Determinants and modeling of specific dynamic action for the Common Garter Snake (*Thamnophis sirtalis*)

Scott M. Bessler, Mary C. Stubblefield, G.R. Ultsch, and Stephen M. Secor

Abstract: Specific dynamic action (SDA), the cumulative energy expended on digestion and assimilation, can contribute significantly to individual daily energy expenditure (DEE). The Common Garter Snake (*Thamnophis sirtalis* (L., 1758)) is a widely distributed generalist predator that could experience considerable variation in SDA and hence the contribution of SDA to DEE. We examined the effects of meal size, meal type, and body temperature on the postprandial metabolic response and SDA of the Eastern Garter Snake (*Thamnophis sirtalis sirtalis* (L., 1758)) and generated predictive models of SDA based on meal size, body mass, and body temperature, and separately based on meal energy. Postprandial peak in oxygen consumption, duration of significantly elevated oxygen consumption, and SDA increased with increasing meal size (5%–45% of body mass). Postprandial metabolic response digesting six different equal-size prey items varied significantly; vertebrate prey generated larger SDA responses than soft-bodied invertebrates. Increases in experimental temperature (15–35 °C) yielded a matched increase in postprandial peak in oxygen consumption and decrease in digestive duration. For a 1-month hypothetical feeding history for an adult *T. sirtalis*, the cumulative predicted SDA varied by 4.5% among the three models (minimal, intermediate, and maximal intake of prey) and averaged 8%, 22%, and 38% of DEE, respectively.

Résumé : L'action dynamique spécifique (SDA), soit l'énergie cumulative dépensée pour la digestion et l'assimilation, peut contribuer significativement à la dépense journalière d'énergie (DEE) individuelle. La couleuvre rayée commune (*Thamnophis sirtalis* (L., 1758)) est un prédateur généraliste à vaste répartition qui pourrait connaître une importante variation de la SDA et donc de la contribution de la SDA à la DEE. Nous avons examiné les effets de la taille du repas, du type de repas et de la température corporelle sur la réponse métabolique postprandiale et sur la SDA chez la couleuvre rayée de l'est (*Thamnophis sirtalis sirtalis* (L., 1758)) et avons mis au point des modèles prédictifs de la SDA basés sur la taille du repas, la masse corporelle et la température du corps et basés séparément sur l'énergie du repas. Il y a une relation positive entre le pic postprandial de consommation d'oxygène, la durée de la consommation d'oxygène significativement élevée et la SDA, d'une part, et la taille du repas (5 % – 45 % de la masse corporelle), d'autre part. La réponse métabolique postprandiale varie significativement lors de la digestion de six proies différentes de tailles semblables : les vertébrés produisent des réponses de SDA plus importantes que les invertébrés à corps mou. Des accroissements de la température expérimentale (15–35 °C) entraînent des augmentations correspondantes de la consommation d'oxygène maximale postprandiale et une réduction du temps de digestion. Au cours d'une séquence hypothétique d'alimentation d'un mois chez un adulte de *T. sirtalis*, les valeurs de SDA cumulative prédites varient de 4,5 % entre les trois modèles (ingestion minimale, moyenne et maximale de proies) et atteignent en moyenne respectivement 8 %, 22 % et 38 % de la DEE.

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Introduction

Food ingestion and assimilation is a required prerequisite for survival, growth, and reproduction. Whereas feeding results in a gain of energy, it is also accompanied by a mandatory expenditure of energy to fuel the breakdown of the meal and the absorption and assimilation of its components (Brody 1945; Kleiber 1975). The cumulative cost of all activities involved in the digestion and assimilation of a meal is commonly referred to as specific dynamic action (SDA; Jobling and Davies 1980). This postprandial response generally constitutes a 25%–200% increase in an individual's metabolic rate (Secor 2009). Although SDA varies tremendously among organisms, it tends to be equivalent to 10%–20% of the meal's energy (Secor 2009). Given that apparent assimilation efficiencies range between 70% and 85% of ingested meal energy, SDA is therefore equal to 12%–30% of available metabolizable energy and hence can be a significant component of an organism's energy budget (Smith 1976; Moors 1977; Barton and Houston 1993; Andrade et al. 1997; Sturm and Horn 1998). This point is exemplified for several species of free-ranging snakes for which SDA contributes to 16%–43% of their daily energy expenditure (DEE) during the activity season (Secor and Nagy 1994; Peterson et al. 1998; Christian et al. 2007).

SDA is significantly affected by meal characteristics and environmental factors (for reviews see McCue 2006, Secor 2009). Larger and (or) tougher food items generate larger SDA responses compared with smaller and (or) softer meals (Janes and Chappell 1995; Secor and Diamond 1997; Hailey

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1998; Fu et al. 2005; Secor and Boehm 2006; Secor et al. 2007). For ectotherms, variation in environmental temperatures, and thus in body temperatures, also significantly effect the SDA response (Wang et al. 2003; Secor et al. 2007; Luo and Xie 2008). Therefore, a species with a generalist food habit that feeds on prey of various sizes and structure, and which possesses a broad geographic range, may experience considerable variation both in its SDA and the contribution of the SDA to its energy budget. In addition, variation in the cost of meal digestion and assimilation may underlie the selection of prey type and size, and the environmental temperatures to digest the meal to maximize net energy gain (Britt et al. 2006).

To examine the determinants of SDA and their influence on the energy budget of a generalist ectothermic predator with a broad geographic range, we quantified the SDA responses of the Eastern Garter Snake (*Thamnophis sirtalis sirtalis* (L., 1758)) across a range of meal sizes, prey types, and body temperatures. With respect to each of these variables, we hypothesized for the Common Garter Snake (*Thamnophis sirtalis* (L., 1758)) that (*i*) SDA would increase with meal size, (*ii*) prey of greater structural integrity would generate larger SDAs than soft-bodied prey, and (*iii*) that while the duration of the SDA response would decrease with increasing body temperature, total SDA would not differ among body temperatures. We developed from these analyses predictive equations of SDA of *T. sirtalis* based on body mass, meal mass, body temperature, or meal energy. Applying field data on snake mass, body temperature, meal mass, and feeding frequency to these equations can provide estimates of the energy expended on digestion and assimilation for free-ranging *T. sirtalis*. Such estimates can be incorporated into a long-term energy budget or be used to determine the contribution of SDA to DEE.

Materials and methods

Snakes and their maintenance

Given its broad geographic and altitudinal range (sea level to 2540 m), *T. s. sirtalis* inhabits a variety of habitats and encounters a wide continuum of environmental temperatures (Rossman et al. 1996). In southern Florida, it is active yearround, whereas in the northern parts of its range, it can be active at colder temperatures (10 °C) and spends from late fall to early spring hibernating (Rossman et al. 1996). *Thamnophis sirtalis* is an active forager, feeding on a wide array of invertebrate and vertebrate prey that include earthworms, leeches, fishes, larval and adult anurans, salamanders, birds, and small mammals (Wright and Wright 1957; Rossman et al. 1996). An individual meal size may range from a small tadpole (~1% of body mass) to a fish, frog, or rodent that may exceed 25% of the snake's body mass. *Thamnophis sirtalis* has also been documented to experience both ontogenetic and seasonal shifts in diet (Rossman et al. 1996).

The 20 *T. sirtalis* (45.1 ± 2.2 g; mean ± SE) used in this study were wild caught in Wisconsin and shipped to the University of Alabama. We housed snakes communally in 60 L plastic containers (3–4 snakes per container) at 24–27 °C, exposed to a photoperiod of 14 h light : 10 h dark. Snakes were fed golden shiners (*Notemigonus crysoleucas* (Mitchill, 1814)) weekly, with water available ad libitum. Prior to metabolic measurements, individuals were fasted for a minimum of 2 weeks to ensure that they were postabsorptive. All animal care and experimentation was conducted with approval from the University of Alabama Institutional Animal Care and Use Committee.

