



Specific Dynamic Action of a Large Carnivorous Lizard, *Varanus albigularis*

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ABSTRACT. *Varanus albigularis* inhabits grasslands of southern and eastern Africa and experiences months of fasting during the dry season (May–December) followed by voracious feeding during the wet season (January–April). Previous studies have found that sit-and-wait foraging snakes, which also experience long intervals between large meals, exhibit unprecedented increases in post-feeding metabolism, which reflects the added cost of up-regulating a previously quiescent gut and digesting a large meal. Hence we measured pre- and post-prandial oxygen consumption rates ($\dot{V}O_2$) of adult *V. albigularis* in order to observe whether they exhibit similarly large metabolic responses to digestion as sit-and-wait foraging snakes. Following the consumption of meals consisting of ground turkey and snails, hard-boiled eggs, or juvenile rats, lizards rapidly increased their $\dot{V}O_2$ to peak within 24–27 hr at 7–10 times pre-feeding values (mean = $0.035 \text{ mL O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$). During the 60–90 hr of significantly elevated $\dot{V}O_2$, the extra oxygen consumed (the specific dynamic action) represented an energy expenditure of 830–1260 kJ. For meals that were fully digested, specific dynamic action equalled 24% of ingested energy. The magnitudes of *V. albigularis* post-prandial metabolic responses are similar to those previously observed for sit-and-wait foraging snakes. Like sit-and-wait foraging snakes, *V. albigularis* may also down-regulate intestinal performance during their months of fasting (suggested by their relatively low standard metabolic rate) and then up-regulate their gut (bearing its high energetic cost) upon feeding. COMP BIOCHEM PHYSIOL 117A;4:515–522, 1997. © 1997 Elsevier Science Inc.

KEY WORDS. Digestive physiology, feeding ecology, lizard, metabolism, reptilia, specific dynamic action, standard metabolic rate, *Varanus albigularis*

INTRODUCTION

The ingestion and subsequent digestion of a meal are accompanied by an increase in metabolic rate, commonly referred to as specific dynamic action [SDA (36)]. Specific dynamic action is the proposed sum of energy expended, in part, on mastication and gut peristalsis, the production and secretion of digestive acids and enzymes, the transport and storage of nutrients, and protein synthesis (11,33,50). A widespread physiological phenomenon, SDA has been reported in organisms ranging from cladocerans (37), to fishes (33), to reptiles (6), and to large mammals (13). Whereas most organisms studied experience modest increases (25–200%) in post-prandial metabolism (13,33,50), sit-and-wait-foraging snakes undergo huge increases (up to 4400%) in metabolic rate during digestion (6,47,50). Sit-and-wait foraging snakes (including pythons, boas, pit vipers, and true vipers) characteristically feed intermittently (once per

1–2 months) on relatively large prey (29,46,52). Recently it was discovered that several sit-and-wait foraging snake species down-regulate intestinal function and reduce intestinal mass following the completion of digestion (47,48). For these snakes, their post-digestive response is viewed as an adaptive mechanism that serves to conserve energy during the long intervals between meals (47,48). Their large increase in post-prandial metabolism reflects the combined costs of up-regulating the function and morphology of a quiescent gut and digesting a large meal (47,50).

In contrast, other reptiles experience more modest increases in post-feeding metabolism; up to 270% for turtles (6), up to 100% for lizards (57), up to 300% for crocodylians (14), and up to 700% for snake species which actively forage and feed frequently (5,30,45). We suggest two factors that contribute to the modest increases in post-prandial metabolism of these other reptiles; first, they typically consume small meals (<10% of body mass) and second, they do not up-regulate a quiescent gut following feeding. For several species of turtles and active foraging snakes, intestinal function and morphology experiences minor changes following feeding and with the completion of digestion [(45), S. Secor and J. Diamond, unpublished observations]. For reptiles

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which feed relatively frequently on small meals, selection has favored the constant maintenance of a functional gut which has modest capacities for regulation (45).

Lizards of the genus *Varanus* exhibit diverse feeding habits, from species that feed frequently on small prey items to those which seasonally or periodically fast and consume large meals (1,15,35,42). For example *V. olivaceus* is partially frugivorous and feeds daily on small meals, whereas the carnivorous *V. komodoensis* consumes meals as large as 71% of its body mass (1,2). Motivated by the consideration that varanid lizards post-feeding metabolic and digestive responses are correlated with their feeding habits, as observed for snakes, we measured pre- and post-prandial metabolic rates of the monitor lizard *V. albigularis*. *Varanus albigularis* fasts for months during the dry season, and with the arrival of the wet season gorge themselves on newly abundant food (41,42). These lizards, like sit-and-wait foraging snakes, may experience relatively large increases in post-prandial metabolism. In this report, we document the large increase in metabolic rate experienced by digesting *V. albigularis* and later comment on the possible significance of their impressive metabolic response.

