REVIEW

Specific dynamic action: a review of the postprandial metabolic response

Stephen M. Secor

Abstract For more than 200 years, the metabolic response that accompanies meal digestion has been characterized, theorized, and experimentally studied. Historically labeled "specific dynamic action" or "SDA", this physiological phenomenon represents the energy expended on all activities of the body incidental to the ingestion, digestion, absorption, and assimilation of a meal. Specific dynamic action or a component of postprandial metabolism has been quantified for more than 250 invertebrate and vertebrate species. Characteristic among all of these species is a rapid postprandial increase in metabolic rate that upon peaking returns more slowly to prefeeding levels. The average maximum increase in metabolic rate stemming from digestion ranges from a modest 25% for humans to 136% for fishes, and to an impressive 687% for snakes. The type, size, composition, and temperature of the meal, as well as body size, body composition, and several environmental factors (e.g., ambient temperature and gas concentration) can each significantly impact the magnitude and duration of the SDA response. Meals that are large, intact or possess a tough exoskeleton require more digestive effort and thus generate a larger SDA than small, fragmented, or soft-bodied meals. Differences in the individual effort of preabsorptive (e.g., swallowing, gastric breakdown, and intestinal transport) and postabsorptive (e.g., catabolism and synthesis) events underlie much of the variation in SDA. Specific dynamic action is an integral part of an organism's energy budget, exemplified by accounting for 19–43% of the daily energy expenditure of free-ranging snakes. There are innumerable opportunities for research in SDA including coverage of unexplored taxa, investigating the underlying sources, determinants, and the central control of postprandial metabolism, and examining the integration of SDA across other physiological systems.

Keywords Specific dynamic action ·
Postprandial metabolism · Digestive energetics

Introduction

For more than two centuries, scientists have observed and reported the increase in energy expenditure that occurs during meal digestion. From the minute copepod to the horse, this reported "cost of digestion" has been described, quantified, and experimentally investigated over a wide array of invertebrate and vertebrate taxa. Originally coined specific dynamic action (SDA) from Max Rubner's descriptions, and later acquiring the additional labels of heat increment of feeding (HIF), diet-induced thermogenesis (DIT), and thermic effect of feeding (TEF), this postprandial physiological phenomenon is considered an obligatory metabolic response of meal digestion and assimilation. Much of the attention in SDA has historically been driven by the desire to identify its underlying mechanisms and the various determinants responsible for the variation in the magnitude and duration of this metabolic response. Defined numerous times, an accepted working definition of SDA (the term used in this review) is the accumulated energy expended (or heat produced) from the ingestion, digestion, absorption, and assimilation of a meal (Jobling 1994).

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Accompanying the many original studies on SDA are the occasional reviews. These reviews have either focused on particular taxa: crustaceans (Whiteley et al. 2001), fishes (Beamish and Trippel 1990; Jobling 1981), amphibians (Andrade et al. 2005), reptiles (Andrade et al. 2005; Wang et al. 2001), ruminants (Blaxter 1989), and humans (de Jonge and Bray 1997; Westerterp 2004); or addressed the determinants or underlying mechanisms of SDA (Borsook 1936; Garrow 1973; James 1992; Lusk 1931; Mitchell 1964; Wilhelmj 1935). Recently McCue (2006) provided a multi-taxa review of SDA with discussions of its various determinants. Evident from these reviews and the rich history of SDA studies is a succession of different theories put forth to explain the metabolic origin of SDA. Combined with the earlier studies of the twentieth century, the more recent investigations of invertebrate, fish, amphibian, and reptile SDA has provided an increasingly expanding data set to examine the determinants and mechanisms of SDA.

The central goal of this review is to provide a comprehensive coverage of SDA. First, a historical account of the study of SDA is presented which identifies the scientists who pioneered the study of the postprandial metabolic response. Second, the various aliases of SDA and the methods employed to quantify SDA are briefly discussed. Third, the available SDA data for invertebrates, fishes, amphibians, reptiles, birds, and mammals, and an abridged data set for humans are tabulated and summarized. Fourth, the various determinants of SDA, the physiological mechanisms that underlie the SDA response, and the contribution of SDA to an organism's energy budget are each reviewed and discussed. Lastly, several areas of SDA that warrant further attention are described. My ultimate aim is that this review will encourage SDA research on yet to be studied taxa and inspire experimental and novel approaches to further explore the features that impact SDA and the sources of this metabolic response.

History of SDA

The roots of SDA can be traced back to the birth of the "modern era of the science of nutrition and chemistry", credited to the French chemist, Antoine-Laurent Lavoisier (Lusk 1928). In the late 1700s, Lavoisier combined that century's discoveries of carbon dioxide, oxygen, nitrogen, and animal calorimetry to demonstrate that oxygen supports metabolism which results in the production of carbon dioxide and heat (Poirier 1996). With fellow chemist Armand Séguin serving as the test subject, Lavoisier found that cold temperatures, exercise, digestion, and exercise with digestion increased Séguin's metabolic rate by 11, 164, 53, and 280%, respectively (Lusk 1928). Despite his

monumental discoveries and his loyal civil service to France, Lavoisier's research and service tenure was unfortunately cut short when on 8 May, 1794, during the height of the French Revolution, he was guillotined by the Revolutionary Tribunal because of his previous membership in the General Farm (ferme générale), a private tax collection agency for the government (Poirier 1996).

Fortunately, the spirit of Lavoisier's work continued through the next century passing from his colleagues and through their academic descendants. Claude Louis Berthollet and Pierre Simon Laplace, two co-workers of Lavoisier, trained Joseph Louis Gay-Lussac, who later trained Justus von Liebig (Crosland 1978). Liebig is acknowledged for his discoveries in organic chemistry and his novel concepts regarding enzymes and chemical transformations within the body. The appointment of Liebig as professor of chemistry at Giessen in 1824 (and later at Munich) marked the transition from France to Germany as the dominant center in the study of metabolism and the training of students. Liebig's most influential student was Carl Voit, who later became professor of physiology at Munich in 1859 where he refined the experimental study of animal metabolism (Mitchell 1937). Voit assisted Max von Pettenkofer in the building of a respiration chamber which he used to measure the metabolism of human subjects fasted, exercising, and on different diets. Upon observing postfeeding increases in carbon dioxide production, Voit proposed his "plethora theory", claiming that the postprandial increase in circulating metabolites (e.g., glucose) are responsible for stimulating tissues to increase their metabolism (Kleiber 1961; Lusk 1928). That era also included the observations of Bidder and Schmidt (1852) of an increase in oxygen consumption and carbon dioxide production for food-deprived cats fed unlimited amounts of meat. Von Mering and Zuntz (1877) proposed from Bidder and Schmidt's observations and from their own on ruminants that the postprandial increase in metabolism represents the "work of digestion", the collective efforts of gut motility, secretion, digestion, and absorption (Benedict and Ritzman 1927; Kleiber 1961).

The students and young colleagues of Carl Voit became some of the most influential animal physiologists and nutritionist at the turn of the twentieth century, and included Max Rubner, Wilbur Olin Atwater, and Graham Lusk. In 1889, Rubner, a professor of physiology at Berlin, constructed a metabolic calorimeter which he used to measure the metabolic rates of dogs fasted and following the consumption of different meals. Rubner's (1902) findings that the heat produced from the digestion of a high protein meal (meat) is greater than that resulting from the digestion of a meal high in either carbohydrates or fats has been demonstrated repeatedly since (Forbes and Swift 1944; Kriss et al. 1934; Lusk 1928; McCue et al. 2005;

Murlin and Lusk 1915; Šimek 1976). Rubner (1902) referred to the postprandial increase in heat production as "spezifisch-dynamische Wirkung", which was mistakenly translated to the commonly used "specific dynamic action" (the proper translation is "specific dynamic effect"; Kleiber 1961; Withers 1992). Rubner did not agree with his mentor on the source of SDA, and proposed instead that SDA stems from the intermediary reactions involved in the transformation of biomolecules (chiefly proteins) prior to their metabolism or storage by cells.

The end of the nineteenth century and the start of the twentieth century also saw the dominance of animal and human energetic studies and training shifting from Germany to USA. Following their training with Voit, Atwater and Lusk returned to the USA and joined Samuel Johnson (a former student of Liebig) in developing research centers of metabolism and nutrition at Wesleyan University, Cornell Medical College, and Yale, respectively (Williams 2003). In 1897, Atwater together with the physicist, Edward Bennett Rosa, completed the construction of the Atwater–Rosa calorimeter which was used to accurately measure both heat production and carbon dioxide production of a man undertaking different activities (Lusk 1928; Williams 2003). Henry Prentiss Armsby, a student of Johnson and Director of the Institute of Animal Nutrition at Pennsylvania State University, likewise constructed a respirometry chamber which he used in his authoritative studies on the nutrition of large farm animals (Benedict 1938).

The first four decades of the twentieth century saw a tremendous influx of SDA studies on humans and domesticated animals. Graham Lusk together with his students and colleagues conducted a meticulous series of studies, primarily on dogs, documenting the postfeeding metabolic responses to a wide array of experimental treatments (e.g., hypothysectomized or phlorizinized) and meals ranging from a single dietary component (e.g., single amino acid solution) to mixtures of sugars, fats, and amino acids, and to intact food items (e.g., beef or chicken). Much of this work was published in the *Journal of Biological Chemistry* from 1912 to 1932 and organized in series (1–42) under the heading of 'Animal Calorimetry', as well as in Lusk's book *The Elements of the Science of Nutrition* (Lusk 1928). Over the decades of study, Lusk was a proponent of several different explanations for SDA, beginning with a modification of Voit's "plethora theory", and then later switching to Rubner's proposed importance of intermediary metabolites (Lusk 1928; Mitchell 1964). Other researchers of that time studying SDA included Francis Benedict, Henry Borsook (California Institute of Technology), Harry Deuel (Mayo Clinic), Max Kriss (Pennsylvania State University), Harold Mitchell (University of Illinois), David Rapport (Western Reserve), Gordon Ring (Ohio State University), and Charles Wilhelmj (Creighton University).

Trained as a chemist in Germany and later as a physiologist under Atwater at Wesleyan University, Francis Benedict was undoubtedly the most comparative among his contemporaries in the study of metabolism and SDA. As Director of the Nutrition Laboratory of the Carnegie Institution of Washington in Boston (1907–1937), Benedict constructed calorimeters of all sizes that enabled him to measure the metabolic rates of humans, and animals ranging from 8 g dwarf mice to 150 g doves to a 132 kg Galapagos tortoise and to a 1,800 kg Asian elephant (Benedict 1915, 1932, 1936; Maynard 1969; Riddle et al. 1932). His SDA studies on humans, steers, and snakes were instrumental in identifying for each, respectively, the modest cost of gut motility, the importance of meal size compared to protein content on the magnitude of postprandial metabolism, and the tremendous increase in metabolism that reptiles can experience after feeding (Benedict and Emmes 1912; Benedict and Ritzman 1927; Benedict 1932).

Equally monumental in the comparative study of animal nutrition and energetics was Samuel Brody, who from the 1920s to the 1940s studied the energy efficiencies, metabolism, and growth of farm animals at the Missouri Agricultural Experimental Station. Much of Brody's work was compiled in his book *Bioenergetics and Growth* (Brody 1945) which illustrates the postfeeding metabolic profiles of hogs, sheep, steers, and horses. Next to dominate the study of farm animal energetics was Sir Kenneth Blaxter who gained his early training with Harold Mitchell at the University of Illinois and then became Director of the Rowett Research Institution in Aberdeen, Scotland. For more than three decades, Blaxter (1962, 1989) likewise studied the growth, energy efficiencies, and metabolism of ruminants. One of his major contributions to the study of SDA, which he shared with A. J. F. Webster, was demonstrating the cost of eating and rumination for sheep (Blaxter and Joyce 1963; Osuji et al. 1975; Webster et al. 1976).

Sparked in part by a handful of studies in the 1960s on fish SDA, the 1970s gave birth to a new era of SDA research as the animals of study switched from those of the barnyards, pastures, and laboratories to those of the rivers, oceans, forests, and deserts (Averett 1969; Saunders 1963). Initiating these research programs were experimental studies on the SDA of invertebrates (Bayne and Scullard 1977; Nelson et al. 1977), fishes (Beamish 1974; Muir and Niimi 1972; Pierce and Wissing 1974), reptiles (Coulson and Hernandez 1979), and mammals (Šimek 1976). The next two decades brought new studies on the SDA of amphibians (Wang et al. 1995; Powell et al. 1999) and birds (Klaassen et al. 1989; Masman et al. 1989), and a renewed interest in the SDA of humans, in part due to the potential link between SDA and obesity (Ravussin et al.

1985; Segal and Gutin 1983; Weststrate 1993). The new millennium has witnessed a surge in SDA studies, especially for amphibians and reptiles. Over a 7-year span (2000–2007), SDA studies (excluding those on humans) were being published at an average rate of slightly more than one study per month. Many of these new studies focused on how biotic and abiotic factors impact the magnitude and duration of the SDA response and the significance of SDA in animal energetics.

The aliases of SDA

Possibly no other physiological phenomenon has garnished as many aliases or acronyms as that for the energy expended on, or the heat produced from, the digestion and assimilation of a meal. Possibly first referred to as the "work of digestion" by von Mering and Zuntz (1877), it was Rubner's (1902) description of the phenomenon as "spezifisch-dynamische Wirkung" and its incorrect translation to specific dynamic action (SDA) that soon became widely accepted. For the first half of the twentieth century, the term SDA was used almost exclusively by physiologists (Lusk, Benedict, Wilhelmj, and Brody to name a few) when describing and quantifying postprandial metabolism. However, during that time and later, physiologists in finding fault with Rubner's definitions began using alternative terms for this response (James 1992; Kriss et al. 1934; Kleiber 1961).

Objections to Rubner's original description include that it is specific to the ingestion of proteins, carbohydrates, or fats, and the postabsorptive fate of those nutrients. We now know that there is a multitude of mechanical and biochemical processes that contribute to elevating metabolism with feeding. Also, it is not an 'action' that is being quantified, but rather the accumulative metabolic outcome of all of these different processes. Hence, throughout the latter half of the twentieth century new terms were created, occasionally with different definitions, to label the postprandial increase in energy expenditure. Terms such as: dietary induced thermogenesis (DIT), postprandial thermogenesis (PPT), thermogenic effects of feeding (TEF), thermic effect of a meal (TEM), heat increment (HI), and heat increment of feeding (HIF) were introduced and each used in a multitude of studies, primarily in reference to the acknowledged production of heat stemming from digestion and assimilation (Beamish and Trippel 1990; James 1992; Kleiber 1961).

James (1992) distinguished PPT from DIT in that the former is used when dealing with the response over a few hours after eating, and the latter is used in reference to longer term effects resulting from sustained overfeeding. Beamish (1974) described SDA as the component of postprandial metabolism specific to the post-absorptive biochemical processing of meal proteins, carbohydrates, and lipids. Because the pre-absorptive mechanical costs of meal breakdown, transport, and absorption cannot be easily separated experimentally from the post-absorptive costs, Beamish (1974) proposed the term "apparent SDA" to be used when the distinction is not made between the mechanical and biochemical costs. For similar reasons, Medland and Beamish (1985) used the term "apparent HI" to describe the entire postprandial response incidental to meal digestion and assimilation.

Other terms that have occasionally surfaced include calorigenic effect of food (Kleiber 1961), digestion-related thermogenesis (DRT; Rashotte et al. 1999), meal-induced thermogenesis (MIT; Even et al. 2002), and postprandial energy expenditure (PEE; Bessard et al. 1983). Even with this myriad of new terms, SDA is still being used commonly in studies of postprandial metabolism, especially those involving ectotherms. For invertebrate and fish studies that state a particular term, 90 and 65%, respectively, use SDA. Other fish studies have used apparent SDA, HIF, HI, or apparent HI. Among all amphibian and reptile studies, SDA is the only term that has been used to date. For bird studies, HIF or HI has been used most frequently (45% of studies), followed by SDA (35%) and DIT (15%). Mammal studies are dominated by the use of SDA (50% of studies) chiefly because it was used by Lusk and his colleagues in their dozens of studies using dogs. More recently, HIF, HI, DIT, and PPT have been used in studies of mammalian postprandial metabolism. If one excludes the early human studies that used SDA, the remaining recent human studies are literally split down the middle in using either DIT or TEF (or TEM), with DIT being used almost exclusively since 2000.

Measuring SDA

For more than a century, studies of SDA have generally employed a similar experimental design. First, a baseline metabolic rate is measured from each individual. For ectotherms, the preferred baseline is their standard metabolic rate (SMR), the minimum metabolic rate of a postabsorptive individual at rest during its non-active period. For endotherms, it is their basal metabolic rate (BMR), the minimum metabolic rate of a postabsorptive, inactive individual within its thermoneutral zone during its non-active period. Whereas many terrestrial and aquatic sedentary ectotherms will remain inactive while fasting (as well as after feeding), others which continuously swim (e.g., fishes) or search for food (e.g., shrews) are more problematic in assigning a prefeeding baseline. Fasting and postprandial metabolic rates are measured using either

direct or indirect calorimetry. The less used and more technologically challenging method of direct calorimetry quantifies energy expenditure from measured heat production (McCollum et al. 2006; Smith et al. 1978). The more wide spread methods of indirect calorimetry quantify energy expenditure from rates of respiratory gas exchange, specifically rates of oxygen consumption ($\dot{V}O_2$ or $\dot{M}O_2$) and/or carbon dioxide production ($\dot{V}CO_2$), and assumptions on the substrate(s) being metabolized.

Once a baseline value has been assigned, the animal is then fed a natural or formulated meal either to satiety or to a targeted percentage of the animal's body mass. Following feeding, metabolic rates are recorded either continuously or intermittently in order to construct an accurate and complete profile of the postprandial metabolic response, commonly illustrated as metabolic rate (on the y-axis) plotted against time postfeeding (on the x-axis; Fig. 1). From this profile variables frequently quantified and analyzed include baseline metabolism (typically SMR or BMR), postprandial peak in metabolism, the factorial scope of that peak, time to peak, the duration of the SDA response, SDA, and the SDA coefficient (Jobling 1981; Secor and Faulkner 2002; Fig. 1; Table 1).

In practice, SDA is calculated from the summed amount of O_2 consumed or CO_2 produced (the area under the curve) above baseline and converted to energy (e.g., calories, joules, or watts). If metabolic measurements are curtailed before rates return back to baseline, the calculated SDA will be an underestimation, a fault considered common to many human studies (D'Alessio et al. 1988; de Jonge and Bray 1997; Reed and Hill 1996). Several studies have identified a circadian rhythm to the activity and metabolism of their study organism (Hopkins et al. 2004; Roe et al. 2004, 2005; Romon et al. 1993). Daily spikes in metabolism due to activity within the experimental chamber must, therefore, be removed from the postprandial
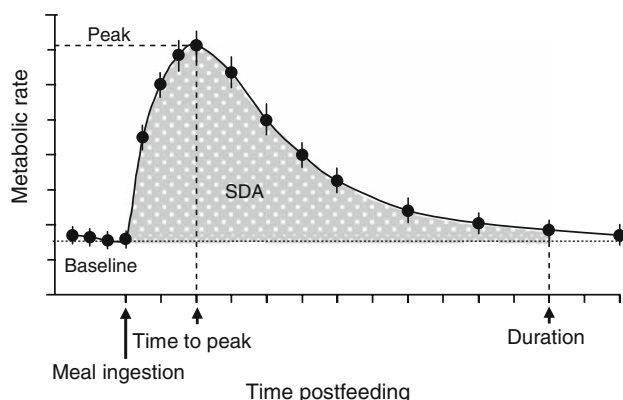
Table 1 Definition of variables commonly used to quantify the postprandial metabolic response to feeding

Variable	Definition
Baseline	Metabolic rate of postabsorptive individuals, quantified as standard metabolic rate (SMR, ectotherms), basal metabolic rate (BMR, endotherms), resting metabolic rate (RMR) or routine metabolic rate (fishes swimming)
Meal size	Wet mass and/or as a percentage of body mass
Meal energy	Meal energy (calories or kilojoules) determined by bomb calorimetry
Peak	Postprandial peak in metabolism
Time to peak	Duration from time of feeding to peak metabolic rate
Scope	Postprandial peak divided by baseline
Duration	Time from feeding when metabolic rate is no longer significantly greater than baseline
SDA	Accumulated energy expended above baseline for duration of SDA response
SDA coefficient	SDA divided by meal energy

Variables are illustrated in Fig. 1

profile in order to accurately quantify SDA (see Roe et al. 2004 for explanation of curve smoothing technique).