Measurements of gas exchange

We measured rates of oxygen consumption ($\dot{V}O_2$) and carbon dioxide production ($\dot{V}CO_2$) of snakes fasted for 2 weeks to 1 month using closed-system respirometry (Vleck 1987; Secor and Faulkner 2002). Snakes were placed individually into respirometry chambers (0.5–1.5 L) fitted with an incurrent and excurrent air port, each connected to a three-way stopcock. Respirometry chambers were placed into an environmental chamber (model DS54SD; Powers Scientific, Pipersville, Pennsylvania, USA) and maintained at a constant target temperature (±0.5 °C). Between measurements, air was constantly pumped through the respirometry chambers. For each measurement trial, a 45 mL air sample was drawn from each chamber's excurrent air port, both ports were then closed, and 1–2 h later, a second 45 mL air sample was drawn from the reopened excurrent air port. Air samples were pumped (75 $mL \cdot min^{-1}$) through a column of water absorbent (Drierite; W.A. Hammond, Xenia, Ohio, USA) and CO_2 absorbent (Ascarite; Thomas Scientific, Swedesboro, New Jersey, USA) into an O_2 analyzer (S-3A/II; AEI Technologies, Pittsburgh, Pennsylvania, USA) and through water absorbent into a CO_2 analyzer (CD-3A: AEI Technologies). We calculated whole animal ($mL \cdot h^{-1}$) and mass-specific ($mL \cdot g^{-1} \cdot h^{-1}$) rates of gas exchange corrected to standard pressure and temperature using a modification of eq. 9 of Vleck (1987).

$\dot{V}O_2$ and $\dot{V}CO_2$ were determined at 12 h intervals for three consecutive days. For each snake, the mean value of the two lowest recorded $\dot{V}O_2$ (and accompanying $\dot{V}CO_2$) was assigned its standard metabolic rate (SMR). Following SMR determination, snakes were fed a particular meal type equal in mass to a targeted percentage of their body mass. Soon after feeding, snakes were returned to their respirometry chambers within the environmental chamber and measurements of gas exchange were resumed that evening and continued at 12 h intervals for 3 days and thereafter at 1 day intervals for 3–7 more days until prefeeding SMR levels were reached.

Experimental procedure

We determined individual effects of meal size, meal type, and body temperature on the postprandial metabolic response and SDA of *T. sirtalis* using the following protocols. Meal-size effects were investigated by feeding a meal of golden shiners that was equal in mass to a targeted percentage (5%, 15%, 25%, 35%, or 45%) of the snake's body mass. Sample size of each meal-size trial was 5–8 and trials were conducted at 30 °C. The meal-type effects were explored by feeding snakes (6–8 per trial) one of the following six meals; larval beetles (Scarabaeidae), earthworms (*Lumbricus terrestris* L., 1758), tadpoles of Bronze Frog (*Lithobates clamitans* (Latreille in Sonnini de Manoncourt and Latreille, 1801)), Bronze Frogs, golden shiners, and neonate house mice (*Mus musculus* (L., 1758)). Meal mass for each meal type was equivalent to ~25% of snake body mass and metabolic measurements were conducted at 30 °C. Body-

Table 1. Wet mass, dry mass, percent dry mass, and energy content of six different meal types fed to the Common Garter Snake (*Thamnophis sirtalis*) to characterize their postprandial metabolic response and quantify specific dynamic action.

		Mass			Energy	
Meal type	*n*	Wet (g)	Dry (g)	Dry (%)	Dry mass ($kJ \cdot g^{-1}$)	Wet mass ($kJ \cdot g^{-1}$)
Larval beetle (Scarabaeidae)	16	2.55±0.10	0.49±0.03	19.1±0.7	19.1±0.6	3.69±0.26
Earthworm (*Lumbricus terrestris*)	17	2.87±0.26	0.44±0.04	15.0±0.6	22.7±0.3	3.40±0.09
Tadpole of Bronze Frog (*Lithobates clamitans*)	12	3.65±0.24	0.43±0.04	11.7±0.4	14.8±0.4	1.74±0.07
Bronze Frog (*Lithobates clamitans*)	5	3.80±0.10	0.70±0.02	18.5±0.3	19.7±0.4	3.63±0.08
Golden shiner (*Notemigonus crysoleucas*)	15	5.37±0.13	1.63±0.13	24.6±0.2	21.8±0.1	5.37±0.05
Neonate house mouse (*Mus musculus*)	5	3.38±0.13	0.87±0.04	25.6±0.6	26.6±0.2	6.81±0.18

Note: Values are means ± 1 SE.

temperature effects were assessed using five different temperatures: 15, 20, 25, 30, and 35 °C. For each temperature trial, snakes were acclimated to the target temperature for 3 days prior to SMR measurements. Following SMR measurements, snakes (6–7 per trial) were removed from the environmental chamber, fed a golden shiner meal equal in mass to ~25% of the snakes' body mass, and returned to their respirometry chamber.

Quantifying the SDA response

For each of the metabolic trials, we quantified the following seven variables: SMR (mean value of the two lowest measured $\dot{V}O_2$ prior to 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, which is $\dot{V}CO_2/\dot{V}O_2$ at peak $\dot{V}O_2$), duration (time from feeding until $\dot{V}O_2$ returned to being not significantly different from SMR), SDA (total energy expended above SMR over the duration of elevated $\dot{V}O_2$), and the SDA coefficient (SDA as a percentage of meal energy). We quantified SDA (kJ and $kJ \cdot kg^{-1}$) by summing the extra O_2 consumed (mL) above SMR over the duration of the significant metabolic response and multiplying that value by 19.8, assuming that 19.8 kJ are expended per millilitre of O_2 consumed given that the dry matter of the catabolized meal is 70% protein, 25% fat, and 5% carbohydrate and generates a respiratory quotient of 0.73 (Gessman and Nagy 1988).

We determined the energy content of each meal type by bomb calorimetry. Five sets of samples of each meal type were weighed (wet mass), dried to a constant mass at 60 °C, reweighed (dry mass), ground to a fine powder, and pressed into pellets. Three pellets of each set were ignited in a bomb calorimeter (model 1266; Parr Instruments, Moline, Illinois, USA) to determine energy content. For each meal type, we determined wet mass energy equivalent ($kJ \cdot g^{-1}$) as the product of dry mass energy content (from bomb calorimetry) and the meal's dry mass percentage (Table 1). A meal's energy content was calculated as the product of the wet mass energy equivalent and meal mass.

Statistical analysis

For each metabolic trial, we used repeated-measures design analysis of variance (ANOVA) to test for significant effects of time (before and after feeding) on $\dot{V}O_2$, $\dot{V}CO_2$, and RER. Each ANOVA was accompanied by a post hoc pairwise mean comparison (Tukey–Kramer) to identify significant differences in $\dot{V}O_2$, $\dot{V}CO_2$, and RER between sampling time points and when $\dot{V}O_2$ did not differ significantly from SMR. To investigate the effects of meal size, meal type, and body temperature on metabolic measures, we used ANOVA for measures of body mass, target meal mass percentage, SMR (mL $O_2 \cdot g^{-1} \cdot h^{-1}$, mL $CO_2 \cdot g^{-1} \cdot h^{-1}$), peak $\dot{V}O_2$ ($mL \cdot g^{-1} \cdot h^{-1}$), scope of peak $\dot{V}O_2$, RER at peak $\dot{V}O_2$, SDA ($kJ \cdot kg^{-1}$), and SDA coefficient, and ANCOVA (body mass as a covariate) for measures of meal size, SMR (mL $O_2 \cdot h^{-1}$, mL $CO_2 \cdot h^{-1}$), peak $\dot{V}O_2$ ($mL \cdot h^{-1}$), and SDA (kJ). These ANOVA and ANCOVA were followed by a pairwise mean comparison to identify differences between treatments. We report the results of the ANOVA and ANCOVA tests in terms of their F and P values and note the P values of significant pairwise mean comparisons. The level of statistical significance for this study was set at $P < 0.05$. Results are reported as means ± 1 SE.

Predictive models of SDA

We utilized our data on snake body mass, body temperature, meal mass, meal energy, and SDA to generate via regression analyses three predictive models of *T. s. sirtalis* SDA. Our first equation incorporated as independent variables body mass, meal mass, and body temperature from the golden shiner meals alone. The second model used body mass, meal mass, and body temperature from all trials. The third equation estimates SDA based only on meal energy. Intercepts were disregarded if shown not to be significantly different from zero.

