The Effect of Meal Composition on Specific Dynamic Action in Burmese Pythons (*Python molurus*)

M. D. McCue
A. F. Bennett*
J. W. Hicks
Department of Ecology and Evolutionary Biology, University of California, Irvine, California 92697-2525

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ABSTRACT

We quantified the specific dynamic action (SDA) resulting from the ingestion of various meal types in Burmese pythons (*Python molurus*) at 30°C. Each snake was fed a series of experimental meals consisting of amino acid mixtures, simple proteins, simple or complex carbohydrates, or lipids as well as meals of whole animal tissue (chicken breast, beef suet, and mouse). Rates of oxygen consumption were measured for approximately 4 d after feeding, and the increment above standard metabolic rate was determined and compared to energy content of the meals. While food type (protein, carbohydrate, and lipid) had a general influence, SDA was highly dependent on meal composition (i.e., amino acid composition and carbohydrate structure). For chicken breast and simple carbohydrates, the SDA coefficient was approximately one-third the energetic content of the meal. Lard, suet, cellulose, and starch were not digested and did not produce measurable SDA. We conclude that the cost of de novo protein synthesis is an important component of SDA after ingestion of protein meals because (1) simple proteins, such as gelatin and collagen, did not stimulate levels of SDA attained after consumption of complete protein, (2) incomplete mixtures of amino acids failed to elicit the SDA of a complete mixture, and (3) the inhibition of de novo protein synthesis with the drug cycloheximide caused a more than 70% decrease in SDA. Stomach distension and mechanical digestion of intact prey did not cause measurable SDA.

Introduction

Many animals have a substantially increased metabolic rate while they are digesting and processing meals (reviewed in Machida 1981; Houlihan 1991; McCue 2003). This increased metabolism above resting levels is termed specific dynamic action (SDA), and its ubiquity among very diverse animals suggests that it is associated with one or more fundamental aspects of food processing. As a result, this seemingly unavoidable phenomenon has long been considered a "tax" on food processing (Rapport 1929; Brody and Procter 1933). It is not at present clear the degree to which energy to fuel SDA is taken from the food (Starck et al. 2004) or from endogenous energy stores of the consumer (Secor and Diamond 1995). In either case, SDA is of particular ecological relevance because it is an unavoidable diversion of energy that might otherwise have been directed to growth and/or activity (Kalarani and Davies 1994; Alsop and Wood 1997).

SDA is particularly high in large carnivorous reptiles (Benedict 1932; Secor and Diamond 1995, 1997). A variety of factors, including low maintenance metabolic rates and large and infrequent meals of high protein content, converge to produce maximum rates of metabolism during the SDA that equal or exceed those during intense physical activity (Andrade et al. 1997; Secor and Diamond 1997; Secor et al. 2000). The SDA coefficient is equivalent to 23%–35% of ingested energy in a variety of reptiles (Pierce and Wissing 1974; Hailey and Davies 1987; Secor and Phillips 1997; Overgaard et al. 2002). One study has estimated that SDA may account for one-third of the overall annual energy expenditure of a viperid snake (McCue and Lillywhite 2002). Snakes of the genus *Python* have been proposed as ideal model organisms for the study of the metabolic physiology of digestion because of the magnitude of their response, their availability, and their experimental tractability (Secor et al. 1994; Secor and Diamond 1998). They have particularly high metabolic increments after feeding, and many aspects of their metabolic digestive physiology have been investigated in a series of studies by Secor (e.g., Secor et al. 1994, 2000, 2002; Secor and Diamond 1995, 1997; Secor 2003) and others (e.g., Starck 1999; Starck and Beese 2001; Overgaard and Wang 2002; Overgaard et al. 2002; Wang et al. 2002; Starck et al. 2004).

It has been known for more than a century that the magnitude of SDA is highly dependent on meal composition in mammals (Rubner 1902; Lusk 1915, 1922), with relatively low values for fats and carbohydrates and substantially higher values for protein (Lusk 1931). Here we examine the effect of food composition on SDA in the digestive model species *Python molurus*. Previous data on this topic come from scattered observations on different reptilian species (e.g., Benedict 1932; Coulson and Hernandez 1968, 1979; Coulson and Herbert

* Author for correspondence; e-mail: abennett@uci.edu.

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1974; Secor et al. 2002). This is the first comprehensive examination of food composition on SDA in a single reptilian species. Specifically, we determined differential SDA responses to a variety of carbohydrates, fats, and proteins. To amplify the latter observations, we also examined the effect of dietary amino acid composition on SDA and the effect of inhibiting protein synthesis on its magnitude.

Material and Methods

Animals

Juvenile Burmese pythons (*Python molurus*) were obtained from Ophiological Services (Gainesville, FL) and raised in the laboratory (30°C; 12L : 12D) on a diet of mice and rats with ad lib water. Eight snakes (body mass 600–700 g) were used in the food type experiments; another eight animals (body mass 200–230 g) were used in the protein composition studies. Body masses of the pythons at the end of these experiments did not differ from initial masses (paired *t*-test, $P = 0.24$). All experiments were conducted in accordance with University of California, Irvine, Institutional Animal Care and Use Committee protocol #1999-2123.

