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# The effects of body temperature and mass on the postprandial metabolic responses of the African egg-eating snakes *Dasypeltis scabra* and *Dasypeltis inornata*

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## ABSTRACT

African egg-eating snakes (*Dasypeltis*) feed only on freshly laid bird eggs which they perforate within their esophagus before swallowing the liquid contents and regurgitating the empty shell. Compared to a snake's typical intact meal, the liquid diet of *Dasypeltis* would expectedly generate a more moderate postprandial metabolic response and specific dynamic action (SDA). Free-ranging *Dasypeltis* feed over a range of ambient temperatures and thereby experience predicted temperature-dependent shifts in the duration and magnitude of their postprandial metabolic response. Such shifts would undoubtedly be shared among different species and age classes of *Dasypeltis*. To examine these expectations, we measured pre- and postprandial metabolic rates of adult *Dasypeltis inornata* and adult and neonate *Dasypeltis scabra* in response to liquid egg meals weighing 20% of snake body mass at 20, 25, 27, 30, and 32 °C. With an increase in body temperature, postprandial metabolic profiles of neonate and adult snakes became narrower and shorter in duration. Specific dynamic action varied among temperature treatments, increasing from 20 to 32 °C. Standard metabolic rate, postprandial peak metabolic rate, and SDA scaled with mass exponents that typically did not differ from 1.0. As expected, *Dasypeltis* digesting a liquid egg diet experienced a more modest postprandial response and SDA, expending on average only 10.6% of the meal's energy on the breakdown, absorption, and assimilation of the egg meal, whereas other colubrids consuming intact rodent or fish meals expend on average 16.3% of the meal's energy on digestion and assimilation. Actively foraging and feeding throughout the avian egg laying season enable *Dasypeltis* to survive when eggs are not available. The adaptive suite of traits that enable *Dasypeltis* to consume eggs of large relative size and ingest only the liquid contents may also be joined by physiological adaptations specific to their liquid diet and extended bouts of fasting.

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## 1. Introduction

To provide the nutrients necessary to fuel maintenance, activity, growth, and reproduction, energy must first be expended on the acquisition, digestion, and assimilation of food (Secor, 2009). These energy consuming processes include gastrointestinal peristalsis, HCl production, secretion of enzymes and buffering solutions, transport of nutrients and ions, and the catabolism and biosynthesis of biomolecules (Secor, 2009). For a wide diversity of invertebrate and vertebrate taxa, feeding generates an increase in metabolic rate that is maintained for the duration of meal digestion and assimilation (Secor, 2009). The cumulative energy expended above maintenance metabolism (basal or standard metabolic rate) on meal digestion and assimilation is commonly referred to as specific dynamic action

(SDA) and is equivalent to 10–30% of the meal's energy (reviewed by McCue, 2006; Secor, 2009).

The magnitude and duration of the postprandial metabolic response and SDA are influenced by the size and composition of the meal, as well as by features of the individual. Larger and more structurally intact meals take more time and effort to digest than smaller, softer, and/or fragmented meals (Secor and Boehm, 2006; Secor et al., 2007). Pre- and postprandial metabolic rates are also affected by body temperature ( $T_b$ ), body mass, and body composition (Secor, 2009). An elevation in  $T_b$  raises metabolic rate, speeds digestion, and reduces the duration of the postprandial metabolic response. In spite of the strong influence of  $T_b$  on postprandial metabolism, SDA tends to remain stable across  $T_b$ 's (Jobling and Davies, 1980; Secor and Faulkner, 2002; Wang et al., 2003). This suggests that regardless of the speed of digestion, a similar amount of energy is expended on any given meal (Secor, 2009). A larger body size inherently generates a greater basal metabolism, peak postprandial metabolism, and SDA (Secor, 2009). Body mass scaling relationships tend to differ among these metabolic variables with SDA scaling isometrically with body mass (Secor and Diamond, 1997;

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Secor et al., 2007). Among snakes, the magnitude of the SDA responses has also been found to differ with respect to feeding habits. When controlling for meal type and size, snakes that feed relatively infrequently in the wild experience significantly greater SDA's than snakes that naturally feed more frequently (Secor and Diamond, 2000).

In addition to a continuum of natural feeding frequency, snakes also exhibit a diversity of feeding habits, from generalist predators to diet specialists. Included in the latter category are Butler's garter snake (*Thamnophis butleri*) which feeds exclusively on earthworms, slug and snail-eating snakes of the genera *Dipsas*, *Pareas*, and *Sibon*, crayfish-eating snakes of the genus *Regina*, and the African egg-eating snakes (*Dasypeltis*) (Greene, 1997). Whereas single and multiple determinants of SDA have been examined for snakes that consume a broader spectrum of prey (e.g., *Agkistrodon piscivorus*, *Boa constrictor*, *Crotalus cerastes*, *Python molurus*, *Thamnophis sirtalis*), little attention has been directed at the determinants that dictate the postprandial metabolic responses of diet specialists (reviewed in Secor, 2009).

As noted, hard and intact meals require more time and energy to digest and assimilate than soft and fragmented meals. Among the aforementioned diet specialists, we postulate that the postprandial effort to digest crayfish for *Regina* is greater than that expended by *Thamnophis*, *Dipsas*, *Pareas*, and *Sibon* in the digestion of worms and slugs. A similar modest postprandial metabolic response and SDA would predictably be experienced by *Dasypeltis* given that they feed exclusively on freshly-laid bird eggs. *Dasypeltis* do not digest intact eggs, but rather longitudinally split and compress the egg within the esophagus, push the fluid contents into the stomach, and then regurgitate the empty shell (Gans, 1952, 1974). Evidence of a reduced metabolic response and SDA generated from the digestion of a liquid egg meal stems from two studies. Großmann and Starck (2006) observed only a two-fold increase in postprandial metabolism for *Dasypeltis scabra* during the digestion of an egg meal that was equal in mass to 20% of snake's body mass. This is markedly less than the 4 to 8-fold increases in postprandial metabolism documented for other colubrid snakes digesting intact rodent meals of similar relative mass (tabulated in Secor, 2009). Gila monsters (*Heloderma suspectum*) were found to expend 24% less energy in digesting an egg meal (no shell) compared to that expended on the digestion of an intact rodent meal of equal mass (Christel et al., 2007).

*Dasypeltis* of all ages feed predominantly during the peak avian egg-laying season. Therefore, to capitalize on this time-limited resource, *Dasypeltis* need to be able to feed and digest their egg meals over a range of environmental temperatures (Gans, 1952; Schulze et al., 2008). Interested in the interactions of body temperature and body size on postprandial metabolism and SDA and the hypothesized generality of a reduced metabolic response to a liquid diet, we characterized and compared the postprandial metabolic profile and SDA of adult *Dasypeltis inornata* and of adult and neonate *D. scabra* over five body temperatures. The goals of our study were to: (1) assess the effects of body temperature on the metabolic response and SDA of *Dasypeltis* and identify whether SDA remains stable regardless of  $T_b$ ; (2) investigate the body mass scaling relationships of pre- and postprandial metabolism and SDA for *D. scabra*; and (3) determine whether species of *Dasypeltis* experiences a moderate postprandial metabolism and SDA, independent of body temperature and size, as a function of their liquid diet. We shall demonstrate in this study that  $T_b$  impacts not only pre- and postprandial metabolic rates, but also SDA, that many of the mass scaling relationships do not differ from 1.0, and as predicted *Dasypeltis* experience a relatively modest postprandial response and SDA compared to other colubrid snakes digesting intact meals.

## 2. Materials and methods

### 2.1. Study species

*Dasypeltis* species are unique among snakes in possessing a highly specialized feeding habit of consuming only freshly-laid bird eggs

(Gans, 1974; Greene, 1997). With poorly developed teeth, long mandibles, and very expandable skin, *Dasypeltis* are able to consume eggs with diameters that are several times greater than the width of the snake's head (Gans, 1952; Gartner and Greene, 2008). Impressive examples of egg swallowing come from reports of *Dasypeltis* with head widths of ~10 mm consuming chicken and duck eggs of 41–46 mm in diameter (Rabb and Snedigar, 1960; Gans, 1974; Krupa, 1985). After entering the esophagus the egg is held in place with ventral extensions of the vertebrae, which saw across the egg surface until it is perforated. The liquid contents are pushed into the stomach and the shell is rolled into itself and regurgitated (Gans, 1974). *Dasypeltis* therefore differ from other oophagous snakes (e.g., *Elaphe*, *Lampropeltis*, and *Pseustes*) in digesting only the egg's contents (Greene, 1997).