Results

Meal-size effects

Mean body mass and SMR (either as $mL \cdot g^{-1} \cdot h^{-1}$ or $mL \cdot h^{-1}$ $\dot{V}O_2$ and $\dot{V}CO_2$) of *T. sirtalis* did not vary significantly among the five meal-size treatments (Table 2). For each meal size, snakes experienced significant variation (P values <0.0001) in $\dot{V}O_2$ and $\dot{V}CO_2$ among pre- and postfeeding time periods, but no variation in RER. After feeding, rates of gas exchange rates of *T. sirtalis* increased rapidly and peaked between 1 and 2 days postfeeding (Fig. 1). Peak $\dot{V}O_2$ varied significantly ($P < 0.0001$) among meal sizes, increasing from a factorial scope above SMR of 3.58 ± 0.21 for the 5% meal size to 9.25 ± 0.27 for the 45% meal size (Table 2). At peak $\dot{V}O_2$, RER did not significantly differ among meal sizes, averaging 0.728 ± 0.008. Following the peaks, rates of gas exchange declined more slowly and became nonsignificantly different from SMR at

Table 2. Body mass, meal size, standard metabolic rate (SMR), and six experimental variables of the postprandial metabolic response of the Common Garter Snake (*Thamnophis sirtalis*) to meals of golden shiners (*Notemigonus crysoleucas*) equaling in mass to 5%–45% of snake's body mass.

	Meal size (% of body mass)						
Variable	5%	15%	25%	35%	45%	*F*	*P*
n	6	7	7	8	5		
Body mass (g)	44.8±4.7	38.6±2.2	47.3±2.0	42.5±3.9	43.9±5.7	81.6	0.461
Meal size (g)	2.22±0.20*a*	5.64±0.29*b*	11.8±0.5*c*	14.9±1.4*d*	19.4±2.7*e*	120	<0.0001
Meal size (% of body mass)	4.99±0.01*a*	14.7±0.3*b*	25.0±0.03*c*	34.9±0.1*d*	43.9±1.1*e*	1032	<0.0001
SMR (mL $O_2 \cdot h^{-1}$)	2.56±0.32	2.06±0.09	2.84±0.14	2.35±0.22	2.47±0.37	1.52	0.351
SMR (mL $O_2 \cdot g^{-1} \cdot h^{-1}$)	0.057±0.002	0.054±0.002	0.060±0.002	0.055±0.001	0.056±0.002	1.47	0.236
SMR (mL $CO_2 \cdot h^{-1}$)	1.85±0.25	1.14±0.04	2.12±0.11	1.68±0.18	1.81±0.31	1.68	0.179
SMR (mL $CO_2 \cdot g^{-1} \cdot h^{-1}$)	0.041±0.002	0.037±0.002	0.045±0.002	0.045±0.002	0.041±0.002	2.32	0.078
Peak $\dot{V}O_2$ (mL·h^{-1})	8.96±1.09*a*	9.60±0.94*a*	19.4±1.0*b*	15.9±1.4*c*	21.9±3.1*d*	58.8	<0.0001
Peak $\dot{V}O_2$ (mL·g·h^{-1})	0.204±0.015*a*	0.256±0.002*b*	0.410±0.005*c*	0.383±0.011*c*	0.515±0.019*d*	73.7	<0.0001
Scope	3.58±0.21*a*	4.78±0.38*b*	6.98±0.23*c*	6.95±0.19*c*	9.25±0.27*d*	80.1	<0.0001
RER	0.730±0.008	0.712±0.007	0.744±0.005	0.721±0.017	0.732±0.001	1.06	0.391
Duration (days)	2.5	4	5	6	7		
SDA (kJ)	3.76±0.76*a*	6.09±0.84*a*	14.4±0.8*b*	16.6±2.1*b*	29.0±1.9*c*	148	<0.0001
SDA (kJ·kg^{-1})	82±11*a*	156±17*b*	305±11*c*	387±25*d*	677±34.5*e*	137	<0.0001
SDA coefficient (%)	29.1±3.8*b*	18.1±2.1*a*	21.6±0.8*a*	19.6±1.3*a*	27.4±1.7*b*	6.21	0.0008

Note: Variables are defined in the text. Values are presented as means ± 1 SE. Values of *F* and *P* are from ANOVAs for SMR (mL $O_2 \cdot g^{-1} \cdot h^{-1}$), SMR (mL $CO_2 \cdot g^{-1} \cdot h^{-1}$), peak oxygen consumption (mL $O_2 \cdot g^{-1} \cdot h^{-1}$), scope, respiratory exchange ratio (RER), specific dynamic action (SDA) (kJ·kg^{-1}), and SDA coefficient, whereas values of *F* and *P* are from ANCOVAs (body mass as a covariate) for SMR (mL $O_2 \cdot h^{-1}$), SMR (mL $CO_2 \cdot h^{-1}$), peak oxygen consumption (mL $O_2 \cdot h^{-1}$), and SDA (kJ). RER values in this table represent individual RER mean values calculated at peak oxygen consumption. Differing letters indicate significant differences ($P < 0.05$) between the five meal-size treatments determined with post hoc pairwise comparison (Tukey's honestly significant difference (HSD) test).

2.5, 4, 5, 6, and 7 days postfeeding for the 5%, 15%, 25%, 35%, and 45% meals, respectively (Table 2). SDA (as kJ and kJ·kg^{-1}) varied significantly among meal sizes, ranging from 3.76 ± 0.76 kJ for the 5% meals to 29.0 ± 0.9 kJ for the 45% meals (Table 2). Plotted against meal energy, SDA increased linearly with a generalized slope of 0.24 (Fig. 2A). Meal size also affected the SDA coefficient, as the cost of digesting and assimilating the 5% and 45% meals was equivalent to a larger percentage of meal energy (29.1% and 27.4%, respectively) compared with the intermediate-size meals (18.1%–21.6%) (Fig. 2B; Table 2).

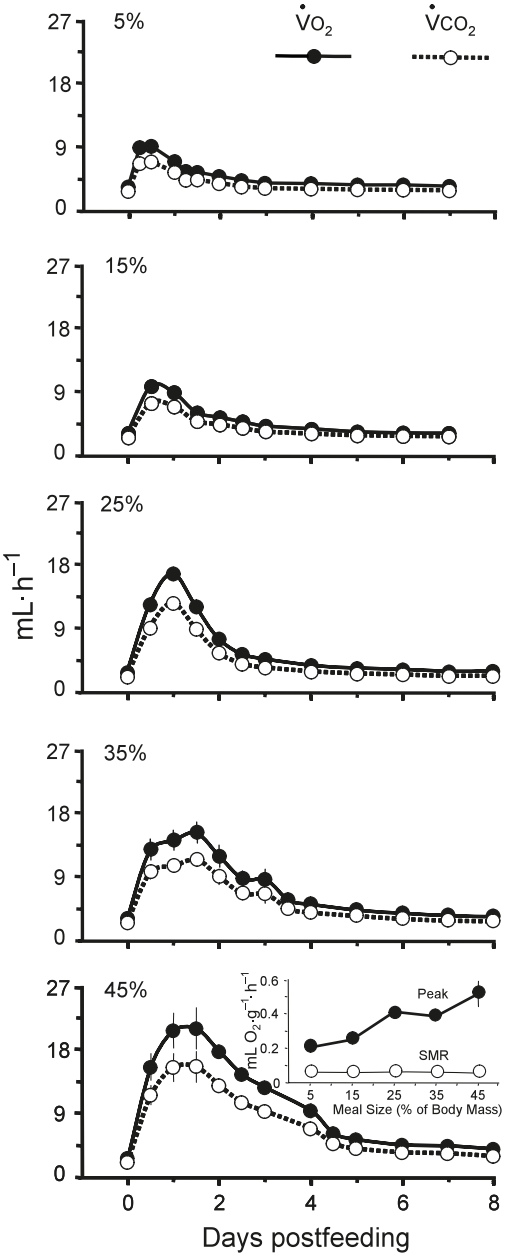
Meal-type effects

For the six meal-type trials, there was no significant variation among trials in mean snake body mass and SMR (Table 3). Regardless of meal type, *T. sirtalis* rapidly increased their rates of gas exchange after feeding, with peaks in $\dot{V}O_2$ and $\dot{V}CO_2$ attained at 12 or 24 h postfeeding (Fig. 3). For each meal-type trial, RER did not vary significantly among sampling periods. Postprandial peaks in $\dot{V}O_2$ varied significantly (*P* values <0.00001) among the different meal types: the meals of beetle grub induced a modest 2.63-fold increase in $\dot{V}O_2$; meals of earthworms, Bronze Frogs, and tadpoles of Bronze Frogs generated a moderate 5.28- to 5.61-fold increase; and meals of mice and golden shiners resulted in larger 6.36- and 6.98-fold increases in $\dot{V}O_2$, respectively (Table 3). At peak $\dot{V}O_2$, there was no significant variation in RER among meal types, with RER at that point averaging 0.729 ± 0.009. Metabolic rates declined slowly after the peak and returned to SMR levels 4–6 days postfeeding (Table 3). Calculated SDA (kJ and kJ·kg^{-1}) varied ($P = 0.0008$) among meal-type trials, differing by nearly 5-fold between the meal of beetle grubs (4.02 ± 0.41 kJ) and the meal of mice (19.9 ± 0.8 kJ). Collectively among meal types, SDA increased as a function of meal energy (Fig. 4A). We found the SDA coefficient to vary significantly among the six meals, ranging from 9.1% ± 0.9% for the meal of beetle grubs to 47.5% ± 4.7% for the tadpole meal (Table 3, Fig. 4B).