Food Type Experiments

These experiments measured SDA after ingestion of isocaloric meals of a variety of nutrients. After a fasting period of 14–21 d, each snake was fed an isoenergetic meal (500 kJ) composed of carbohydrates, lipids, or proteins of varying composition. For sucrose and glucose meals, energy content was 250 kJ because preliminary trials resulted in the death of two snakes fed 500-kJ meals of these compounds. All meals (except whole mice) were fed by inserting a rigid acrylic feeding tube (1.5-cm diameter) into the center of the stomach, and meals were then slowly inserted into each snake's stomach through this tube. Postprandial oxygen consumption was measured until it returned to preingestion values (see "Respirometry"). Meal type was randomly assigned to individuals. After the completion of two sequential experimental feedings, snakes were allowed to ingest a mouse or small rat so they could maintain body mass and nutritional health (Anderson and Lusk 1917; Dann and Chambers 1930; Ashworth 1969).

The four carbohydrate meals were wheat starch, cellulose, sucrose, and D-glucose. The two lipid meals consisted of purified lard and beef suet. The six protein meals were whole dead mice, pureed mice, ground lean chicken breast, casein, collagen, and gelatin. Purified chemicals (starch, cellulose, sucrose, glucose, casein, collagen, and gelatin) were purchased from Sigma Biochemicals, and water was added to these to approximate the water content of natural foods and to reduce osmotic stress on the animals. Meal volume and water and energy content of each food type are given in Table 1. Meal volume was not standardized because of the major differences in energy content among the experimental nutrients; volumes of experimental meals ranged from 25 mL (lard) to 250 mL (gelatin). Meal volume for the mouse and chicken was approximately 15% body mass.

Energy content of chicken breast, beef suet, and mouse sam-

Table 1: Volume, water, and energy content of meals, SDA, and SDA coefficient in the food type experiments (mean ± SEM)

Units	Meal Volume[a] (mL)	Water Content (%)	Energy Content (kJ/g)	Meal Energy (kJ)	SDA (kJ)	SDA Coefficient (%)	*n*
Protein:							
Chicken	100	70.5 ± .1	26.7 ± .4	500	157.9 ± 3.8	32	5
Mouse (whole)	100	66.8 ± .2	24.5 ± .2	500	72.8 ± 7.1	15	8
Mouse (puree)	100	66.8 ± .2	24.5 ± .2	500	98.8 ± 7.3	20	6
Casein	100	70[a]	21.7[c]	500	89.3 ± 10.6	18	5
Collagen	100	60[a]	23.8[b]	500	58.3 ± 9.1	12	3
Gelatin	250	80[a]	19.23[c]	500	0	0	2
Carbohydrate:							
Glucose	50	70[a]	15.5[b]	250	79.2 ± 9.4	32	4
Sucrose	50	70[a]	15.5[b]	250	79.0 ± 8.8	32	4
Starch	100	70[a]	17.6[b]	500	0	0	2
Cellulose	100	70[a]	17.6[b]	500	0	0	2
Lipid:							
Lard	25	0	39.7[b]	500	0	0	3
Suet	25	17.8 ± 1.0	37.9 ± .5	500	0	0	3

[a] Approximate.
[b] From Kleiber (1975).
[c] From Kriss and Voris (1937) and Kriss (1938).

ples were measured directly using a Phillipson Microbomb Calorimeter (Phillipson 1964). Samples were first dried at 50°C for 7 d and then homogenized in a blender and powdered. Energy values (kJ/g ash-free dry mass) were determined by combusting 20–30 samples (approx. 75 mg each) of each material, along with benzoic acid standards. Energy contents of purified substances (e.g., casein, glucose, and gelatin) were obtained from published values (Kriss and Voris 1937; Kriss 1938; Kleiber 1975). The food type and amino acid compositions of the chicken breast and mouse samples were determined by Food Products Laboratory (Portland, OR).

Protein Composition Studies

The effect of protein meal composition on SDA was further analyzed by feeding pythons various combinations of purified L-amino acids (Sigma; ICN Biochemicals). Five different amino acid mixtures were used. The "Complete" mixture was an artificial mixture identical in amino acid composition to the whole mice used in the food type experiments (as determined by Food Products Laboratory). Four additional "Incomplete" amino acid mixtures were deficient in sets of some specific amino acids: the "Nonessential" mixture lacked 10 essential amino acids (O'Neil et al. 2001), the "Essential" mixture was deficient in 10 nonessential amino acids (O'Neil et al. 2001), the "Oxidative" mixture was deficient in amino acids that undergo reductive deamination (Brody 1945), and the "Reductive" mixture was deficient in amino acids that undergo oxidative deamination (Brody 1945). The amino acid composition of each of these mixtures is reported in Table 2. The percentage of the amino acids in each of the Incomplete mixtures was increased in proportion to its composition in the Complete mixture. Each mixture was isomolar (7.5 mmol/meal) and had a dry mass and energy content of approximately 1 g and 25 kJ, respectively. Snakes were also fed empty gelatin capsules as a control.