MATERIALS AND METHODS

Animals, Maintenance, and Feeding

Varanus albigularis inhabits savannah grasslands and woodlands of southern and eastern Africa (12,42,43). In the wild, adult males and females reach snout-vent lengths (SVL) of 77 cm and 62 cm, respectively, and masses of 8 kg and 6.5 kg, respectively (42). In northern Namibia, *V. albigularis* is active during the hot and wet season (January–April) and feeds regularly on a catholic diet of invertebrates, other reptiles, birds and their eggs, and occasionally small-mammals (42). During the cool and dry season (May–August), male lizards search for and mate with females which spend most of this time in burrows and/or trees. During the following hot and dry season (September–December), both sexes retreat to refuges (burrows and trees) while remaining alert and partially active. *Varanus albigularis* rarely feed from July to December (they lose about 4% of their body mass per month) and then resume feeding in January with the arrival of the rainy season (41,42).

In this study, we measured pre- and post-prandial metabolism of four adult male *V. albigularis* maintained by the Center for Reproduction of Endangered Species (Zoological Society of San Diego). Mean \pm 1 SE and range (in parenthesis) SVL, total length, and mass of these four lizards were 69 ± 4 cm (59–77), 136 ± 6 cm (125–147), and 8.1 ± 0.7 kg (6.2–9.2), respectively. Lizards in this study originated from wild-caught gravid females and at the time of the study were four years old. During the study, lizards were housed at UCLA in a temperature-controlled room (Sure-Temp, Apex, North Carolina) set at 30°C with a L:D photoperiod of 14hr:10hr. Prior to metabolic measurements,

lizards were fasted for 2–3 week (water was available *ad libitum*) to ensure that they had reached a post-absorptive state (defecation occurs 4–6 days after feeding, J. Phillips, personal observations). All housing and experimental procedures were conducted with the approval of UCLA Animal Research Committee.

We conducted three separate metabolic trials, each with a different meal type: a mixture (7:1) of ground turkey and land snails (*Helix*, removed from their shell); hard-boiled chicken eggs; and juvenile rats (*Rattus norvegicus*). We selected these meals because of their similarity to the lizards' natural diet and we had previously observed these individuals to feed readily on these meals. For each trial, lizards were allowed to consume as much food as they wanted, and thus consumed (mean \pm 1 SE) 980 ± 120 g of the turkey and snail mixture, 560 ± 60 g of hard-boiled eggs, and 750 ± 120 g of rats.

Metabolic Measurements

We used closed-system respirometry [described in (50) and (56)] to measure oxygen consumption rates ($\dot{V}O_2$ as mL $O_2 \cdot g^{-1} \cdot hr^{-1}$) of fasting and digesting *V. albigularis*. Each lizard was placed within a large respirometry chamber (100–150 L) fitted with air-ports for continuous ventilation of pumped air. A thermocouple probe taped to the inside floor of each chamber was used to monitor chamber temperatures and indirectly lizard body temperatures (lizards would lie on the thermocouple probes). Room temperature was periodically adjusted to maintain chamber temperatures at $30 \pm 1^\circ C$. To measure $\dot{V}O_2$, 50-mL air samples were drawn through excurrent air-ports from each respirometry chamber, all air-ports were then closed, and a second set of air samples were drawn from re-opened air-ports 0.5–1 hr later. Air samples were pumped (150 mL $\cdot min^{-1}$) through columns of H_2O absorbent (Drierite) and CO_2 absorbent (Ascarite) into an Applied Electrochemistry S-3A O_2 analyzer (Sunnyvale, California). We measured $\dot{V}O_2$ (calculated from the depletion of O_2 in each chamber and corrected for standard pressure and temperature) at 3–24 hr intervals for 2 days prior to feeding and 5–6 days after feeding.

For each feeding trial we quantified for each lizard the following six parameters of the metabolic response [described and illustrated in (33,50)]: *standard metabolic rate* (SMR) as the minimum $\dot{V}O_2$ measured prior to feeding, *peak $\dot{V}O_2$* as the highest recorded $\dot{V}O_2$ during digestion, *scope* as the factorial increase of peak $\dot{V}O_2$ from SMR (peak $\dot{V}O_2$ /SMR), *duration* as the period of significantly elevated $\dot{V}O_2$ (from SMR) following ingestion, *average $\dot{V}O_2$* as the average rate of O_2 consumption during the duration of significantly elevated rates, and *SDA* quantified as the extra energy expended (kJ) during significantly elevated $\dot{V}O_2$ [assuming 19.8 J expended per mL O_2 consumed (23)] and as a percent of ingested and digested (ingested minus regurgitated) energy [assuming energy equivalents of 7.5 kJ $\cdot g^{-1}$

wet mass, $6.5 \text{ kJ} \cdot \text{g}^{-1}$ wet mass, and $8 \text{ kJ} \cdot \text{g}^{-1}$ wet mass, respectively, for the turkey and snail mixture, hard-boiled eggs, and juvenile rats (40,48)].