Body-temperature effects

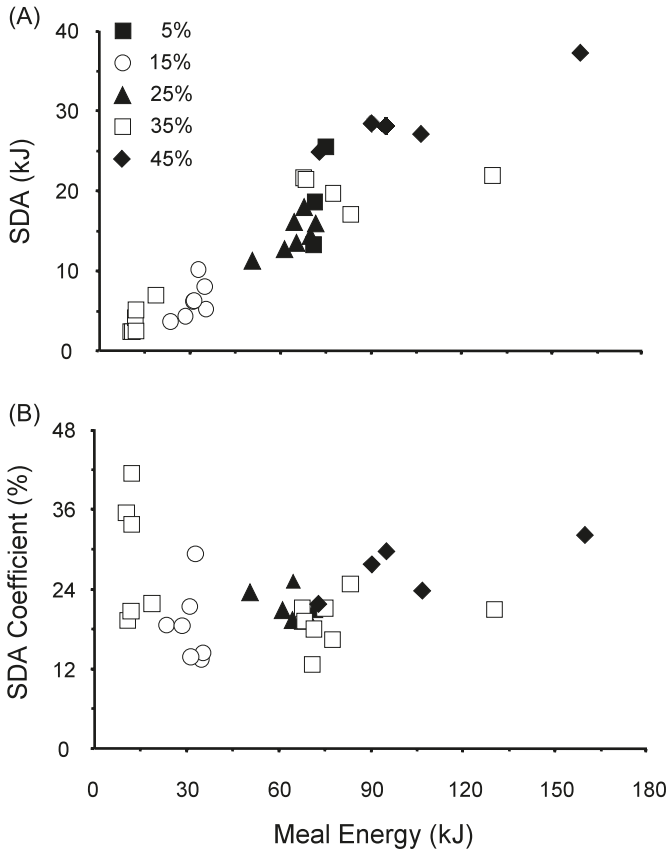
Mean body mass did not vary among the five body temperature trials. Body temperature had a significant impact on SMR, as SMR increased (*P* values <0.021) with each 5 °C increase in temperature (Table 4). For each temperature treatment, $\dot{V}O_2$ and $\dot{V}CO_2$ varied significantly (*P* values <0.0001) among sampling periods. Again, we observed no variation in RER among sampling periods at any of the treatment temperatures. The shape of the postprandial metabolic profile shifted from being shallow and elongated at 15 °C to becoming increasingly more narrow and shorter in duration with each increase in temperature (Fig. 5). The postprandial peak in $\dot{V}O_2$ varied significantly among temperature treatments, increasing significantly (*P* values <0.0002) with each 5 °C increase in body temperature. For each 5 °C increase in body temperature, Q_{10} of SMR (mL $O_2 \cdot g^{-1} \cdot h^{-1}$) and peak $\dot{V}O_2$ ranged from 1.70 to 2.66 and from 1.99 to 6.90, respectively, with respective mean values of 2.19 and 3.54. Factorial scope of peak $\dot{V}O_2$ also varied significantly ($P < 0.0001$) among temperatures, owing in part to the much lower scope (2.93) at 15 °C compared with the other four temperature treatments (5.09–6.68; Table 4). At peak $\dot{V}O_2$, RER did not vary significantly among the five body temperatures. With an increase in body temperature, the du-

Fig. 1. Mean oxygen consumption and carbon dioxide production ($mL \cdot h^{-1}$) for the Common Garter Snake (*Thamnophis sirtalis*) at 30 °C prior to day 0 and following ingestion of a meal of golden shiners (*Notemigonus crysoleucas*) equaling in mass to 5%, 15%, 25%, 35%, and 45% of snake's body mass. For each trial, n = 5–8. The inset on the last panel depicts the lack of any meal-size effects on standard metabolic rate (SMR) and the increase in peak oxygen consumptions with increasing meal size. For this and similar figures, error bars represent SE and are omitted if the SE is smaller than the symbol for the mean.



ration of elevated metabolism decreased from 9 days at 15 °C to 3 days at 35 °C (Table 4). Although predicted not to vary among temperature treatments, SDA did differ significantly ($P < 0.0001$) among temperature trials, largely owing to a SDA at 15 °C that averaged one-third the SDA for the other four higher temperatures. Likewise, we observed significant variation among temperature trials for the

Fig. 2. (A) Meal energy plotted against specific dynamic action (SDA) for meals of golden shiners (*Notemigonus crysoleucas*) equaling in mass to 5%, 15%, 25%, 35%, and 45% of the body mass of the Common Garter Snake (*Thamnophis sirtalis*) and digested at 30 °C. Note the increase in SDA with an increase in meal size and thus meal energy. (B) SDA coefficients plotted against meal energy for the same meal trials.



SDA coefficient, i.e., 7.1% ± 0.6% at 15 °C and 18.5%–23.6% for the other four temperatures (Table 4).

Models of SDA

We generated three predictive models of SDA (kJ) for *T. sirtalis*. Model 1 was developed from the nine trials of meals of golden shiners and incorporates body mass (BM; g), body temperature (T_b; °C), and meal mass (MM; g). Model 2 was generated from all 14 trials and likewise incorporates body mass, body temperature, and meal mass. Model 3 estimates SDA based on meal energy (ME; kJ) with data from all 14 trials.

$$[1] \quad \mathrm{SDA} = -0.17\mathrm{BM} + 1.38\mathrm{MM} - 8.42T_b + 0.50 \quad (r^2 = 0.835,\ P < 0.0001)$$

$$[2] \quad \mathrm{SDA} = -0.26\mathrm{BM} + 1.40\mathrm{MM} + 0.37T_b + 0.50 \quad (r^2 = 0.835,\ P < 0.0001)$$

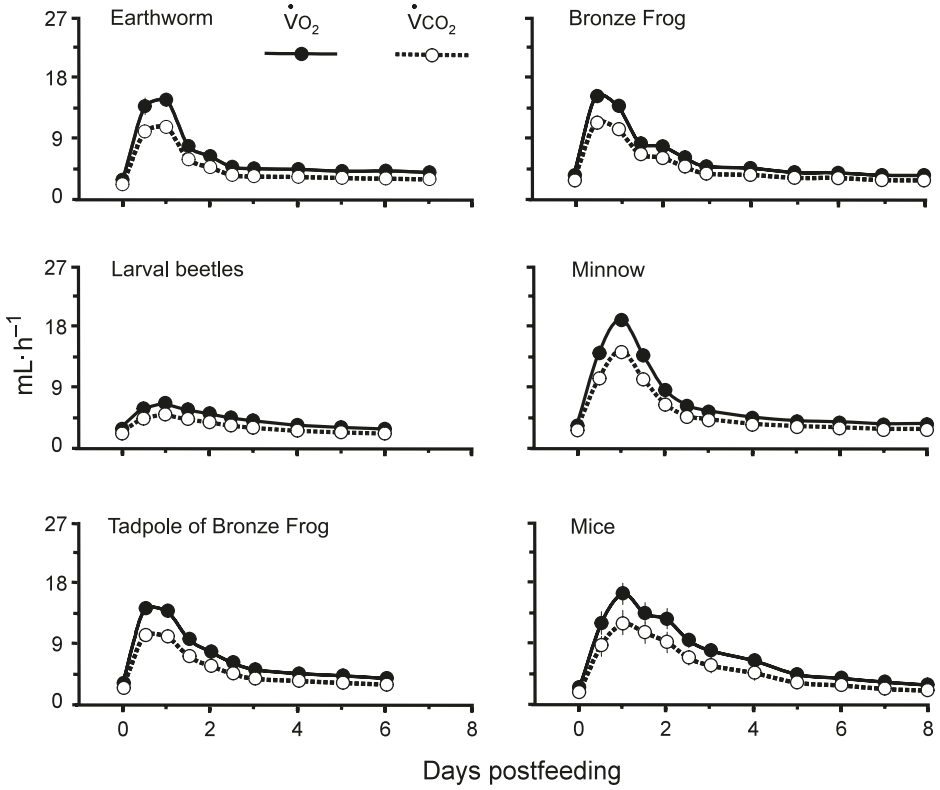
$$[3] \quad \mathrm{SDA} = 0.22\mathrm{ME} + 1.86 \quad (r^2 = 0.615,\ P < 0.0001)$$

Table 3. Body mass, meal size, standard metabolic rate (SMR), and six experimental variables of the postprandial metabolic response of the Common Garter Snake (*Thamnophis sirtalis*) to six differing meal types equaling in mass to 25% of their body mass.