We examined the postprandial metabolic response of the southern brown egg-eating snake (*Dasypeltis inornata*) and the common or rhombic egg-eating snake (*Dasypeltis scabra*). The former species is endemic to the eastern parts of South Africa and western Swaziland, whereas the latter species is distributed throughout much of sub-Saharan Africa (Branch, 1998; Marais, 2004; Escoriza, 2010). Both species possess a relatively slender body with maximum lengths of 70–90 cm (Marais, 2004). They are excellent climbers and actively forage, typically at night, for freshly-laid eggs of ground and tree-nesting birds (Lloyd, 2004; Nalwanga et al., 2004). The adult *D. inornata* used in this study were captured in the wild in KwaZulu-Natal, South Africa, and the adult *D. scabra* were captured in the Northwest Province, South Africa. Neonate *D. scabra* originated from clutches laid in the laboratory by six of the captured *D. scabra*.

Snakes were housed in custom-made wooden and glass terraria (60 × 30 × 45 cm or 90 × 30 × 60 cm) within a temperature-controlled room and maintained on a 12L:12D cycle at 24 ± 2 °C. Snakes were fed 2 or 3 eggs mid-morning once every 3–4 weeks with water available *ad libitum*. Eggs were obtained from local bird breeders and included those of budgerigar (*Melopsittacus undulatus*), quail species (*Coturnix coturnix* and *C. japonica*) and bantam chickens (*Cochin bantum*). Snake care, maintenance, and experimentation were conducted with approval from the Animal Ethics Committee of the University of KwaZulu-Natal (reference 014/08/Animal).

### 2.2. Experimental procedure and measurements of oxygen consumption

We used closed-system respirometry to measure oxygen consumption rates ( $\dot{V}O_2$ ) of fasted and fed snakes (see Vleck, 1987; Secor and Nagy, 1994) at 20, 25, 27, 30 and 32 °C. The sequence of trials was randomized to prevent habituation to a constant temperature increase. Prior to metabolic trials, snakes were fasted for a minimum of three weeks to ensure they were post-absorptive. All metabolic trials were conducted in a constant environment room with a 12L:12D cycle. Before each trial, snakes were weighed and placed into individual plastic opaque air-tight respirometry chambers (0.43–2.60 L, Lock & Lock, Seoul, South Korea) and allowed to acclimate to the chambers for a minimum of 48 h. Each chamber was fitted with incurrent and excurrent air ports, each attached to a 3-way stop cock.

An initial 50-mL air sample was withdrawn from the excurrent air port and then both the incurrent and excurrent air ports were closed. One hour later, the excurrent port was opened and a second 50-mL sample was withdrawn. After withdrawing the second air sample, both air ports were re-opened and room air was pumped continuously through each chamber. Air samples were pumped (100 mL min<sup>-1</sup>; New Era Pump NE-510, Wantagh, NY, USA) through a column of water absorbent Drierite (W.A. Hammond Drierite Co., Xenia, OH, USA) and CO<sub>2</sub> absorbent (soda lime) into an O<sub>2</sub> analyzer (Ametek S-3A/1, AEI Technologies, Pittsburgh, Pennsylvania, USA). We calculated whole-animal (mL g<sup>-1</sup>) and mass-specific (mL g<sup>-1</sup> h<sup>-1</sup>) rates of O<sub>2</sub> consumption corrected for standard pressure and temperature.

Each trial began with a measurement of  $\dot{V}O_2$  of fasted snakes to determine individual standard metabolic rate (SMR).  $\dot{V}O_2$  was measured

twice a day (08:00 h and 20:00 h) for three consecutive days. We assigned the average of the two lowest measured  $\dot{V}O_2$  as an individual's SMR. Following SMR measurement, snakes were tube-fed a meal of mixed yolk and albumen from chicken eggs, equivalent in mass to 20% of the snake's body mass. Following feeding, snakes were returned to their respirometry chambers and  $\dot{V}O_2$  was measured twice daily (08:00 h and 20:00 h) for the next five days. Thereafter,  $\dot{V}O_2$  was measured only in the morning (08:00 h) for 7 to 13 additional days.

### 2.3. Quantification of the postprandial metabolic response and SDA

We found that during respirometry trials, both species of *Dasypeltis*, including neonate *D. scabra*, exhibited distinct circadian rhythms of elevated metabolism indicating activity. During SMR trials,  $\dot{V}O_2$  measured at 20:00 h averaged 42.5% greater than at 08:00 h and following feeding there were distinct spikes in metabolic rate during nighttime readings. Similar nighttime spikes in pre- and postprandial  $\dot{V}O_2$  have previously been documented for the nocturnally-active colubrids *Nerodia fasciata* and *Lamprophis fuliginosus* (Hopkins et al., 2004; Roe et al., 2004). To reduce the variability stemming from differences in night-time activity among individuals and the addition of activity expenditure, we used only  $\dot{V}O_2$  measurements taken at 08:00 h to characterize postprandial metabolic response and quantify SDA. We quantified the following variables as described by Secor (2009): SMR, peak  $\dot{V}O_2$  (highest  $\dot{V}O_2$  after feeding), scope of peak  $\dot{V}O_2$  (peak  $\dot{V}O_2$ /SMR),

duration (time from feeding that postprandial  $\dot{V}O_2$  is no longer significantly greater than SMR), SDA (total energy expended above SMR over the duration of significantly elevated  $\dot{V}O_2$ , quantified as kJ and kJ kg<sup>-1</sup>), and SDA coefficient (SDA quantified as a percentage of the meal's energy content). We quantified SDA by summing the extra O<sub>2</sub> consumed above SMR over the duration of the significant metabolic response and multiplying by 19.8 J mL<sup>-1</sup> O<sub>2</sub>, assuming a dry matter catabolism of 65% protein, 30% fat, and 5% carbohydrate and a respiratory quotient of 0.72 (Gessaman and Nagy, 1988).

The energy content of the meal was calculated as the product of meal wet mass and its energy equivalent (kJ g<sup>-1</sup> wet mass) determined using bomb calorimetry. Chicken egg yolk and albumen were collected individually and freeze dried. Samples were burned in a bomb calorimeter (isothermal CP500, Digital Data Systems, Randburg, Johannesburg, South Africa) to determine dry mass energy content. Wet mass energy equivalent of the yolk-albumen mixture (7.59 kJ g<sup>-1</sup>) was calculated by summing the products of dry mass energy content and dry mass percentages for yolk and albumen.

### 2.4. Data analyses

We used repeated-measures analysis of variance (RMANOVA) for each metabolic trial to test for significant variation in mean  $\dot{V}O_2$  among pre- and postprandial sampling periods. These analyses were followed by post-hoc pairwise mean comparisons (Tukey tests) to

**Table 1**

Body mass, meal size, pre- and postfeeding whole animal and mass-specific metabolic response variables including standard metabolic rate (SMR), peak oxygen consumption, scope of peak, duration, specific dynamic action (SDA) and SDA coefficient for *Dasypeltis inornata* and *D. scabra* adults and neonates in response to five temperature treatments.