Each amino acid mixture was placed into a 20 × 7 mm gelatin capsule (size 000; Torpac, Fairfield, NJ) and deposited directly into the snake's stomach through a feeding tube (10 mm outside diameter) similar to that used in the food type experiments. Postprandial oxygen consumption was measured until it returned to preingestion values (see "Respirometry"). The five amino acid mixtures were a priori randomly assigned to individuals and fed to snakes fasted for 2 wk. Dead mice were fed to pythons between experimental trials to minimize the risk of residual effects between experimental meals and to ensure they were adequately nourished.

Table 2: Millimolar concentrations of amino acid mixtures fed to pythons

Amino acid	Complete	Nonessential	Essential	Reductive	Oxidative
Alanine	.38	.83			.53
Arginine	.60		1.20	.75	
Asparagine	.30	.60		.38	
Aspartic acid	.30	.60		.38	
Cystine	.08	.15		.08	.08
Glutamic acid	.60	1.20		.68	
Glutamine	.60	1.20		.68	.75
Glycine	.30	.60			.38
Histidine	.38		.68	.45	.45
Isoleucine	.30		.53	.30	.38
Leucine	.60		1.13	.68	.75
Lysine	.83		1.50	.90	1.05
Methionine	.15		.30	.23	.23
Phenylalanine	.45		.75		.53
Proline	.30	.68		.38	.45
Serine	.30	.60		.30	.38
Threonine	.30		.53	.30	.38
Tryptophan	.15		.30	.15	.15
Tyrosine	.45	.90		.53	.60
Valine	.30		.60	.38	.38

Note. All meals totaled 7.5 mmol of amino acids. The amino acid composition of the Complete meal is based on the amino acid composition of whole mice in the food type experiments. Incomplete mixtures were made by increasing the percentage of the residual amino acids while maintaining total amino acid content.

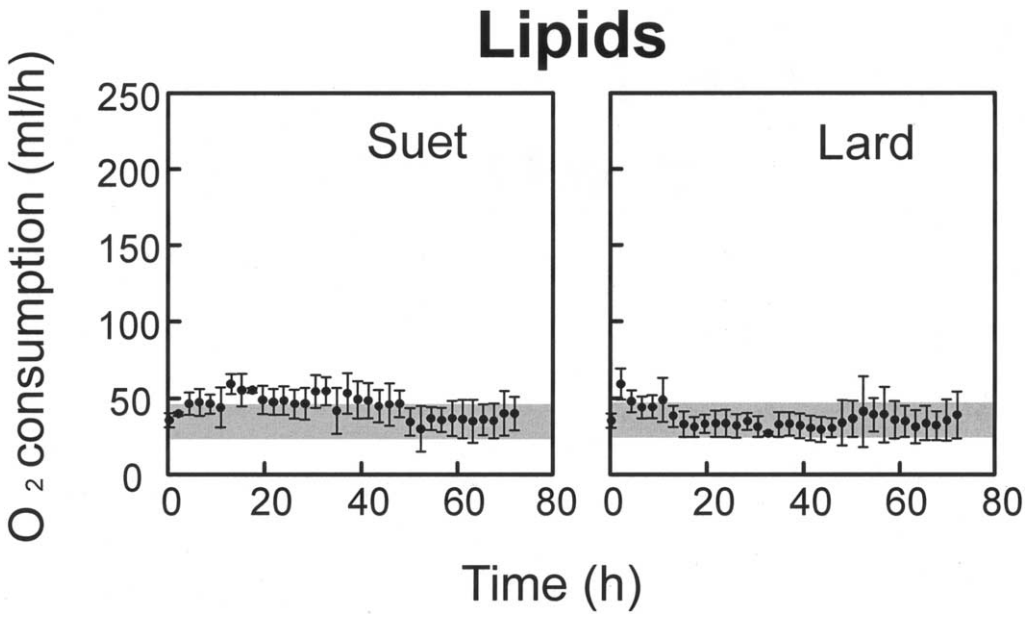

Figure 1. Postprandial oxygen consumption after ingestion of lipids by *Python molurus*. Circles represent mean oxygen consumption (± 1 SD) measured every 2 h; the gray bar is for mean standard rate of metabolism ± 95% confidence limit.

Inhibition of Protein Synthesis

To determine the impact of de novo protein synthesis on SDA, cycloheximide (CAS no. 66-81-9, ICN Biochemicals), a protein synthesis inhibitor (O'Neil et al. 2001), was administered before a final repetition of the Complete amino acid mixture feeding. Individual cycloheximide doses (10 mg/kg; Coulson and Hernandez 1971) were dissolved in 1 mL 0.9% NaCl and injected intraperitoneally. Injected solutions were allowed 4 h to equilibrate before feeding (Korner 1966; Coulson and Herbert 1974; Hubbard and Licht 1986; Brown and Cameron 1991*a*). Then a Complete amino acid mixture was fed to the snake, and oxygen consumption was measured until it returned to preingestion values. These meals were the last in the protein composition series, and the snakes were then killed for later tissue analyses.