	Meal type							
Variable	Earthworms	Bronze Frogs	Tadpoles	Larval beetles	House mice	Golden shiners	*F*	*P*
n	6	7	8	8	6	7		
Body mass (g)	49.7±3.8	48.6±1.8	49.7±2.9	47.1±2.9	49.5±2.1	47.3±2.0	0.200	0.960
Meal size (g)	12.1±0.8	12.1±0.5	11.7±0.7	11.8±0.7	12.4±0.5	11.8±0.5	5.68	0.001
Meal size (% body mass)	24.5±0.4	25.0±0.1	23.6±0.4	25.0±0.02	25.0±0.03	24.9±0.03	6.40	0.001
SMR (mL $O_2 \cdot h^{-1}$)	2.84±0.22	2.76±0.14	2.87±0.13	2.66±0.16	2.82±0.12	2.84±0.14	0.443	0.815
SMR (mL $O_2 \cdot g^{-1} \cdot h^{-1}$)	0.057±0.002	0.057±0.001	0.059±0.003	0.057±0.001	0.057±0.001	0.060±0.002	0.435	0.821
SMR (mL $CO_2 \cdot h^{-1}$)	2.06±0.17	1.99±0.10	2.10±0.09	1.92±0.11	2.03±0.08	2.12±0.11	0.714	0.617
SMR (mL $CO_2 \cdot g^{-1} \cdot h^{-1}$)	0.042±0.002	0.041±0.002	0.043±0.003	0.041±0.001	0.041±0.001	0.045±0.002	0.903	0.490
Peak $\dot{V}_{O2}$ (mL·h^{-1})	15.4±1.0*b*	15.2±1.0*b*	14.6±0.8*b*	6.73±0.3*a*	17.6±0.7*c*	19.4±1.0*e*	44.1	<0.0001
Peak $\dot{V}_{O2}$ (mL·g^{-1}·h^{-1})	0.313±0.010*b*	0.310±0.002*b*	0.310±0.02*b*	0.149±0.008*a*	0.362±0.01*b*,*c*	0.410±0.005*c*	45.4	<0.0001
Scope	5.61±0.38*b*	5.53±0.28*b*	5.28±0.17*b*	2.63±0.12*a*	6.36±0.25*c*	6.98±0.23*c*	42.9	<0.0001
RER	0.726±0.007	0.725±0.011	0.722±0.012	0.726±0.013	0.728±0.007	0.744±0.005	0.499	0.774
Duration (days)	4	4	4	4	6	5		
SDA (kJ)	9.23±0.6*b*	9.53±0.75*b*	10.0±0.8*b*	4.02±0.41*a*	19.9±0.8*d*	12.7±0.5*c*	52.3	<0.0001
SDA (kJ·kg^{-1})	191±18*b*	196±14*b*	200±20*b*	84±10*a*	406±25*d*	270±8*c*	37.9	<0.0001
SDA coefficient (%)	16.3±1.4*b*	21.6±1.6*b*	47.5±4.7*c*	9.1±0.9*a*	20.8±0.3*b*	19.7±0.6*b*	34.7	<0.0001

Note: Meal types are as follows: earthworms (*Lumbricus terrestris*); Bronze Frogs (*Lithobates clamitans*); tadpoles, tadpoles of Bronze Frogs; larval beetles (Scarabaeidae); house mice (*Mus musculus*); and golden shiners (*Notemigonus crysoleucas*). Variables are defined in the text. Values are presented as means ± 1 SE. Values of *F* and *P* from ANOVAs for SMR (mL $O_2 \cdot g^{-1} \cdot h^{-1}$), SMR (mL $CO_2 \cdot g^{-1} \cdot h^{-1}$), peak oxygen consumption (mL $O_2 \cdot g^{-1} \cdot h^{-1}$), scope, respiratory exchange ratio (RER), specific dynamic action (SDA) (kJ·kg^{-1}), and SDA coefficient, whereas values of *F* and *P* are from ANCOVAs (body mass as a covariate) for SMR (mL $O_2 \cdot h^{-1}$), SMR (mL $CO_2 \cdot h^{-1}$), peak oxygen consumption (mL $O_2 \cdot h^{-1}$), and SDA (kJ). RER values in this table represent individual RER mean values calculated at peak oxygen consumption. Differing letters indicate significant differences ($P < 0.05$) between the five meal-size treatments determined with post hoc pairwise comparison (Tukey's honestly significant difference (HSD) test).

Fig. 3. Mean oxygen consumption and carbon dioxide production ($mL \cdot h^{-1}$) for the Common Garter Snake (*Thamnophis sirtalis*) at 30 °C prior to day 0 and following the ingestion of six different meal types equaling to 25% of snake body mass. For each meal type, n = 5–8. Note that vertebrate meals generated larger metabolic responses than invertebrate meals.



Discussion

Upon feeding, *T. sirtalis* experiences a rapid increase in metabolic rate that peaks 1–2 days postfeeding and then gradually returns to prefeeding levels within an additional 1–7 days. As previously observed for a variety of aquatic and terrestrial organisms, the magnitude and duration of the postprandial metabolic response for *T. sirtalis* is significantly affected by variation in meal size, meal type, and body temperature (Secor 2009). In the following, we will comment further on the individual impact of each of these determinants of *T. sirtalis* postprandial metabolic response and SDA. With field information on snake body mass and body temperature, and meal mass, our models can estimate the total energy expended on the digestion and assimilation of that meal for a free-ranging snake. Combined with field data on feeding frequency, assumptions of standard metabolism, and activity cost, we will demonstrate an application of our model to estimate the contribution of SDA to DEE.

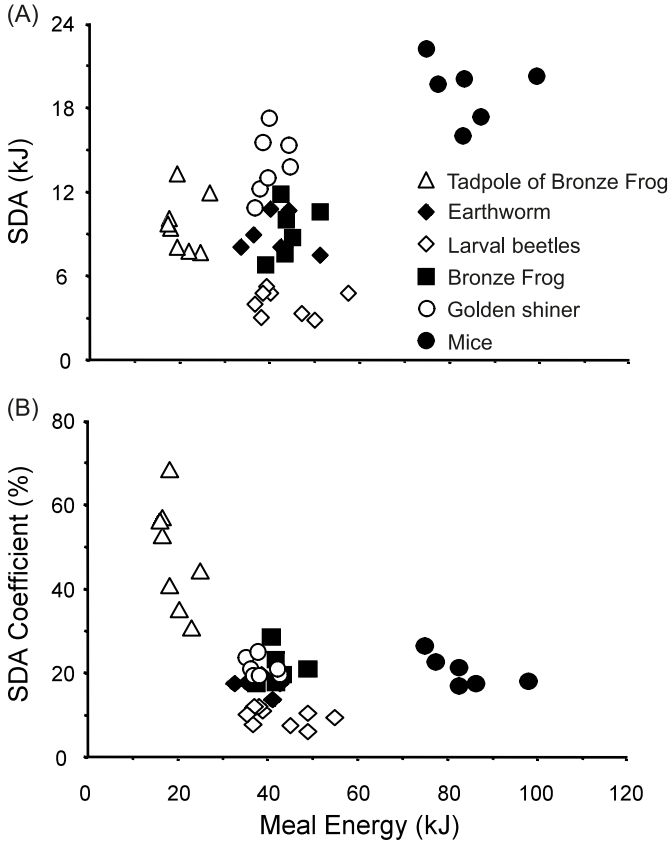
Meal-size effects on SDA

Thamnophis sirtalis experienced a characteristic increase in the magnitude and duration of the postprandial metabolic response and SDA with an increase in meal size (Andrade et al. 1997; Secor and Diamond 1997; Fu et al. 2005; Secor et al. 2007). Controlling for meal type, body temperature, and body size, larger meals require more energy for breakdown and assimilation and thus generate a greater SDA. In this study, a 9-fold increase in meal size (from 5% to 45% of body mass) resulted in a 7.7-fold greater SDA. Over the same span in meal size (5%–45%), the Burmese Python (*Python molurus* (L., 1758)) experiences a 9.5-fold increase in SDA (Secor and Diamond 2000). On average, *T. sirtalis* responded to a doubling of meal size by increasing peak $\dot{V}O_2$ by 52%, duration by 44%, and SDA by 130%. For eight other species of snakes, SDA increased by a factor of 95%–168% with a doubling of meal size (Secor 2009).