Variable	Temperature (°C)					F	P
	20	25	27	30	32		
<i>Dasypeltis inornata</i>							
N	4	4	4	4	4		
Body mass (g)	65.2 ± 14.2	61.7 ± 12.7	62.9 ± 12.9	71.3 ± 16.3	65.1 ± 13.6	0.070	0.990
SMR (mL O <sub>2</sub> h <sup>-1</sup> )	1.03 ± 0.20 <sup>a</sup>	1.70 ± 0.38 <sup>a,b</sup>	2.30 ± 0.45 <sup>c</sup>	3.14 ± 0.67 <sup>c</sup>	3.27 ± 0.58 <sup>c</sup>	18.9	<0.0001
SMR (mL O <sub>2</sub> g <sup>-1</sup> h <sup>-1</sup> )	0.016 ± 0.001 <sup>a</sup>	0.033 ± 0.002 <sup>b</sup>	0.037 ± 0.003 <sup>c</sup>	0.044 ± 0.002 <sup>c,d</sup>	0.052 ± 0.001 <sup>d</sup>	35.6	<0.0001
Peak $\dot{V}O_2$ (mL O <sub>2</sub> h <sup>-1</sup> )	2.36 ± 0.48 <sup>a</sup>	4.00 ± 0.52 <sup>a,b</sup>	6.66 ± 1.39 <sup>b,c</sup>	8.81 ± 2.00 <sup>c</sup>	10.15 ± 1.90 <sup>c</sup>	11.8	0.0002
Peak $\dot{V}O_2$ (mL O <sub>2</sub> g <sup>-1</sup> h <sup>-1</sup> )	0.038 ± 0.004 <sup>a</sup>	0.071 ± 0.010 <sup>a,b</sup>	0.109 ± 0.014 <sup>b,c</sup>	0.124 ± 0.005 <sup>c,d</sup>	0.165 ± 0.019 <sup>d</sup>	16.9	<0.0001
Scope (peak $\dot{V}O_2$ /SMR)	2.33 ± 0.24	2.64 ± 0.42	2.90 ± 0.13	2.76 ± 0.10	3.16 ± 0.31	1.33	0.304
Duration (days)	13.5	12.5	7.5	6.5	6.5		
SDA (kJ)	6.00 ± 1.59	9.93 ± 1.14	10.84 ± 2.57	13.18 ± 3.03	13.19 ± 3.33	2.03	0.146
SDA (kJ kg <sup>-1</sup> )	94.8 ± 16.4	182.1 ± 35.1	184.1 ± 34.7	186.9 ± 17.9	216.4 ± 39.4	2.29	0.107
SDA coefficient (%)	6.24 ± 1.08	12.00 ± 2.31	12.13 ± 2.28	12.31 ± 1.18	13.55 ± 2.75	1.98	0.149
<i>Dasypeltis scabra</i> adults							
N	8	9	10	8	9		
Body mass (g)	54.2 ± 7.4	47.3 ± 6.5	51.2 ± 6.2	59.1 ± 8.3	54.5 ± 5.7	0.404	0.804
SMR (mL O <sub>2</sub> h <sup>-1</sup> )	0.70 ± 0.12 <sup>a</sup>	1.48 ± 0.18 <sup>b</sup>	1.69 ± 0.18 <sup>b,c</sup>	2.37 ± 0.35 <sup>c,d</sup>	2.40 ± 0.32 <sup>d</sup>	15.3	<0.0001
SMR (mL O <sub>2</sub> g <sup>-1</sup> h <sup>-1</sup> )	0.013 ± 0.001 <sup>a</sup>	0.032 ± 0.003 <sup>b</sup>	0.035 ± 0.003 <sup>b</sup>	0.041 ± 0.003 <sup>b</sup>	0.044 ± 0.004 <sup>b</sup>	13.9	<0.0001
Peak $\dot{V}O_2$ (mL O <sub>2</sub> h <sup>-1</sup> )	1.53 ± 0.25 <sup>a</sup>	3.10 ± 0.34 <sup>b</sup>	4.24 ± 0.38 <sup>b</sup>	5.73 ± 0.74 <sup>c</sup>	7.22 ± 0.53 <sup>d</sup>	43.5	<0.0001
Peak $\dot{V}O_2$ (mL O <sub>2</sub> g <sup>-1</sup> h <sup>-1</sup> )	0.028 ± 0.002 <sup>a</sup>	0.069 ± 0.005 <sup>b</sup>	0.088 ± 0.007 <sup>b</sup>	0.102 ± 0.010 <sup>b</sup>	0.139 ± 0.012 <sup>c</sup>	24.6	<0.0001
Scope (peak $\dot{V}O_2$ /SMR)	2.23 ± 0.09 <sup>a</sup>	2.18 ± 0.19 <sup>a</sup>	2.62 ± 0.21 <sup>a,b</sup>	2.47 ± 0.12 <sup>a,b</sup>	3.30 ± 0.32 <sup>b</sup>	4.57	0.0040
Duration (days)	14.5	13.5	10.5	9.5	7.5		
SDA (kJ)	3.89 ± 0.68 <sup>a</sup>	6.18 ± 1.12 <sup>a,b</sup>	6.76 ± 0.96 <sup>a,b,c</sup>	9.90 ± 1.36 <sup>c</sup>	9.12 ± 0.82 <sup>b,c</sup>	6.92	0.0003
SDA (kJ kg <sup>-1</sup> )	72.3 ± 8.9 <sup>a</sup>	129.7 ± 19.8 <sup>a,b</sup>	137.9 ± 17.1 <sup>a,b</sup>	182.5 ± 25.0 <sup>b</sup>	178.7 ± 21.2 <sup>b</sup>	5.07	0.0022
SDA coefficient (%)	4.76 ± 0.59 <sup>a</sup>	8.54 ± 1.30 <sup>a,b</sup>	9.09 ± 1.12 <sup>a,b</sup>	12.02 ± 1.65 <sup>b</sup>	11.77 ± 1.40 <sup>b</sup>	5.07	0.0022
<i>Dasypeltis scabra</i> neonates							
N	11	8	11	11	8		
Body mass (g)	4.66 ± 0.27 <sup>a,b</sup>	3.98 ± 0.20 <sup>a</sup>	4.46 ± 0.27 <sup>a,b</sup>	5.30 ± 0.26 <sup>b</sup>	4.45 ± 0.28 <sup>a,b</sup>	3.27	0.0198
SMR (mL O <sub>2</sub> h <sup>-1</sup> )	0.07 ± 0.001 <sup>a</sup>	0.11 ± 0.01 <sup>b</sup>	0.14 ± 0.01 <sup>b</sup>	0.19 ± 0.01 <sup>c</sup>	0.21 ± 0.01 <sup>c</sup>	36.5	<0.0001
SMR (mL O <sub>2</sub> g <sup>-1</sup> h <sup>-1</sup> )	0.015 ± 0.001 <sup>a</sup>	0.029 ± 0.002 <sup>b</sup>	0.030 ± 0.002 <sup>b</sup>	0.036 ± 0.003 <sup>b</sup>	0.049 ± 0.004 <sup>c</sup>	29.6	<0.0001
Peak $\dot{V}O_2$ (mL O <sub>2</sub> h <sup>-1</sup> )	0.16 ± 0.01 <sup>a</sup>	0.32 ± 0.02 <sup>b</sup>	0.44 ± 0.04 <sup>b</sup>	0.56 ± 0.03 <sup>c</sup>	0.79 ± 0.05 <sup>d</sup>	56.4	<0.0001
Peak $\dot{V}O_2$ (mL O <sub>2</sub> g <sup>-1</sup> h <sup>-1</sup> )	0.034 ± 0.001 <sup>a</sup>	0.082 ± 0.003 <sup>b</sup>	0.100 ± 0.008 <sup>b</sup>	0.107 ± 0.006 <sup>b</sup>	0.185 ± 0.019 <sup>c</sup>	36.4	<0.0001
Scope (Peak $\dot{V}O_2$ /SMR)	2.39 ± 0.12 <sup>a</sup>	2.94 ± 0.21 <sup>a,b</sup>	3.36 ± 0.28 <sup>b</sup>	3.12 ± 0.29 <sup>a,b</sup>	3.73 ± 0.26 <sup>b</sup>	4.19	0.0058
Duration (days)	16.5	12.5	9.5	8.5	7.5		
SDA (kJ)	0.38 ± 0.03 <sup>a</sup>	0.81 ± 0.05 <sup>b,c</sup>	0.64 ± 0.07 <sup>b</sup>	1.03 ± 0.08 <sup>c</sup>	1.02 ± 0.06 <sup>c</sup>	18.7	<0.0001
SDA (kJ kg <sup>-1</sup> )	82.0 ± 5.8 <sup>a</sup>	207.0 ± 17.3 <sup>b,c</sup>	146.2 ± 12.9 <sup>b</sup>	198.7 ± 17.8 <sup>b,c</sup>	235.3 ± 20.6 <sup>c</sup>	16.4	<0.0001
SDA coefficient (%)	5.40 ± 0.38 <sup>a</sup>	13.63 ± 1.14 <sup>b,c</sup>	9.63 ± 0.85 <sup>b</sup>	13.09 ± 1.17 <sup>b,c</sup>	15.50 ± 1.36 <sup>c</sup>	16.4	<0.0001

Note: Variables are defined in the text. Values are presented as mean ± 1 SE. P and F values result from GLM RMANOVA for body mass, SMR (mL O<sub>2</sub> g<sup>-1</sup> h<sup>-1</sup>), peak  $\dot{V}O_2$  (mL O<sub>2</sub> g<sup>-1</sup> h<sup>-1</sup>), scope, SDA (kJ kg<sup>-1</sup>) and SDA coefficient, and from GLM RMANCOVA (body mass as the covariate) for SMR (mL O<sub>2</sub> h<sup>-1</sup>), peak  $\dot{V}O_2$  (mL O<sub>2</sub> h<sup>-1</sup>) and SDA (kJ). Superscript letters that differ denote significant differences (P < 0.05) between means among temperature treatments determined from post-hoc pairwise mean comparisons (Tukey tests) for each variable.