The SDA coefficient is often quantified by dividing SDA by meal energy as determined by bomb calorimetry (Beaupre 2005; Jobling and Davies 1980; Secor and Boehm 2006). A popular rationale for presenting SDA coefficients is that it allows for intraspecific and interspecific comparisons of SDA that are independent of meal size, meal type, body size, and body temperature (LeGrow and Beamish 1986; McCue 2007; Ross et al. 1992). Objections to the application of SDA coefficients for comparative analyzes includes the possible false assumption that the scaling between SDA and ingested energy is isometric and that different meal types will not share equivalent mass-specific cost of digestion and/or energy content (Beaupre 2005; Secor and Boehm 2006).

Taxonomic summary of SDA

Published accounts of SDA are tabulated and summarized for each of the major groups of animals. All attempts were made to be as thorough as possible and to include those studies published up to the time of final submission with the exception of an abridged set of studies for humans. Because the amount of available data associated with these studies is more than can be presented in this format, the variables presented in the tables are limited to body mass, body (ectotherms) or ambient (endotherm) temperature, meal type, relative meal size (meal mass as a percentage of body mass), scope of peak postprandial metabolism (peak

Fig. 1 Hypothetical postprandial metabolic profile of metabolic rate plotted against time postfeeding. Noted are variables commonly quantified in characterizing and comparing the SDA response

Table 2 Tabulation of invertebrate SDA studies

Species	Body mass (g)	T_b (°C)	Meal type	Meal mass (%)	Scope	Duration (h)	SDA (kJ)	SDA coefficient (%)	Treatments	Source
Cnidaria										
Anthozoa										
Astrangia danae		22	Brine shrimp		1.87					Szmant-Froelich and Pilson (1984)
Platyhelminthes										
Turbellaria										
Planaria dorotocephala[a]	0.5	22	Liver		2.01	48	0.046			Hyman (1919)
Planaria velata[a]	0.5	22	Liver		1.88	36	0.098			Hyman (1919)
Nemertea										
Parborlasia corrugatus[a]	8.63	0.3	Limpet	45.5	1.70	840	0.083	0.5		Clarke and Prothero-Thomas (1997)
Annelids										
Hirudinea										
Erpobdella testacea	0.045	20	Tubificid worm		2.50	120	0.014			Mann (1958)
Hirudo medicinalis[a]	1.2	18	Blood	500	6.00		1.10			Zebe et al. (1986)
Nephelopsis obscura	0.04	20	Tubificid worm	25.3	1.79	14	0.0017	4.2	BT	Kalarani and Davies (1994)
Mollusk										
Gastropoda										
Ancylus fluviatilis	0.02	13	Algae		1.54					Berg et al. (1958)
Australorbis glabratus[a]	0.16[b]	30	Lettuce/fish food		4.74					Von Brand et al. (1948)
Crepidula fornicata		25	Algae		1.40					Newell and Kofoed (1977)
Helisoma duryi[a]		30	Lettuce/fish food		4.11					Von Brand et al. (1948)
Nacella concinna	0.17[b]	−0.65	Algae	3.3	2.30	360	0.045	48.4		Peck and Veal (2001)
Nassarius reticulatus[a]	0.1[b]	17.5	Crab		2.77		0.023			Crisp et al. (1978)
Physa gyrina[a]		30	Lettuce/fish food		4.00					Von Brand et al. (1948)
Bivalvia										
Corbicula fluminea	0.3	25	Algae		1.25					Soucek (2007)
Gnathophausia ingens	2.8	5.5	Shrimp	2.14	1.53	7	0.10	29.0		Hiller-Adams and Childress (1983)
Littorina littorea	0.08[b]	15	Algae		1.44					Shumway et al. (1993)
Littorina obtusata	0.005[b]	15	Algae		1.47					Shumway et al. (1993)
Mulinia lateralis[a]	0.01		Algae		2.04	384	0.051			Shumway et al. (1993)
Mytilus edulis	0.01[b]	15	Algae	9.8	1.38	10	0.00096	5.0	MS	Widdows and Hawkins (1989)
Mytilus edulis[a]	0.064[b]	15	Algae				0.0017			Gaffney and Diehl (1986)
Mytilus edulis[a]	1.0[b]	15	Algae		2.02					Thompson and Bayne (1972)
Mytilus edulis	1.33[b]	13.5	Algae	0.23	2.36	30	0.015	27.7		Bayne and Scullard (1977)

Table 2 continued

Species	Body mass (g)	T_b (°C)	Meal type	Meal mass (%)	Scope	Duration (h)	SDA (kJ)	SDA coefficient (%)	Treatments	Source
Cephalopoda										
Octopus vulgaris	571	21	Crab	2.04	3.00	12	2.06	5.9		Wells et al. (1983)
Arthropoda										
Arachnida										
Alaskozetes antarcticus	0.00022	10	Algae		1.42				BT	Young and Block (1980)
Crustacea										
Acartia tonsa[a]	0.0000044[b]	14	Algae		2.00	8	0.00096			Thor (2000)
Acartia tonsa	0.0000074[b]	18	Algae		5.20					Kiørboe et al. (1985)
Acartia tonsa[a]		20	Algae		3.36			19.0		Thor et al. (2002)
Asellus aquaticus[a]	0.016	11	Meat		1.58					Hervant et al. (1997)
Calanus euxinus	0.00091	20	Dinoflagellate		1.30				BS	Svetlichny and Hubareva (2005)
Calanus finmarchicus	0.0002	14	Algae		2.80					Thor (2000)
Callinectes sapidus[a]	195	20	Clam/fish		2.30	45	7.11			McGaw and Reiber (2000)
Cancer gracilis	250	11	Fish	2.0	2.54	55	3.33			McGaw (2006)
Cancer pagurus	200	11	Mussel		2.62					Ansell (1973)
Carcinus maenas[a]	10	10	Squid	5.4	1.44	120	0.074	3.4		Wallace (1973)
Carcinus maenas	20	15	Squid	3.33	3.08	20	0.24	10.5		Robertson et al. (2002)
Carcinus maenas[a]	36.8	15	Mussel	1.96	2.30	20	0.34	13.3		Houlihan et al. (1990)
Carcinus maenas	49	15	Mussel	4.1	1.79					Legeay and Massabuau (1999)
Carcinus maenas[a]	53	15	Mussel		2.43	48	0.70			Mente et al. (2003)
Cardisoma guanhumi[a]	241	30	Fish	2.0	2.53	50	2.79	11.5		Burggren et al. (1993)
Crangon franciscorum	0.185[b]	18	Fish		1.11	3	0.0019		MT	Nelson et al. (1985)
Daphnia magna	0.00013[b]	20	Algae		1.42					Porter et al. (1982)
Daphnia magna	0.0009[b]	20	Algae		2.00					Lampert (1986)
Euphausia superba[a]	0.212	−0.5	Diatom		1.45					Ikeda and Dixon (1984)
Gammarus fossarum[a]	0.0335	11	Meat		1.66					Hervant et al. (1997)
Glyptonotus antarcticus	37.1	0	Krill	4.66	2.46		0.93	11.7	BT	Robertson et al. (2001a)
Goniopsis cruentata[a]	61.4	24	Fish	3.0	1.75	50	0.76	8.3		Burggren et al. (1993)
Homarus americanus	3.2		Formulated diet		1.51				MC	Koshio et al. (1992)
Jasus edwardsii[a]	16	15	Squid	3.0	1.78	30	0.54	29.2		Radford et al. (2004)
Jasus edwardsii[a]	750	13	Squid	3.0	1.80	42	5.73	6.6		Crear and Forteath (2000)
Ligia oceanica	0.10[b]	10	Pear		2.56					Newell et al. (1976)
Ligia pallasii[a]	0.25	15	Formulated diet	17.6	2.48	11	0.0025	3.6	BS, MC	Carefoot (1990a)
Ligia pallasii[a]	0.25	15	Algae	1.33			0.0016	24.2	MS	Carefoot (1990b)

Table 2 continued

Species	Body mass (g)	T_b (°C)	Meal type	Meal mass (%)	Scope	Duration (h)	SDA (kJ)	SDA coefficient (%)	Treatments	Source
Liothyrella uva[a]	0.29[b]	0.76	Algae		1.66	432	0.044			Peck (1996)
Litopenaeus vannamei	2.6	28	Formulated diet	2.3	2.08	96	0.031	3.9	MC	Rosas et al. (2001)
Macrobrachium rosenbergii	0.035[b]	28	Tubificid worm		1.41				MT	Nelson et al. (1977)
Macrobrachium rosenbergii	0.57	28	Formulated diet		1.73	17	0.024	7.1	MC	Du and Niu (2002)
Macrobrachium rosenbergii[a]	13.4	30	Formulated diet		2.84		0.55		MC	González-Peña and Moreira (2003)
Niphargus rhenorhodanensis[a]	0.0127	11	Meat		2.27					Hervant et al. (1997)
Niphargus virei	0.0925	11	Meat		2.50					Hervant et al. (1997)
Ocypode quadrata[a]	20.5	30	Fish	7.0	3.31	42	0.42	5.9		Burggren et al. (1993)
Panulirus cygnus	450	23	Squid	3.0	2.19	44	7.13	13.7		Crear and Forteath (2001)
Penaeus duorarum	0.031	28	Formulated diet	10.0	2.89				MC	Rosas et al. (1996)
Penaeus esculentus	0.27	30	Formulated diet		1.33				MC	Hewitt and Irving (1990)
Penaeus esculentus	17.7	25	Shrimp		1.39					Dall and Smith (1986)
Penaeus monodon[a]	5.08	28	Shrimp	2.86	2.25	5	0.061	9.0	MT, S	Du Preez et al. (1992)
Penaeus notialis	0.027	28	Formulated diet	10.0	3.12				MC	Rosas et al. (1996)
Penaeus schmitti	0.028	28	Formulated diet	10.0	2.84				MC	Rosas et al. (1996)
Penaeus setiferus	0.023	28	Formulated diet	10.0	2.11				MC	Rosas et al. (1996)
Penaeus setiferus[a]	0.40	28	Formulated diet		2.50	6	0.0024		MC	Taboada et al. (1998)
Penaeus setiferus[a]	37.6	28	Squid	2.68	1.68	8	0.41	6.8		Rosas et al. (1995)
Saduria entomon[a]	4.76	13	Fish	3.77	2.48	52	0.083	8.4		Robertson et al. (2001b)
Stenasellus virei	0.012	11	Meat		2.18					Hervant et al. (1997)
Waldeckia obsea	0.233[b]	0	Fish		4.75	7	0.00083			Chapelle et al. (1994)
Uca pugnax	2.9	28			1.58					Vernberg (1959)
Insecta										
Culex tarsalis[a]	0.002	25	Blood		2.03	57	0.0032			Gray and Bradley (2003)
Gryllus firmus	0.5	25	Formulated diet		1.78					Nespolo et al. (2005)
Gynaephora groenlandica[a] (larva)	0.052[b]	15	Leaves		4.29	36	0.020			Bennett et al. (1999)
Locusta migratoria[a]	0.53	30	Formulated diet	151	2.46	20	0.040			Zanotto et al. (1997)
Rhodnius prolixus[a]	0.02	20	Blood	991	9.20	16	0.102	22.9		Bradley et al. (2003)
Spodoptera exempta (larva)	0.33	25	Corn	8.8	2.01		0.0035	2.9	MT	Aidley (1976)
Tyria jacobaeae[a] (larva)	0.21	25	Leaves	1.29	1.52		0.00025	2.5		McEvoy (1984)
Echinodermata										
Stelleroidea										
Asterias rubens	5.0	15	Mussel	31.0	2.47	1,200	0.57	10.2		Vahl (1984)

Table 2 continued

Species	Body mass (g)	T_b (°C)	Meal type	Meal mass (%)	Scope	Duration (h)	SDA (kJ)	SDA coefficient (%)	Treatments	Source
Echinoidea										
Eucidaris tribuloides		30	Sponge		1.42					McPherson (1968)
Mellita quinquiesperforata	5.0[b]	25			1.37					Lane and Lawrence (1979)
Strongylocentrotus droebachiensis	44.0	14	Algae		2.11					Lilly (1979)
Urochordata										
Ascidiacea										
Ciona intestinalis[a]	0.1	15	Algae		6.55	53	0.029	20.0		Sigsgaard et al. (2003)

Meal mass (%) is reported as a percentage of body mass. Scope, duration, SDA, and SDA coefficient are defined in Table 1

T_b body temperature; studies with experimental treatments are noted as BS body size, BT experimental temperature, MC meal composition, MS meal size, MT meal type, S salinity

[a] Studies for which scope, SDA, and/or SDA coefficient are calculated from published information

[b] Body mass reported as dry mass

rate divided by baseline), duration of the SDA response, SDA, and SDA coefficient (Table 1). For studies that quantify SDA for one or more treatment effects (e.g., meal size, meal type, body temperature, etc.), a single set of data is presented that best characterize the SDA of that species for that study. For those studies, the treatment(s) investigated are noted in the tables. For each taxonomic summary, the average mean meal size, scope, and SDA coefficient was calculated from all available treatment data from every study. This total data set was also used to generate predicted equations of SDA.

Not every SDA report presented all of the tabulated variables. If a postprandial metabolic profile was presented graphically values were extracted from the figure using a digital caliper to calculate the missing variable(s). Occasionally, SDA was calculated from the reported SDA coefficient and meal energy, or the SDA coefficient was calculated from reported meal energy and SDA. Studies for which a tabled variable was calculated are noted by superscript a ([a]) next to the species name. The SDA of each study was standardized to kilojoules using the conversion factors of: 1 cal = 4.184 J, 1 mg O_2 = 14 J, 1 mL O_2 = 19.5 J, and 1 μmol O_2 = 0.45 J (Geesaman and Nagy 1988; Moyes and Schulte 2006; Wieser and Medgyesy 1990).

Invertebrates

The majority of invertebrate species whose postprandial metabolic responses have been measured are either aquatic or semi-aquatic (e.g., crabs), with many of those being marine (Table 2). Nearly half of the studied species are crustaceans, whereas insects represent most of the studied terrestrial species. Compared to the other major taxa in this review, invertebrates exhibit the greatest variation in body size, body temperature, and relative meal size. From copepods (~ 0.02 mg) to the rock lobster (750 g), individual body mass ranges over seven orders of magnitude, although are commonly between 0.1 and 50 g (Table 2). Studies have been conducted at body temperatures as low as -0.65°C for the Antarctic limpet, *Nacella concinna*, to as high as 30°C for the locust, *Locusta migratoria*, and the tropical land crabs, *Cardisoma guanhumi* and *Ocypode quadrata* (Burggren et al. 1993; Peck and Veal 2001; Zanotto et al. 1997). Meal sizes ranged from a very modest 0.2% of body mass for a study on the mussel, *Mytilus edilus*, to more than 990% of body mass for the blood-sucking insect, *Rhodnius prolixus* (Bayne and Scullard 1977; Bradley et al. 2003). Meal type is also quite variable among studies; brown and green algae were consumed by bivalves and small crustaceans, bivalves, crustaceans, and fish were consumed by medium size and larger crustaceans, leaves were consumed by moth larva, and blood was ingested by the leech, *Hirudo*

medicinalis, and the insects, *R. prolixus* and *Culex tarsalis* (Table 2).

For such a diverse group of organisms, feeding generated a shared rapid increase in metabolism that generally peaked at between two and three times prefeeding rates (Fig. 2). Across all invertebrate studies, the factorial scope of peak postprandial metabolism averaged 2.45 ± 0.12. Two of the largest factorial scopes in postprandial metabolism, 6.0 for the leech *H. medicinalis* and 9.2 for *R. prolixus*, occurred following the ingestion of a blood meal equaling in mass to 500 and 991%, respectively, of the animal's body mass (Fig. 2). Following the peak, metabolic rate returned more slowly back to baseline levels (Fig. 2). The impressive range of invertebrate SDA

(0.00025–7.11 kJ) reflects the large variation in body mass, body temperature, and meal size among studies (Table 2). For those studies for which both meal energy and SDA are calculated, SDA coefficients averaged 11.0 ± 1.4%, ranging from 0.50% for the Antarctic nemertean, *Parborlasia corrugatus,* to 48.4% for the limpet *N. concinna* (Clarke and Prothero-Thomas 1997; Peck and Veal 2001). Irrespective of meal type and ambient temperature, invertebrate SDA increases linearly as a function of meal energy (Fig. 3). The available data allows the SDA of an individual invertebrate to be predicted from equations with the input of body mass and either meal mass or meal energy (Table 3).

Fishes

Of all the groups covered in this review, fishes were chronologically the last to be subjected to studies of SDA, even though investigations of oxygen consumption of aquatic organisms had been conducted much earlier (Ege and Krogh 1914; Jolyet and Regnard 1877). Interestingly, the first fish SDA study was undertaken on the air-breathing African lungfish, *Protopterus aethopicus*, by Homer Smith (1935). For the first half of the twentieth century, studies of fish metabolism, frequently on the goldfish, *Carassius auratus*, focused on the effects of temperature and activity (Ege and Krogh 1914; Fry and Hart 1948; Toryu 1928). Then in the early 1960s, the study of fish energetics was literally jump-started by the efforts of several Canadian researchers, most notably Beamish (1964), Brett (1964), and Saunders (1963). Their investigations lead to studies of fish SDA, beginning in the 1970s and continuing until today. Many fish SDA studies have been conducted on species important to commercial (e.g., cod, salmon, and tuna) or recreational (e.g., sunfish, bass, and walleye) fishing, or on those used in aquaculture (e.g., catfish, trout, and tilapia). Many of these studies explored the effects of meal composition, meal size, body temperature, and density on fish SDA (Table 4). One central aim of these studies is to identify the optimal meal size, meal composition, water temperature, and/or fish density that minimize SDA and therefore increase the amount of absorbed energy allocated to growth (Chakraborty et al. 1992; Fu and Xie 2004; LeGrow and Beamish 1986; Peres and Oliva-Teles 2001). Comparatively, fewer SDA studies have been conducted on fishes of non-economic interests (Boyce and Clarke 1997; Johnston and Battram 1993; Vahl and Davenport 1979).