Over the range of meal sizes tested, *T. sirtalis* continued to experience an increase in peak $\dot{V}O_2$ with larger meals (Fig. 1). Several studies have shown the postprandial peak $\dot{V}O_2$ to plateau with the largest meal sizes, suggesting that maximum aerobic capacity of the animal is reached during the digestion of these larger meals (Jobling and Davies 1980; Roe et al. 2004; Secor and Boehm 2006). We suspect that it is unlikely that peak $\dot{V}O_2$ will plateau with larger meals (>45% of body mass) for *T. sirtalis.* Postprandial peak $\dot{V}O_2$ of *P. molurus* continued to increase, without an obvious plateau, as meal size increased from 5% to 100% of body mass (Secor and Diamond 1997). Although *T. sirtalis* may be able to consume a meal heavier than 45% of its body mass, it may seldom do so in the wild. Additionally, the largest peak $\dot{V}O_2$ that we measured, 0.515 $mL \cdot g^{-1} \cdot h^{-1}$ for the 45% meal, is less than half the estimated $\dot{V}O_{2\ max}$ (~1.06 $mL \cdot g^{-1} \cdot h^{-1}$) for similar size *T. sirtalis* (Garland and Bennett 1990).

When consuming small and large meals (5% and 45% of body mass at 30 °C), *T. sirtalis* generates larger SDA coefficients (29.1% ± 3.8% and 27.4% ± 1.7%, respectively), suggesting a potential "energetically preferred" (i.e., lower

Fig. 4. (A) Meal energy plotted against specific dyanamic action (SDA) for the six meal types (tadpoles of Bronze Frog (*Lithobates clamitans*), earthworms (*Lumbricus terrestris*), larval beetles (Scarabaeidae), Bronze Frogs, golden shiners (*Notemigonus crysoleucas*), and house mice (*Mus musculus*)) digested at 30 °C. Note that higher energy meals (mice, golden shiners) exhibit larger SDAs. (B) SDA coefficient plotted against SDA for the same meal trials.



SDA coefficient) range of meal sizes between 15% and 35% of body mass (Table 2). The consumption of smaller meals (5% and 10% of body mass) by the Cane Toad (*Rhinella marina* (L., 1758)) generated lower SDA coefficients (13.0% ± 0.9% and 16.5% ± 1.9%, respectively) compared with meals 15% and 20% of body mass (20.5% ± 1.7% and 22.8% ± 0.7%, respectively; Secor and Faulkner 2002). In contrast, *P. molurus* and Eastern Tiger Salamanders (*Ambystoma tigrinum* (Green, 1825)) exhibited similar SDA coefficients across a range of meal sizes (5%–100% and 2.5%–12.5% of body mass, respectively) (Secor and Diamond 1997; Secor and Boehm 2006). Hence, not evident among these studies is the existence of an optimal range of meal sizes that minimizes the SDA coefficient of a species.

Meal-type effects on SDA

Meal composition and structure can impact the magnitude and duration of the SDA response (Secor 2009). Meals high in protein content relative to carbohydrates and fat tend to generate greater SDAs than high-carbohydrate or high-fat meals (Tandler and Beamish 1980; Karst et al. 1984; McCue et al. 2005). Given the carnivorous diet of *T. sirtalis*, all of their meals are expectedly high in protein with varying amounts of fat and minimal amounts of carbohydrates. Based on data from bomb calorimetry (kJ·g^{-1} of dry mass) and percentage dry mass (which increases with fat content), we estimate that the food items used in this study ranged from having literally no or very little fat (e.g., tadpoles of Bronze Frogs, larval beetles, and Bronze Frogs) to an estimated 3%–8% fat content (earthworms, golden shiners, and mice).

The effect that different types of meals have on SDA can be examined while controlling for meal size and body temperature (Secor 2009). Amphibians experience larger SDAs during the digestion and assimilation of hard-bodied, chitinous prey (e.g., crickets, larval tenebrids) than during the digestion of soft-bodied earthworm and moth larva (Secor and Boehm 2006; Secor et al. 2007). Similarly, we predicted that *T. sirtalis* would expend more energy digesting Bronze Frogs, mice, and golden shiners owing to the presence of a developed skeleton, than spent digesting earthworm, larval beetles, and tadpoles of Bronze Frogs. We found that the SDAs generated from meals of Bronze Frog, mice, and golden shiner averaged 50% greater than the SDAs for the meals of earthworm, larval beetles, and tadpoles of Bronze Frogs. In addition to expending more energy to digest and assimilate these vertebrate prey, more effort may be required for their capture and swallowing. For *T. sirtalis*, the greater cost of consuming and digesting mice and golden shiners is offset energetically by their greater total energy content (Table 1).

For the Valley Garter Snake (*Thamnophis sirtalis fitchi* Fox, 1951), the digestion and assimilation of a meal of Treefrogs equal in mass to 33% of snake body mass at 30 °C generates a SDA of 168 kJ·kg^{-1} (Peterson et al. 1998). In comparison, *T. sirtalis* of this study responded to a meal of Bronze Frogs (25% of body mass) with a SDA of 196 kJ·kg^{-1} (Table 3). For four other active foraging snake species, rodent meals weighing 25% of snake body mass generated SDAs of 258–309 kJ·kg^{-1}, a range that while encompassing the SDA of *T. sirtalis* of this study digesting fish meals, is less than their SDA (406 ± 25 kJ·kg^{-1}) for the meal of mice (Secor and Diamond 2000).

Body-temperature effects on SDA

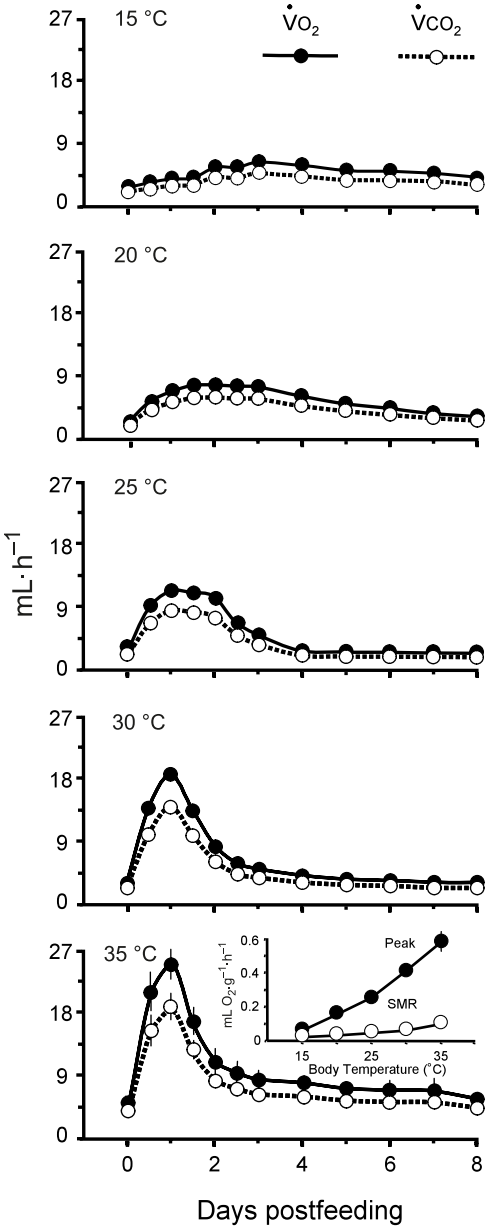
For ectotherms, a shift in environmental temperature and hence body temperature will significantly affect the postprandial metabolic profile by altering SMR, peak $\dot{V}O_2$, and the duration of the metabolic response (Soofiani and Hawkins 1982; Kalarani and Davies 1994; Powell et al. 1999; Secor and Faulkner 2002). At the lowest temperature treatment (15 °C) of this study, *T. sirtalis* experienced only a 3-fold postprandial increase in $\dot{V}O_2$ and maintained a low, flat metabolic profile for 9 days (Fig. 3). At higher temperatures, the scope of peak $\dot{V}O_2$ was greater (5.1- to 6.7-fold) and the profile became increasing more narrow and higher with each increase in experimental temperature. This trend towards a taller and narrower postprandial metabolic profile with an increase in ambient temperature has been observed for fishes, amphibians, and reptiles (Wang et al. 2003; Secor and Boehm 2006; Secor et al. 2007; Luo and Xie 2008; Tsai et al. 2008). This pattern illustrates that at higher body temperatures, digestion and assimilation are occurring more rapidly and intensely for a shorter period of time. For