identify when postprandial  $\dot{V}O_2$  was significantly greater than SMR and when it was no longer significantly greater than SMR. To test for significant effects of species, age and  $T_b$ , analysis of covariance (ANCOVA, body mass as the covariate) was used for whole-animal measures of SMR, peak  $\dot{V}O_2$  and SDA (kJ), and analysis of variance (ANOVA) for mass-specific variables, scope, and SDA coefficient. In the results, we report only the outcome of analysis based on whole animal measures of SMR and peak  $\dot{V}O_2$ . Since the same individuals were used for the five temperature treatments, we analyzed the  $T_b$  data using RMANOVA and found the results to be equivalent to the ANOVA and ANCOVA tests. We also used post-hoc pairwise comparison (Tukey tests) to identify significant differences for each variable between  $T_b$ . We used least squares linear regression analysis to examine the scaling relationships between  $\log_{10}$  transformed body mass and  $\log_{10}$  transformed whole-animal SMR, peak  $\dot{V}O_2$ , and SDA, and to generate predictive equations. Resultant  $P$  values from the RMANOVA and RMANCOVA are reported, and  $P$  values of selected significant pairwise mean comparisons are provided. We designated the level of statistical significance as  $P < 0.05$  and report mean values as means  $\pm 1$  standard error (SE). Statistical tests were performed using Statistica 9.0 (Statsoft®, Tulsa, Oklahoma USA).

### 3. Results

#### 3.1. Postprandial response at different body temperatures

Body mass of adult *D. inornata* and *D. scabra* did not significantly vary among the five body temperature treatments (Table 1). However, for neonate *D. scabra* mean body mass varied ( $P = 0.020$ ) due to neonates being heavier in the 30 °C trial compared to the 25 °C trial (Table 1). For adults and neonates, SMR increased with an increase in  $T_b$  (Table 1). From 20 °C to 32 °C, SMR tripled with respective  $Q_{10}$ 's of

2.62, 2.81 and 2.61 for adult *D. inornata*, adult *D. scabra*, and neonate *D. scabra*.

For all three sets of snakes,  $T_b$  had a very observable impact on the profile of their postprandial metabolism (Fig. 1). At 20 °C, there was an immediate increase in  $\dot{V}O_2$ , after which rates remained at a plateau for more than two weeks. With the increase to 25 °C, snakes responded similarly with an elevated  $\dot{V}O_2$  that plateaued over 10 days. Beginning at 27 °C,  $\dot{V}O_2$  was characterized by a distinct peak that became more evident at 30 °C and 32 °C as the profiles became narrower and shorter (Fig. 1). The postprandial peak in  $\dot{V}O_2$  differed significantly ( $P$  values  $< 0.0002$ ) among temperature treatments, increasing more than 4-fold from 20 °C to 32 °C for each set of snakes ( $Q_{10}$ 's = 3.38–3.82; Table 1). Across temperature treatments, the factorial scope of peak  $\dot{V}O_2$  did not vary significantly for *D. inornata*, but was significantly different among temperatures for adult and neonate *D. scabra* ( $P$  values  $< 0.006$ ; Table 1). For neonate and adult *D. scabra*, the scope of peak  $\dot{V}O_2$  were significantly greater at 32 °C than at 20 °C (Table 1). With an increase in  $T_b$ , the duration of the metabolic response decreased from 13.5–16.5 days at 20 °C to 6.5–7.5 days at 32 °C (Table 1). Adult and neonate *D. scabra* experienced significant ( $P$  values  $\leq 0.0022$ ) variations in SDA (kJ and  $\text{kJ kg}^{-1}$ ) across temperature treatments. SDA was noticeably low at 20 °C, increased at 25 °C and 27 °C, and increased further at 30 °C and 32 °C (Table 1). In similar fashion, SDA coefficients varied significantly ( $P$  values  $\leq 0.0022$ ) among temperature treatments; more than doubling from 20 °C to 32 °C for neonates and adults (Table 1).

#### 3.2. Effects of body size

Neonate and adult *D. scabra* experience near identical postprandial metabolic profiles for each of the tested  $T_b$ 's (Fig. 1). Although SMR

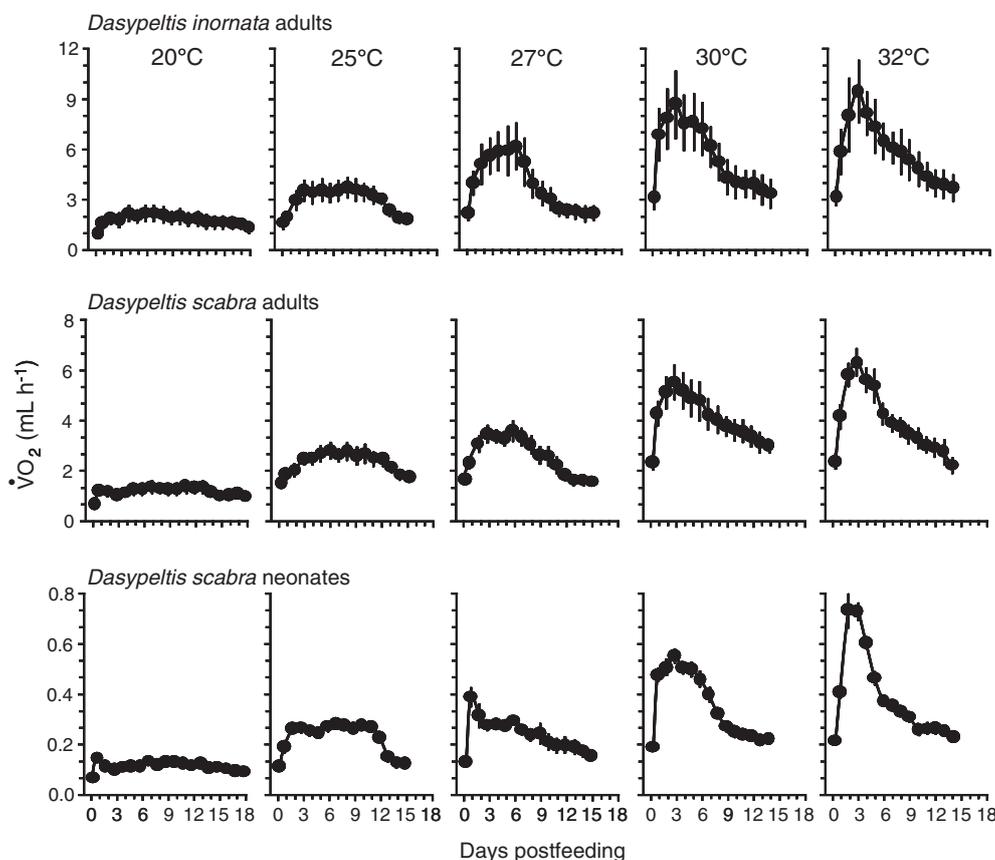


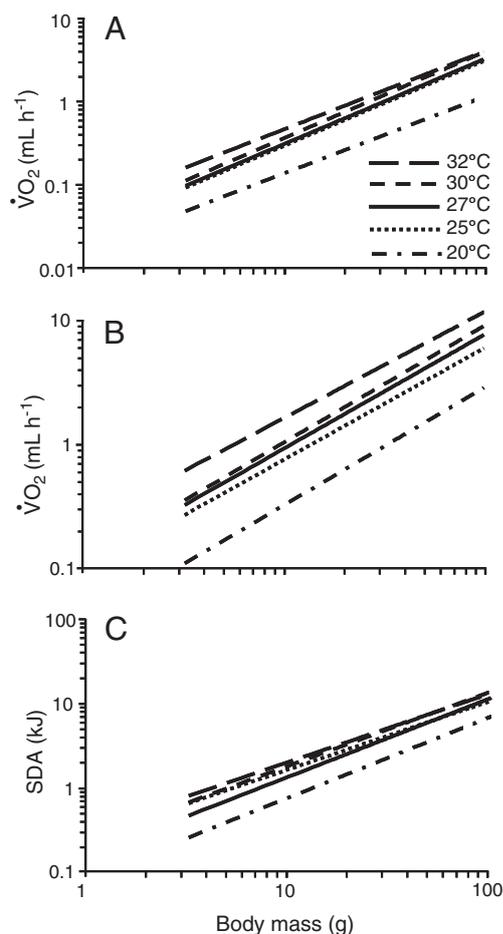
Fig. 1. Mean  $\dot{V}O_2$  ( $\text{mL h}^{-1}$ ) of adult *Dasypeltis inornata*, adult *Dasypeltis scabra*, and neonate *Dasypeltis scabra* before (day 0) and up to 18 days following the consumption of a liquid egg meal weighing 20% of snake body mass at body temperatures of 20, 25, 27, 30, and 32 °C. Postprandial metabolic profiles of *Dasypeltis* become shorter in duration and more elevated with increasing body temperature. Error bars are  $\pm 1$  SE and are omitted if the SE is smaller than the symbol for mean value.