Statistical Analyses

For each meal trial, we used a repeated measures ANOVA [GLM procedure of SAS (44)] to test whether there was a significant effect of sampling time (prior to and after feeding) on lizard $\dot{V}\text{O}_2$. In addition, we made a priori-planned pairwise mean comparisons between sampling times to identify significant changes in $\dot{V}\text{O}_2$ and when post-feeding $\dot{V}\text{O}_2$ had declined to values not significantly greater than pre-feeding rates. We similarly used a repeated design ANOVA to test for significant effects of meal type on feeding and metabolic measures. We used least-squares regression analyses [REG procedure of SAS (44)] to test the relationship between SDA and meal mass or energy and between SMR and body mass. In the text we report the results of ANOVA in terms of their *F* and *P* values and we state the *P* values of significant pairwise comparisons. Results are presented as mean ± 1 standard error and we designate statistical significance as $P < 0.05$. We carried out all statistical analyses using the microcomputer version of SAS (PC-SAS).

RESULTS

Profiles of Post-prandial Metabolism

Following a 2–3 week fast, SMR averaged $0.035 \pm 0.004 \text{ mL O}_2 \cdot \text{g}^{-1} \cdot \text{hr}^{-1}$ (range = 0.029–0.043) and for each individual were consistent among trials (coefficient of variation = $4.5 \pm 0.6\%$). Following feeding, $\dot{V}\text{O}_2$ increased rapidly and was significantly (planned pairwise comparisons; $P_s < 0.021$) elevated within 6–12 hr. For each meal, $\dot{V}\text{O}_2$ continued to increase, peaking at 24–30 hr post-feeding (Fig. 1). Thereafter, $\dot{V}\text{O}_2$ declined at a slower pace before returning to levels not significantly greater than those prior to feeding (Fig. 1). We found for each meal trial, $\dot{V}\text{O}_2$ to differ significantly (ANOVA; $P_s \leq 0.0001$) among pre- and post-feeding measurements.

Trial 1: Turkey/Snail Meal

Lizards consumed an average of $11.7 \pm 1.1\%$ of their body mass of the ground turkey and snail mixture, the largest meal consumed of the three trials (Table 1). Following this meal, $\dot{V}\text{O}_2$ peaked 27 hr post-feeding at $0.33 \pm 0.02 \text{ mL} \cdot \text{g}^{-1} \cdot \text{hr}^{-1}$, 9.4 times SMR (Fig. 1A). Unfortunately after $\dot{V}\text{O}_2$ had peaked and was declining, each lizard regurgitated a portion ($43 \pm 8\%$) of its meal, thus the resulting digested meals (ingested minus regurgitated) equalled $6.7 \pm 1.4\%$ of body mass. Thereafter, $\dot{V}\text{O}_2$ declined more rapidly for those lizards which had regurgitated a larger portion of their ingested meal. For example, lizards 1 and 4, which regurgitated 65 and 45% of their meal, respectively, experi-