In addition to the impact of meal size, meal composition, body size, and body temperature on fish SDA (to be discussed later), the effects of swimming speed, fish density, feeding frequency, and oxygen saturation has also been explored. Whereas swimming speed (1.4–2.5 body
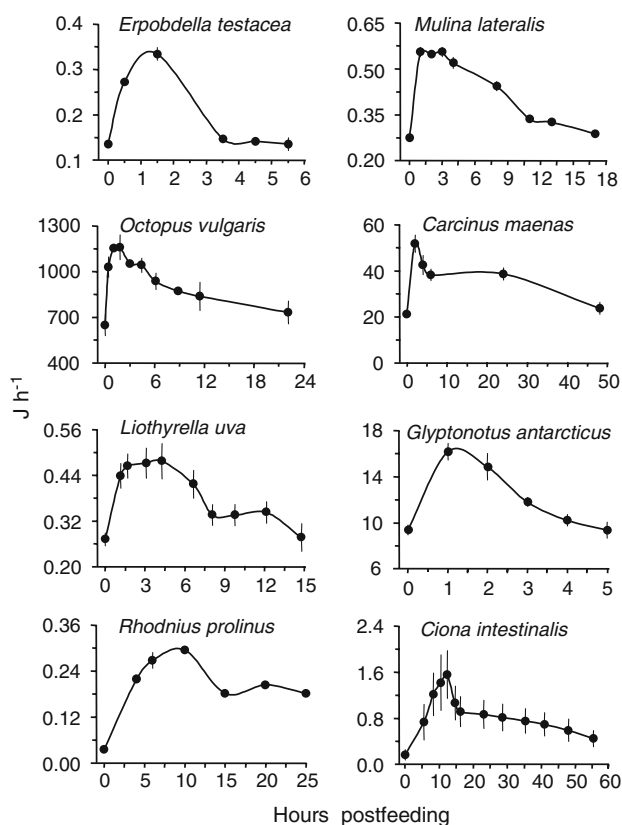

Fig. 2 Postprandial metabolic profiles of eight species of invertebrates. For each, feeding generated a rapid increase in metabolic rate that gradually returned to prefeeding levels. In this and subsequent figures, *error bars* represent ±1 SE and are omitted if the SE is smaller than the symbol for the mean value. Body mass, body temperature, meal type, and meal mass (if known) for each figure are presented in Table 2. Figures were drawn from the data presented in the following original articles; *Erpobdella testaceas* (Mann 1958), *Mulina lateralis* (Shumway 1983), *Octopus vulgaris* (Wells et al. 1983), *Carcinus maenas* (Mente et al. 2003), *Liothyrella uva* (Peck 1996), *Glyptonotus antarcticus* (Robertson et al. 2001a), *Rhodnius prolinus* (Bradley et al. 2003), and *Ciona intestinalis* (Sigsgaard et al. 2003)

Fig. 3 SDA (kJ) plotted against meal energy (kJ) for invertebrates, fishes, amphibians, reptiles, birds, mammals, humans (*open circles* single meal, *closed circles* full day), and all combined data. Data were collected from each experimental trial for the tabulated studies. Data are graphed on log–log plots to better visualize the variation in SDA and meal energy. Regression equations for each plot are presented in Table 3
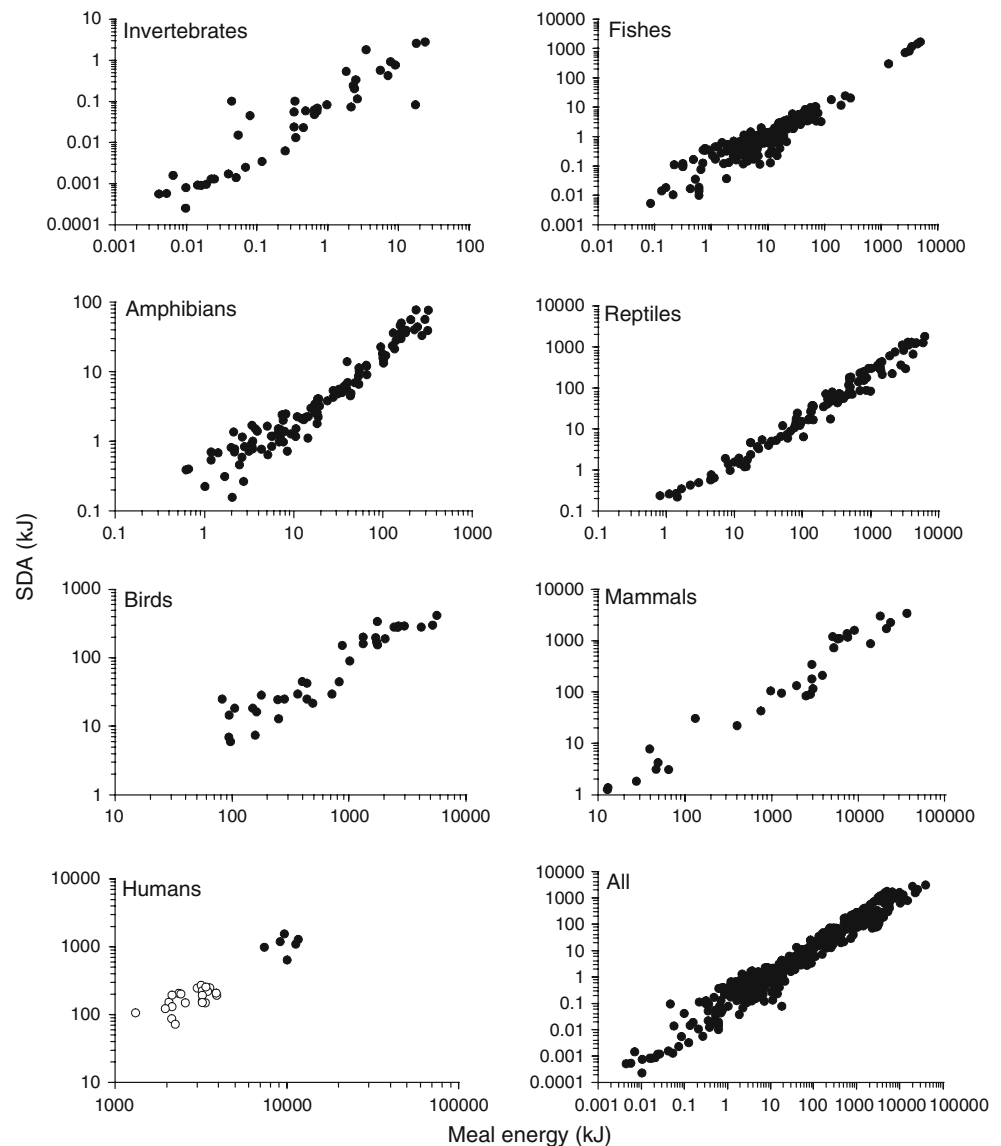
lengths/s) has no influence on the SDA of young large-mouth bass, *Micropterus salmoides*, a doubling of swimming speed results in a threefold increase in SDA for cod, *Gadus morhua* (Beamish 1974; Blaikie and Kerr 1996). Maintained over a threefold range in fish density (10–30 fish/67 L), walleyes, *Stizostedion vitreum*, experienced no significant variation in SDA with respect to density (Beamish and MacMahon 1988). Controlling for total food intake, feeding frequency (one large meal vs. several small meals) had no obvious effect on the SDA of the southern catfish, *Silurus meridionalis*, the walleye, or the gilthead sea bream, *Sparus aurata* (Beamish and MacMahon 1988; Fu et al. 2005a; Guinea and Fernandez 1997).

The fish species covered in this review span a 22,000-fold range in adult body mass, from 0.5 g zebrafish, *Brachydanio rerio*, to 11 kg bluefin tunas, *Thunnus maccoyii*

(Table 4). Experimental temperatures range from −0.5 to 30°C, although the majority of studies were conducted with water temperatures between 20 and 28°C. Many studies, especially those looking at the effects of meal composition, fed fish a formulated diet in pellet form for which protein and lipid concentrations were controlled. Other studies used natural food items, including mollusks, crustaceans, and other types of fish. For all studies, and their experimental treatments, meal mass averaged $3.35 \pm 0.23\%$ of fish body mass (range 0.25–24.2%). For fish, feeding generates a rapid increase in metabolic rate that peaks 3–12 h later (depending on body temperature) and is followed by a slower return to prefeeding rates (Fig. 4). The factorial scope of the postprandial peak in $\dot{V}O_2$ averages 2.36 ± 0.07, exhibiting its highest value (11.0) for the European eel in part due to the eel's low SMR (Table 4). Among these studies, the duration of elevated postprandial metabolism

Table 3 Equations for the estimation of SDA (kJ) based on body mass (bm) and meal mass (mm), and based on meal energy (me)

Taxa	r^2	P
Invertebrates		
SDA = 0.0034 bm + 0.12 mm + 0.13	0.57	<0.0001
log SDA = 0.31 log bm + 0.72 log mm − 0.83	0.89	<0.0001
SDA = 0.068 me + 0.065	0.62	<0.0001
log SDA = 0.97 log me − 1.091	0.85	<0.0001
Fishes		
SDA = −0.027 bm + 2.53 mm − 0.72	0.99	<0.0001
log SDA = 0.33 log bm + 0.67 log mm − 0.45	0.83	<0.0001
SDA = 0.11 me + 0.32	0.85	<0.0001
log SDA = 0.91 log me − 0.83	0.80	<0.0001
Amphibians		
SDA = −0.04 bm + 1.72 mm + 0.84	0.92	<0.0001
log SDA = −0.20 log bm + 1.11 log mm + 0.40	0.93	<0.0001
SDA = 0.21 me − 0.24	0.88	<0.0001
log SDA = 0.90 log me − 0.56	0.93	<0.0001
Reptiles		
SDA = −0.07 bm + 2.45 mm − 12.0	0.93	<0.0001
log SDA = −0.08 log bm + 1.13 log mm + 0.11	0.96	<0.0001
SDA = 0.26 me − 10.65	0.90	<0.0001
log SDA = 1.06 log me − 0.85	0.97	<0.0001
Birds		
SDA = 0.024 bm + 1.29 mm + 0.74	0.49	<0.0001
log SDA = 0.17 log bm + 1.00 log mm + 0.60	0.89	<0.0001
SDA = 0.08 me + 26.72	0.82	<0.0001
log SDA = 1.04 log me − 1.10	0.93	<0.0001
Mammals		
SDA = 7.33 bm (kg) + 0.92 mm − 133.6	0.87	<0.0001
log SDA = 0.32 log bm (kg) + 0.70 log mm + 0.28	0.92	<0.0001
SDA = 0.095 me + 81.5	0.84	<0.0001
log SDA = 0.93 log me + 1.21	0.95	<0.0001
Humans		
SDA = 1.38 bm (kg) + 0.26 mm + 123.6	0.57	<0.0001
log SDA = −0.43 log bm (kg) + 0.88 log mm + 0.61	0.61	<0.0001
SDA = 0.055 me − 46.03	0.36	<0.0001
log SDA = 0.81 log me − 0.50	0.37	<0.0001
Combined		
SDA = 0.013 bm + 1.48 mm − 72.7	0.90	<0.0001
log SDA = 0.18 log bm + 0.82 log mm − 0.23	0.91	<0.0001
SDA = 0.13 me + 14.0	0.76	<0.0001
log SDA = 1.01 log me − 0.88	0.95	<0.0001

Equations are generated from raw and logged ($\log_{10}$) data. For all non-mammalian taxa and combined data set body mass is in g and for mammals and humans in kg. Meal mass is in g and meal energy is in kJ for all taxa and the combined data set

varies greatly (1.3–390 h; Fig. 4), a function of differences in meal mass (duration increases with larger meals) and body temperature (duration decreases with increasing body temperature). Fish SDA ranges over six orders of magnitude (0.006–1,901 kJ), a function of variation in body mass and meal size (Tables 3, 4). Across studies, SDA coefficients averaged 15.6 ± 0.7, with low coefficients (<5%) generally stemming from formulated pellet diets and high coefficients (>25%) resulting from natural foods (e.g., fish or krill). Regardless of meal type, fish SDA increases as a function of meal energy (Fig. 3, Table 3).

Amphibians

The first published SDA studies on an amphibian were conducted by two French physiologists, R. Bonnet and

Table 4 Tabulation of fish SDA studies

Species	Body mass (g)	T_b (°C)	Meal type	Meal size (%)	Scope	Duration (h)	SDA (kJ)	SDA coefficient (%)	Treatments	Source
Elasmobranchii										
Carcharhiniformes										
Cephaloscyllium ventriosum	190	16	Fish	5.1	2.30	12	7.20	12.0		Ferry-Graham and Gibb (2001)
Scyliorhinus canicula	740	15	Squid	6.5	2.99	84	27.7	12.5	BS	Sims and Davies (1994)
Dipnoi										
Protopterus annectens	510	25	Beef heart	0.98	2.30					Smith (1935)
Actinopterygii										
Anguilliformes										
Anguilla anguilla	72.8	25	Formulated diet	1.3	11.0		1.97	11.3		Owen (2001)
Anguilla rostrata	1.5	20	Formulated diet		6.6	18	0.15			Gallagher and Matthews (1987)
Cypriniformes										
Acheilognathus lanceolate[a]	3.5	25	Algae	6.7	3.43		0.084	13.3		Hamada and Ida (1973)
Brachydanio rerio	0.5	24	Formulated diet	5.0	1.80	20	0.019	4.6	MS	Lucas and Priede (1992)
Carassius auratus	1.18	25	Tubificid worm		6.56		0.49	44.0		Cui and Liu (1990)
Carassius auratus[a]	143	25	Algae	2.2	1.84		1.14	10.1	BS, BT, MS	Hamada and Ida (1973)
Chalcalburnus chalcoides	0.1	20	Brine shrimp		1.98					Wieser et al. (1992)
Ctenopharyngodon idella[a]	16.7		Algae				0.25	7.0	MC	Carter and Brafield (1992)
Cyprinus carpio	1.36	23	Formulated diet		1.51	12	0.038		MT	Kaushik and Dabrowski (1983)
Cyprinus carpio	72.0	28	Formulated diet	1.0	2.66	18	2.24	15.5	MC, MS	Chakraborty et al. (1992)
Cyprinus carpio	150	20	Formulated diet		2.10					Yarzhombek et al. (1984)
Cyprinus carpio	318	25	Formulated diet	0.94	2.00		2.57	21.0	MC, MS	Hamada and Maeda (1983)
Leuciscus cephalus[a]	0.1	20	Brine shrimp		1.82					Wieser et al. (1992)
Phoxinus phoxinus[a]	2.5	15	Whiteworm	3.0	7.03		0.11	35.0	BT	Cui and Wootton (1988)
Pseudorasbora parva	1.18	25	Tubificid worm				0.44	58.6		Cui and Liu (1990)
Rhodeus rhombeus	10.5	30	Tubificid worm	8.2	1.73	8.0	0.18	7.7		Machida (1981)
Rhodeus lanceolatus	3.27	30	Tubificid worm	7.6	2.35	7.5	0.14			Machida (1981)
Scardinius erythrophthalmus[a]	0.1	20	Brine shrimp		1.57					Wieser et al. (1992)
Siluriformes										
Clarias gariepinus	0.002	28	Brine shrimp		1.63					Coneição et al. (1998)
Ictalurus punctatus	1,025	22	Formulated diet	2.0	2.28	18				Brown and Cameron (1991a, b)
Pseudobagrus fulvidraco	1.18	25	Tubificid worm		5.39		0.38	50.8		Cui and Liu (1990)
Silurus asotus	37.4	25	Fish	9.0	3.19	42	2.69	16.3	MS	Fu et al. (2006)
Silurus meridionalis	22.2	27.5	Formulated diet	4.0	3.41	68	3.16	10.4	BT	Luo and Xie (2008)
Silurus meridionalis	40.0	27.5	Formulated diet	6.0	2.19	56	2.64	15.6	MS	Fu et al. (2005a)
Silurus meridionalis	51.6	27.5	Fish	7.9	2.98	32	2.50	10.5		Fu et al. (2005b)
Silurus meridionalis	46.5	27.5	Fish	8.3	2.92	32	2.52	12.7	MS	Fu et al. (2005c)
Silurus meridionalis	40.8	27.5	Formulated diet	1.6	2.34	27	1.49	13.7	MC	Fu et al. (2005d)

Table 4 continued

Species	Body mass (g)	T_b (°C)	Meal type	Meal size (%)	Scope	Duration (h)	SDA (kJ)	SDA coefficient (%)	Treatments	Source
Salmoniformes										
Oncorhynchus rhodurus	50.0	10	Fish	2.4		30	0.68	16.6		Miura et al. (1976)
Oncorhynchus tshawytscha	520	10	Formulated diet		2.28					Thorarensen and Farrell (2006)
Salmo gairdneri	12.5	15	Formulated diet	2.0			0.71	15.1	MC	LeGrow and Beamish (1986)
Salmo gairdneri	15.0	15	Formulated diet	2.0			0.38	7.6	MC	Medland and Beamish (1985)
Salmo gairdneri	15.3		Formulated diet	2.4	1.60	3.4	0.13	1.6	MC	Smith et al. (1978)
Salmo gairdneri	38.0		Formulated diet	8.2			3.83	5.6		Oliva-Teles and Kaushik (1987)
Salmo salar	3.7		Formulated diet	2.7	1.71	3.5	0.041	2.5		Smith et al. (1978)
Gadiformes										
Gadus morhua	0.00038[b]	10	Rotifers		2.08				BS	McCollum et al. (2006)
Gadus morhua	5.0	15.5	Formulated diet	0.65	1.51	6.5	0.021	3.6	BT	Peck et al. (2003)
Gadus morhua	7.81	10	Formulated diet		1.45	10	0.11		BS	Hunt von Herbing and White (2002)
Gadus morhua[a]	61.0	18	Formulated diet	5.2	2.71		7.59	17.1	BT, MS	Soofiani and Hawkins (1982)
Gadus morhua	147	10	Fish	5.0	2.25	95	7.10	9.7		Jordan and Steffensen (2007)
Gadus morhua	180	10.5	Fish	6.4	1.68	48	3.61	4.4		Lyndon et al. (1992)
Gadus morhua	1,530	8	Fish	2.5	1.47	51	13.2	7.0		Blaikie and Kerr (1996)
Gadus morhua	3,050	15	Fish		1.51				BS, BT	Saunders (1963)
Scorpaeniformes										
Anoplopoma fimbria[a]	993	8.5	Fish	5.0	1.44	100	23.2	8.4		Furnell (1987)
Myoxocephalus scorpius	74.5	15	Shrimp	12.7	2.86	162	7.64	16.0	BS, BT	Johnston and Battram (1993)
Perciformes										
Blennius pholis[a]	15.6	10	Mussel	3.0	1.60	19	0.13	7.9		Vahl and Davenport (1979)
Channa argus	201	28	Fish	1.0			0.68	6.8		Liu et al. (2000)
Coregonus lavaretus	0.051	10	Brine shrimp				0.021	13.0	BT	Huuskonen et al. (1998)
Cirrhitichys bleekeri	21.1	25	Shrimp	5.3	1.97	39	0.81	14.9		Johnston and Battram (1993)
Dicentrarchus labrax	42.0	25	Formulated diet	2.0	2.07		2.49	14.9	BS, BT, MC	Peres and Oliva-Teles (2001)
Eleotris oxycephala	40.0	30	Fish	3.6	2.15	15	0.75	13.7	BT	Machida (1981)
Esox lucius	3.05	20	Fish	18.1	3.08		0.39	13.0		Wieser and Medgyesy (1991)
Esox lucius[a]	18.6	12	Fish	7.8	2.35	120	0.92	12.6		Armstrong et al. (2004)
Etroplus suratensis[a]	30.0	28	Formulated diet		2.33		0.48		MT	Somanath et al. (2000)
Harpagifer antarcticus	4.33	−0.5	Krill	14.6	2.38	390	0.41	10.1	BS, MS	Boyce and Clarke (1997)
Harpagifer bispinis[a]	3.0	10	Amphipod	15.0	3.60	118	0.13		BT	Brodeur et al. (2003)
Kuhlia sandvicensis	44.0	23	Fish	4.6	2.42	48	2.21	17.5	MS	Muir and Niimi (1972)
Lepomis macrochirus	19.2	30	Fish	3.8	1.48	12	0.15	8.0	BT	Machida (1981)
Lepomis macrochirus[a]	63.4	25	Mayfly nymph	2.9	1.29		0.72	12.8	BT	Pierce and Wissing (1974)
Lepomis macrochirus	72.9	25	Formulated diet	1.8	1.80	40	3.11	16.1	MC	Scalles and Wissing (1976)
Lichia amia[a]	86.7	20	Fish	6.0	1.81		6.65	24.0		Du Preez (1987)