**Table 2**

Mass coefficients, mass exponents, and  $\dot{V}O_2$  equations generated from linear regression analysis for standard metabolic rate (SMR), postprandial peak  $\dot{V}O_2$ , and specific dynamic action (SDA) against body mass. We indicate the slopes (e.g., mass exponents) that were not significantly different from 1.0.

	Mass coefficient	Mass exponent	Equation	r <sup>2</sup>	b = 1.0
<b>SMR (<math>\dot{V}O_2</math>)</b>					
20 °C	-1.788 ± 0.044	0.929 ± 0.036	0.016 W <sup>0.929</sup>	0.975	NS
25 °C	-1.555 ± 0.061	1.029 ± 0.048	0.028 W <sup>1.029</sup>	0.968	NS
27 °C	-1.531 ± 0.057	1.027 ± 0.046	0.029 W <sup>1.027</sup>	0.964	NS
30 °C	-1.480 ± 0.060	1.044 ± 0.048	0.033 W <sup>1.044</sup>	0.964	NS
32 °C	-1.271 ± 0.064	0.941 ± 0.048	0.054 W <sup>0.941</sup>	0.962	NS
<b>Peak <math>\dot{V}O_2</math></b>					
20 °C	-1.442 ± 0.060	0.956 ± 0.049	0.036 W <sup>0.956</sup>	0.957	NS
25 °C	-1.026 ± 0.037	0.907 ± 0.029	0.094 W <sup>0.907</sup>	0.985	<0.01
27 °C	-0.956 ± 0.058	0.926 ± 0.047	0.111 W <sup>0.926</sup>	0.954	NS
30 °C	-0.930 ± 0.054	0.950 ± 0.043	0.117 W <sup>0.950</sup>	0.966	NS
32 °C	-0.648 ± 0.063	0.865 ± 0.047	0.225 W <sup>0.865</sup>	0.957	<0.05
<b>SDA (kJ)</b>					
20 °C	-1.080 ± 0.069	0.968 ± 0.057	0.083 W <sup>0.968</sup>	0.945	NS
25 °C	-0.598 ± 0.087	0.819 ± 0.069	0.252 W <sup>0.819</sup>	0.905	<0.05
27 °C	-0.808 ± 0.087	0.942 ± 0.069	0.156 W <sup>0.942</sup>	0.908	NS
30 °C	-0.624 ± 0.085	0.886 ± 0.068	0.237 W <sup>0.886</sup>	0.910	NS
32 °C	-0.512 ± 0.075	0.822 ± 0.056	0.308 W <sup>0.822</sup>	0.934	<0.01

and peak  $\dot{V}O_2$  were greater for adults, given their larger body mass, both age classes experience similar factorial scopes of peak  $\dot{V}O_2$  (Table 1). At each temperature, the duration of elevated metabolism



**Fig. 2.** Standard metabolic rate (A), postprandial peak  $\dot{V}O_2$  (B), and specific dynamic action (SDA, C) plotted against body mass for *Dasyveltis scabra* ranging in mass from 3.21 to 97.5 g for each tested temperature (20, 25, 27, 30 and 32 °C). Postprandial peak  $\dot{V}O_2$  and SDA were generated from liquid egg meals equaling in mass to 20% of snake body mass. Body mass, SMR, Peak  $\dot{V}O_2$ , and SDA were  $\log_{10}$  transformed proper to generating equations. Y-intercepts varied as a function of body temperature whereas scaling exponents were generally similar among the different temperatures.

**Table 3**

Predicted equations for SMR ( $\text{mL O}_2 \text{ h}^{-1}$ ), peak  $\dot{V}O_2$  ( $\text{mL h}^{-1}$ ), and SDA (kJ) for *Dasyveltis scabra* using logged ( $\log_{10}$ ) data. Body mass and meal mass are in g,  $T_b$  is in °C, and meal energy is in kJ. For each equation, the factors of body mass, body temperature, meal mass, and meal energy contribute significantly to the equation.

Equation	r <sup>2</sup>	P
Log SMR = 0.995 log bm + 0.041 $T_b$ - 2.64	0.961	<0.0001
Log peak $\dot{V}O_2$ = 0.923 log bm + 0.053 $T_b$ - 2.44	0.963	<0.0001
Log SDA = 0.891 log bm + 0.032 $T_b$ - 1.59	0.913	<0.0001
Log SDA = 0.479 log bm + 0.413 log meal mass - 0.38	0.913	<0.0001
Log SDA = 0.656 log bm + 0.234 log meal mass + 0.018 $T_b$ - 1.0	0.919	<0.0001
Log SDA = 0.760 log meal energy - 0.59	0.853	<0.0001
Log SDA = 0.811 log meal energy - 0.017 $T_b$ - 0.19	0.867	<0.0001

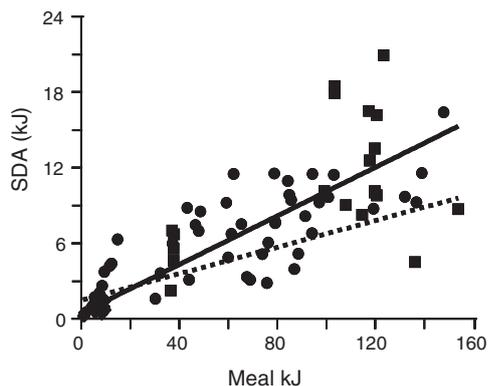
averaged a day different between age classes (Table 1). Weighing on average 11.6-fold heavier than neonates, adult *D. scabra* experienced SDA's that averaged 9.5 times greater. When adjusted to body mass or meal energy, SDA did not differ between age classes at each temperature (with the exception of 25 °C). Standard metabolic rate, postprandial peak  $\dot{V}O_2$  and SDA plotted against body mass ( $\log_{10}$ - $\log_{10}$ ) for all temperature treatments scaled with respective mass exponents between 0.929–1.044, 0.864–0.956, and 0.819–0.968 (Table 2, Fig. 2). For SMR, scaling exponents did not differ significantly from 1.0 at any temperature, whereas exponents were significantly less than 1.0 for peak  $\dot{V}O_2$  and SDA at 25 °C and 32 °C (Table 2). *Dasyveltis scabra* specific equations that incorporate both body mass and  $T_b$  possess similar mass scaling exponents and provide an additional means to predict SMR, peak  $\dot{V}O_2$ , and SDA (Table 3).

### 3.3. Species comparisons

Adults of *D. inornata* and *D. scabra* experienced very similar postprandial metabolic profiles across tested temperatures (Fig. 1). With few exceptions, body mass and metabolic variables did not differ significantly between the two species at each tested temperature (Table 1). Although peak  $\dot{V}O_2$  at 27 °C and 30 °C did differ significantly ( $P$  values < 0.05) between the two species, they exhibited very similar factorial scopes of peak  $\dot{V}O_2$ . Mean  $\dot{V}O_2$  ( $\text{mL h}^{-1}$ ) and SDA were generally greater for *D. inornata* than for *D. scabra* owing to differences in body mass (Table 1). However, the duration of elevated postprandial  $\dot{V}O_2$  at each temperature was 1–3 days longer for *D. scabra* than for *D. inornata* (Table 1).

### 4. Discussion

Adult and neonate *Dasyveltis inornata* and *D. scabra* experience postprandial metabolic responses that are characteristic of other reptiles (Secor, 2009). Feeding triggers a rapid increase in gas exchange rates that usually peaks within 48 hours before returning to prefeeding levels within a week (see Secor, 2009 for model response). Body temperature influences the shape of the postprandial profile for ectotherms, as it did for *Dasyveltis*. The duration of their postprandial metabolic response decreased with increasing  $T_b$ , as observed for other ectotherms (Wang et al., 2003; Secor and Boehm, 2006; Secor et al., 2007). For *D. scabra*, SMR, postprandial peak  $\dot{V}O_2$ , and SDA scaled with mass exponents ranging from 0.819 to 1.044. The energy expended by neonate and adult *Dasyveltis* to digest and assimilate their egg meals represented a relatively modest 4.8–15.5% of the meal's energy (Fig. 3). In the ensuing discussion, we will highlight the effects of body temperature and body size on the pre- and postprandial metabolic responses and SDA of *Dasyveltis* and comment on the differences in SDA experienced by snakes when digesting a liquid egg meal compared to an intact prey item.