Respirometry

Animals were maintained at 30°C for all feeding and metabolic measurements. Rates of oxygen consumption were quantified using flow-through respirometry (Withers 1977). Snakes were placed in 1.5-L metabolic chambers, and dry room air was metered continuously through chambers at 300–600 mL/min. Over each 2-h period, an eight-channel solenoid manifold was used to subsample excurrent air from each chamber for 15 min (including empty-chamber controls) during the postprandial period. Excurrent gas samples were dried with calcium sulfate (DriRite) before the oxygen fraction was measured with an AEI S3-A oxygen analyzer. Outputs were recorded continuously on a strip chart recorder. All reported oxygen consumption values are STPD. On the basis of preliminary trials of digesting pythons (McCue et al. 2002), respiratory quotients of 0.8 were assumed throughout all experiments (Gessaman and Nagy 1988). Metabolic equivalents of energy (kJ) are estimated at 20.2 kJ/mL O_2 (Jobling 1981; Merker and Nagy 1984; Chappell and Ellis 1987).

Standard rates of metabolism (SMR) were measured on 2-wk fasting individuals at the beginning and end of the project. Average SMR ± 95% confidence limits (CLs) were calculated by pooling the SMR measurements from all individuals within each of the two experiments. SDA duration was defined as the time at which the postprandial metabolic rate first equaled the upper boundary of the 95% CL of mean SMR. This method, rather than defining the postprandial period as the time when metabolic rate exceeds the mean or lowest measured preingestion metabolic rate, gives a more conservative measure for determining SDA (F. Zaidan, personal communication). Here, SDA was measured as the difference between the total integrated metabolic rate and the 95% upper CL of SMR.

Mean values for SDA were compared with one another using *t*-tests with a critical *P* value of 0.05 and are reported ± 1 standard error, except as specifically noted. A linear regression was used to examine the relationship between meal size and SDA.