Table 4 continued

Species	Body mass (g)	T_b (°C)	Meal type	Meal size (%)	Scope	Duration (h)	SDA (kJ)	SDA coefficient (%)	Treatments	Source
Lithognathus lithognathus[a]	731	20	Clam	6.0	1.88		20.5	20.7		Du Preez et al. (1986a)
Lithognathus mormyrus[a]	110	20	Clam	6.0	1.81		3.71	18.8		Du Preez et al. (1986a)
Macropodus chinensis	1.18	25	Tubificid worm		6.27		0.39	44.5		Cui and Liu (1990)
Micropterus salmoides[a]	13.9	25	Formulated diet	1.0		48	0.56	13.4	MC	Tandler and Beamish (1980)
Micropterus salmoides	34.6	30	Fish	4.4	1.46	16	0.40	6.7	MT	Machida (1981)
Micropterus salmoides	42.5	20	Fish		2.76					Glass (1968)
Micropterus salmoides[a]	100	25	Fish	8.0		49	8.05	15.5	MS	Beamish (1974)
Micropterus salmoides[a]	100	25	Formulated diet	2.0		64	7.15	18.1	BS, MS	Tandler and Beamish (1981)
Notothenia neglecta	95.3	0.5	Shrimp	8.7	2.34	211	9.24	20.0	BS, BT	Johnston and Battram (1993)
Odontobutis obscura	37.2	30	Fish	5.0	2.44	12	0.64	9.2	BT, MT	Machida (1981)
Oreochromis mossambicus	1.18	25	Tubificid worm		5.01		0.52	40.0		Cui and Liu (1990)
Oreochromis niloticus	6.3	30	Formulated diet	6.0	2.83		0.96	26.9	MS	Xie et al. (1997)
Oreochromis niloticus	58.0	27	Formulated diet	1.3	2.81		3.08	20.6	G	Mamun et al. (2007)
Oreochromis niloticus	95.0	28	Formulated diet	1.0	1.70	15	1.05	6.4	MC, MS	Ross et al. (1992)
Orthodon microlepidotus	0.85	25.5	Brine shrimp	1.7	1.47					Sanderson and Cech (1992)
Perca fluviatilis	2.45	20	Fish		4.19		0.65	13.5		Wieser and Medgyesy (1991)
Pomadasys commersonni[a]	474	20	Clam	4.0	1.83		11.0	24.7		Du Preez et al. (1986b)
Sciaenops ocellatus	0.0001[b]	24	Rotifer		2.52					Torres et al. (1996)
Seriola dumerili	308	19	Formulated diet		1.52					De la Gándara et al. (2002)
Siniperca chuatsi	202	28	Fish	1.0			0.87	8.7		Liu et al. (2000)
Sparus aurata	99.8	21	Formulated diet	1.5	3.18		0.95	19.8	BS, BT, MS	Guinea and Fernandez (1997)
Stizostedion vitreum vitreum	35.0	20	Formulated diet	1.6	1.80	34	0.70	5.6	MS	Beamish and MacMahon (1988)
Tilapia rendalli[a]	100	23.5	Algae	6.8			0.88	8.5		Caulton (1978)
Thunnus maccoyii	11,000	19.4	Fish	6.8	2.36	45	1,628	38.9		Fitzgibbon et al. (2007)
Tridentiger obscurus	5.5	25	Algae		3.38		0.05			Hamada and Ida (1973)
Pleuronectiformes										
Pleuronectes platessa	32	10	Fish paste	3.8	1.97	70	1.12	16.5	BT, MC, MS	Jobling and Davies (1980)

Meal mass (%) is reported as a percentage of body mass. Scope, duration, SDA, and SDA coefficient are defined in Table 1

T_b body temperature; studies with experimental treatments are noted as *BS* body size, *BT* experimental temperature, *G* genetic strain, *MC* meal composition, *MS* meal size, *MT* meal type

[a] Studies for scope, SDA, and/or SDA coefficient are calculated from published information
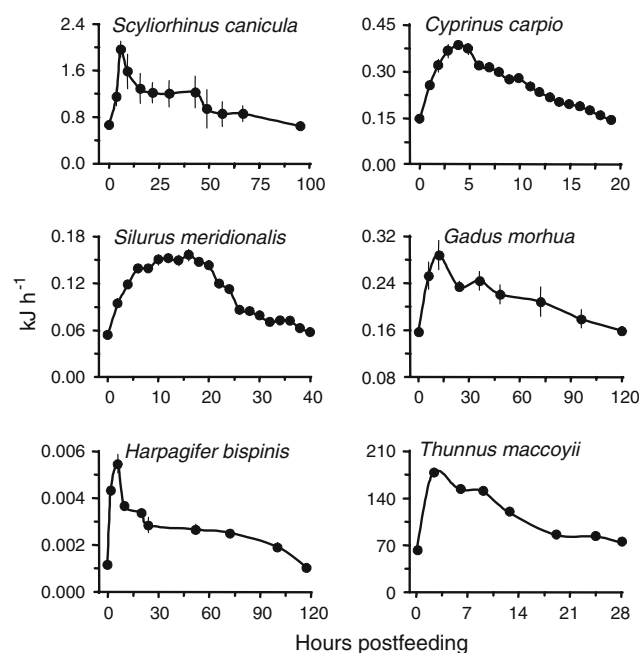
[b] Body mass reported as dry mass

Fig. 4 Postprandial metabolic profile for six species of fishes. Peaks in postprandial metabolism were usually attained within 20 h after feeding at rates two to three times prefeeding levels. Body mass, body temperature, meal type, and meal mass for each figure are presented in Table 4. Figures were drawn from data presented in the following original articles; *Scyliorhinus canicula* (Sims and Davies 1994), *Cyprinus carpio* (Chakraborty et al. 1992), *Silurus meridonalis* (Fu et al. 2005c), *Gadus morhua* (Jordan and Steffensen 2007), *Harpagifer bispinis* (Brodeur et al. 2003), and *Thunnus maccoyii* (Fitzgibbon et al. 2007)

E. F. Terroine published in the mid 1920s on the European frog, *Rana temporaria* (Bonnet 1926; Terroine and Bonnet 1926). They explored the effects of meal composition (protein, sugars, and fats) and of individual amino acids on the SDA response. Since, only a handful of studies have been published on amphibian SDA: a dozen on anurans (frogs and toads), three on salamanders, and none on caecilians (Table 5). For the 19 anuran and 9 salamander species investigated, body mass spans nearly a 200-fold range. Most studies were conducted with a body temperature between 20 and 30°C and meals, typically neonatal rodents or crickets, were equal to 5, 10 or 15% of body mass (Table 5). Amphibians respond to feeding with a rapid increase in metabolic rate that after peaking declines more slowly to prefeeding levels (Fig. 5). For all amphibian studies and their respective treatments, the factorial scope of peak postprandial $\dot{V}O_2$ averages 3.43 ± 0.18, and varies with respect to meal size (larger meals generate larger peak rates). The largest postprandial scopes (6.5–11.6-fold) are exhibited by *Bufo alverius*, *Ceratophrys ornata*, and *Pyxicephalus adspersus*, three anuran species that estivate during their dry season (Secor 2005a). The duration of elevated postprandial $\dot{V}O_2$ range from 1 day for the marine

toad, *Bufo marinus*, following the gastric administration of a peptide solution equaling 1% of body mass, to 9 days for *B. marinus* and the tomato frog, *Dyscophus antongilli*, digesting neonate rat and cricket meals, respectively, equaling 10% of body mass at 20°C (Secor and Faulkner 2002; Secor et al. 2007; Wang et al. 1995). For anuran species digesting meals 10% of body mass and six ambystomatid salamander species digesting meals 5% of body mass, the duration of elevated metabolic rates averaged 4.99 ± 0.26 and 4.17 ± 0.33 days, respectively.

Amphibian SDA varies with body size and meal size, such that an increase in body size and/or meal size generates a larger SDA (Table 5). Additionally, meal type (hard-bodied vs. soft-bodied prey) and body temperature also significantly impacts amphibian SDA. These determinants of SDA are covered later in this review. For amphibians, SDA likewise increases as a function of meal energy and among current amphibian studies, the SDA coefficient averages $23.3 \pm 1.1\%$ (Fig. 3; Table 3).

Reptiles

Whereas Buytendijk (1910) may be credited with the first documentation of SDA for a reptile, the boa constrictor (*Boa constrictor*), it was Francis Benedict that pioneered experimental studies on reptile metabolism and SDA (Benedict 1932). Benedict reported the postprandial metabolic profiles of boa constrictors, indigo snakes (*Drymarchon corais*), and Indian pythons (*Python molurus*) maintained at different body temperatures (17.6–37.1°C) and fed meals ranging from 3 to 28% of snake body mass (Benedict 1932). Following Benedict's studies there was a hiatus of reptiles SDA studies, with the exception of the work of Rapatz and Musacchia (1957) and Roberts (1968) until the late 1970s and 1980s beginning with the seminal work of Roland Coulson and Thomas Hernandez on the nutrition and physiology of the American alligator, *Alligator mississippiensis* (Coulson and Hernandez 1979, 1980). In the mid 1990s, studies documenting large postprandial responses of snakes sparked a surge in reptile SDA studies (Andrade et al. 1997; Secor et al. 1994, Secor and Diamond 1997). Prior to 1997, only 15 studies explored the SDA of reptiles, and since an average of 5 new studies are published each year. Among reptiles, postprandial metabolic responses has been documented for 4 species of crocodilians, 8 species of turtles, 16 species of lizards, and 30 species of snakes (Table 6). Because of their attractiveness for studies in digestive, respiratory, and cardiovascular physiology, there are five published accounts on the SDA of *B. constrictor* and 11 for *P. molurus* (Table 6).

Among tabulated studies, body mass ranges from 3.5 g for the side-blotched lizard, *Uta stansburiana*, to 8,100 g for the white-throated monitor lizard, *Varanus albigularis*

Table 5 Tabulation of amphibian SDA studies

Species	Body mass (g)	T_b (°C)	Meal type	Meal size (%)	Scope	Duration (days)	SDA (kJ)	SDA coefficient (%)	Treatments	Source
Anura										
Bombina orientalis	4.53	30	Cricket	10	3.64	5	1.17	45.3	BT, MS, MT	Secor et al. (2007)
Bufo alverius	161	30	Rodent	15	6.50	7	37.6	23.9	MS	Secor and Faulkner (2002)
Bufo alverius	140	30	Rodent	15	6.46	7	36.6	28.9		Secor (2005a)
Bufo boreas	78.6	30	Cricket	10	3.29	3	12.7	20.2	BT, MS, MT	Secor and Faulkner (2002)
Bufo cognatus	76.3	30	Cricket	10	5.13	5	12.2	19.2		Secor et al. (2007)
Bufo marinus	115	30	Cricket	10	5.30	4	23.2	25.2	BS, BT, MS, MT	Secor and Faulkner (2002)
Bufo marinus	137	30	Rodent	15	3.90	5	23.8	19.2		Secor (2005a)
Bufo marinus	293	24	Peptone solution	1	2.00	1	4.14	23.0		Wang et al. (1995)
Bufo marinus	300	25	Rodent	8.5	2.80					Andersen and Wang (2003)
Bufo terrestris	19.3	30	Cricket	10	2.90	3	3.05	20.2		Secor and Faulkner (2002)
Bufo woodhousei	23.3	30	Cricket	10	2.80	3	3.31	17.5		Secor and Faulkner (2002)
Bufo woodhousei	82.0	23	Cricket	5	1.70					Sievert and Bailey (2000)
Ceratophrys cranwelli	8.42	25	Rodent	10	4.16	2.7	0.79	18.8	MT	Grayson et al. (2005)
Ceratophrys cranwelli	23.2	30	Rodent	16.6	3.75	2.4	3.89	16.7	BS, BT, MC	Powell et al. (1999)
Ceratophrys ornata	169	30	Rodent	15	11.6	5	50.8	32.3		Secor (2005a)
Ceratophrys ornata	110	30	Rodent	15	8.70	4	28.0	27.8	MS	Secor et al. (2007)
Dyscophus antongilli	39.8	30	Cricket	10	4.71	6	5.57	17.3	BT, MS, MT	Secor et al. (2007)
Hyla cinerea	8.83	30	Cricket	10	3.09	4	1.69	34.4	BT, MS, MT	Secor et al. (2007)
Kassina maculata	5.85	30	Cricket	10	4.09	3	0.93	28.7	BT, MT	Secor et al. (2007)
Kassina senegalensis	5.67	30	Cricket	10	4.40	5	1.74	52.5	MS	Secor et al. (2007)
Leptodactylus pentadactylus	173	30	Rodent	15	3.50	5	30.5	19.6		Secor (2005a)
Psuedacris cadaverina	3.40	30	Cricket	10	2.80	3	0.27	10.4		Secor (2001)
Psuedacris regilla	2.40	30	Cricket	10	2.60	3	0.16	7.9		Secor (2001)
Pxyicephalus adspersus	225	30	Rodent	15	9.65	6	57.3	28.6		Secor (2005a)
Rana catesbeiana	161	30	Cricket	10	3.83	4	21.8	16.6	BT, MS, MT	Secor et al. (2007)
Rana catesbeiana	238	30	Rodent	15	3.94	4	41.2	18.9		Secor (2005a)
Rana catesbeiana	445	22	Rodent	10	2.90					Busk et al. (2000a, 2000b)
Rana temporaria	45.3	24	Meat	0.81	1.61				BT, MT	Bonnet (1926)
Rana temporaria		15	Leucine		2.19	5	0.50	14.2	MC	Terrione and Bonnet (1926)
Caudata										
Ambystoma jeffersonianum	10.9	25	Cricket	5	2.54	4	0.74	24.2		Secor and Boehm (2006)
Ambystoma maculatum	17.9	25	Cricket	5	2.85	4	1.15	16.6		Secor and Boehm (2006)
Ambystoma opacum	3.41	25	Cricket	5	2.27	3	0.23	23.4		Secor and Boehm (2006)

Table 5 continued

Species	Body mass (g)	T_b (°C)	Meal type	Meal size (%)	Scope	Duration (days)	SDA (kJ)	SDA coefficient (%)	Treatments	Source
Ambystoma talpoideum	5.75	25	Cricket	5	2.85	3	0.32	19.5		Secor and Boehm (2006)
Ambystoma texanum	8.22	25	Cricket	5	3.40	3	0.47	19.6		Secor and Boehm (2006)
Ambystoma t. tigrinum	30.1	25	Cricket	5	2.72	5	2.08	16.6	BT, MS, MT	Secor and Boehm (2006)
Ambystoma t. mavortium	14.4	25	Cricket	5	3.24	3	0.86	15.7		Secor and Boehm (2006)
Plethodon jordani	4.30	17.5	Fly larva		1.77					Feder et al. (1984)
Tarchica granulosa	13.3	30	Cricket	8.8	2.10		1.20	11.8		Secor (2001)
Tarchica torosa	11.0	30	Cricket	7.5	2.90		1.00	13.5		Secor (2001)

Meal mass (%) is reported as a percentage of body mass. Scope, duration, SDA, and SDA coefficient are defined in Table 1

T_b body temperature; studies with experimental treatments are noted as *BS* body size, *BT* experimental temperature, *MC* meal composition, *MS* meal size, *MT* meal type
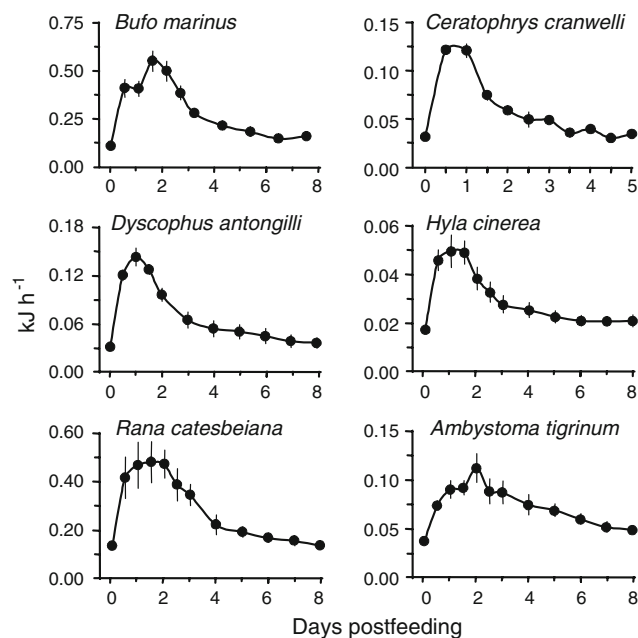
Fig. 5 Postprandial metabolic profiles for six species of amphibians. Postprandial metabolic rates of amphibians peak within 2 days after feeding at three to fourfold of standard metabolic rates. Body mass, body temperature, meal type, and meal mass for each figure are presented in Table 5. Figures are drawn from data presented in the following original articles; *Bufo marinus* (Secor and Faulkner 2002), *Ceratophrys cranwelli* (Powell et al. 1999), *Dyscophus antongilli* (Secor et al. 2007), *Hyla cinerea* (Secor et al. 2007), *Rana catesbeiana* (Secor et al. 2007), and *Ambystoma tigrinum* (Secor and Boehm 2006)

(Table 7). For most studies, body temperatures were maintained between 25 and 30°C. The food consumed was typically a natural prey item, including: insects for small turtles and lizards, rodents for large lizards and snakes, and fish for turtles, crocodilians, and aquatic snakes. Although meal sizes range from 1.25% (for *A. mississippiensis*; Coulson and Hernandez 1983) to 100% (for *P. molurus*; Secor and Diamond 1997) of reptile body mass, most meals for turtles, lizards, and crocodilians are less than 10% of body mass, whereas for most snake studies, meals are between 20 and 30% of snake body mass (Table 6). The factorial scope of the postprandial peak in metabolism averages 1.90 ± 0.12 for turtles, 2.17 ± 0.22 for crocodilians, 3.17 ± 0.44 for lizards, and 7.87 ± 0.63 for snakes (Table 7). The much larger scopes for snakes stems predominantly from their larger meals and lower SMR, exemplified by the 43-fold increase in $\dot{V}O_2$ of *P. molurus* during the digestion of rodent meals equaling 100% of snake body mass (Secor and Diamond 1997). The impressive postprandial increase in metabolic rates for snakes is accompanied by 1–4°C increases in core and skin temperatures, the latter easily visualized using an infrared camera (Marcellini and Peters 1982; Tattersall et al. 2004). The duration of elevated postprandial metabolism averages