**Fig. 3.** Specific dynamic action (SDA, kJ) plotted against ingested meal energy (kJ) for adult *Dasypleltis inornata* (■), adult *Dasypleltis scabra* (●), and neonate *Dasypleltis scabra* (◆). The solid line represents the predicted relationship between meal energy and SDA for trials conducted at 25, 27, 30, and 32 °C, whereas the dotted line represents this relationship for the trials conducted at 20 °C.

#### 4.1. Temperature effects on postprandial metabolism and SDA

For the ectothermic *Dasypleltis*, metabolic rates and the speed of physiological processes are dictated by ambient temperatures, which determines body temperatures. With each 10 °C increase in body temperature, metabolic rates of ectotherms typically increase by 2- to 3-fold (Bennett and Dawson, 1976). The temperature-dependent shifts in SMR we observed for *Dasypleltis* are very similar to those noted for other snake species (Benedict, 1932; Greenwald, 1971; Jacobson and Whitford, 1971; Secor and Nagy, 1994; Dorcas et al., 2004). Studies that have examined the effects of temperature on postprandial metabolism illustrate a near identical pattern of metabolic profiles across different temperatures. At low temperatures (15–20 °C), the increase in  $\dot{V}O_2$  is relatively modest, and the profile has a characteristic plateau shape with rates remaining elevated for 1–2 weeks before slowly returning to baseline (Secor and Faulkner, 2002; Secor and Boehm, 2006; Tsai et al., 2008; Bessler et al., 2010). With each increase in  $T_b$  (2–5 °C), the profile exhibits a more distinct peak and metabolic rates return to baseline sooner. At the highest experimental temperatures (30–35 °C), postprandial metabolism rises very rapidly, peaks within 48 h and returns to baseline within a week (Secor and Faulkner, 2002; Secor and Boehm, 2006; Tsai et al., 2008; Bessler et al., 2010). Postprandial  $\dot{V}O_2$  of *Dasypleltis* remained at a plateau for two weeks at 20 °C, exhibited a distinct peak at 27 °C, and at 32 °C had returned to baseline after one week (Fig. 1). Suggestive from the metabolic data is that *Dasypleltis* takes at least twice as long to digest and assimilate a meal at 20 °C compared to 32 °C.

In similar fashion to SMR, peak  $\dot{V}O_2$  increases with  $T_b$  for all three groups of *Dasypleltis*. For *D. scabra*, peak  $\dot{V}O_2$  tended to increase with temperature at a greater rate than SMR, resulting in an increase in the factorial scope of peak  $\dot{V}O_2$  with temperature. Whereas other studies have documented increases in peak  $\dot{V}O_2$  with  $T_b$ , the scope of peak  $\dot{V}O_2$  generally does not vary with  $T_b$ ; SMR and peak  $\dot{V}O_2$  respond similarly to changes in  $T_b$  (Secor and Faulkner, 2002; Secor and Boehm, 2006; Secor et al., 2007). In addition to *Dasypleltis*, temperature-dependent variation in the scope of peak  $\dot{V}O_2$  has been documented for *Rana catesbeiana* and *Thamnophis sirtalis* (Secor et al., 2007; Bessler et al., 2010).

Body temperature strongly impacts the speed of digestion and passage, as rates of gastric breakdown, intestinal absorption, and substrate assimilation increase with  $T_b$ . Thus, the duration of meal digestion is shortened with increasing  $T_b$  (Skoczylas, 1970; Freed, 1980). Similar temperature-dependent effects on the duration of the SDA response have also been observed for amphibians and other snakes (Secor and Faulkner, 2002; Wang et al., 2003; Secor and Boehm, 2006; Secor et al., 2007; Tsai et al., 2008; Bessler et al., 2010). For

studies that include a 20 °C and a 30 °C treatment, the duration of the SDA response decreases on average by  $41.3 \pm 3.6\%$  (range 16.6–55.4%) from 20 °C to 30 °C, similar to the average of 45% observed for the three sets of *Dasypleltis* in this study (Secor and Faulkner, 2002; Secor and Boehm, 2006; Secor et al., 2007; Tsai et al., 2008; Bessler et al., 2010).

We earlier proposed that SDA would remain stable regardless of  $T_b$ . Other studies have found SDA not to significantly vary over a range of experimental temperatures (Jobling and Davies, 1980; Powell et al., 1999; Secor and Faulkner, 2002; Wang et al., 2003; Secor et al., 2007). Hypothesized is that regardless of the speed of digestion and the shape of the postprandial metabolic profile, the digestion and assimilation of a given meal entails the same amount of expended energy (Secor and Faulkner, 2002). For all three sets of *Dasypleltis*, SDA was impacted by  $T_b$ , most notably for neonate and adult *D. scabra* (Table 1). For adult *D. inornata*, SDA was matched among the 25, 27, 30, and 32 °C trials, however mean SDA at 20 °C was half of that of the other temperatures (Table 1). Adult *D. scabra* likewise exhibited the lowest SDA at 20 °C, with SDA nearly doubling at 25 °C and 27 °C and increasing further (~50%) at 30 °C and 32 °C. Neonate *D. scabra* also experienced their lowest SDA at 20 °C with SDA increasing 2- to 3-fold at the four higher temperature treatments. Counter to the stable SDA hypothesis, *Dasypleltis* expend varying amounts of energy in the digestion of their egg meal at different  $T_b$ . Temperature-dependent variation in SDA has also been observed for the tiger salamander (*Ambystoma tigrinum*), green treefrog (*Hyla cinerea*), American bullfrog (*Rana catesbeiana*), common garter snake (*Thamnophis sirtalis*) and timber rattlesnake (*Crotalus horridus*) (Zaidan and Beaupre, 2003; Secor and Boehm, 2006; Secor et al., 2007; Bessler et al., 2010). A pattern similar to that of *D. inornata*; low SDA at the lowest temperature and stable SDA at all higher temperatures, was also observed for *A. tigrinum* and the grass snake *Natrix natrix*, whereas stepwise increases in SDA with higher  $T_b$ , as seen for *D. scabra*, was observed for *T. sirtalis* (Hailey and Davies, 1987; Secor and Boehm, 2006; Bessler et al., 2010). A potential explanation for the depressed SDA at the lower  $T_b$  is that these animals experience a reduction in overall digestive performance, and hence effort, at such low temperatures (Bessler et al., 2010).

#### 4.2. Body size and pre- and postprandial metabolism

Few studies have simultaneously examined pre- and postfeeding metabolic responses across age classes or over a range of body sizes (see Secor and Diamond, 1997; Secor and Faulkner, 2002; Zaidan and Beaupre, 2003). When comparing the postprandial metabolic responses to the same relative meal size, meal type, and body temperature, neonate and adult individuals exhibit similar metabolic profiles (Secor, 1995; Secor and Diamond, 1997). Standard metabolic rates of snakes traditionally scale allometrically with body mass with intraspecific mass exponents ranging from 0.57 to 0.88 when SMR is measured at 30 °C (Andrews and Pough, 1985; Chappell and Ellis, 1987; Secor and Diamond, 1997; Peterson et al., 1998). In the present study, over a 30-fold range in body mass and for each tested temperature, *D. scabra* SMR scaled with mass exponents that were never significantly different than 1.0, hence greater than the scaling exponents for SMR observed for other snakes.

In this study, a steeper scaling relationship may stem from a relatively low metabolic rate for neonates, a relatively high metabolic rate for adults, or both. Unfortunately there are few intraspecific scaling equations of SMR for snakes, and among such studies the variation in SMR is due in part to the different methods used to quantify SMR (Andrews and Pough, 1985). We applied scaling equations generated for *Trimeresurus stejnegeri* (Viperidae), *Eryx colubrinus* (Boidae), and *Thamnophis sirtalis* (Colubridae) to calculate predicted SMR at 30 °C for a 5 and 55 g *D. scabra* (Chappell and Ellis, 1987; Peterson et al., 1998; Tsai et al., 2008). These studies were selected because they each include a range of body masses that overlap the range of body

masses of *D. scabra* used in this study. The predicted SMR of 0.179 mL h<sup>-1</sup> (at 5 g) and 2.172 mL h<sup>-1</sup> (at 55 g) for *D. scabra* at 30 °C (Table 2) were found to be 37%, 46%, and 18.3% of that predicted for a 5-g snake, and 72%, 92%, and 44% of that predicted for a 55-g snake, respectively, for *T. stejnegeri*, *E. colubrinus*, and *T. sirtalis* from scaling equations presented in those studies. While certainly not conclusive, the seemingly low SMR of neonate *D. scabra* appear to drive the higher (than expected) mass scaling exponents of SMR observed in this study.