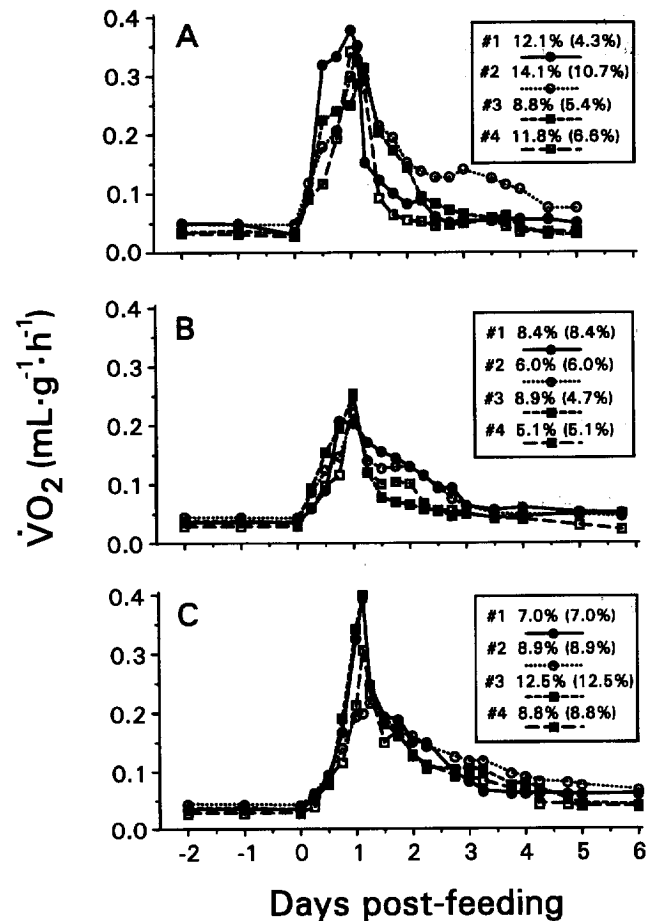


FIG. 1. Oxygen consumption rates ($\dot{V}\text{O}_2$ as $\text{mL O}_2 \cdot \text{g}^{-1} \cdot \text{hr}^{-1}$ at 30°C) of four adult male *Varanus albigularis* (mean mass = $8.1 \pm 0.7 \text{ kg}$) for 2 days prior to and up to 6 days following the consumption of meals consisting of turkey and snail mixture (A), hard-boiled eggs (B), and juvenile rats (C). Figure legends note for each lizard (nos. 1–4) the relative mass (% of body mass) of the meal ingested and digested (ingested–regurgitated, noted in parentheses). Note in A and B that as more of the meal was lost to regurgitation, $\dot{V}\text{O}_2$ declined quicker and returned to pre-feeding levels sooner.

enced a faster decline in $\dot{V}\text{O}_2$ than lizard 2 which had regurgitated only 24% of its meal (Fig. 1A). $\dot{V}\text{O}_2$ eventually returned to levels not significantly ($P = 0.113$) greater than prefeeding rates by 60-hr post-feeding (Table 1). During the 60 hr significantly elevated rates, $\dot{V}\text{O}_2$ averaged $0.163 \pm 0.011 \text{ mL} \cdot \text{g}^{-1} \cdot \text{hr}^{-1}$ (Table 1). Specific dynamic action (the energy expended on digestion) averaged $1200 \pm 110 \text{ kJ}$, equalling $17 \pm 3\%$ and $30 \pm 6\%$ of the energy ingested and digested, respectively (Table 1).

Trial 2: Hard-boiled Egg Meal

Each lizard consumed 7 to 14 hard-boiled eggs (mean egg wet mass = $55 \pm 2 \text{ g}$), resulting in a total meal mass equaling $7.1 \pm 0.9\%$ of body mass (Table 1). In response to this

TABLE 1. Comparison (mean \pm 1 SE and ANOVA) among three meals (ground turkey and snail mixture, hard-boiled eggs, and juvenile rats) in size, energy content, and metabolic response during their digestion by adult male *Varanus albigularis* (mean mass = 8.1 \pm 0.7 kg, n = 4). Definition of variables are given in the text

Variable	Trial			ANOVA <i>P</i>
	I	II	III	
Meal type	turkey and snails	hard-boiled eggs	juvenile rats	
Mass ingested (g)	980 \pm 120	560 \pm 60	750 \pm 120	0.077
Mass as % of body mass	11.7 \pm 1.1	7.1 \pm 0.9	9.3 \pm 1.1	0.100
Energy ingested (kJ)	7310 \pm 910	3660 \pm 410	5980 \pm 970	0.041
Mass digested (g)	580 \pm 140	470 \pm 30	750 \pm 120	0.223
Mass as % of body mass	6.7 \pm 1.4	6.0 \pm 0.8	9.3 \pm 1.1	0.251
Energy digested (kJ)	4520 \pm 1030	3080 \pm 190	5980 \pm 970	0.088
SMR (mL O ₂ · g ⁻¹ · hr ⁻¹)	0.035 \pm 0.005	0.035 \pm 0.003	0.035 \pm 0.004	0.865
Peak $\dot{V}O_2$ (mL O ₂ · g ⁻¹ · hr ⁻¹)	0.33 \pm 0.02	0.23 \pm 0.01	0.33 \pm 0.05	0.048
H post-feeding of peak $\dot{V}O_2$	27	24	27	
Scope (peak $\dot{V}O_2$ /SMR)	10.4 \pm 1.3	6.7 \pm 0.8	9.9 \pm 1.7	0.038
Duration (h)	60	72	90	
Average $\dot{V}O_2$ (mL O ₂ · g ⁻¹ · hr ⁻¹)	0.163 \pm 0.011	0.110 \pm 0.007	0.136 \pm 0.005	0.001
SDA (kJ)	1200 \pm 110	830 \pm 30	1260 \pm 70	0.007
SDA as % of ingested energy	17 \pm 3	24 \pm 3	23 \pm 3	0.368
SDA as % of digested energy	30 \pm 6	27 \pm 1	23 \pm 3	0.381

