_2$max scaled with an interspecific mass exponent of 0.91 (Taigen et al. 1982). None of these scaling exponents significantly differed from the scaling of *B. marinus* peak $\dot{V}O_2$. For the treefrogs *Hyla arborea* and *Hyla versicolor*, $\dot{V}O_2$ during calling (averaging 24-fold and 13-fold of $\dot{V}O_2$ at rest, respectively) scaled with respective mass exponents of 0.88 and 1.16 (calculated from Table 1 of Grafe and Thein 2001 and Table 1 of Taigen and Wells 1985), similar to the respective scaling of peak postprandial $\dot{V}O_2$ and exercise $\dot{V}O_2$ of *B. marinus*. As observed for *P. molurus* (Secor and Diamond 1997*a*), peak postprandial $\dot{V}O_2$ of *B. marinus* scaled with a higher mass exponent than SMR; therefore, the factorial scope of peak $\dot{V}O_2$ increases with body size. Evidently, the factorial scope of elevated metabolism, occurring during digestion, exercise, or calling, increases with body size.

The allometric exponent of SDA (kJ) is almost identical for *B. marinus* (1.02) and *P. molurus* (1.01; Secor and Diamond 1997*a*). Whereas a similar scaling relationship was noted for python small intestinal mass (1.02), suggestive of a causal relationship between gut mass and SDA (Secor and Diamond 1997*a*), we found toad stomach and small intestinal masses to scale with significantly lower mass exponents (0.72–0.82; Table 5). Even the combined wet or dry masses of the nutritive organs scaled with a lower exponent (P values < 0.001) than SDA. We did find that peak $\dot{V}O_2$ and combined nutritive organ mass scaled similarly and that residuals of nutritive organ mass, peak $\dot{V}O_2$, and SDA are correlated (toads with larger-than-predicted gut organ masses also possessed larger-than-predicted peak $\dot{V}O_2$ and SDA), therefore suggesting the existence of a causal link between gut mass (and thus metabolic performance) and the magnitude of postprandial metabolism.

Across animal taxa, interspecific allometric relationships have been presented for SMR, basal metabolic rates, field metabolic rates, active metabolic rates, and $\dot{V}O_2$max (Kleiber 1975; Taylor et al. 1981; Andrews and Pough 1985; Bennett and Harvey 1987; Nagy 1987). It has been theorized and shown that interspecific scaling relationships are generally greater than intraspecific allometries (Heusner 1982; Andrews and Pough 1985; Chappell and Ellis 1987). We introduce an interspecific scaling of SDA by plotting the SDA of six anuran species digesting cricket meals 10% of body mass at 30°C against body mass (Fig. 9). Interspecifically, SDA scaled with a mass exponent ($\log_{10}$-$\log_{10}$ re-

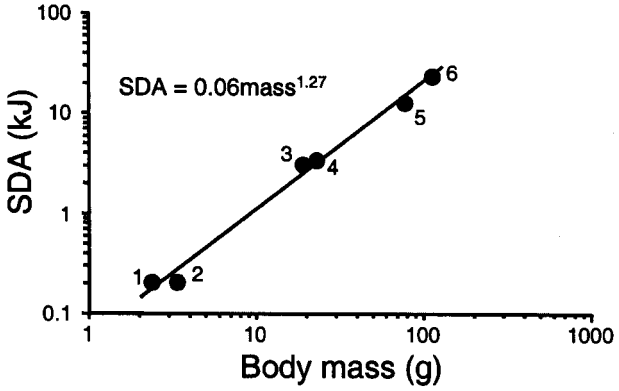

Figure 9. Interspecific allometric relationship of SDA generated from six anurans species digesting cricket meals equaling 10% of body mass at 30°C. Numbers signify the following species: 1, *Hyla regilla*; 2, *Hyla cadaverina*; 3, *Bufo terrestris*; 4, *Bufo woodhousei*; 5, *Bufo boreas*; and 6, *Bufo marinus*. Data are from this study and Secor (2001).

gression) of 1.27 ($r^2 = 0.99$; $P < 0.0001$), significantly (P values < 0.001) greater than the intraspecific exponents of 1.02 for *B. marinus* and 1.01 for *P. molurus*.

Interspecific Evaluation of SDA

Finding that meal size, meal type, body temperature, and body size each significantly impact the SDA response emphasizes the importance of controlling and standardizing variables when undertaking a comparative evaluation of SDA. This is especially relevant when comparing published accounts of SDA: Close attention must be paid to the methods, controls, and features of the meals and animals of each study. In addition to the established effects of meal size and type and animal size and feeding habits, even subtle differences among individual meals (e.g., one large food item vs. several small food items) and animals (e.g., originating from different populations, or wild-caught vs. captive raised) may contribute to the variation in postprandial metabolic measures.

It has been popular in SDA studies to report the SDA coefficient–SDA expressed as a percentage of the ingested (or absorbed) energy (Jobling and Davies 1980). This quantifier of SDA can serve to reduce some of the inherent variation in the magnitude of the SDA response caused by differences in meal size and composition and animal size and type. A review of the SDA of 31 species of amphibians and reptiles found SDA coefficients to range from 4% to 33%, with a characteristic lower coefficient (mean 15% ± 1%) for frequently feeding species and higher coefficient (23% ± 2%) for infrequently feeding species (Secor 2001). In that review (independent of feeding habits) and in this study, it is apparent that the SDA coefficient is significantly impacted by meal size and type.

Meal size and type effects both the numerator (SDA) and denominator (meal energy) in calculating the SDA coefficient. SDA varies with the ease or difficulty of digesting and absorbing a meal, and meal energy is a product of meal size and its mass-specific energy content (kJ/g). Therefore, meals difficult to digest (incurring a high SDA) but low in energy will generate a high SDA coefficient relative to a high-energy meal that is easily digested. The twofold difference in SDA as a percentage of ingested energy between *B. marinus* digesting rodents (16.5% ± 1.9%) and digesting earthworms (36.9% ± 3.7%) is not caused by difference in the cost of digestion (17.3 vs. 14.2 kJ) but, rather, by differences in the energy content of the meals (99.7 vs. 38.1 kJ), as rodents are 2.5 times more energy rich than earthworms. In contrast, the 53% greater SDA coefficient for *B. marinus* digesting crickets compared with digesting rodents likely results from crickets being more costly to digest (23.2 ± 2.3 kJ) than rodents (17.3 ± 3.2 kJ), given that they both have equal energy content (8 kJ g^{-1} wet mass).

A growing consensus is that meal size and type and body size and temperature significantly affect an individual's postprandial metabolism and SDA. Large and/or hard-to-digest meals require more energy and time to break down and absorb than small and/or easy-to-digest meals. Increasing body temperature shortens the postprandial profile, whereas increasing body mass elevates the factorial scope of peak postprandial $\dot{V}O_2$. Therefore, the design of any experiment to characterize and compare SDA must consider all of these determinants. This approach is valuable if SDA is to be modeled for incorporation into an energy budget (Beaupre et al. 1993). SDA has been previously estimated to contribute to 19%, 40%, and 43% of the daily energy expenditure of free-ranging coachwhips (*Masticophis flagellum*), garter snakes (*Thamnophis sirtalis*), and sidewinders (*Crotalus cerastes*), respectively (Secor and Nagy 1994; Peterson et al. 1998). Therefore, models should include meal type and size, daily body temperature profiles, and body size if they are to accurately define SDA and its contribution to an individual's energy budget.

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