Table 6 Tabulation of reptile SDA studies

Species	Body mass (g)	T_b (°C)	Meal type	Meal size (%)	Scope	Duration (days)	SDA (kJ)	SDA coefficient (%)	Treatments	Source
Testudines										
Caretta caretta	56.6	24	Formulated diet	2.0	1.60				BS	Kowalski (2005)
Chelonia mydas	79.8	24	Formulated diet	2.0	1.80				BS	Kowalski (2005)
Chelydra serpentina	101	30	Beef	11.3	3.40	5	18.0	22.0		Secor and Diamond (1999)
Chrysemys picta	400	28	Meal/lettuce		1.72					Rapatz and Musacchia (1957)
Chrysemys picta marginata[a]	7.7	25	Mealworm	3.9	2.14	6	0.5	16.7		Sievert et al. (1988)
Kinixys spekii	640	30	Kale	5.3	1.90	4	12.4	15.8	MT	Hailey (1998)
Ocadia sinensis[a]	18.8	30	Mealworm	5.0	1.81	3	0.98	11.2	MT	Pan et al. (2005a)
Sternotherus odoratus	61	30	Beef	5.0	2.10	4	3.7	17.0		Secor and Diamond (1999)
Trachemys scripta elegans[a]	8.3	30	Mealworm	1.5	1.53	1.9	0.26	23.6	MT	Pan et al. (2004)
Trachemys scripta elegans	356	30	Beef	5.2	2.70	3	27.0	21.0		Secor and Diamond (1999)
Lacertilia										
Angolosaurus skoogi[a]	65	30	Carrot	7.0	1.78				MS	Clarke and Nicolson (1994)
Anolis carolinensis[a]	5	28	Beef	5.0	1.39	2.3	0.22	14.9		Coulson and Hernandez (1980)
Cnemidophorus murinus	56.1	40	Formulated diet	2.0	2.33	3.5	11.7		MC	O'Grady (2006)
Dipsosaurus dorsalis	43.6	40	Formulated diet	2.0	3.10	3.4	12.0		MC	O'Grady (2006)
Eulamprus quoyii	26.9	30	Mealworm	4.9	2.21	2	1.23	8.3		Iglesias et al. (2003)
Eulamprus tympanum[a]	10	30	Mealworm	4.6	1.70	2	0.76	16.5		Robert and Thompson (2000)
Eumeces chinensis[a]	30	30	Mealworm	4.9	1.54	3	1.21	8.6	MT	Pan et al. (2005b)
Heloderma suspectum	480	30	Rodent	10.0	4.80	6	59.9	18.2	MT	Christel et al. (2007)
Hemidactylus bowringii[a]	3.4	30	Mealworm	5.3	1.86	1.7	0.26	14.8		Xu et al. (2006)
Sceloporus merriami	4.0	32	Cricket	10.0	1.51				BT	Niewiarolwski and Waldschmidt (1992)
Sceloporus merriami[a]	5	34	Cricket	5.0		1	0.064	4.6		Beaupre et al. (1992)
Sceloporus occidentalis[a]	10	30	Cricket	2.9	4.40	2	0.35	20.8	MS	Roe et al. (2005)
Sphenomorphus indicus[a]	11.1	30	Mealworm	4.6	2.10	2.5	0.64	12.6		Lu et al. (2004)
Tubinambis merianae	797	30	Beef	10.9	2.77	4.8	187	36.3		Klein et al. (2006)
Uta stansburiana[a]	3.5	30	Mealworm	2.7	1.31	0.4	0.025	3.1		Roberts (1968)
Varanus albigularis	8,100	30	Rodent	9.3	9.90	3.8	1,260	23.0	MT	Secor and Phillips (1997)
Varanus exanthematicus[a]	430	35	Rodent	8.9	3.08	3	50.7	19.9		Hicks et al. (2000)
Varanus exanthematicus[a]	740	35	Rodent	9.7	2.70	4.8	105.4	21.0		Hartzler et al. (2006)
Serpentes										
Acanthophis praelongus[a]	448	30	Rodent	11.4	5.30	6	70.5	18.4		Christian et al. (2007)
Acrantophis dumerili	206	30	Rodent	25.1	7.60	6	67.6	21.9		Ott and Secor (2007b)
Agkistrodon piscivorus[a]	139	25	Fish	23.4	5.70	9.2	37.1	26.5		McCue and Lillywhite (2002)

Table 6 continued

Species	Body mass (g)	T_b (°C)	Meal type	Meal size (%)	Scope	Duration (days)	SDA (kJ)	SDA coefficient (%)	Treatments	Source
Boa constrictor	69.8	30	Rodent	25	7.83	6	24.5	29.0		Ott and Secor (2007b)
Boa constrictor	137	30	Rodent	20	3.96	4.8	34.4	16.8	BT, MS	Toledo et al. (2003)
Boa constrictor	170	30	Rodent	30	3.77	6	51.8	14.8		Andrade et al. (2007)
Boa constrictor	346	30	Rodent	25.1	18.5	8	232	33.0		Secor and Diamond (2000)
Boa constrictor[a]	6,303	31.3	Rabbit	7.4	3.56	3.3	296	9.3		Benedict (1932)
Coluber constrictor	223	30	Rodent	25	5.40	4	68.9	15.0		Secor and Diamond (2000)
Corallus hortulanus	308	30	Rodent	25	5.88	5	84.6	16.9		Ott and Secor (2007b)
Crotalus atrox	200	30	Rodent	9.9	3.90	3.2	35.5	26.0		McCue (2007)
Crotalus cerastes	63	30	Rodent	25	6.11		17.7	14.0		Zaidan and Beaupre (2003)
Crotalus cerastes	127	30	Rodent	26	7.86	9	60.0	23.0		Secor et al. (1994)
Crotalus cerastes	161	30	Rodent	25	9.90	12	73.2	21.0		Secor and Diamond (2000)
Crotalus durissus	42	30	Rodent	20	3.72	3.5	7.3	12.2	MS	Andrade et al. (1997)
Crotalus horridus	350		Rodent	25	6.90		86.0	12.3	MS	Zaidan and Beaupre (2003)
Dasypeltis scabra[a]	47	30	Egg	20	1.97	11	8.88	13.2		Großmann and Starck (2006)
Drymarchon corais[a]	2,520	29.3	Rodent	5.8	3.20	1.9	83.7	8.4		Benedict (1932)
Eunectes murinus	781	30	Rodent	25	7.79	8	269	18.9	MS	Ott and Secor (2007b)
Lampropeltis getula	188	30	Rodent	24.8	7.00	4	56.0	14.0		Secor and Diamond (2000)
Lamprophis fuliginosus	16.3	25	Rodent	20	5.10	6	3.3	14.5	MS	Roe et al. (2004)
Liasis fuscus	43	30	Rodent	25	6.59					Bedford and Christian (2001)
Lichanura trivirgata	163	30	Rodent	25	15.9	9	58.2	18.0		Secor and Diamond (2000)
Masticophis flagellum	273	30	Rodent	25	5.90	5	70.4	13.0		Secor and Diamond (2000)
Morelia spilota	64.8	30	Rodent	25	8.03	5	15.1	18.7		Ott and Secor (2007b)
Morelia spilota imbricata[a]	130	30	Rodent	23	6.31	6	52.6	22.1		Thompson and Withers (1999)
Natrix natrix	30	25	Fish	11.7	4.24	4	4.6	26.3	BT	Hailey and Davies (1987)
Nerodia fasciata fasciata	30.2	25	Fish	19.7	5.64	3.5	5.4	21.1		Hopkins et al. (2004)
Nerodia sipedon[a]	13	27	Fish	10	3.24	3.7	1.93	26.3		Sievert & Andreadis (1999)
Pituophis melanoleucus	431	30	Rodent	25	5.26		87.4	10.1		Zaidan and Beaupre (2003)
Pituophis melanoleucus	732	30	Rodent	25.1	8.00	5	211	14.0		Secor and Diamond (2000)
Python brongersmai	763	30	Rodent	25	11.3	8	322	23.1		Ott and Secor (2007a)
Python molurus	113	30	Rodent	25	11.6	6	71.0	32.0		Secor (1995)
Python molurus	215	30	Rodent	25	3.23					Overgaard et al. (1999)
Python molurus[a]	300	30	Rodent	20	8.59		118	24.5		Overgaard et al. (2002)
Python molurus[a]	500	30	Rodent	20	6.30	8	248	31.0	BT	Wang et al. (2003)
Python molurus[a]	650	30	Rodent	9.4	5.12	4.5	72.8	15.0	MC	McCue et al. (2005)

Table 6 continued

Species	Body mass (g)	T_b (°C)	Meal type	Meal size (%)	Scope	Duration (days)	SDA (kJ)	SDA coefficient (%)	Treatments	Source
Python molurus	690	30	Rodent	25	15.3	8	420	30.0	BS, MS	Secor and Diamond (1997)
Python molurus	719	30	Rodent	25.1	14.5	6	317	24.5	MS	Ott and Secor (2007a)
Python molurus	736	30	Rodent	25	17.1	8	438	29.8		Secor and Diamond (1995)
Python molurus	1,380	30	Rodent	25	9.50	8			MC	Secor et al. (2000)
Python molurus	2,394	30	Rodent	25	16.8	8	1,259	26.5		Secor (2003)
Python molurus[a]	6,403	28.2	Rabbit	9.2	5.58	5.1	665	15.4		Benedict (1932)
Python regius[a]	147	30	Rodent	25	5.23	10	51.7	18.8		Starck et al. (2004)
Python regius[a]	147	30	Rodent	25	4.74	9	17.4	6.7		Starck and Wimmer (2005)
Python regius	715	30	Rodent	25	9.90	8	326	25.1		Ott and Secor (2007a)
Python reticulatus	730	30	Rodent	25	10.4	7	340	25.6	MS	Ott and Secor (2007a)
Python sebae	706	30	Rodent	24.9	11.7	6	347	27.3		Ott and Secor (2007a)
Thamnophis elegans[a]	25.2	30	Fish	11	2.93	3.8	1.42	11.7		Britt et al. (2006)
Thamnophis sirtalis[a]	24	30	Frog	33	4.08	2	4.04	12.6		Peterson et al. (1998)
Crocodilian										
Alligator mississippensis[a]	700	28	Fish	10	4.17	10	180	36.7	MC, MS	Coulson and Hernandez (1983)
Alligator mississippensis[a]	700	28	Fish	5.0	2.95	5.2	43.7	17.8		Coulson and Hernandez (1979)
Alligator mississippensis	4,500	30	Fish/chicken	7.5	3.68					Busk et al. (2000a, b)
Caiman crocodilus	1,684	25	Rodent		1.62					Gatten (1980)
Caiman latirostris	1,680	30	Chicken	11.5	1.63	8	36.1			Starck et al. (2007)
Crocodylus porosus[a]	400	30	Pork	2.0	1.34		6.6	13.8	MC	Garnett (1988)

Meal mass (%) is reported as a percentage of body mass. Scope, duration, SDA, and SDA coefficient are defined in Table 1

T_b body temperature; studies with experimental treatments are noted as *BS* body size, *BT* body temperature, *MC* meal composition, *MS* meal size, *MT* meal type

[a] Studies for scope, SDA, and/or SDA coefficient are calculated from published information

Table 7 Tabulation of avian SDA studies

Species	Body mass (g)	T_a (°C)	Meal type	Meal size (%)	Scope	Duration (h)	SDA (kJ)	SDA coefficient (%)	Treatments	Source
Sphenisciformes										
Eudyptula minor	1,055	22.6	Fish	7.10	1.87	4.7	48.8	12.8	MS	Green et al. (2006)
Pygoscelis adeliae	1,030	10–30	Krill	26.4	1.82	10	97.3	10.0	MS	Janes and Chappell (1995)
Procellariiformes										
Diomedea gibsoni[b]	6,288	14	Cuttlefish	17.3			201	5.2	MT	Battam et al. (2008)
Thalassarche carteri	2,158	14	Cuttlefish	19.1			76.5	5.3	MT	Battam et al. (2008)
Pelecaniformes										
Phalacrocorax auritus	2,080	21	Fish	4.90	1.71	5.5	53.1	4.2	AT	Enstipp et al. (2008)
Anseriformes										
Anas platyrhynchos	1,043	23	Grain	4.40		1.7	31.8	4.6	AT	Kaseloo and Lovvorn (2003)
Aythya affinis	580	23	Mussel				19.8	10.6	AT	Kaseloo and Lovvorn (2006)
Duck	914		Corn	5.50	1.49		165	19.7		Hári and Kriwuscha (1918)
Goose	3,140		Corn	3.10	1.53		368	21.9		Hári (1917)
Falconiformes										
Falco tinnunculus[a]	200	25	Rodent	15.1	1.91	20	26.6	11.3	AT, MS	Masman et al. (1989)
Galliformes										
Coturnix coturnix	27.4	33	Formulated diet		1.68					Marjoniemi (2000)
Gallus gallus	65	38	Formulated diet		1.73		30.8	18.1	BC, MS	Kleiber and Dougherty (1934)
Gallus gallus	400		Formulated diet				451	8.3	BS, MC, MS	Swennen et al. (2006)
Gallus gallus	695		Casein	1.33	1.14		50.1	34.3		Barott et al. (1938)
Gallus gallus	1,148	25	Formulated diet	11.9	1.48		307	13.1	AT, BC	Geraert et al. (1988)
Gallus gallus	2,000	20	Corn starch		1.32	24	23.5	5.0	MC	Tasaki and Kushima (1980)
Gallus gallus	2,870	12–37	Corn	2.60	1.23	48	174	13.8	SX	Mitchell and Haines (1927)
Gallus gallus	3,150		Wheat feed	0.80	1.12		27.1	6.4	MT	Sarmiento-Franco et al. (2000)
Gallus gallus	3,250		Formulated diet	1.43	1.32	9	48.0	6.1		MacLeod (1991)
Gallus gallus	3,282		Formulated diet	2.40			217	17.2		Gabarrou et al. (1997)
Gallus gallus	3,850	29	Formulated diet		1.13				AT	Berman and Snapir (1965)
Meleagris gallopavo	235	35	Mash food		1.74				AT	MacLeod et al. (1980)
Charadriiformes										
Sterna paradisaea	100		Fish		1.40					Klaassen et al. (1989)
Uria lomvia	820	7	Fish	2.30	1.40	1.4	6.50	7.0		Hawkins et al. (1997)
Columbiformes										
Columbia livia	375	20	Formulated diet	5.30	1.26		32.0	9.1	MS	Rashotte et al. (1995)
Columbia livia	393	21	Formulated diet		1.63				MS	Rashotte et al. (1999)

Table 7 continued

Species	Body mass (g)	T_a (°C)	Meal type	Meal size (%)	Scope	Duration (h)	SDA (kJ)	SDA coefficient (%)	Treatments	Source
Strigiformes										
Strix aluco	419	20	Rodent	7.54	1.60	12.6	27.0	11.3	AT, MS	Bech and Presteng (2004)
Apodiformes										
Selasphorus rufus	3.3	20	Sucrose solution		1.73				MC	Lotz et al. (2003)
Passeriformes										
Lonchura cucullata[a]	10.0	35	Seed		1.44		0.81			Seagram et al. (2001)
Padda oryzivora	23.7	30	Formulated diet		1.24		13.3		AT	Meienberger and Dauberschmidt (1992)
Sturnus vulgaris	79.6	25	Formulated diet		1.50					Biebach (1984)
Troglodytes aedon	8.0	34.5	Cricket	6.40	1.51	1.1	0.16	5.1	BS, MS	Chappell et al. (1997)

Meal mass (%) is reported as a percentage of body mass. Scope, duration, SDA, and SDA coefficient are defined in Table 1

T_a ambient temperature; studies with experimental treatments are noted as AT ambient temperature, BC body composition, BS body size, MC meal composition, MS meal size, MT meal type, SX sex

[a] Studies for scope, SDA, and/or SDA coefficient are calculated from published information

[b] Values for Diomedea gibsoni also includes data from a single individual Diomedea exulans (Battam et al. 2008)

about 3 days for crocodilians, lizards, and turtles, and 6 days for snakes (Table 6). Intraspecific variation in duration is again largely explained by differences in meal size (increasing with meal size) and body temperature (decreasing with temperature).

For reptiles, feeding generates the characteristic rapid increase in rates of gas exchange that peak usually a day or two after feeding before undergoing a slower decline in returning to prefeeding rates (Fig. 6). As noted previously for other taxa, SDA of reptiles is governed by body size and meal size as both variables have a significant impact on the magnitude of SDA (Table 4). An increase in meal energy is matched by a corresponding increase in SDA (Fig. 3; Table 4). Calculated SDA coefficients for natural meals average $17.6 \pm 2.9\%$ for crocodilians, $17.9 \pm 1.3\%$ for turtles, $17.9.1 \pm 1.9\%$ for lizards, $20.9 \pm 0.7\%$ for snakes, and $20.0 \pm 0.6\%$ overall for reptiles.

Birds

Avian SDA studies can be divided between those on domesticated poultry species (e.g., chickens and turkeys) and investigations on wild species, including waterfowl,
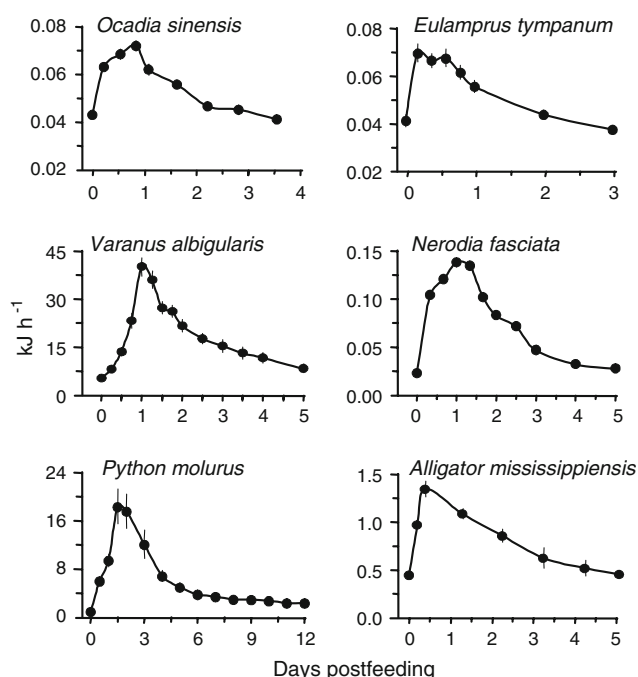
Fig. 6 Postprandial metabolic profiles for six species of reptiles. For reptiles, feeding triggers 3-fold to 15-fold increases in metabolic rate within 1 or 2 days. Body mass, body temperature, meal type, and meal mass for each figure are presented in Table 6. Figures are drawn from data presented in the following original articles; Ocadia sinensis (Pan et al. 2005a), Eulamprus tympanum (Robert and Thompson 2000), Varanus albigularis (Secor and Phillips 1997), Nerodia fasciata (Hopkins et al. 2004), Python molurus (Secor and Diamond 1997), and Alligator mississippiensis (Coulson and Hernandez 1979)

birds of prey, and passerines (Fig. 7; Table 8). Regardless, all species experience a postprandial increase in metabolic rate that peaks within 2 h after feeding and returns to baseline usually within 12 h (Fig. 7). For the chicken, *Gallus gallus*, SDA studies include individuals that span a 60-fold range in body mass (65–3,850 g), whereas for wild species, body mass ranges from 8 g for the rufous hummingbird, *Selasphorus rufus*, to 1,055 g for the little penguin, *Eudyptula minor*. Ambient temperature of avian studies range between 7 and 38°C and the meals consumed were equally variable and include formulated pellets and natural foods of seeds, insects, fish, and rodents (Table 7). Meal sizes range from less than 1% to over 26% of bird body mass, and on average feeding generates a 45 ± 5% increase in metabolic rate. Research on chicken SDA has explored various determinants of SDA, especially the effects of meal size and meal composition. For wild species, there has been an experimental emphasis to assess the effects of ambient temperature on SDA, a subject covered later in this review. Avian SDA is likewise dependent on body mass and meal size and increases with meal energy (Fig. 3; Table 3). Among avian studies, the SDA coefficient averages 9.8 ± 0.9%.

Mammals

The study of mammalian (non-human) SDA can be divided into two major eras of research. Following the turn of the twentieth century a collection of researchers lead by Graham Lusk, Francis Benedict, and David Rapport explored

the effects of meal composition and meal size on SDA, largely using dogs (Table 9). In many of the published studies of that time, a single dog was used to compare the postprandial rise in metabolism following the feeding meat or administration of various solutions composed of a single amino acid, sugar, or fat, or a combination of these. Samuel Brody (1945) followed these studies with measurements of the postprandial metabolic responses of farm animals, including horses, steers, pigs, and sheep (Fig. 8). The second era of mammal SDA studies began in the 1980s and continues until today with experimental studies on dogs and rats, and explorations of the SDA responses of wild mammals ranging from 35-g short-tailed shrews, *Blarina brevicauda*, to 150-kg muskoxen, *Ovibus moschatus*, and harp seals, *Phoca groenlandica* (Fig. 8; Table 8).