meal, lizard $\dot{V}O_2$ increased rapidly to peak at 0.23 \pm 0.01 mL · g⁻¹ · h⁻¹ at 24 hr post-feeding (Fig. 1B). Whereas three lizards (nos. 1, 2, and 4) did not regurgitate any of their egg meal, one lizard (no. 3) regurgitated 350 g of this meal at 32 hr post-feeding, decreasing its meal size from 8.4 to 4.7% of body mass. As observed previously with lizards that regurgitated portions of their turkey and snail meal, this individual then experienced a quicker decline in $\dot{V}O_2$ (Fig. 1B). By 72 hr post-feeding, $\dot{V}O_2$ had returned to values not significantly (P = 0.162) greater than SMR. During these 72 hr, $\dot{V}O_2$ averaged 0.110 \pm 0.007 mL · g⁻¹ · hr⁻¹ and SDA averaged 830 \pm 30 kJ, equalling 24 \pm 3% and 27 \pm 1%, respectively, of ingested and digested meal energy (Table 1).

Trial 3: Rat Meal

Monitor lizards consumed 5 to 12 young rats (mean rat mass = 88 \pm 4 g) such that their ingested and digested (no regurgitation during this trial) meal mass equalled 9.3 \pm 1.1% of their body mass (Table 1). Lizard $\dot{V}O_2$ responded with a peak of 0.33 \pm 0.05 mL · g⁻¹ · h⁻¹ (9.4-fold SMR) at 27 hr post-feeding (Figs. 1C and 2). Thereafter, $\dot{V}O_2$ experienced significant (P s < 0.023) decreases at hour 30, 36, 54, and 90, at which time $\dot{V}O_2$ had returned to values not significantly (P = 0.06) greater than SMR. During the 90 hr of elevated $\dot{V}O_2$, rates averaged 0.136 \pm 0.005 mL · g⁻¹ · h⁻¹ and the resultant SDA averaged 1260 \pm 70 kJ, equalling 23 \pm 3% of the ingested and digested energy.

Comparison Among Meals

Mass of ingested and digested meals did not differ significantly (P s > 0.077) among trials, although in pairwise com-

parisons, ingested turkey and snail meals were significantly (P s < 0.03) heavier than ingested eggs. The energy ingested differed significantly among meals ($F_{2,6}$ = 5.68, P = 0.041; in pairwise comparisons, turkey and snail meal > egg meal), whereas the energy eventually digested ($F_{2,6}$ = 3.76, P = 0.088) did not (Table 1). The difference in ingested energy could be responsible for the significant meal-type effects on peak $\dot{V}O_2$ ($F_{2,6}$ = 4.88, P = 0.048), the scope of peak rates ($F_{2,6}$ = 5.96, P = 0.038), and mean $\dot{V}O_2$ during the duration of elevated rates ($F_{2,6}$ = 27.7, P = 0.001) (Table 1). For

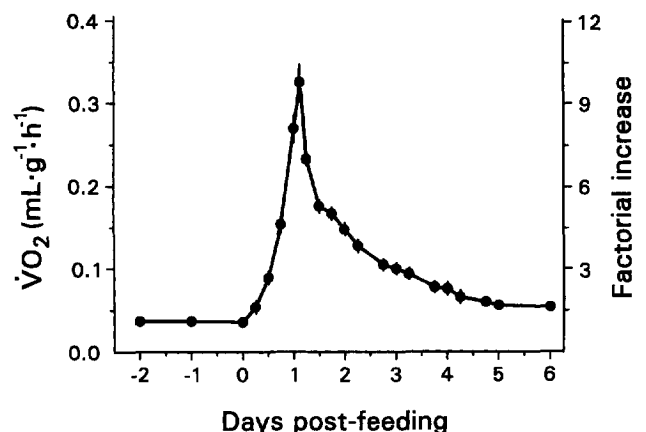


FIG. 2. Metabolic profile (mean $\dot{V}O_2$ at 30°C) of adult male *Varanus albigularis* (n = 4) prior to and after ingesting juvenile rat meals equalling 9.3 \pm 1.1% of body mass. Error bars note \pm 1 SE from the mean and are included if they extend beyond the edges of the mean symbol. Note the rapid increase in $\dot{V}O_2$ prior to peak at 27 hr post-feeding, and the subsequent slower decline in $\dot{V}O_2$ over the next several days. The right hand ordinate scale is the factorial increase of post-feeding $\dot{V}O_2$ over mean SMR.