Table 4. Body mass, meal size, standard metabolic rate (SMR), and six experimental variables of the postprandial metabolic response of the Common Garter Snake (*Thamnophis sirtalis*) to meals of golden shiners (*Notemigonus crysoleucas*) equaling in mass to 25% of snake's body mass being digested at temperatures from 15 to 35 °C.

	Body temperature (°C)						
Variable	15	20	25	30	35	*F*	*P*
n	6	7	7	7	6		
Body mass (g)	46.3±1.3	46.6±1.9	47.3±3.9	47.3±2.0	46.5±3.1	0.030	0.998
Meal size (g)	11.6±0.3	11.6±0.5	11.8±1.0	11.8±0.5	11.6±0.8	0.874	0.492
Meal size (% body mass)	25.0±0.02	25.0±0.04	25.0±0.01	25.0±0.03	25.0±0.01	0.861	0.499
SMR (mL $O_2 \cdot h^{-1}$)	0.96±0.08*a*	1.43±0.07*b*	2.15±0.18*c*	2.84±0.14*d*	4.47±0.23*e*	112	<0.0001
SMR (mL $O_2 \cdot g^{-1} \cdot h^{-1}$)	0.021±0.002*a*	0.031±0.002^b	0.046±0.003*c*	0.060±0.002*d*	0.098±0.007*e*	68.5	<0.0001
SMR (mL $CO_2 \cdot h^{-1}$)	0.70±0.05*a*	1.02±0.05*b*	1.57±0.14*c*	2.12±0.11*d*	3.24±0.17*e*	98.6	<0.0001
SMR (mL $CO_2 \cdot g^{-1} \cdot h^{-1}$)	0.015±0.001*a*	0.022±0.001*a*	0.034±0.002*b*	0.045±0.002*c*	0.071±0.005*d*	61.2	<0.0001
Peak $\dot{V}_{O_2}$ (mL·h^{-1})	2.68±0.15*a*	6.95±0.41*b*	11.66±0.91*c*	19.43±0.95*d*	25.29±2.15*e*	155	<0.0001
Peak $\dot{V}_{O_2}$ (mL·g^{-1}·h^{-1})	0.059±0.002*a*	0.155±0.005*b*	0.254±0.004*c*	0.410±0.005*d*	0.578±0.019*e*	126	<0.0001
Scope	2.93±0.17*a*	5.09±0.33*b*	5.68±0.38*b*	6.68±0.23*c*	5.90±0.19*b*	23.6	<0.0001
RER	0.708±0.012	0.738±0.013	0.729±0.010	0.744±0.013	0.734±0.012	1.14	0.354
Duration (days)	9	8	6	5	3		
SDA (kJ)	4.45±0.33*a*	13.1±0.9*b*	12.1±1.0*b*	14.4±0.8*c*	14.8±0.9*c*	38.9	<0.0001
SDA (kJ·kg^{-1})	97±8*a*	279±12*b*	254±8*b*	305±11*c*	325±26*c*	38.9	<0.0001
SDA coefficient (%)	7.1±0.6*a*	20.3±0.9*b*	18.5±0.6*b*	21.6±0.8*c*	23.6±1.9*c*	38.1	<0.0001

Note: Variables are defined in the text. Values are presented as means ± 1 SE. Values of *F* and *P* are from ANOVAs for SMR (mL $O_2 \cdot g^{-1} \cdot h^{-1}$), SMR (mL $CO_2 \cdot g^{-1} \cdot h^{-1}$), peak oxygen consumption (mL $O_2 \cdot g^{-1} \cdot h^{-1}$), scope, respiratory exchange ratio (RER), specific dynamic action (SDA) (kJ·kg^{-1}), and SDA coefficient, whereas values of *F* and *P* are from ANCOVAs (body mass as a covariate) for SMR (mL $O_2 \cdot h^{-1}$), SMR (mL $CO_2 \cdot h^{-1}$), peak oxygen consumption (mL $O_2 \cdot h^{-1}$), and SDA (kJ). RER values in this table represent individual RER mean values calculated at peak oxygen consumption. Differing letters indicate significant differences ($P < 0.05$) between the five meal-size treatments determined with post hoc pairwise comparison (Tukey's honestly significant difference (HSD) test).

Fig. 5. Mean oxygen consumption and carbon dioxide production ($mL \cdot h^{-1}$) for the Common Garter Snake (*Thamnophis sirtalis*) prior to day 0 and following the ingestion of meals of golden shiners (*Notemigonus crysoleucas*) equaling in mass to 25% of snake body mass at body temperatures of 15, 20, 25, 30, and 35 °C. For each temperature trial, n = 5–8. Note that with an increase in body temperature, the postprandial metabolic profile becomes more elevated and shorter. The inset on the last panel depicts the temperature-dependent increase of SMR and peak oxygen consumption.



T. sirtalis, increasing body temperature from 20 to 30 °C decreases the digestive duration of the SDA response by approximately 40% and thus increases the potential to feed more frequently. The benefits of decreasing the duration of digestion might explain why some snakes have been observed exhibiting postprandial thermophily (Sievert and Andreadis 1999).

Our hypothesis that SDA would not significantly vary among body-temperature treatments was based on the assumption that the same amount of cumulative energy would be expended regardless of the speed of digestion. Support for this hypothesis stems from SDA studies on fishes, anurans, and snakes (Jobling and Davies 1980; Peres and Oliva-Teles 2001; Wang et al. 2003; Secor et al. 2007; Tsai et al. 2008). However, we found significant differences in SDA of *T. sirtalis* among the five temperature treatments, largely owing to the much lower SDA (4.45 kJ) that *T. sirtalis* experienced at 15 °C (Table 4). At the four higher body temperatures (20, 25, 30, and 35 °C), SDA was more consistent (12.1–14.8 kJ). *Ambystoma tigrinum* and the European Grass Snake (*Natrix natrix* (L., 1758)) likewise experienced a significantly reduced SDA at 15 °C compared with measurements made at higher body temperatures (20–35 °C) (Hailey and Davies 1987; Secor and Boehm 2006). A reduction in SDA at lower temperatures may be due to a decrease in assimilation efficiency at lower temperatures as observed for some reptiles (Greenwald and Kanter 1979; Angilletta 2001). For *T. sirtalis*, if less of the meal is absorbed and assimilated at 15 °C, then this could account for their lower SDA at that temperature.

Modeling SDA

Models to predict SDA can be specific to a single species, encompass a major taxa, or span invertebrates or vertebrates (Secor and Phillips 1997; Peterson et al. 1998; Beaupre 2002; Secor 2009; Tsai et al. 2009). One objective of this program was to develop a model to predict SDA for *T. sirtalis* using field-collected data. Our models incorporate body mass, body temperature, and meal mass to derive an estimate of SDA specific to golden shiners or for any meal in general. To illustrate the application of these models, we have constructed a hypothetical feeding history for an adult *T. sirtalis* (Table 5). For this exercise, we have varied body size (assuming positive growth), body temperature (assuming an increase in daily temperature), and meal mass (assuming the availability of prey of different sizes). For each feeding, the model derives a SDA that when summed over the period of study provides an estimate of the total energy allocated to meal digestion and assimilation. In this example of five meals, body mass ranged from 45 to 52 g, mean body temperature ranged from 26 to 31 °C, and meal masses ranged from 6 to 9 g. The cumulative SDAs equaled to 38.4 and 39.8 kJ, respectively, for meals of golden shiner only and mixed prey (Table 5).