The meals used in these studies included formulated concoctions of nutrients and a wide variety of natural food items. Meals weighed less than 10% of body mass with the exception of meals consumed by the insectivores *B. brevicauda* (10% of body mass) and *Condylura cristata* (15%). Regardless of meal type and size, mammals respond with a very characteristic 25–50% increase in metabolic rate (Fig. 8). The factorial scope of postprandial metabolism for 130 mammal trials averaged 1.37 ± 0.02. The duration of the postprandial response was as short as 2 h for a dog following the consumption of a glucose solution to as long as 60–70 h for livestock feeding on straw (Fig. 8; Table 8). Among mammal studies, there is more than a 32,000-fold range in SDA, due largely to the 18,000-fold range in body mass (Table 9). Both body mass and meal mass are significant determinants of mammalian SDA, combining to explain close to 90% of the variation in SDA (Table 3). Meal energy is an additional good predictor of SDA as illustrated in Fig. 3. For studies that quantified both meal energy and SDA, the SDA coefficient averages 9.9 ± 1.0%.

Humans

The earliest and most extensive collection of SDA studies are those conducted on humans. From Lavoisier's inaugurate measurements of the postprandial metabolism of his colleague Armand Séguin, through an expanding series of studies beginning in the late 1800s, to more recent inquiries in human nutrition, the volume of human SDA studies well exceeds the number of published SDA studies for any other covered taxa (Mitchell 1964). For the first half of the twentieth century, much of the attention on human SDA was directed at the effects of meal composition (Deuel 1927; Mason 1927; McClellan et al. 1931; Mitchell 1964). Since, human studies have also focused on the effects of exercise and body composition, specifically obesity, on SDA. With regards to the latter, it has been hypothesized that individuals which are postprandially "more efficient",

Fig. 7 Postprandial metabolic profiles for four species of birds. Postprandial metabolism of birds peaks within a couple of hours after feeding at less than fold of prefeeding rates. Body mass, ambient temperature, meal type, and meal mass for each figure are presented in Table 7. Figures are drawn from data presented in the following original articles; *Pygoscelis adeliae* (Janes and Chappell 1995), *Falco tinnunculus* (Masman et al. 1989), *Strix aluco* (Bech and Præsteng 2004), and *Troglodytes aedon* (Chappell et al. 1997)

Table 8 Tabulation of mammalian SDA studies

Species	Body mass (kg)	T_a (°C)	Meal type	Meal size (%)	Scope	Duration (h)	SDA (kJ)	SDA coefficient (%)	Treatments	Source
Insectivora										
Blarina breviceauda[a]	0.035	28	Earthworm	10.0	1.36		1.23	9.5		Hindle et al. (2003)
Condylura cristata	0.05	26	Earthworm	15.0	1.45	4	1.77	6.3	AT, MS	Campbell et al. (2000)
Carnivora										
Canis familiaris	6.3		Glycine	1.7	1.31				MC	Plummer et al. (1926)
Canis familiaris	6.5		Casein		1.32	4	65.6			Rapport and Beard (1927)
Canis familiaris	6.5		Gelatin	0.1	1.39				MC	Rapport (1926)
Canis familiaris	7.0		Meat	7.1	1.44	24	335	11.2	MS	Benedict and Pratt (1913)
Canis familiaris	7.7		Meat	2.6	1.31					Dann et al. (1931)
Canis familiaris	8.4		Meat		1.40				MC	Rapport and Beard (1928)
Canis familiaris	9.3		Dextrose sol.		1.30	5	68.4	5.9		Lusk (1912a, b, c), dextrose
Canis familiaris	9.5		Mixed diet	2.3	1.54		89.1	3.1	MS, MT	Lusk (1912a, b, c)
Canis familiaris	9.9		Glucose sol.	4.1	1.27	4	78.4	8.6	MC	Lusk (1921)
Canis familiaris	10.0		Meat	2.0	1.26					Gaebler (1929)
Canis familiaris	10.2		Glycine		1.18					Nord and Deuel (1928)
Canis familiaris	10.8		Glucose		1.25		11.6	2.8	MC	Dann and Chambers (1933)
Canis familiaris	11.4		Meat	2.6	1.52				MC	Chambers and Lusk (1930)
Canis familiaris	11.5		Glucose		1.20	3	66.6	7.1	MC	Lusk (1915)
Canis familiaris	11.5	25.5	Meat		1.35				MC, MT	Rapport (1924)
Canis familiaris	11.5		Meat	7.0	1.59	5	205	5.1	MC, MS	Weiss and Rapport (1924)
Canis familiaris	11.6	25.5	Meat	9.3	1.95				MC	Atkinson and Lusk (1919)
Canis familiaris	12.0		Glucose sol.	1.7	1.29	2	36	4.1		Dann and Chambers (1930)
Canis familiaris	13.0	26	Fat	0.6	1.30				MC	Murlin and Lusk (1915)
Canis familiaris	13.5		Meat	8.9	1.88	21	1,142	14.7	MS	Williams et al. (1912)
Canis familiaris	16.6	21	Dog food		2.05					Diamond et al. (1985)
Canis familiaris[a]	17.9	22	Dog food	2.8	1.75	6	114	3.7	MF, MS	LeBlanc and Diamond (1986)
Canis familiaris	18.8	22	Dog food	3.8	2.04					Diamond and LeBlanc (1988)
Canis familiaris	19.0	22	Dog food	3.8	1.84					Diamond and LeBlanc (1987a, b), hormone
Canis familiaris	19.2		Dog food	3.8	1.96					Diamond and LeBlanc (1987a, b)
Canis familiaris	30.0		Meat	0.7	1.20		185		BC	Gibbons (1924)
Enhydra lutris	18.4		Squid	8.2	2.02	5.3	712	13.2		Costa and Kooyman (1984)
Felis domesticus	2.62	27.6	Protein	0.6	1.38					Haimovici (1939)
Pinnipedia										
Eumetopias jubatus[a]	117	8	Fish	1.9	1.47				AT	Rosen and Trites (2003)
Phoca groenlandica[a]	150		Fish	1.3	1.67	10	2,924	15.7	MS	Gallivan and Ronald (1981)
Phoca vitulina[a]	43.7	4	Fish	3.5	1.27	10	864	6.8		Markussen et al. (1994)

Table 8 continued

Species	Body mass (kg)	T_a (°C)	Meal type	Meal size (%)	Scope	Duration (h)	SDA (kJ)	SDA coefficient (%)	Treatments	Source
Rodentia										
Cynomys ludovicianus	1.0		Vegetables		1.25					Pfeiffer et al. (1979)
Mesocricetus auratus[a]	0.099	30	Casein		1.31		2.08		MC	Šimek (1976)
Phyllotis darwini	0.064	25	Formulated diet		1.22		0.51			Nespolo et al. (2003)
Rattus noviegicus[a]	0.10		Formulated diet	2.0	1.73	4	29.7	22.0	MS	Forbes et al. (1934)
Rattus noviegicus	0.10		Casein	8.0	1.31			19.6	MC, SX	Kriss et al. (1934)
Rattus noviegicus	0.147	26	Formulated diet	3.8	1.27	7.5	3.08	6.5		Even et al. (2002)
Rattus noviegicus	0.175	26	Glucose	2.0	1.54				MC	Sadhu and Brody (1947)
Rattus noviegicus[a]	0.2		Formulated diet	5.5	1.37		27.9	43.0	MC	Kriss (1938)
Rattus noviegicus[a]	0.2	25	Formulated diet	7.6	1.31	3.5	4.15	8.3		Luz et al. (2000)
Rattus noviegicus[a]	0.21	27.5	Formulated diet		1.44				MT	Curcio et al. (1999)
Rattus noviegicus[a]	0.33	29	Corn flour	0.8	1.15	36	7.56	18.9		Rothwell et al. (1982)
Rattus noviegicus	0.335		Formulated diet	0.9	1.62	1.1	3.03	4.6		Forsum et al. (1981)
Lagomorpha										
Oryctolagus cuniculus	2.56		Formulated diet	1.0			21.5	5.3		Baumann and Hunt (1925)
Artiodactyla										
Bos taurus	336		Corn		1.51		18,010		MC	Eisemann and Nienaber (1990)
Bos taurus	392		Hay	1.8	1.48		16,213		MS, MT	Benedict and Ritzman (1927)
Bos taurus	628		Straw		1.86	70	15,537			Brody (1945)
Camelus dromedarius	317		Grain/straw	1.8	1.97		14,828	16.8	MS	Guerouali et al. (2004)
Odocoileus virginianus[a]	35.6	5	Mixed browse	1.4	1.40		1,100	17.6	AT	Jensen et al. (1999)
Ovibus moschatus[a]	150	17.4	Hay		1.54	1.8	1,344	3.5	AT	Lawler and White (2003)
Ovis aries	73.5		Straw		1.84	60	3,335			Brody (1945)
Rangifer tarandus[a]	83.5	15			1.20	24	2,232	9.1		McEwan (1970)
Sus scrofa	13.5		Starch	3.1	1.60		1,267	10.3		Wierzuchowski and Ling (1925)
Sus scrofa	20.0		Formulated diet		1.42	16	1,175	22.4		Gray and McCraken (1980)
Sus scrofa	22.4		Casein		1.13				MT	Rapport et al. (1924)
Sus scrofa	66.4	24	Formulated diet	3.6	2.04	62	3,360	8.9	MS	Lovatto et al. (2006)
Sus scrofa	193		Straw			60	7,548			Brody (1945)
Perissodactyla										
Equus caballus	581		Straw		1.59	60	16,700			Brody (1945)

Meal mass (%) is reported as a percentage of body mass. Scope, duration, SDA, and SDA coefficient are defined in Table 1

T_a ambient temperature; studies with experimental treatments are noted as *AT* ambient temperature, *BC* body composition, *MC* meal composition, *MF* meal frequency, *MS* meal size, *MT* meal type, *SX* sex

[a] Studies for scope, SDA, and/or SDA coefficient are calculated from published information

Table 9 Tabulation of 28 human SDA studies

Sex	Body mass (kg)	T_a (°C)	Meal type	Meal size (%)	Scope	Duration (h)	SDA (kJ)	SDA coefficient (%)	Source
Single meal									
Female[a]	35.1	23	Liquid	1.50	1.37	5	266	9.1	Moukaddem et al. (1997)
Female	40.0	24	Mixed	1.31	1.14	5	161	6.4	Maffeis et al. (2001)
Female	53.2	22.5	Mixed		1.23		209	5.5	Segal and Gutin (1983)
Female[a]	55.1	23.5	Liquid	1.60	1.27	5	293	9.5	Bessard et al. (1983)
Female[a]	56.1	23.5	Liquid	1.32	1.27	3.4	171	5.4	Tai et al. (1997)
Female	57.9	24	Liquid	1.28	1.29	5	241	7.7	Tai et al. (1991)
Female[a]	59.8		Liquid		1.20	4	95.0	4.6	Labayen et al. (1999)
Female	60.0		Mixed		1.38	5	226	6.0	Swindells (1972)
Female[a]	60.3		Mixed		1.35	4	269	7.8	Bronstein et al. (1995)
Female	63.4		Liquid	0.55	1.22	3	115	9.0	Visser et al. (1995)
Male[a]	67.5	23	Liquid	0.83	1.34	4	240	7.2	Katzeff and Danforth (1989)
Male	71.0		Liquid		1.20	6	219	9.3	Nacht et al. (1987)
Male	71.2	24	Liquid		1.22	4	211	10.0	Morgan et al. (1982)
Male	73.3	23	Liquid	0.48	1.16	5	141	6.8	D'Alessio et al. (1988)
Male	73.7	24	Mixed		1.27	4	161	4.9	Elia et al. (1988)
Male[a]	74.4	24	Liquid	0.99	1.24	3	208	6.6	Segal et al. (1987)
Male[a]	75.4	24	Liquid		1.17	4	132	6.9	Westrate et al. (1989)
Male[a]	78.0		Mixed	0.46	1.21	3	78.0	3.6	Belko et al. (1986)
Male[a]	79.8	24	Liquid	1.02	1.32	3	277	8.5	Poehlman et al. (1989)
Male[a]	95.0	24	Liquid	0.78	1.19	3.5	164	5.2	Segal et al. (1985)
Both	62.1		Mixed		1.30	5	224	9.8	Bandini et al. (1989)
Both[a]	66.2		Liquid	0.73	1.23	4	166	8.3	Weststrate et al. (1990)
Full day									
Female	55.0		Mixed		1.32		1,065	14.8	Schutz et al. (1984)
Female	67.0		Mixed		1.22		1,295	14.6	Westerterp et al. (1999)
Male	71.3		Mixed		1.22		1,176	10.8	Ravussin et al. (1985)
Both	69.7		Mixed		1.19		1,400	12.4	Verboeket-van de Venne et al. (1996)
Both	93.1		Mixed		1.75		1,697	18.9	Tataranni et al. (1995)
Both	96.9		Mixed		1.40		690	7.1	Ravussin et al. (1986)

Meal mass (%) is reported as a percentage of body mass. Scope, duration, SDA, and SDA coefficient are defined in Table 1. Studies are divided into those involving a single meal and those that include multiple meals and monitoring for over a full day

T_a ambient temperature

[a] Studies for scope, SDA, and/or SDA coefficient are calculated from published information

and hence generate a lower SDA, will allocate more of ingested energy into body stores (e.g., adipose tissue) and thus are predestined to becoming obese. It has also been hypothesized that exercise after a meal should enhance the SDA response beyond that predicted from the sum of exercise $\dot{V}O_2$ when fasting and postprandial $\dot{V}O_2$ at rest (Segal and Gutin 1983). Whereas several studies have observed exercise to further potentiate SDA (Miller et al. 1967; Segal and Gutin 1983; Zahorska-Markiewicz 1980), there is a greater number of studies that have found that human postprandial $\dot{V}O_2$ during exercise can be accounted for by the additive effects of exercise and digestion (Belko et al. 1986; Bray et al. 1974; Dallosso and James 1984; Swindells 1972).

Studies have explored the impact of athletic training, pregnancy, menstrual cycle, stress, and age (discussed later) on human SDA. Compared to sedentary controls, trained athletes have been found to possess either a higher or lower SDA (Poehlman et al. 1989; Tremblay et al. 1983). For either normal weight or overweight women, SDA was found not to differ between pregnant and non-pregnant individuals (Bronstein et al. 1995). For three studies, an increase, a decrease, and no change in SDA have been noted from the follicular (preovulation) phase to the luteal (postovulation) phase of the menstrual cycle (Piers et al. 1995; Tai et al. 1997; Weststrate 1993). Westrate et al. (1989) explored the influence of psychological stress on SDA and found that when watching a horror film, humans experienced a higher SDA response compared to when watching a romantic family film.

In addition to the effects on SDA of meal composition and size (discussed later), the effects of meal palatability and familiarity have also been explored. LeBlanc and Brondel (1985) found that compared to a highly palatable meal, a tasteless, nonpalatable meal of matched ingredients generated a reduced SDA response. In contrast, other studies observed no differences in SDA between palatable and unpalatable meals, nor found any effect of meal sweetness on SDA (Prat-Larquemin et al. 2000; Weststrate et al. 1990). Among normal weight and overweight women, unfamiliar foods elicited a 19% greater SDA compared to familiar foods (Westerterp-Plantenga et al. 1992).

The majority of human SDA studies are conducted following a fairly standard protocol involving measurements of RMR taken the morning following an overnight fast, a single meal consumed, and measurements of $\dot{V}O_2$ taken at regular intervals for 3–6 h at an ambient temperature of 22–25°C. Meals generally are either a normal meal of mixed foods or a custom-made or commercial (e.g., Ensure®) liquid diet of balanced nutrients. Typical meals range in mass from 0.5 to 1.5% of body mass and in energy from 1,200 to 8,000 kJ. Compared to other organisms, humans exhibit a very modest postprandial metabolic response (Fig. 9). For 22 single-meal studies involving men and/or women, postprandial metabolic rate increased only $25 \pm 1\%$ above fasting values with the duration of this response only lasting 3–6 h (Table 9). Because of the less than threefold range in body mass, much of the variation in human SDA is explained by differences in meal mass (Table 3). For the tabulated set of single-meal studies,

Fig. 8 Postprandial metabolic profiles for four species of mammals. Mammals experience a relatively modest postprandial increase in metabolism that usually only lasts 6–10 h. Body mass, ambient temperature, meal type, and meal mass (if known) for each figure are presented in Table 8. Figures are drawn from data presented in the following original articles; *Canis familiaris* (LeBlanc and Diamond 1986), *Phoca groenlandica* (Gallivan and Ronald 1981), *Rattus noviegicus* (Even et al. 2002), and *Bos taurus* (Brody 1945)

Fig. 9 Postprandial metabolic profiles for two sets of male and two sets of female human subjects. Average body mass are noted in *parentheses*. Humans experience a 20–30% increase in metabolism with feeding that returns to prefeeding levels within 4–6 h. Body mass, ambient temperature, meal type, and meal mass (if known) for each figure are presented in Table 9. Figures were drawn from data presented in the following original articles; males (Elia et al. 1988; Segal et al. 1987) and females (Moukaddem et al. 1997; Bessard et al. 1983)

SDA increases with meal energy and the SDA coefficient averages $7.2 \pm 0.4\%$ (Fig. 3; Table 9).

An alternative method to calculate human SDA is by continuously monitoring an individual's rate of gas exchange within a room-size respirometry chamber (Ravussin et al. 1986). Such chambers are typically furnished with a bed, chair, television, sink, and toilet allowing subjects to experience a near normal regiment of daily activities (minus strenuous activities). Activities of subjects are monitored by radar and the SDA resulting from breakfast, lunch, and dinner is calculated from any increase in gas exchange above BMR at zero level of activity. Studies using a respiratory chamber generally find SDA to constitute a higher percentage of meal energy compared to single-meal studies that generally employ a ventilated hood apparatus to monitor gas exchange. For six studies using the room chambers, SDA averaged $13.1 \pm 1.6\%$ of daily ingested energy (Table 9). Suggested reasons for the higher SDA and SDA coefficients for these studies include the establishment of a lower baseline from subjects while they are sleeping in the chamber and that the full postprandial metabolic response is measured (Ravussin et al. 1986). It has been commented that many single-meal studies terminate measurements before postprandial metabolic rates fully return to baseline levels (Reed and Hill 1996).

Determinants of SDA

The magnitude and duration of the postprandial metabolic response is dependent upon features of the meal, characteristics of the animal, and environmental conditions. Across all major taxa, individual determinants of SDA have been experimentally explored (Tables 2, 4, 5, 6, 7, 8). The impact on SDA of individual features of the meal (composition, type, size, and temperature), of the animal (body size, body composition, sex, and age), and of the environment (ambient temperature, gas concentration, and salinity) are summarized below.

Meal composition

Rubner (1902) is credited with being the first to describe the effects of meal composition on SDA by comparing the postprandial metabolism of dogs following the digestion of meat, sugar, or fat. Following Rubner's lead, Lusk and others documented the magnitude of postprandial metabolism of dogs following the administration of meal ranging from solutions of a single amino acid, sugar, or fat to combinations of nutrients, and to intact pieces of meat (Lusk 1912a, b, c; Murlin and Lusk 1915; Weiss and Rapport 1924; Williams et al. 1912). During that same time period, Bonnet and Terroine explored the effects of meat, fat, starch, and individual amino acids on the SDA of the frog, *Rana temporaria* (Bonnet 1926; Terroine and Bonnet 1926). More recently, the attention on the effects of meal composition on SDA has been examined using fish. One impetus for these studies is the consideration that the more balanced a meal is in satisfying the animal's nutritional requirements, the smaller the SDA and the greater the net energy gained (Chakraborty et al. 1992; Peres and Oliva-Teles 2001).