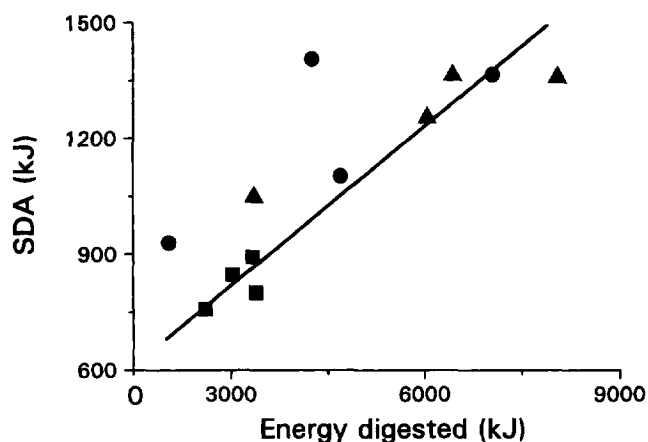


FIG. 3. Specific dynamic action, expressed as kJ, plotted against digested meal energy (kJ). The circle, square, and triangle symbols represent values from the four individual *Varanus albigularis* digesting, respectively, the turkey and snail, hard-boiled egg, and rat meal. Note that SDA increases significantly ($P = 0.001$, $r^2 = 0.69$) with the increase in digested energy.

each of these variables, values resulting from the turkey and snail or rat meals were significantly ($P_s < 0.048$) greater than those resulting from the egg meal.

Specific dynamic action differed among meals ($F_{2,6} = 12.8$, $P = 0.007$) as the energy expended on digesting the turkey and snail or rat meals were significantly ($P_s = 0.007$) greater than that for hard-boiled eggs. Interestingly, there were no meal-type effects ($P_s > 0.36$) on SDA calculated either as a percent of ingested energy or as a percent of digested energy. After pooling data from the three meal treatments, a regression analyses demonstrated that SDA increased significantly with the mass of the meal consumed ($F_{1,11} = 5.69$, $r^2 = 0.36$, $P = 0.038$) and digested ($F_{1,11} = 15.2$, $r^2 = 0.60$, $P = 0.003$), and the amount of energy consumed ($F_{1,11} = 9.85$, $r^2 = 0.50$, $P = 0.011$) and digested ($F_{1,11} = 22.5$, $r^2 = 0.69$, $P = 0.001$). The latter relationship, which explains a greater percentage of the variation in SDA, can be explained by the equation, $SDA \text{ (kJ)} = 0.11 \text{ (kJ digested)} + 616$ (Fig. 3).

DISCUSSION

Varanus albigularis experiences large increases in metabolic rate following feeding. The scope of their post-prandial metabolic response is the highest known for lizards and is within the range of metabolic scopes of digesting sit-and-wait foraging snakes (45,47,48,57). Sit-and-wait foraging snakes down-regulate intestinal function and morphology with the completion of digestion, a proposed adaptive measure that reduces energy expenditure between meals (47,48). Their large increase in post-feeding metabolism reflects the added cost of up-regulating gut performance from a quiescent state (47,48). We speculate that the large post-prandial meta-

bolic response of *V. albigularis* also originates from their up-regulation of intestinal function and morphology. Like sit-and-wait foraging snakes, *V. albigularis* would benefit energetically from an adaptive response which conserves energy during their months of fasting. In the ensuing discussion we will comment on the metabolic profile and proximate causes of SDA for *V. albigularis*, the contribution of SDA in *V. albigularis* bioenergetics, and the implications of their post-prandial metabolic response.

Specific Dynamic Action for *V. albigularis*

The metabolic profile of digesting *V. albigularis* is similar in shape to those of digesting fishes, toads, snakes, alligators, birds, and mammals (14,18,32,33,50,58). Post-prandial metabolism is generally characterized by a rapid increase in $\dot{V}O_2$ after ingestion, peak $\dot{V}O_2$ reached within 10 to 36 hr, and a subsequent slower decline in $\dot{V}O_2$ until rates return to pre-feeding levels (50). For *V. albigularis*, post-prandial peak $\dot{V}O_2$ increases with the amount of energy ingested as it does for fishes, snakes, and mammals (21,33,50). The factorial scopes of *V. albigularis* post-prandial $\dot{V}O_2$ (7–10) are within the range of scopes (8–17) measured from sit-and-wait foraging snakes (*Python molurus*, *Crotalus cerastes*, *Boa constrictor*, and *Lichanura trivirgata*) and frogs (*Ceratophrys ornata* and *Pyxicephalus adspersus*) digesting meals equalling 25% of body mass (45,47,48,49, S. Secor and J. Diamond, unpublished observations). More comparable to the meal sizes of this study, *P. molurus* increase their $\dot{V}O_2$ 5.1-fold and 11-fold, respectively, while digesting meals 5 and 15% of body mass (50).