The scaling exponents for peak  $\dot{V}O_2$  for *D. scabra*, ranging from 0.865 to 0.956, did not significantly differ from that determined for *P. molurus* digesting 25% sized meals at 30 °C (mass exponent =  $0.90 \pm 0.03$ ; Secor and Diamond, 1997). In the python study, the mass exponent was significantly less than 1.0, and greater than the exponent for SMR. For three temperatures (20, 27, and 32 °C), the mass exponent of peak  $\dot{V}O_2$  for *D. scabra* did not significantly differ from 1.0 (the other two were less than 1.0), and the scaling exponents for SMR were greater than those for peak  $\dot{V}O_2$  (except at 20 °C), being significant at 25, 27, and 30 °C. Whereas *P. molurus* experience an increase in the factorial scope of peak  $\dot{V}O_2$  with body mass, this was not observed for *D. scabra* (Secor and Diamond, 1997). In contrast at 25 °C, the scope of peak  $\dot{V}O_2$  declined with an increase in body mass.

The body mass scaling of SDA can be examined by feeding animals the same food type, weighing the same relative mass (e.g., 10% or 25%), and conducting metabolic studies at the same  $T_b$  (Secor and Diamond, 1997; Secor and Faulkner, 2002). Over a respective 100-fold and 120-fold range in body mass, SDA of *B. marinus* and *P. molurus* (both at  $T_b = 30$  °C) scaled with mass exponents of  $1.02 \pm 0.04$  and  $1.01 \pm 0.02$  (Secor and Diamond, 1997; Secor and Faulkner, 2002). For 19 taxa of snakes that had consumed rodent meals equaling 25% of body mass and studied at 30 °C, the interspecific mass scaling exponent was 1.11 (Secor, 2009). Mass exponents of SDA for *D. scabra* are less than those observed previously and significantly less than 1.0 at 25 and 32 °C. Currently lacking are studies that would enable an evaluation, from a comparative perspective, of the intraspecific scaling of SDA for *Dasypeltis*. New studies, especially on colubrid snakes, that examine the scaling relationships of postprandial metabolism and SDA would identify whether *Dasypeltis* exhibit a uniquely low SDA scaling, or whether the intraspecific scaling relationship for SDA is variable among snakes.

#### 4.3. The postprandial metabolic response of an oophagus snake

One aim of this study was to explore whether the liquid diet of *Dasypeltis* generates a postprandial metabolic profile and SDA distinctly different from that observed for snakes that consume solid and intact prey. Given that SMR sets the baseline for the postprandial profile and hence the calculation of SDA, a first start is to compare SMR among species while considering the differences in body mass and temperature. At 30 °C, the SMR of *D. inornata* (body mass =  $71.3 \pm 16.3$  g) and *D. scabra* (body mass =  $59.0 \pm 8.3$  g) averaged  $3.14 \pm 0.67$  and  $2.37 \pm 0.35$  mL h<sup>-1</sup> (Table 1). Without an interspecific scaling equation for SMR specific for colubrid snakes, we can only compare *Dasypeltis* SMR to the predicted values generated from intraspecific analysis conducted on other colubrid species of similar size. For the colubrids *Helicops modestus*, *Liophis miliaris*, and *T. sirtalis*, predicted SMR (30 °C) at 71.3 g (*D. inornata*) and 59.0 g (*D. scabra*) were on average 110% and 140% greater, respectively, than the SMR of *D. inornata* and *D. scabra* (Abe and Mendes, 1980; Peterson et al., 1998). Interestingly, the SMR of both species of *Dasypeltis* in this study, and *D. scabra* (47 g, 2.82 mL O<sub>2</sub> h<sup>-1</sup>) studied by Großmann and Starck (2006), were more similar to the predicted SMR at those body masses of the boid *E. colubrinus* (2.90 and 2.51 mL O<sub>2</sub> h<sup>-1</sup>, respectively) and the viperid *T. stejnegeri* (3.69 and 3.19 mL h<sup>-1</sup>, respectively) (Chappell and Ellis, 1987; Peterson et al., 1998; Tsai et al., 2008). Previously noted is that infrequently feeding snakes of

the families Boidae, Pythonidae, and Viperidae tend to possess SMR that are 50% less than the SMR of frequently feeding snakes of the family Colubridae (Ott and Secor, 2007). Secor and Diamond (2000) suggested that the lower SMR exhibited by infrequently feeding snakes stem from an adaptive response that downregulates the gastrointestinal tract between meals thereby reducing metabolic expenditure. A generated equation that incorporates both body mass and temperature suggests that *D. scabra* possess SMR more similar to that of infrequently feeding snakes compared to that of other colubrid snakes (Table 1). Yet to be determined is whether *Dasypeltis*, like boas, pythons, and vipers, downregulate their gastrointestinal tract between meals.

Interspecific comparisons of postprandial metabolic responses and SDA are best conducted with matched meal type, relative meal mass, and body temperature (Secor, 2009). The only other investigation of the postprandial metabolic responses to an egg meal, 20% of body mass at 30 °C, is the Großmann and Starck (2006) study on *D. scabra*. In that study snakes experienced an 80% increase in postprandial metabolism, maintained significantly elevated  $\dot{V}O_2$  for 11 days, and experienced a SDA coefficient of 13.2% (calculated from Fig. 4, Großmann and Starck, 2006). Independent of body mass, SMR, peak  $\dot{V}O_2$ , SDA, and SDA coefficient did not differ between adult *Dasypeltis* of the two studies. All other studies conducted at 30 °C that included a 20% meal size had fed snakes intact rodents (Table 4). For those five studies involving *Boa constrictor*, *Crotalus durissus*, *P. molurus*, and *T. stejnegeri*, the factorial scope of peak  $\dot{V}O_2$  averaged 5.29 (3.72–8.59), the duration of the metabolic response averaged 5.8 days (3.5–8), and SDA averaged 317 kJ kg<sup>-1</sup> (174–490) (Table 4; Andrade et al., 1997; Overgaard et al., 2002; Toledo et al., 2003; Wang et al., 2003; Tsai et al., 2008).

There are several features of the postprandial metabolic response and SDA of *Dasypeltis* that stand out from other snakes. First, *Dasypeltis* experiences a relatively modest scope of postprandial metabolism, with  $\dot{V}O_2$  little more than doubling after feeding. Snakes typically experience a 3.5- to 8-fold increase in  $\dot{V}O_2$  following the consumption of a rodent meal of similar size (Secor, 2009). Second, *Dasypeltis* maintains an elevated  $\dot{V}O_2$  after feeding longer than generally observed for colubrid snakes, even those that have consumed meals equaling 25% of body mass (Secor, 2009). Third, the SDA of *Dasypeltis* (accounting for body mass) sits at the low end of the range of SDA documented for snakes consuming similar sized meals at 30 °C (Table 4). A similarly low SDA was documented for *C. durissus*, and the authors of that study suggested that the peak  $\dot{V}O_2$  is, in part, suppressed due to the facilitation of gastric breakdown by the injected venom's proteolytic enzymes (Andrade et al., 1997). For 12 other species of colubrids that have consumed intact rodent or fish meals (20–25% of body mass), the SDA coefficient averages  $16.3 \pm 1.7$ , whereas for the three groups of *Dasypeltis* of this study and including *D. scabra* from Großmann and Starck (2006), SDA coefficient averaged  $12.7 \pm 0.3$  (Secor, 2009; Bessler et al., 2010). This difference is extended to other reptiles as well. For a 50-g animal at 25 °C, SDA is 48% less for *D. scabra* compared to reptiles in general as predicted from two equations incorporating meal mass or meal energy (Table 3; Table 3 of Secor, 2009).