In these fish studies, meals vary in their relative percentages of protein, lipids, and carbohydrates, and include meals that are as much as 100% protein, 100% carbohydrates, or 30% lipids (Chakraborty et al. 1992; Fu et al. 2005d; LeGrow and Beamish 1986; Peres and Oliva-Teles 2001; Ross et al. 1992; Tandler and Beamish 1980; Fig. 10). Coulson and Hernandez (1979) documented the SDA responses of *Alligator mississippiensis* following their consumption of different protein meals (fish, casein, and gelatin; Fig. 10) and mixtures of amino acids (complete, essential, and nonessential). McCue et al. (2005) performed a similar study on *Python molurus* using different protein and mixed amino acid meals (Fig. 10), as well as meals of carbohydrates (glucose, sucrose, starch, and cellulose) and fats (lard and suet). Metabolic responses to experimental diets of casein, gelatin, and mixtures of low and high concentrations of fats and proteins have also been documented for the chicken (Barott et al. 1938; Swennen et al. 2006).

From the time of Rubner's studies, the general consensus has been that protein-based meals generate larger SDA responses than meals relatively high in carbohydrates or fats. This has been found true for fishes, amphibians, reptiles, birds, and mammals (Bonnet 1926; Karst et al. 1984; McCue et al. 2005; Šimek 1976; Swennen et al. 2006; Tandler and Beamish 1980; Weiss and Rapport 1924). Additionally, it had been found for several studies that SDA increases with relative protein content of a meal. A 50, 150, and 700% increase in percent meal protein generated respective increases of 23, 78, and 300% in SDA for the fishes *Salmo gairdneri*, *Cyprinus carpio*, and *Oreochromis niloticus* (Chakraborty et al. 1992; LeGrow and Beamish 1986; Ross et al. 1992; Fig. 10). Contrary to these findings, the magnitude of SDA was found not to be affected by either a 56 or 88% increase in meal protein for the fishes *Dicentrarchus labrax* and *Lepomis macrochirus*, respectively (Peres and Oliva-Teles 2001; Schalles and Wissing 1976). When controlling for protein content, increasing lipid content also generated mixed results. Both *D. labrax* and *O. niloticus* experience a decrease in SDA with an increase in lipid meal content, whereas two studies on *Salmo gairdneri* found that changing meal lipid content had no impact on SDA (LeGrow and Beamish 1986; Medland and Beamish 1985; Peres and Oliva-Teles 2001;
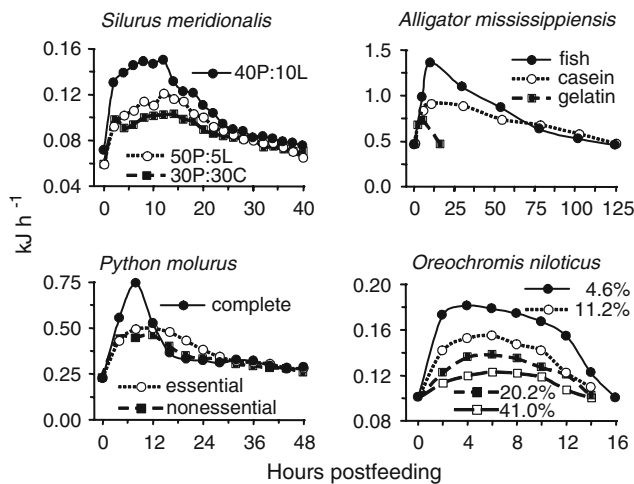
Fig. 10 Effects of meal composition on the postprandial metabolic response of the fishes *Silurus meridionalis* and *Oreochromis niloticus* and the reptiles *Python molurus* and *Alligator mississippiensis*. For *S. meridionalis*, meal treatment include diets of 40% protein and 10% lipid (40P:10L), 50% protein and 5% lipid (50P:5L), and 30% protein and 30% carbohydrates (30P:30C) (Fu et al. 2005d). For *O. niloticus*, meal treatments include diets of 4.6, 11.2, 20.2, and 41.0% protein (Ross et al. 1992). For *P. molurus*, meal treatments include solutions of complete, essential, and nonessential amino acids (McCue et al. 2005). For *A. mississippiensis*, meal treatments include diets of fish and solutions of casein and gelatin (Coulson and Hernandez 1979). Figures were drawn from data presented in the original articles

Ross et al. 1992). In replacing the previous emphasis on protein alone, the new opinion is that SDA is affected by the interactions among the relative amounts of proteins, carbohydrates and lipids (LeGrow and Beamish 1986; Peres and Oliva-Teles 2001).

Meal type

Few studies have explored the effects of different natural food items on SDA while also controlling for meal size and body mass. For the crustaceans, *Crangon franciscorum* and *Macrobrachium rosenbergii*, tubificid worms elicited a larger metabolic response than diets of fish, mysid shrimp, or algae (Nelson et al. 1977, 1985). After adjusting for meal mass, the digestion of millipedes was several time more costly than the digestion of either mushrooms or kale for the turtle, *Kinixys spekii* (Hailey 1998). For the lizard, *Heloderma suspectum*, a meal of rats resulted in a greater metabolic response than the digestion of chicken egg contents (Christel et al. 2007). Cows feeding upon alfalfa hay experienced larger SDA's than when feeding on similar amounts of timothy hay (Benedict and Ritzman 1927).

To date, the greatest amount of attention on meal type effects on SDA has been on amphibians, both for anurans and a salamander (Fig. 11). For six species of anurans (*Bombina orientalis*, *Bufo marinus*, *Dyscophus antongilli*,
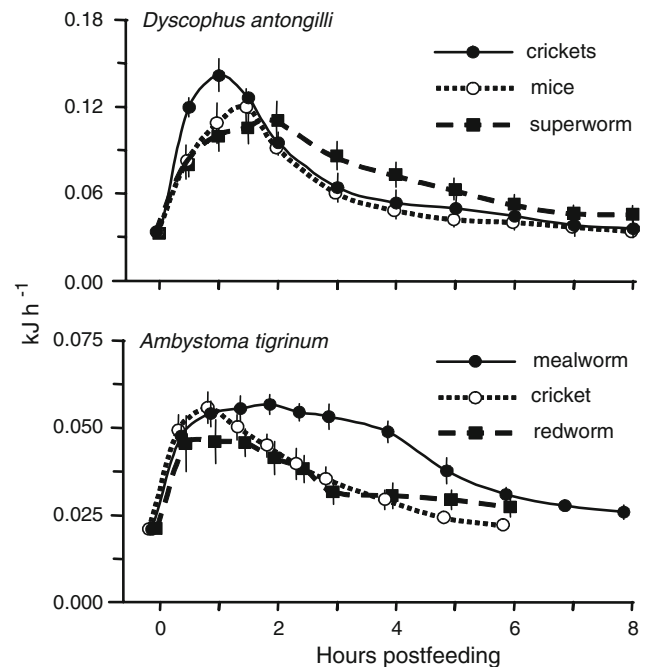
Fig. 11 Effects of meal type on the postprandial metabolic response of the anuran *Dyscophus antongilli* and the salamander *Ambystoma tigrinum*. For both amphibians, peak and duration of the metabolic response varied with meal type. Figures were drawn from data presented in the following original articles; *D. antongilli* (Secor et al. 2007) and *A. tigrinum* (Secor and Boehm 2006)

Hyla cinerea, *Kassina maculatus*, and *Rana catesbeiana*) the ingestion of three or four different natural prey items, all of the same relative mass (10% of body mass) revealed that the digestion and assimilation of chitinous beetle larva (*Tenebrio molitor* and *Zophobas morio*) and crickets generated significantly larger SDA responses than the digestion of soft-bodied earthworms, moth larva, and neonatal rodents (Secor and Faulkner 2002; Secor et al. 2007; Fig. 12). Similarly for the tiger salamander, *Ambystoma tigrinum*, a study comparing the responses to nine different meals (5% of body mass) found that the ingestion of hard-bodied prey (beetle larva, beetles, crickets) resulted in SDA's that averaged 75% greater than the SDA's generated from the consumption of soft-bodied prey (earthworms, salamanders, grubs) (Secor and Boehm 2006) Presumably these differences can be attributed to the greater effort expended to breakdown and assimilate the hard chitinous exoskeleton of the insect prey compared to that used to digest the soft-bodied prey.

Meal size

Meal size is a well documented determinant of SDA. Multiple studies have found that when controlling for meal type and body temperature and body size, any increase in meal size is matched by a corresponding increase in
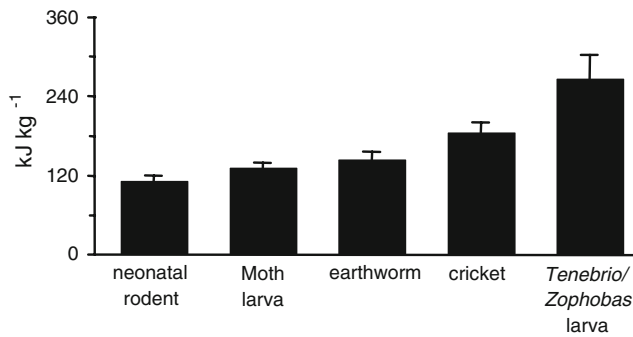
Fig. 12 Meal type effects on anuran SDA. Data were obtained from six anuran species (*Bombina orientalis*, *Bufo marinus*, *Dyscophus antongilli*, *Hyla cinerea*, *Kassina maculatus*, and *Rana catesbeiana*) digesting meals equaling 10% of anuran body mass. Note that the SDA generated from digesting chitinous meals (crickets and *Tenebrio* and *Zophobas* larva) is greater than the SDA resulting from the digesting of soft-bodied neonate rodents, moth larva, and earthworms. Data from Secor and Faulkner (2002) and Secor et al. (2007)

Fig. 13 Effects of meal size (% of body mass) on the postprandial metabolic response of the fish *Silurus meridionalis* and the snake *Python molurus*. Note that with an increase in relative meal size there is a corresponding increase in the peak and duration of the metabolic response. Figures were drawn from data presented in the original articles; *S. meridionalis* (Fu et al. 2005c) and *P. molurus* (Secor and Diamond 1997)

postprandial peak metabolism, the duration of elevated metabolism, and SDA (Campbell et al. 2000; D'Alessio et al. 1988; Fu et al. 2005c; Masman et al. 1989; Secor and Diamond 1997; Secor et al. 2007; Fig. 13). The direction of this response can easily be explained by the increase in time and effort needed to digest and assimilate a larger meal. The number and range of meal sizes compared per study extends from only two meals spanning a twofold range in size (Benedict and Ritzman 1927; Jordan and Steffensen 2007) to seven or eight meals spanning a 20–40-fold range in size (Secor and Diamond 1997; Fu et al. 2005c, 2006). For many of these studies, a linear relationship exists between meal size and peak metabolism, duration, and SDA (Fu et al. 2005c; Ross et al. 1992; Secor and Diamond 1997; Fig. 14). In contrast, several studies have found that the peak in postprandial metabolism plateaus with larger meals (Jobling and Davies 1980; Secor and Boehm 2006). Jobling and Davies (1980) suggested that the metabolic processes of SDA may reach a maximum level which is set by the oxidative capacities of gut tissue. For the vast majority of animals, the maximum postprandial metabolism (two to fourfold of basal) is less than the maximum metabolic rate attained during strenuous activities (5–20-fold of basal; Brett 1965; Gatten et al. 1992; Hinds et al. 1993; Hoppeler and Weibel 1998; Secor and Faulkner 2002). Exceptions to this pattern are sit-and-wait foraging snakes that while digesting can experience rates of O_2 consumption that exceed their crawling-induced $\dot{V}O_2$ max (Andrade et al. 1997; Secor and Diamond 1997; Secor et al. 2000). For example, the Burmese python can experience a 31-fold increase in $\dot{V}O_2$ while digesting a meal equaling 65% of its body mass, whereas vigorous crawling on an empty stomach generates a less impressive 14-fold increase in $\dot{V}O_2$ (Secor and Diamond 1997; Secor et al. 2000).

The doubling of meal size would predictably result in a doubling of SDA. To assess the extent that postprandial peak metabolism, duration of the postprandial response, and SDA are affected by a doubling of meal size, response coefficients were calculated for those studies in which postprandial metabolic responses were quantified for two or more meal sizes (Table 10). The response coefficient ($Q_{2\times}$) represents the factorial increase in a parameter with a doubling of demand, in this case, meal size (Secor and Boehm 2006). For the two invertebrate studies, doubling meal size resulted in an average $Q_{2\times}$ for SDA of 1.45 ± 0.16 (Fig. 15). For these animals, a double of meal size generates on average a 45% increase in SDA. For fishes, a doubling of meal size has a more predicted outcome, as the $Q_{2\times}$ for postprandial peak metabolism, duration, and SDA averaged 1.29 ± 0.04, 1.46 ± 0.06, and 2.00 ± 0.09, respectively (Fig. 15; Table 10). Amphibian and reptile $Q_{2\times}$ for peak metabolism and duration averaged greater than that for fishes, resulting in significantly greater $Q_{2\times}$ for SDA (Fig. 15; Table 10). Doubling meal size for birds generated a $Q_{2\times}$ of 2.11 ± 0.20% for SDA, whereas for mammals $Q_{2\times}$ of SDA is a more modest 1.61 ± 0.10 (Fig. 15; Table 10). Across all taxa, $Q_{2\times}$ for SDA averages
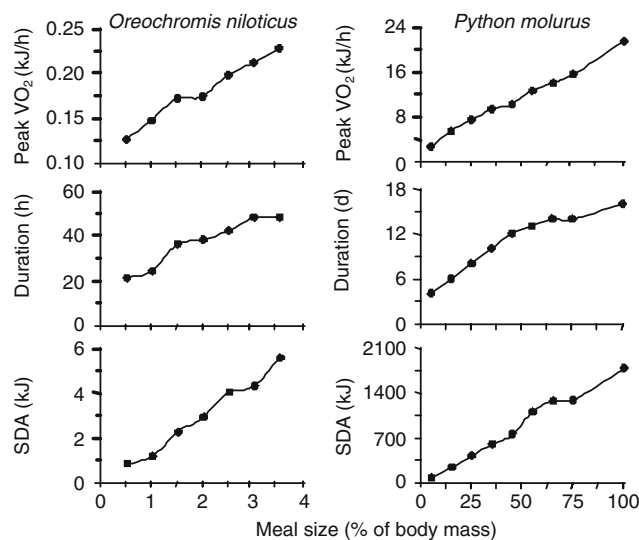
Fig. 14 Postprandial peak $\dot{V}O_2$, duration of the SDA response, and SDA plotted against meal size (% of body mass) for the fish *Oreochromis niloticus* and the snake *Python molurus*. Note the near linear increase in the peak, duration, and magnitude of the SDA response with increasing meal size. Figures were drawn from data presented in the original articles; *O. niloticuss* (Ross et al. 1992) and *P. molurus* (Secor and Diamond 1997)

2.06 ± 0.06, which is not significantly different from 2.0, and therefore, supports the prediction that a doubling of meal size generates a doubling of SDA. The increase in SDA with meal size appears to be contributed to equally by increases in peak metabolism and the duration of the elevated response.

Meal temperature

Endotherms commonly ingest food of a lower temperature (usually equal to ambient temperature) than their core body temperature. Hence, extra heat must be generated to elevate food temperature to body temperature. The cost of food warming is therefore included in the SDA response. The contribution of food warming to SDA will vary as a function of food temperature and mass: more energy will be expended warming a large, cold meal compared to a smaller, warmer meal (Berteaux 2000). The effects of meal temperature are most evident for endotherms living in cold environments that consume food that may be more than 30°C lower than their body temperature (Battam et al. 2008; Lotz et al. 2003; Wilson and Culik 1991). For Brünnich's guillemont, *Uria lomvia*, the ingestion of a 19-g cod meal of 0–2°C was immediately followed by a slight drop in abdominal temperature (39.93–39.78°C) that was recovered within 20 min and which increased thereafter (Hawkins et al. 1997). Within 7 min the temperature of the cod meal had increased to match that of the bird's stomach (Hawkins et al. 1997). The estimated cost of heating the

cod meal (3 kJ) was approximately one-third of the overall metabolic response (9.5 kJ), with the remaining expenditure (6.5 kJ) attributed to digestion and assimilation (Hawkins et al. 1997). For rufous hummingbirds, *Selasphorus rufus*, digesting a 5% sucrose solution of 4°C, mallard ducks, *Anas platyrhynchos*, digesting a mixed grain meal of 8°C, and albatrosses, *Diomedea gibsoni* and *Thalassarche carteri*, digesting fish of 0 and 20°C, the cost of warming these meals is estimated to be equal to 13–44% of the total postprandial metabolic response (Battam et al. 2008; Kaseloo and Lovvorn 2003; Lotz et al. 2003). Wilson and Culik (1991) found for adult Adélie penguins (*Pygoscelis adeliae*, core temperature 37.5°C), that the ingestion of a 300-g cold krill meal (0°C) generated a fourfold increase in oxygen consumption, whereas a warm krill meal (37°C) produced no significant rise in metabolic rate. In not observing a SDA response specific to meal ingestion and assimilation they concluded that all of the postprandial energy expended above BMR was attributed to the cost of heating the meal. In contrast, Janes and Chappell (1995) later observed a distinct SDA response for Adélie penguin chicks when given krill meals warmed to 40°C. The results of these studies illustrate the need to experimentally test or control for the effects of meal temperature when it is significantly different from body temperature.

Body size

An increase in body size, while maintaining constant relative meal size, meal type, and body temperature, will predictably generate a corresponding increase in metabolic rate and the SDA response. This has been found to be true in almost all cases; basal and peak metabolic rates and SDA increase with an increase in body mass (Benedict 1932; Boyce and Clarke 1997; Kaushik and Dabrowski 1983; Sims and Davies 1994). However, the effect of body mass on the duration of the SDA response has been mixed; duration decreases with body mass for the birds *Pygoscelis adeliae* and *Troglodytes aedon* (Janes and Chappell 1995; Chappell et al. 1997), duration does not change with body mass for the fishes *Gadus morhua* and *Myoxocephalus scorpius* (Hunt von Herbing and White 2002; Johnston and Battram 1993), and duration increases with body mass for the fishes *Micropterus salmoides* and *Harpagifer antarcticus* (Tandler and Beamish 1981; Boyce and Clarke 1997).