The post-peak decline in $\dot{V}O_2$ was influenced by the size of the meal that was eventually digested (ingested minus regurgitated). In comparing post-prandial metabolic profiles (Fig. 1), $\dot{V}O_2$ declined faster and returned to pre-feeding levels sooner as more of the meal was lost to regurgitation. Thus, the metabolic profiles during the digestion of rodent meals more accurately represent the magnitude and duration of their post-prandial metabolic response (Figs. 1C and 2). The duration (90 hr) of elevated $\dot{V}O_2$ while digesting the rodent meals (9.3% of body mass) is similar to that (96 hr) experienced by *P. molurus* digesting rodent meals equaling 5% of body mass (50).

Specific dynamic action has commonly been quantified as a percent of ingested energy [referred to as the SDA coefficient (34)]. For two meals in our study, this value differed whether SDA was quantified as a percent of ingested or digested (non-regurgitated) energy (Table 1). Understandably, more accurate values are calculated when meals are not regurgitated. For the seven instances in which meals were not regurgitated, SDA averaged $24 \pm 2\%$ of ingested energy. This mean value for *V. albigularis* is within the range of SDA coefficients (22–34%) for several species of sit-and-wait foraging snakes and greater than SDA coefficients calculated for more frequently-feeding organisms (50).

Numerous causal mechanisms potentially contribute to SDA for *V. albigularis*. Mastication, swallowing, and peristalsis occur via muscular contractions. The arrival of the meal into the stomach and eventually into the small intestine triggers the production and secretion of acids, enzymes, bile, and buffering agents. Nutrients are actively transported across the intestinal epithelium. These digestive processes occur with a metabolic cost, but few attempts have been made to measure their contributions to SDA (22). Absorbed nutrients are metabolized, stored, or used in tissue synthesis. The transport and storage costs of fats and carbohydrates are relatively low, whereas the synthesis of protein from absorbed amino acids (amino acids are not stored long-term) is costly (11). Contributing to the large magnitude of SDA for *V. albigularis* is the digestion and eventual fate of their protein-rich meals; protein synthesis alone is estimated to account for 20–44% of SDA of other ectotherms (31,39,50).

Specific Dynamic Action in *V. albigularis* Bioenergetics

We suggest three factors that contributed to the large post-prandial metabolic scope observed in our study. First, lizards of our study possessed low SMR ($297 \pm 31 \text{ mL O}_2 \cdot \text{hr}^{-1}$ at 30°C) averaging 30 and 22% less than predicted, respectively, from a generalized allometric equation for lizards at 30°C (9) and our allometric equation generated from SMR of 13 species of *Varanus* (Fig. 4). Second, these lizards experienced remarkably high $\dot{\text{V}}\text{O}_2$ during digestion. Our highest measure of $0.40 \text{ mL O}_2 \cdot \text{g}^{-1} \cdot \text{hr}^{-1}$ from two digesting, non-moving, individuals is 76% greater than the $\dot{\text{V}}\text{O}_{2\text{max}}$ estimated for a 8.1 kg lizard at 30°C based upon an allometric equation for exercising lizards which includes several varanids (8) (note that these allometric equations were calculated from lizards whose body masses were less than 8.1 kg). And third, our lizards consumed relatively large meals, at times exceeding 10% of their body mass.

$\dot{\text{V}}\text{O}_{2\text{max}}$ has been measured from several species of varanid lizards, but none as large as 8.1 kg (10,24,25). The results of those studies lead us to speculate that our adult *V. albigularis* attains post-prandial $\dot{\text{V}}\text{O}_2$ that may exceed their $\dot{\text{V}}\text{O}_{2\text{max}}$ during activity. Similarly, several species of snakes (*P. molurus*, *L. trivirgata*, and *Lampropeltis getula*) experience post-prandial $\dot{\text{V}}\text{O}_2$ that surpass their $\dot{\text{V}}\text{O}_{2\text{max}}$ during strenuous activity [(48), S. Secor, unpublished observations]. Monitor lizards possess high aerobic capacities enabling them to sustain high $\dot{\text{V}}\text{O}_2$ while searching, chasing, and capturing prey (7,10,24). An added benefit of their high aerobic capacity is the ability to endure large increases in $\dot{\text{V}}\text{O}_2$ during digestion.