The scope of peak  $\dot{V}O_2$  and SDA for *Dasypeltis* can best be explained by the liquid consistency of the meal. A fragmented or liquid meal would intuitively take less effort to be broken down for absorption. The python, *P. molurus*, expends 12% less energy in the digestion and assimilation of a ground steak meal compared to that of an intact steak meal (Boback et al., 2007). For snakes, the cost of gastric breakdown of an intact rodent meal can contribute significantly to postprandial metabolism and SDA (Secor, 2003; Andrade et al., 2004). Ingesting an already liquefied meal ready for intestinal passage reduces gastric effort, thereby generating a lower SDA. In support, a liquid meal of casein and a homogenized liquid meal of casein, chicken fat, and glucose reduced SDA by a respective 43% and 56% compared to that generated from intact meals for *P. molurus* (Secor, 2003; McCue et al., 2005). Specific to an egg meal (no shell), Gila monsters (*Heloderma suspectum*)

**Table 4**  
Tabulation of data illustrating the scope of peak  $\dot{V}O_2$ , duration, SDA, and SDA coefficient for studies on snakes conducted at 30 °C and with a meal size 20% of snake body mass.

Species	Body mass (g)	Meal type	Scope	Duration (days)	SDA (kJ)	SDA (kJ kg <sup>-1</sup> )	SDA coefficient	Source
<i>Boa constrictor</i>	137	Rodent	3.96	4.8	34.4	251	16.8	Toledo et al. (2003)
<i>Crotalus durissus</i>	42	Rodent	3.72	3.5	7.3	174	12.2	Andrade et al. (1997)
<i>Python molurus</i>	300	Rodent	8.59		118	393	24.5	Overgaard et al. (2002)
<i>Python molurus</i>	500	Rodent	6.30	8.0	248	490	31.0	Wang et al. (2003)
<i>Trimeresurus stejnegeri</i>	53.7	Rodent	3.88	7.0	14.8	276	16.0	Tsai et al. (2008)
<i>Dasypeltis scabra</i>	47	Egg	1.97	11.0	8.88	189	13.2	Großmann and Starck (2006)
<i>Dasypeltis inornatus</i>	71.3	Egg	2.76	6.5	13.2	187	12.3	This study
<i>Dasypeltis scabra</i>	59.1	Egg	2.47	9.5	9.9	183	12.0	This study

expend 24% less energy in digesting and processing egg meals weighing 10% of the lizard body mass compared to intact rodent meals of the same size (Christel et al., 2007). Whereas differences in the SDA coefficient could be explained by differences in meal energy, the mass-specific energy of the egg meal (7.59 kJ g<sup>-1</sup>) is similar to that of rodent meals used in the other studies (6.81–8.00 kJ g<sup>-1</sup>; Secor and Diamond, 2000; Roe et al., 2004; Bessler et al., 2010).

The second feature, a longer duration of elevated postprandial metabolism, is puzzling. If a liquid egg meal is easier to digest and assimilate, then why does it seem to take longer than the digestion of a similar-size intact rodent meal? For *H. suspectum*, the duration of the SDA response for the egg meal was a day less than that resulting from the digestion of an intact rodent meal (Christel et al., 2007). A relatively long duration of the SDA response for *D. scabra* was observed both in the present study and in the study of Großmann and Starck (2006). Plausible explanations include that the consistency of the egg requires more time for passage through the snake's gastrointestinal tract, that their small intestine invests more time and effort in the breakdown of the egg proteins and absorption of the amino acids, and/or that a longer time is needed for the assimilation of those amino acids. Each of these scenarios is speculative and would require studies on gastrointestinal passage, intestinal hydrolase and transporter capacities, and assimilation efficiencies to be firmly addressed.

#### 4.4. Ecological and evolutionary implications

*Dasypeltis* forage at night, actively searching for freshly-laid eggs of ground and arboreal nesting birds (Lloyd, 2004; Nalwanga et al., 2004). Hence they are most successful, and may only feed when eggs are most abundant during the peak egg laying season that generally extends from August to February in South Africa (Hockey et al., 2005). During this period, and encompassing the geographic range of *Dasypeltis* in South Africa, ambient temperatures range between 10 (nighttime) and 32.5 °C (daytime) (Schulze et al., 2008). Over much of this temperature range we demonstrate that *Dasypeltis* are able to digest and assimilate their egg meals. At lower nighttime temperatures (<20 °C), rates of digestion would further decrease and may practically cease. Such a depression in digestion would be temporary, lasting until warmer daytime temperatures sparked an increase in digestive performance. Expectedly with declining temperatures in fall and winter (March–July) and the cessation of egg-laying by many bird species, it is believed that *Dasypeltis* becomes relatively dormant and fasts during the winter months.

The reports of *Dasypeltis* feeding in the wild are largely anecdotal, and make note that a snake will consume one to all of the eggs in a nest (depending on egg size), as evident by the discarded collapsed shells within or outside the nest (Dyer, 1996; Lloyd et al., 2001; Krüger, 2004; Pryke and Lawes, 2004; Underhill et al., 2009). In southern Africa, it is estimated that *Dasypeltis* is capable of consuming the eggs of 232 species of ground and arboreal nesting birds, of which the eggs of finches (Fringillidae, Estrilididae) and weaverbirds (Ploceidae) are considered the most preyed upon (Gartner and Greene, 2008). Among these bird species, clutch sizes are typically 2–4 eggs, each weighing 1 (finches) to 3 g (weaverbirds) (Payne, 1977). Therefore, if

an adult *Dasypeltis* (~50 g) raids a nest, it may consume as much as 4 to 12 g of egg liquid, which would be equivalent to 8–24% of its body mass. In this study, and that of Großmann and Starck (2006), snakes were fed egg meals equivalent to 20% of body mass, and there are observations of snakes consuming egg meals of much greater relative masses (Rabb and Snedigar, 1960; Gans, 1974; Krupa, 1985). This suggests that *Dasypeltis* could readily consume all the eggs in one or a couple of finch nests or in a single weaver bird's nest. A week or more would then be spent digesting that meal before resuming foraging (Lloyd et al., 2001). During peak foraging months, an adult *Dasypeltis* could be responsible for the complete predation of as many as 25–50 nests. For the ground-nesting Namaqua sandgrouse (*Pterocles namaqua*) and grass/shrub-nesting red-collared widowbirds (*Euplectes ardens*) it is estimated that *Dasypeltis* is responsible for 20% (13.0–43.5% per year) and 27% of all egg predation events, respectively (Lloyd et al., 2001; Pryke and Lawes, 2004).

*Dasypeltis* possess a remarkable suite of morphological adaptations for their obligate diet of freshly-laid bird eggs (Gans, 1974). To swallow a relatively large (several times the diameter of their head), smooth-surface, spherical (in cross section) item, they largely lack teeth and possess elongated mandibles and expandable skin (Gans, 1974). Elongated and anteriorly facing the hypapophyses on the 17th through 38th vertebrae hold the swallowed egg in place within the esophagus and by extending through folds in the esophagus bear down in a sawing-like fashion cracking the egg shell (Gans, 1974; Gartner and Greene, 2008). The egg contents are squeezed out and propelled into the stomach and the collapsed egg shell reverses its path and is regurgitated. All other snakes that facultatively consume eggs swallow and digest the entire egg (see for example Gans and Oshima, 1952; Savidge, 1988; Gardner and Mendelson, 2003). Lacking the cranial adaptations of *Dasypeltis*, these snakes (e.g., *Elaphe* and *Lampropeltis*) tend to struggle with egg swallowing (Gartner and Greene, 2008). For facultative egg-eaters, the egg shell is either mechanically cracked within the stomach (compressed by gastric smooth or axial skeletal muscles) or dissolved by stomach acid. In either case, gastric acid production must be sufficient enough to dissolve the shell prior to passage into the small intestine, in similar fashion to the breakdown of a prey's skeleton (Secor, 2003).

Without having to deal with a shell or a skeleton, the efforts of the stomach would be more modest in preparing a liquid egg meal for intestinal passage. As part of the selective regime that encompasses the morphological and behavioral traits for egg eating, we could envision two anatomical and physiological traits of the gastrointestinal tract of *Dasypeltis* that arose concurrently to facilitate the digestion and absorption of an egg meal. Such adaptations would serve to maximize egg breakdown and absorption, while minimizing the expense of gut maintenance and food processing. First, relaxed pressure on gastric performance might have led to a reduction in stomach size or tissue architecture, as well as depression of pepsin and HCl production. Second, their long episodes of digestive quiescence due to the lack of nesting birds may have provided adequate selective pressure for *Dasypeltis* to evolve the capacity to downregulate gastrointestinal performance in an integrative manner as exemplified by the infrequently feeding Burmese python (Secor, 2008). An advantage of such an adaptive response would be the lowering of their maintenance

costs outside of the peak avian egg-laying season. Future studies that examine postprandial changes in gut histology and function for *Dasyptis* would shed light on whether the adaptive regime associated with their unique diet also encompasses gastrointestinal form and function.

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