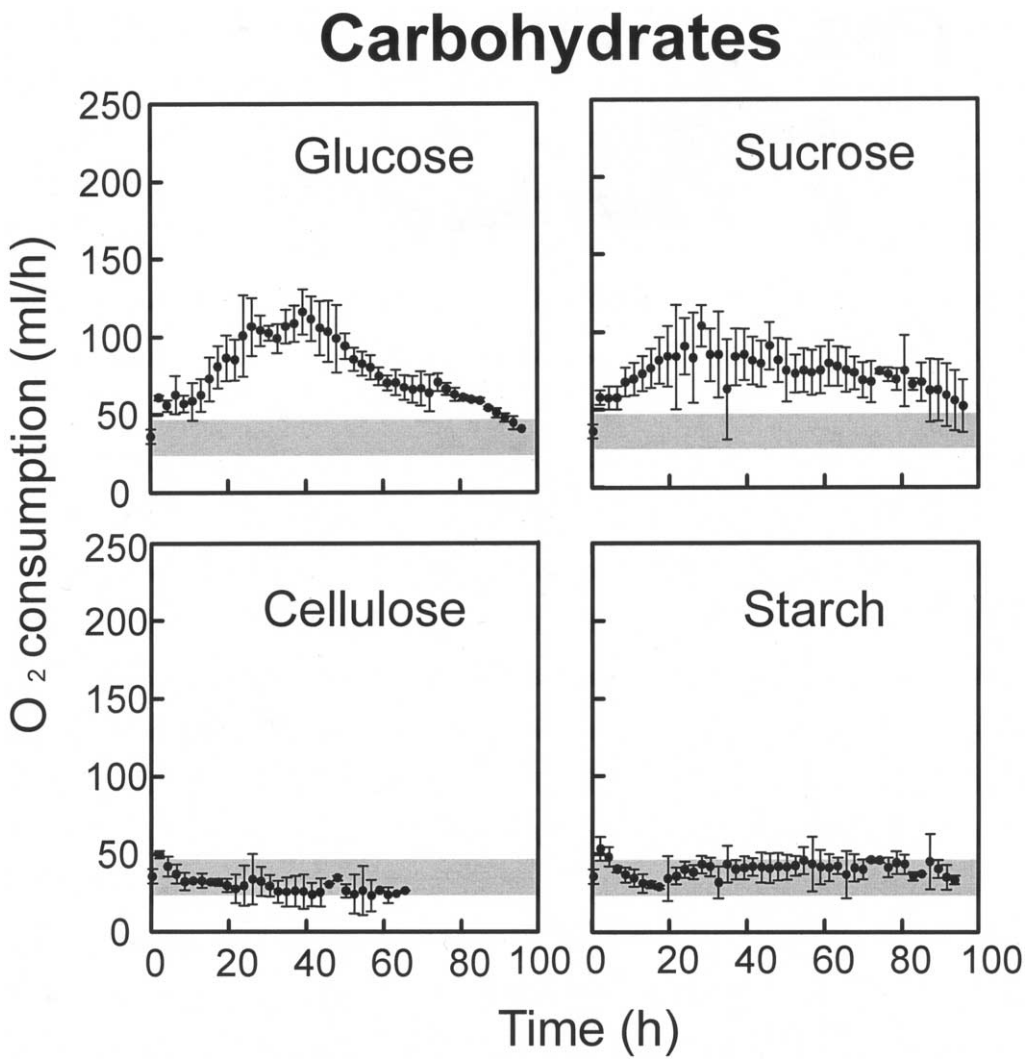

Figure 2. Postprandial oxygen consumption after ingestion of carbohydrates by *Python molurus*; symbols as in Figure 1

Results

Food Type Experiments

The mean rate of standard rate of oxygen consumption was 34.11 ± 2.08 (95% cl) mL/h (126% of the predicted SMR for this species; Chappell and Ellis 1987; 89% of the predicted SMR for a snake at 30°C; Bennett and Dawson 1976). No diel patterns in SMRs were observed.

Food type and composition had strongly differential effects on SDA (Table 1; Figs. 1–3). Lipid meals did not result in measurable SDA ($P = 0.39$; Fig. 1) and appeared to pass through the digestive tract unmodified, resulting in very oily stools. Although, in general, protein produced a greater SDA than did carbohydrate, there was significant heterogeneity in both of these, depending on the type of protein or carbohydrate in the meal. Proteins containing a complete balance of amino acids (mouse, chicken breast, and casein) induced a larger SDA (14%–33% energy content) than those composed of only a few amino acids (collagen and gelatin; Fig. 3; $P < 0.001$). The SDA after ingestion of different carbohydrates varied widely (Fig. 2). Neither starch nor cellulose induced a measurable SDA ($P = 0.18$), and both appeared to pass intact through the digestive system, while glucose and sucrose induced a SDA equivalent to approximately 1/3 of the energy in the meal. None of the administered diets induced apparent intestinal distress or diarrhea. Across all meal types, meal volume was not correlated with SDA ($P = 0.51$). Whole- and pureed-mouse meals induced different SDA responses: pureed meals had a 36% greater SDA than did whole-mouse meals ($P = 0.03$; Fig. 3).