Recently, field and laboratory studies have shown that SDA is an important component of the daily energy budget for snakes. *Thamnophis sirtalis*, *Masticophis flagellum*, and *C. cerastes* devote 19 to 43% of their daily energy expenditure, measured as field metabolic rates (FMR), to SDA (5,46). Field metabolic rates have not been measured for *V. albigu-*

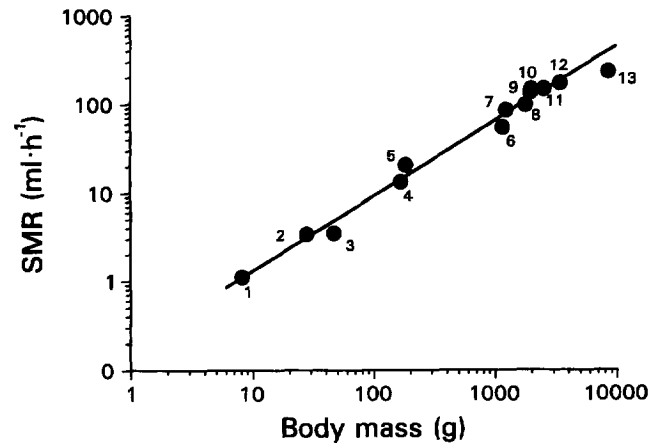


FIG. 4 Allometric plot (log–log) of standard metabolic rates (SMR as $\text{mL O}_2 \cdot \text{hr}^{-1}$) of 13 species of *Varanus* at 30°C . The allometric equation of the straight line generated by published values and for *V. albigularis* of this study is $\dot{\text{V}}\text{O}_2 (\text{ml} \cdot \text{hr}^{-1}) = 0.19 M^{0.64}$. Numbers on the plot note the mean values for the following species: 1 *V. caudolineatus* (54), 2 *V. gilleni* (10), 3 *V. acanthurus* (54), 4 *V. gouldii* (53), 5 *V. punctatus* (4), 6 *V. mertensi* (17), 7 *V. rosenbergii* (15), 8 *V. exanthematicus* (59), 9 *V. varius* (4), 10 *V. panoptes* (53), 11 *V. giganteus* (55), 12 *V. bengalensis* (20), and 13 *V. albigularis* (this study). First, we note that the mass exponent of our interspecific allometric equation is similar to that ($0.25 M^{0.86}$) reported for the SMR of eight species of *Varanus* at 35°C (54). And, second the SMR of *V. albigularis* of our study is 26% less than the value predicted for a 8.1 kg varanid from our allometric equation.

laris, although FMR of eight other varanid species (16,17,19,26–28) suggest that a 8 kg varanid would experience FMR of approximately $100 \text{ kJ} \cdot \text{kg}^{-1} \cdot \text{d}^{-1}$. In our study, the digestion of the rat meal resulted in a total expenditure, above SMR, of $173 \text{ kJ} \cdot \text{kg}^{-1}$. Adult *V. albigularis* in the wild occasionally eat similar size meals once a week (J. Phillips, personal observations), thus they allocate approximately 25% of their weekly energy expenditure to SDA.

Adaptive Correlates of SDA for *Varanus*

The diversity of feeding habits among snake species lead to studies which demonstrated that species which naturally feed frequently (active foragers) experience modest post-feeding intestinal and metabolic responses (45). In contrast, species which feed infrequently (sit-and-wait foragers) up regulate gut function and morphology with feeding, resulting in a large metabolic response (47,50). Varanid lizards also exhibit a moderate diversity in their feeding habits (38,51). Many, especially smaller species, are active foragers that feed frequently on small prey items, whereas larger species, including *V. komodoensis* and *V. giganteus*, are ambush foragers as adults and feed relatively infrequently on large prey (1,3,35,38). Like snakes, monitor lizards may possess an adaptive correlation between their feeding habits and

their digestive responses. In order to elucidate the adaptive trends of *Varanus* digestive response requires the systematic measurements of intestinal function (e.g., nutrient transport) and morphology and metabolic rate during fasting and digesting periods [see (47,48)] of species differing in feeding habits. This comparative study would have the advantage of reduced phylogenetic interactions (compared to the multi-taxa snake study [45]) and thus be favorable for testing hypotheses regarding the evolution of gastrointestinal adaptations.

In summary, *V. albigularis* inhabits grasslands of southern and eastern Africa. They fast for long periods when prey is not available and feed voraciously when food becomes abundant. After feeding they experience large increases in metabolic rate, similar in scope to that of sit-and-wait-foraging snakes that naturally feed infrequently on large prey items and regulate intestinal performance. Hypothetically, the large post-prandial metabolic response of *V. albigularis* also reflects the up-regulation of an adaptively quiescent gut.

We thank Allison Alberts, Vincent Lai, and Caleb Slotnick for their assistance in this study. This study was supported by National Institutes of Health National Research Service Award DK 08878, National Institutes of Health grant GM 14772, and National Science Foundation grant BNS 90-00100.

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