We also present an alternative model that uses only meal energy, determined as the product of meal wet mass (which could be recorded in the field) and that meal's wet-mass energy equivalent ($kJ \cdot g^{-1}$). Energy equivalents of prey can possibly be retrieved from the literature or obtained directly from bomb calorimetry. Using the aforementioned feeding history, the SDA of each meal was calculated based on meal energy and summed for the cumulative SDA (Table 5). Among these three models, summed SDA varied by only 4.5% ± 1.1%.

SDAs contribution to DEE

An additional application of our models is the incorporation of calculated SDA into an energy budget for *T. sirtalis* and the determination of how much DEE of an individual *T. sirtalis* is devoted to SDA. DEE of a free-ranging terres-

Table 5. Cumulative specific dynamic action (SDA) based on eqs. 1, 2, or 3 for a hypothetical 1-month feeding schedule (with increasing environmental temperature) of a growing Common Garter Snake (*Thamnophis sirtalis*) digesting meals of golden shiners (*Notemigonus crysoleucas*) or mixed prey.

						Cumulative SDA (kJ)
Meal of golden shiner	1	2	3	4	5	
Body mass (BM; g)	45	47	48.5	50.5	52	
Meal mass (MM; g)	8	6	9	6	8	
Body temperature (T_b; °C)	26	27	29	30	31	
SDA (kJ; eq. 1)	7.8	5.2	10.1	6.1	9.1	38.4
Meal of mixed prey	Mouse	Shiner	Tadpole	Grub	Mouse	
BM (g)	45	47	48.5	50.5	52	
MM (g)	8	6	9	6	8	
T_b (°C)	26	27	29	30	31	
SDA (kJ; eq. 2)	8.8	5.9	10.4	6	8.8	39.9
Meal of mixed prey	Mouse	Shiner	Tadpole	Grub	Mouse	
Meal energy (ME; kJ)	54.5	32.2	15.7	20.4	29	
SDA (kJ; eq. 3)	13.3	8.6	5.2	6.1	8	41.2

Note: Meal types are as follows: mouse, house mice (*Mus musculus*); shiner, golden shiners; tadpole, tadpoles of Bronze Frog (*Lithobates clamitans*); grub, larval beetles (Scarabaeidae).

Table 6. Three 1-month feeding schedules of Common Garter Snakes (*Thamnophis sirtalis*) representing (*a*) moderate normal feeding, (*b*) continuous feeding, and (*c*) a single meal (all meals were golden shiners (*Notemigonus crysoleucas*)) with calculated contributions of standard metabolic rate (SMR), activity cost, and specific dynamic action (SDA) to their daily energy expenditure (DEE).

(*a*) Normal feeding (5 meals).

	BM; T_b; duration							
	45; 26; 3	47; 27; 7	48.5; 29; 7	50.5; 30; 6	52; 31; 7	Sum	DEE (kJ)	Percentage of DEE
Meal mass (g)	8.0	6.0	9.0	6.0	8.0			
SMR (kJ)	3.5	8.9	10.2	9.4	11.7	43.7	1.46	22.8
Activity (kJ)	8.7	22.3	25.5	23.5	29.2	109.2	3.64	57.1
SDA (kJ)	7.8	5.2	10.1	6.1	9.1	39.9	1.33	20.1
Sum (kJ)	20.0	36.4	45.8	39.0	50.0	191.3	6.38	

(*b*) Continuous feeding (6 meals).

	BM; T_b; duration								
	45; 26; 5	48; 27; 5	51; 29; 5	54; 30; 5	57; 31; 5	59.5; 31; 5	Sum	DEE (kJ)	Percentage of DEE
Meal mass (g)	11.5	12.0	12.8	13.5	14.3	14.9			
SMR (kJ)	5.8	6.4	7.5	8.1	8.7	8.9	45.4	1.5	18.2
Activity (kJ)	14.6	16.1	18.7	20.2	21.8	22.3	113.6	3.8	45.4
SDA (kJ)	12.7	13.4	14.9	15.9	17.0	17.4	91.2	3.0	36.4
Sum (kJ)	33.1	35.9	41.1	44.2	47.5	48.5	250.3	8.3	

(*c*) Single meal.

	BM; T_b; duration							
	45; 26; 3	45; 27; 7	47; 29; 7	46; 30; 6	45; 31; 7	Sum	DEE (kJ)	Percentage of DEE
Meal mass (g)	0	11.5	0	0	0			
SMR (kJ)	3.5	8.7	10.0	9.0	10.9	42.2	1.4	26.1
Activity (kJ)	8.7	21.8	25.1	22.5	27.3	105.4	3.5	65.2
SDA (kJ)	0	14.1	0	0	0	14.1	0.5	8.7
Sum (kJ)	12.2	44.6	35.1	31.5	38.3	161.7	5.4	

Note: BM, body mass (g); T_b, body temperature (°C); duration of digestion (days).

trial vertebrate can be determined from its field metabolic rates, measured using the doubly labeled water technique (Nagy 1980; Nagy and Costa 1980). An individual's DEE can be partitioned into three metabolic compartments, basal metabolism (SMR or basal metabolic rate (BMR)), SDA, and activity metabolism. Basal metabolism can be measured in the laboratory or estimated from published allometric models. For ectotherms, an added determinant of SMR is

body temperature. Subtracting SMR or BMR from DEE reveals the combined expenditure on SDA and activity, both of which can vary day to day. Hypothetically, this element of DEE could range from 100% being devoted to SDA to 100% being devoted to activity. To estimate the energy allocated to SDA and activity requires focal observations of the animal's activities. Of particular importance would be the time spent inactive and active, the intensity of activities, meal size, meal type, and feeding frequency. Possessing daily profiles of body temperature can aid in more accurately estimating SMR, SDA, and activity costs.

To demonstrate the utility of our models to estimate the contribution of SDA to DEE and to illustrate the variation to which SDA does contribute to DEE, we developed three hypothetical monthly feeding schedules for *T. sirtalis*. In the first exercise, we use the feeding schedule of Table 5 and assume that the scope of the activity cost is constant day to day (2.5× SMR). During this hypothetical month, SMR and activity costs increased owing to the increase in body mass and temperature. For the month, SMR, SDA, and activity costs were 43.7, 39.9, and 109.2 kJ, respectively (Table 6*a*). Time averaged over the month, 20.1% of DEE was allocated to SDA. Free-ranging Coachwhips (*Masticophis flagellum* (Shaw, 1802)), another active foraging colubrid snake that feeds frequently, were shown to partition an estimated 19% of their DEE to SDA (Secor and Nagy 1994). A second exercise assumes that meal mass is equivalent to 25% of snake body mass, that digestion is completed in 5 days after feeding, and that snakes feed immediately after digesting the previous meal (no intermeal fasts). With the resulting increase in body mass and an extra meal, SMR, activity costs, and SDA are greater in this exercise. Averaged over the month, SDA is equal to 36.4% of DEE (Table 6*b*). From a doubly labeled water study on free-ranging *T. s. fitchi*, it was concluded that snakes of the studied population fed continuously and that 40% of their DEE was partitioned to SDA (Peterson et al. 1998). For the third exercise, only a single meal is consumed. *Thamnophis sirtalis* loses body mass later in the month and SDA averages only 8.7% of DEE (Table 6*c*).

Conclusion

For *T. sirtalis*, the ingestion of different prey items of different sizes under varying environmental conditions generates a spectrum of postprandial metabolic responses. Our measurements and model of SDA for *T. sirtalis* are representative of a small frequently feeding colubrid snake, applicable to examining the ecological energetics of other species. Combining models of SDA with laboratory measurements of SMR and field measurements of FMR can provide an accurate account of how energy is allocated daily for a free-ranging individual. It is increasingly apparent that SDA can be a significant component (10%–40%) of an individual's DEE. Therefore, we encourage research in animal energetics, particularly for ectotherms, to incorporate SDA, measured or modeled, to an individual's energy budget.

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