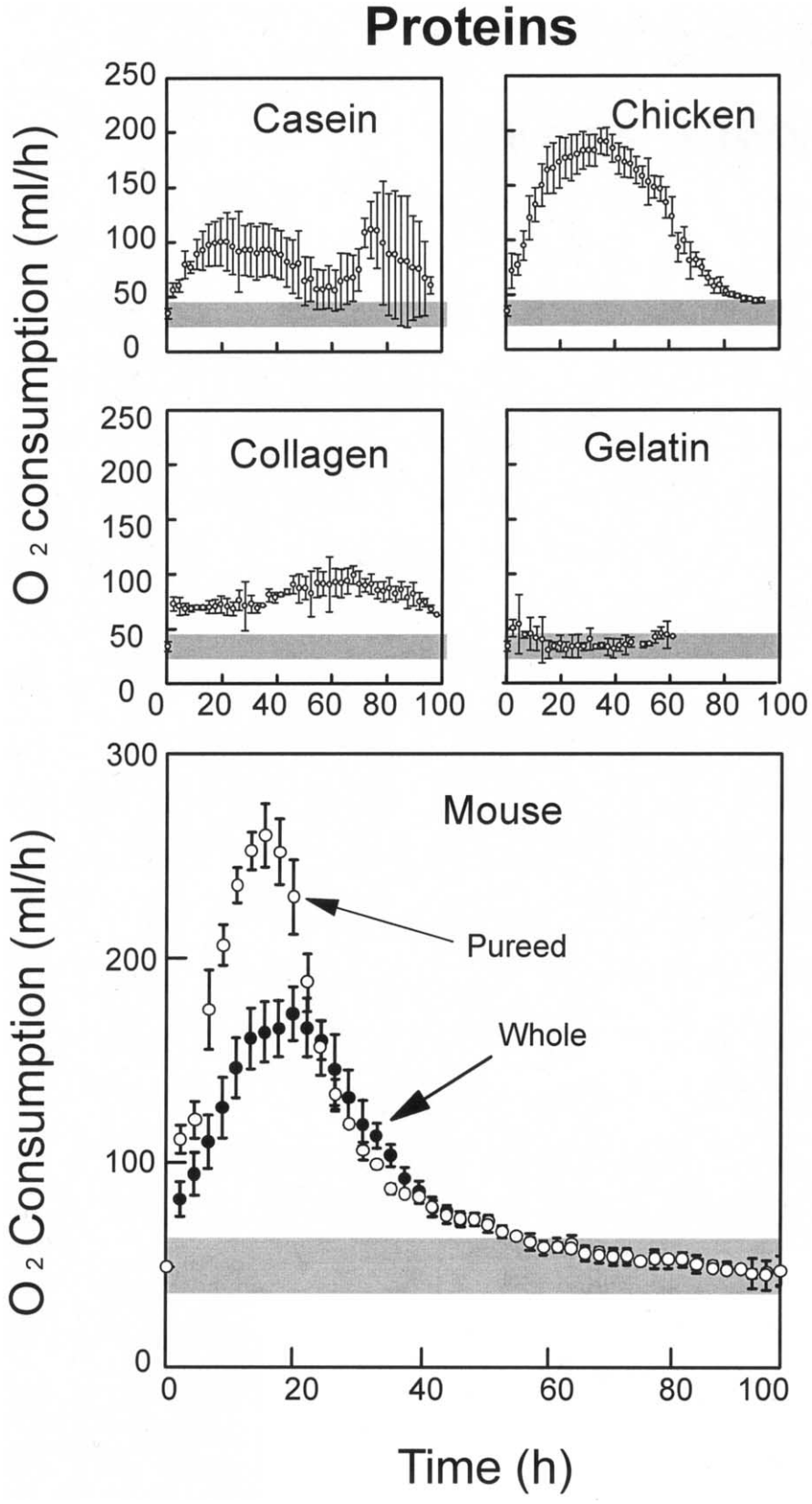

Figure 3. Postprandial oxygen consumption after ingestion of proteins by *Python molurus*. Symbols as in Figure 1: filled and open circles represent oxygen consumption after ingestion of whole and pureed mouse, respectively.

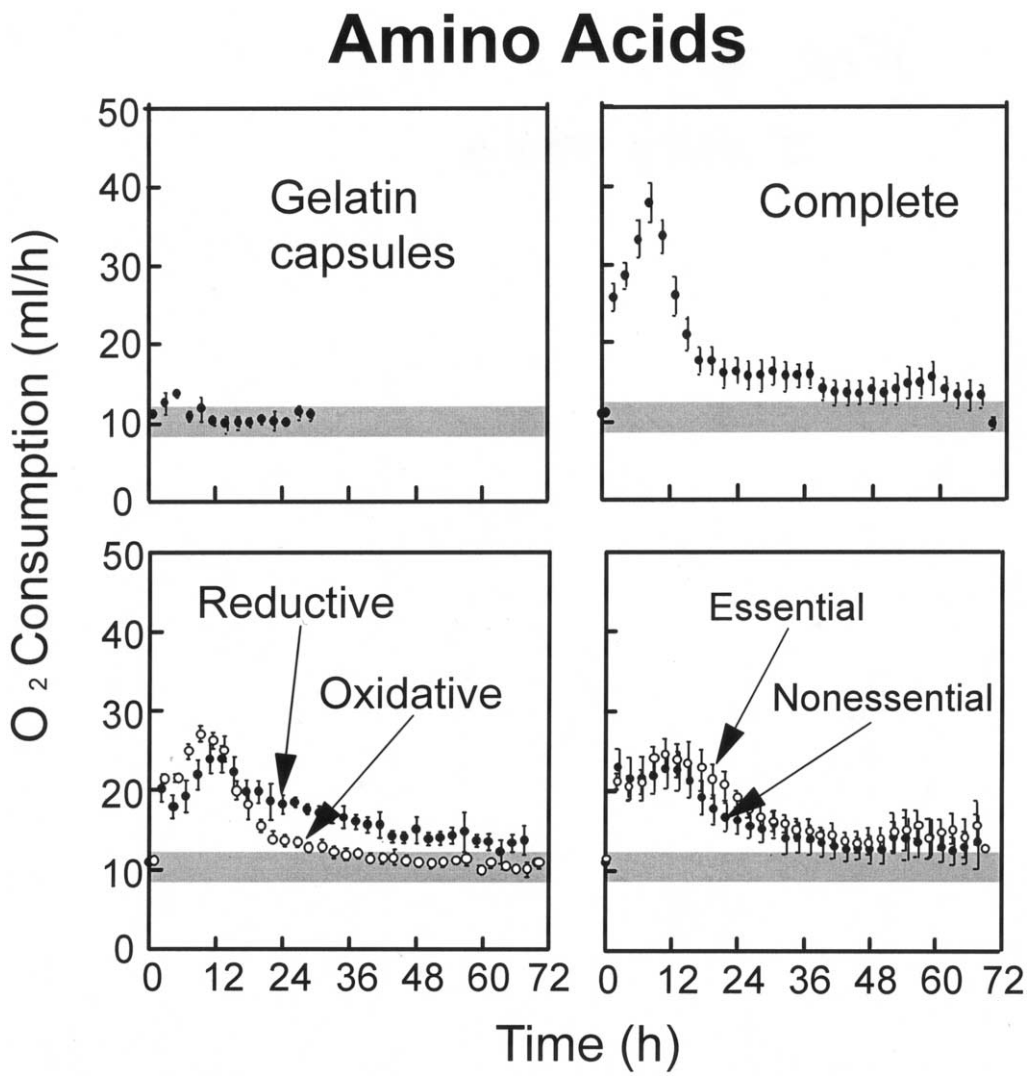

Figure 4. Postprandial oxygen consumption after ingestion of Reductive or Nonessential amino acid mixtures (*filled circles*) or Oxidative or Essential amino acid mixtures (*open circles*) by *Python molurus*. See Table 2 for composition of mixtures. Symbols as in Figure 1.

Protein Composition and Protein Synthesis Inhibition Studies

Consonant with the gelatin data in the food type experiments, the gelatin capsules used as vehicles for amino acid meal delivery did not induce measurable SDA ($P = 0.17$; Fig. 4). Among the Incomplete amino acid mixtures, there was no difference in SDA between the Essential (5.28 ± 1.13 kJ) and the Nonessential mixtures (4.96 ± 0.99 kJ, $P = 0.84$; Fig. 4) or between the Oxidative (3.86 ± 0.18 kJ) and the Reductive mixtures (4.89 ± 0.61 kJ, $P = 0.13$; Fig. 4). In contrast, the Complete amino acid mixture (7.61 ± 1.15 kJ) resulted in a greater overall SDA than did the Incomplete mixtures (4.74 ± 0.40 kJ, $P = 0.006$; Fig. 4). A large part of this greater SDA can be attributed to the higher peak metabolic rates generated by the Complete amino acid mixture ($P < 0.0001$; Fig. 4). The SDA coefficient for the Complete mixture was approximately 30%, a value consistent with the data for complete protein meals in the food type experiments. The administration of cycloheximide before ingestion of a Complete amino acid mixture resulted in a 71% reduction in SDA (Complete mixture with cycloheximide = 2.17 ± 0.37 kJ, $P < 0.001$; Fig. 5).

Discussion

Our results support previous conclusions that some protein meals can elicit a very high SDA and that SDA after lipid meals is low or absent. However, our results also point out how very dependent SDA is on the exact chemical composition of the meal. For instance, animal tissue containing complete protein or complete mixtures of amino acids produces high SDA, but

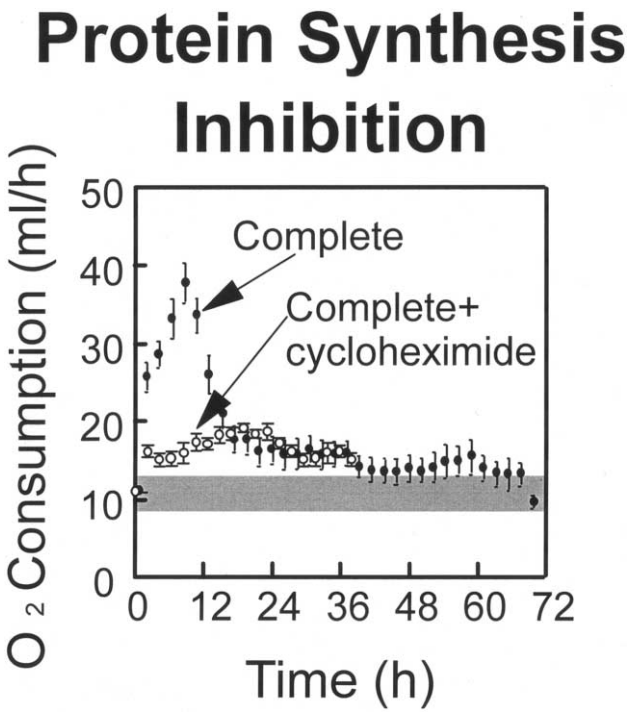

Figure 5. Postprandial oxygen consumption of *Python molurus* after ingestion of Complete amino acid mixture in the absence (*filled circles*) and presence (*open circles*) of the protein synthesis inhibitor cycloheximide. Symbols as in Figure 1.

simpler proteins or incomplete mixtures of amino acids produce a smaller or immeasurable SDA.

Lipid and Carbohydrate

Meals of pure lipid (lard or suet) were neither digested nor assimilated by pythons. They appeared to pass unmodified through the snakes' digestive systems and did not generate measurable SDA. Benedict (1932) reported SDA coefficients averaging only 4% for *Boa constrictor* eating fat. Similarly, dogs neither digest meals of pure lard nor generate a significant SDA from them (Chambers and Lusk 1930).

Because pythons are carnivorous, it is perhaps not surprising that their carbohydrate digestion is poor. Cellulose is not typically digested by vertebrates and was not by these snakes. Neither was starch digested; instead, it passed through the digestive tract intact. In most vertebrates, starch digestion is catalyzed by an α- or β-amylase; pythons apparently do not posses sufficient amylase to digest these large starch meals. In contrast, glucose and sucrose induced very high ratios of SDA to ingested energy, similar to those of complete animal protein. (Note, however, that these carbohydrate meals had only half the energy content of the protein meals and that SDA may not scale linearly with meal energy content.) These results are generally in agreement with the observations of Coulson and Hernandez (1983) for carbohydrate digestion (or lack of it) in caimans and turtles (*Pseudemys scripta*). They fed these animals a variety of saccharides and starches (e.g., glucose, sucrose, maltose, lactose, starch, rice, wheat, corn, and potato). Most of these passed through the digestive tract unabsorbed, except glucose, which was absorbed very rapidly. Only glucose was effective at raising postprandial blood saccharide levels. Apparently, pythons can hydrolyze and absorb the components of sucrose but otherwise resemble caimans and turtles in their carbohydrate utilization ability. It is possible that the high SDA observed for glucose and sucrose are the result of glycogen formation and storage in the liver, in addition to transport across the intestinal epithelium.

Protein and Amino Acids

Although whole animal tissues, such as chicken breast and mice, produced a high SDA, simpler animal proteins, such as gelatin and collagen, did not. While the former are composed of complete protein, the latter are made of nutritionally unbalanced ratios of amino acids. Gelatin and collagen are similar in amino acid composition. Although collagen constitutes nearly one-third of the total protein found in birds and mammals, it remains a poor dietary component because it is deficient in essential amino acids (O'Neil et al. 2001). Casein, in contrast, is relatively rich in most essential amino acids, but it lacks sufficient amounts of arginine and glycine to be considered a complete diet (Rapport 1927; Coulson et al. 1987). Casein induced a greater SDA than did gelatin and collagen but a lower SDA than whole-tissue meals. Lean chicken breast induced a higher SDA than did mouse meals, likely because a significant proportion of energy and protein stores in the mouse meals are in the indigestible keratin of the mouse fur (Greenwald and Kanter 1979). In addition, the chicken breast had greater protein content (73.7% dry) than did the mouse tissue (53.4% dry). The observation that pureed mouse meals induced a greater SDA than did intact mouse meals was surprising, particularly because it is the opposite response found by Secor (2003) for this same species. We did, however, obtain identical results in a colubrid snake (*Pituophis catinifer*) consuming both whole- and pureed-mouse meals (M.D. McCue, unpublished data). In view of the recent observations of Starck et al. (2004), which document the use of energy stored within the prey to fuel SDA, it is possible that homogenization of the carcass releases nutrients for more rapid and complete access than is afforded by whole prey.

The hypothesized significance of amino acid composition in determining SDA of protein meals is further reinforced by the amino acid mixture experiments. The Complete amino acid mixture generated a significantly greater SDA than did the Incomplete mixtures. Meals rich in amino acids that typically undergo oxidative forms of deamination did not result in

greater SDA than those undergoing reductive deamination (see Brody 1945 for a detailed explanation). This finding suggests that the costs of oxidative deamination do not contribute differentially to SDA; a similar conclusion has been reported for humans (Garrow and Hawes 1972). Likewise, there was no difference in the SDA between meals of essential and nonessential amino acids. Although, theoretically, some of the former could have been converted to the latter to permit synthesis of complete protein, with attendant higher metabolic cost, this apparently did not happen.

The Physiological Basis of SDA

The physiological processes responsible for SDA have been under investigation for nearly a century (e.g., Lusk 1915, 1922), and their nature is still controversial. Probably there is a suite of factors of differential importance, depending on food type and previous feeding status. For instance, we obtained equal ratios of SDA to meal energy for meals of complete protein and simple sugars, and these must have different underlying physiological mechanisms for processing.

The results of these experiments suggest the importance of de novo protein synthesis as an important factor in SDA of pythons eating protein meals. The importance of protein synthesis is supported by the failure of simple proteins, such as gelatin and collagen, to stimulate levels of SDA attained after consumption of complete protein. Further support is provided by the failure of Incomplete mixtures of amino acids to elicit an SDA response as large as that following the ingestion of a Complete mixture. And finally, the inhibition of de novo protein synthesis with the drug cycloheximide caused a more than 70% decrease in SDA. These observations and conclusions are in accord with those measured for crocodilians (Coulson and Hernandez 1968, 1979, 1983; Coulson and Herbert 1974) and fish (Brown and Cameron 1991*a*, 1991*b*). In the crocodilians, simple proteins such as gelatin and casein failed to promote extensive SDA, and incomplete mixtures of amino acids were metabolized differently than were complete mixtures. Cycloheximide was used to inhibit protein synthesis in both sets of studies, and both concluded that protein synthesis is responsible for a large amount of the cost of SDA.

Our data fail to suggest an important role for gastric distension or mechanical digestive effects as causal factors of SDA. The failure of the voluminous but nonnutrient meals of gelatin, cellulose, and starch to induce SDA are particularly persuasive in the regard. These results are not surprising and accord with the classical studies of Lusk (1922) in regard to nonnutrient meals. Overall, we found no correlation between meal volume and SDA. Nor did we find a significant cost associated with mechanical digestion of mice: our pureed mice had a higher, not a lower, SDA than did intact mice. These findings support with the conclusions of Tandler and Beamish (1979), who suggested that the mechanical component of SDA is substantially smaller than the chemical component.

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