Whereas the effects of body mass on basal metabolic rate has been examined intra- and interspecifically for all animal taxa, few studies have explored the scaling relationship of the SDA responses (Peters 1989; Schmidt-Nielsen 1989). Important to these SDA studies is controlling for meal type, relative meal mass, and for ectotherms,

Table 10 Meal size range and response coefficients ($Q_{2\times}$) of peak $\dot{V}O_2$, duration, and SDA for species for which SDA responses were measured for two or more meal sizes

Species	Meal sizes (% of body mass)	Response coefficient ($Q_{2\times}$)			Source
		Peak $\dot{V}O_2$	Duration	SDA	
Invertebrates					
Mytilus edulis	2.0–7.3			1.30 ± 0.09	Widdows and Hawkins (1989)
Nephelopsis obscura	10.3–25.3			1.61	Kalarani and Davies (1994)
Fish					
Brachydanio rerio	1–5	1.06 ± 0.03	1.24 ± 0.01	1.62 ± 0.01	Lucas and Priede (1992)
Cyrpinus carpio	0.4–1.0	1.24 ± 0.11	1.47 ± 0.15	2.06 ± 0.15	Chakraborty et al. (1992)
Gadus morhua	1.35–5.21	1.38 ± 0.50	1.29 ± 0.07	1.48 ± 0.62	Soofiani and Hawkins (1982)
Gadus morhua	2.5–5.0		1.96	2.33	Jordan and Steffensen (2007)
Kuhlia sandvicensis	2.3–4.6	1.35	1.34	2.11	Muir and Niimi (1972)
Micropterus salmoides	2–8		1.54 ± 0.01	2.18 ± 0.09	Beamish (1974)
Micropterus salmoides	0.25–2.0	1.54 ± 0.05	1.55 ± 0.01	2.36 ± 0.12	Tandler and Beamish (1981)
Oreochromis niloticus	0.5–3.5	1.32 ± 0.08	1.41 ± 0.16	2.12 ± 0.27	Ross et al. (1992)
Oreochromis niloticus	2–10	1.42 ± 0.17		1.61	Xie et al. (1997)
Silurus asotus	0.74–21.9	1.33 ± 0.10	1.38 ± 0.06	1.95 ± 0.16	Fu et al. (2006)
Silurus meridionalis	0.6–24.2	1.22 ± 0.08	1.46 ± 0.15	2.04 ± 0.16	Fu et al. (2005a, b, c, d; CBP 140:451)
Pleuronectes platessa	0.63–3.75	1.27 ± 0.16	1.38 ± 0.14	2.16 ± 0.32	Jobling and Davies (1980)
Stizostedion vitreum	0.4–1.6	1.10 ± 0.02		1.52 ± 0.41	Beamish and MacMahon (1988)
Amphibians					
Ambystoma tigrinum	2.5–12.5	1.28 ± 0.16	1.43 ± 0.16	1.94 ± 0.25	Secor and Boehm (2006)
Bombina orientalis	2.5–10	1.47 ± 0.60	1.64 ± 0.07	1.61 ± 0.13	Secor et al. (2007)
Bufo cognatus	2.5–10	1.52 ± 0.35	1.64 ± 0.07	2.12 ± 0.17	Secor et al. (2007)
Bufo marinus	5–20	1.46 ± 0.19	1.70 ± 0.44	2.54 ± 0.09	Secor and Faulkner (2002)
Ceratophrys ornata	5–35	1.53 ± 0.09	1.79 ± 0.36	2.53 ± 0.17	Secor et al. (2007)
Dyscophus antongilli	2.5–10	1.66 ± 0.31	1.89 ± 0.31	2.85 ± 0.43	Secor et al. (2007)
Hyla cinerea	5–15	1.43 ± 0.17	1.75 ± 0.25	2.49 ± 0.45	Secor et al. (2007)
Kassina senegalensis	2.5–10	1.71 ± 0.33	1.89 ± 0.31	1.92 ± 0.63	Secor et al. (2007)
Pyxicephalus adspersus	5–25	1.98 ± 0.70	1.53 ± 0.23	2.99 ± 1.01	Secor et al. (2007)
Rana catesbeiana	2.5–10	1.28 ± 0.17	1.55 ± 0.23	2.18 ± 0.32	Secor et al. (2007)
Reptiles					
Alligator mississippensis	1.25–10	1.40 ± 0.11	1.81 ± 0.09	3.16 ± 0.48	Coulson and Hernandez (1983)
Angolosaurus skoogi	5–11	1.50 ± 0.81			Clarke and Nicolson (1994)
Boa constrictor	5–40	1.39 ± 0.15	1.57 ± 0.22	2.14 ± 0.37	Toledo et al. (2003)
Crotalus durissus	10–50	1.43 ± 0.10	1.59 ± 0.21	2.35 ± 0.24	Andrade et al. (1997)
Crotalus horridus	10–50	1.62 ± 0.29	1.50 ± 0.28	2.12 ± 0.17	Zaidan and Beaupre (2003)
Eunectes murinus	5–25	1.35 ± 0.00	1.38 ± 0.12	2.15 ± 0.15	Ott and Secor (2007b)
Lamprophis fuliginosus	10–30	1.35 ± 0.10		2.22 ± 0.13	Roe et al. (2004)
Python molurus	5–100	1.62 ± 0.04	1.41 ± 0.08	1.95 ± 0.18	Secor and Diamond (1997)
Python molurus	5–25	1.52 ± 0.09	1.21 ± 0.09	2.35 ± 0.29	Ott and Secor (2007b)
Python reticulatus	5–25	1.39 ± 0.06	1.65 ± 0.48	2.28 ± 0.43	Ott and Secor (2007b)
Python sebae	5–25	1.70 ± 0.39	1.46 ± 0.29	2.68 ± 0.44	Ott and Secor (2007b)
Sceloporus occidentalis	1.44–3.92	0.96 ± 0.09	1.49 ± 0.49	1.55 ± 0.10	Roe et al. (2005)
Birds					
Columba livia	2.3–5.3	1.40 ± 0.18		3.10 ± 0.87	Rashotte et al. (1995)
Eudyptula minor	2.9–7.1	1.12	1.71	2.23	Green et al. (2006)
Falco tinnunculus	5.8–15.1	1.28 ± 0.18	1.28 ± 0.01	1.48 ± 0.06	Masman et al. (1989)
Gallus gallus	1.0–2.1	1.02		2.04	Barott et al. (1938)

Table 10 continued

Species	Meal sizes (% of body mass)	Response coefficient ($Q_{2\times}$)			Source
		Peak $\dot{V}O_2$	Duration	SDA	
Pygoscelis adeliae	7.8–31.1			2.00	Janes and Chappell (1995)
Strix aluco	2.74–8.26		1.44	2.29	Bech and Præsteng (2004)
Troglodytes aedon	2–8	1.00	1.19	1.58	Chappell et al. (1997)
Mammals					
Bos taurus	0.9–1.8	1.37		1.62	Benedict and Ritzman (1927)
Bos taurus	0.9–1.8	1.46		1.87	Benedict and Ritzman (1927)
Canis familiaris	0.7–2.8	1.03	1.33	1.57	LeBlanc and Diamond (1986)
Canis familiaris	1.74–6.96	1.14 ± 0.04		1.48 ± 0.12	Weiss and Rapport (1924)
Condylura cristata	6.5–15	1.05	1.76	1.24	Campbell et al. (2000)
Phoca groenlandica	0.67–2.0	1.20		1.89	Gallivan and Ronald (1981)

The response coefficient represents the factorial increase in a parameter with a doubling of meal size (Secor and Boehm 2006). Response coefficients are presented as mean ± 1 SE determined by calculating for each species a response coefficient between each consecutive pair of meal sizes

body temperature. For the toad *B. marinus* and the snake *P. molurus* digesting rodent meals weighing 10 and 25% of their body mass, respectively, and maintained at 30°C, SMR, peak $\dot{V}O_2$ and SDA scaled against body mass (log–log) with respective mass exponents of 0.69, 0.85, and 1.02 for *B. marinus* and 0.68, 0.90, and 1.01 for *P. molurus* (Secor and Diamond 1997; Secor and Faulkner 2002; Fig. 16). For both species, the higher scaling exponent for peak $\dot{V}O_2$ compared to SMR results in an increase in the scope of peak $\dot{V}O_2$ with body mass. Interspecific body mass scaling of SDA response has been examined for several groups of amphibians and reptiles (Ott and Secor 2007b; Secor and Boehm 2006; Secor et al. 2007). For 13 species of anurans that consumed cricket meals weighing

10% of body mass (from Table 5), SMR, peak $\dot{V}O_2$, and SDA scaled with mass exponents of 0.83, 0.92, and 1.08 (Fig. 16). Similarly for six species of ambystomatid salamanders, each fed cricket meals weighing 5% of body mass, these mass exponents equaled 0.72, 0.78, and 1.05, respectively (Secor and Boehm 2006). For 19 taxa of snakes that had consumed rodent meals weighing 25% of snake body mass and maintained at 30°C (from Table 7), SMR, peak $\dot{V}O_2$, and SDA scaled with mass exponents of 0.84, 0.99, and 1.11, respectively (Fig. 16). For each of these intraspecific and interspecific analyzes, the scaling exponent of SDA (1.01–1.11) does not differ significantly from 1.0.

Body composition, sex, and age

Outside of human studies exploring the effects of obesity on SDA, there have been very few attempts to examine the impact of body composition on SDA. Between genetic strains of lean and fat (possessing three times the abdominal fat as lean) chickens, SDA did not differ significantly following the consumption of a commercial pellet diet, a high protein/low fat, or a low protein/high fat diet (Geraert et al. 1988; Swennen et al. 2006). For two individual dogs of similar body mass (29–30 kg), one "thin" (a greyhound) and the other "fat" (mastiff mix), a meal of 200 g of beef heart generated a higher postprandial peak in metabolism and a twofold greater SDA for the thin dog compared to the fat dog (Gibbons 1924).

The interest in the relationship between body composition and SDA for humans stems from the hypothesis that obesity results from an inherent reduced SDA response, thereby more of the ingested meal is invested in body stores rather than in metabolism (Bessard et al. 1983;
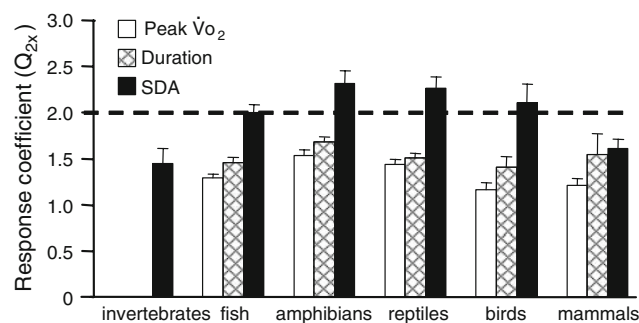
Fig. 15 Response coefficient ($Q_{2\times}$) of postprandial peak $\dot{V}O_2$, duration of the SDA response, and SDA averaged for invertebrates, fish, amphibians, reptiles, birds, and mammals. The response coefficient here represents the factorial increase in a parameter with a doubling of meal size. Species specific response coefficients are presented in Table 10. With a doubling of meal size, peak $\dot{V}O_2$ and duration increases by factors of 1.2–1.6-fold, whereas SDA on average doubles (*dashed line*)
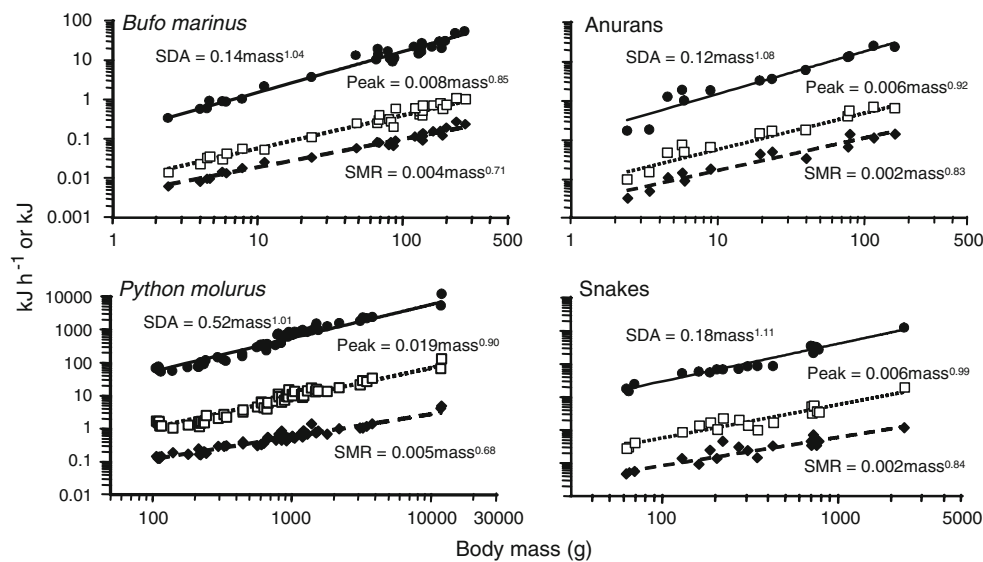
Fig. 16 Intraspecific (*Bufo marinus* and *Python molurus*) and inter-specific (anurans and snakes) scaling (log₁₀–log₁₀ plots) of SMR (kJ/ h, *closed diamonds*), postprandial peak $\dot{V}O_2$ (kJ/h, *open squares*), and SDA (kJ, *closed circles*). *Bufo marinus* and *P. molurus* plots were drawn from data originating from Secor and Faulkner (2002) and Secor and Diamond (1997), respectively. Anuran and snake plots were drawn from data originating from studies in Tables 5 and 6. For each plot, experimental body temperature, meal type and relative meal size were held constant. For each plot, the mass exponent of peak $\dot{V}O_2$ was greater than the exponent for SMR and the mass exponent of SDA did not significantly differ from 1.0

D'Alessio et al. 1988). Proposed mechanisms for a reduced SDA response include decreased postprandial response of the sympathetic nervous system and hence a decrease facultative metabolic response, and a resistance to insulin thereby lowering rates of tissue glucose uptake (de Jonge and Bray 1997; Weststrate 1993). In a review of 49 studies that compared SDA responses between lean and obese individuals, 20 studies found no difference in SDA, whereas 29 studies found a difference, of which 22 studies documented a lower SDA for obese individuals (de Jonge and Bray 1997). It has also been asked whether obesity is due to a low SDA or is a low SDA characteristic of obesity (James 1992). Support for the former connection comes from studies that have found that when following weight loss, previously obese subjects still retained a reduced SDA (Bessard et al. 1983; Schutz et al. 1984). However, when finding no difference in SDA between previously obese and non-obese subjects, Thörne et al. (1990) concluded that a reduced SDA is not the primary pathogenic factor in human obesity, but rather a corollary phenomenon.

Few non-human studies identify the sex of their test subjects and present separate SDA data for males and females. For chickens fed 75 g of corn, hens (mean body mass 1.95 kg) experienced an SDA of 155 ± 10 kJ, whereas for cocks (2.87 kg), SDA averaged 167 ± 12 kJ (Mitchell and Haines 1927). Although hens consumed relatively larger meals than cocks (3.8 vs. 2.6% of body mass), the SDA coefficients of hens (12.3 ± 0.8%) did not significantly differ from that of cocks (13.2 ± 0.9%). For 100-g rats, meals of 3.8 g of casein or 1.56 g of olive oil generated on average a higher SDA for females compared to males, whereas a meal of 3.92 g of starch produced a larger SDA for male rats (Kriss et al. 1934). Although human studies routinely note the sex of their subjects, few include both male and female individuals, and only a handful of those studies provide separate data for each sex. In such studies, there are no apparent differences in SDA between male and female subjects when correcting for body mass (Visser et al. 1995; Weststrate and Hautvast 1990).

Separate from those studies that examine intraspecific body size effects on SDA with individuals differing in body size because of age, the effects of age on SDA of adult individuals has only been investigated for humans. Because of the decrease in daily energy expenditure with age, it is hypothesized that SDA also declines with age. For studies that compared the SDA of elderly men (>65 years) with younger subjects (20–33 years), several observed a decrease in SDA with age (Morgan and York 1983; Thörne and Wahren 1990), one study found no difference with age (Tuttle et al. 1953), and others were able to explain the difference with age due to differences in body composition (Bloesch et al. 1988; Visser et al. 1995) or physical activity levels (Poehlman et al. 1989). In a single study with women, there was no significant difference in SDA between young (average age 23 years) and elderly (average age 72 years) individuals (Visser et al. 1995).

Ambient temperature—ectotherms

Metabolic rates of ectotherms vary as a function of ambient temperature, and hence body temperature. An increase in body temperature results in an increase in metabolic rates, as well as an increase in rates of meal digestion and assimilation. Thus, any shift in body temperature will change the postprandial metabolic profile (McCue 2006). Studies examining the effects of body temperature on ectotherm SDA have found that with an increase in temperature there is a corresponding increase in SMR and peak metabolism and a decrease in the duration of the metabolic response (Machida 1981; Robertson et al. 2002; Secor et al. 2007; Wang et al. 2003). The postprandial metabolic profile becomes narrower and taller with an increase in body temperature, and the postprandial peak in metabolism is reached sooner after feeding (Wang et al. 2003; Secor et al. 2007; Fig. 17). Given that both SMR and peak metabolism increase with body temperature, the scope of peak metabolism would theoretically not change. This has generally been found to be true (Machida 1981; Soofiani and Hawkins 1982; Peck et al. 2003; Secor and Faulkner 2002; Secor et al. 2007; Toledo et al. 2003; Wang et al. 2003),
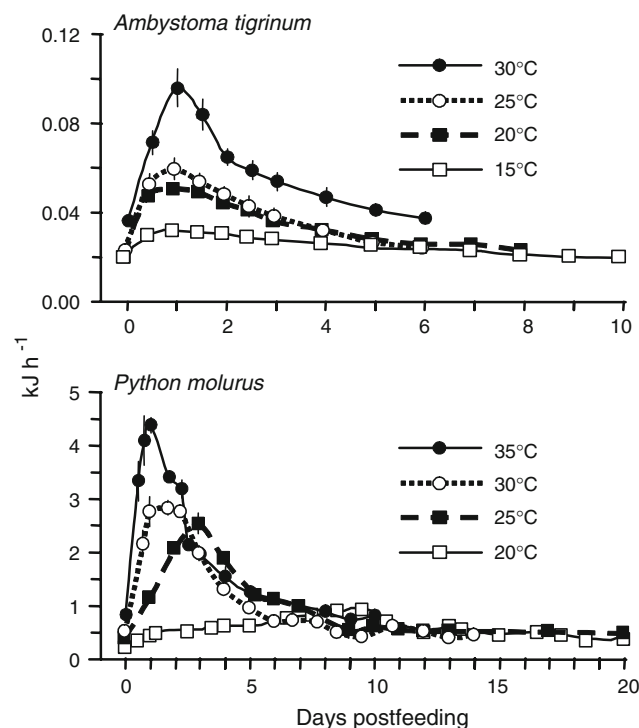
Fig. 17 Body temperature effects on the postprandial metabolic response of the salamander *Ambystoma tigrinum* and the snake *Python molurus*. For both species, the metabolic profile becomes more elevated and narrower with an increase in body temperature. Figures were drawn from data presented in the original articles; *A. tigrinum* (Secor and Boehm 2006) and *P. molurus* (Wang et al. 2003)

although increases and decreases in the scope with body temperature have also been observed (Hamada and Ida 1973; Robertson et al. 2002; Secor and Boehm 2006; Secor et al. 2007). One possible explanation for differences in the factorial scope of peak metabolic rate with temperature is that the aerobic scope of the particular species is limited at one end of the temperature range being tested.

In assuming that a fixed amount of energy is expended to digest and assimilate a given meal regardless of the rate of digestion, then SDA would predictably not vary with body temperature (Secor et al. 2007). Lack of significant temperature effects on SDA has been documented for the fishes *D. labrax*, *Pleuronectes platessa*, and *Odontobutis obscura*, the anurans *Bombina orientalis*, *Bufo cognatus*, *B. marinus*, *Ceratophrys cranwelli*, *D. antongilli*, and *Kassina maculata*, and the snake *Python molurus* (Jobling and Davies 1980; Machida 1981; Peres and Oliva-Teles 2001; Powell et al. 1999; Secor and Faulkner 2002; Secor et al. 2007; Wang et al. 2003). For a similar number of other species, SDA has been found to vary with body temperature. Elevating body temperature results in an increase in SDA for the fishes *G. morhua*, *Silurus meridionalis*, and *Sparus aurata*, the amphibians *Hyla cinerea*, *Rana catesbeiana*, and *Ambystoma tigrinum*, and the snakes *Crotalus horridus* and *Natrix natrix* (Guinea and Fernandez 1997; Hailey and Davies 1987; Luo and Xie 2008; Peck et al. 2003; Secor and Boehm 2006; Secor et al. 2007; Zaidan and Beaupre 2003). In contrast, a decrease in SDA was observed with an increase in body temperature for the fish *Phoxinus phoxinus* and the snake *Boa constrictor* digesting meals equaling 20% of snake body mass (Cui and Wootton 1988; Toledo et al. 2003).

Ambient temperature—endotherms

In 1902, Rubner proposed for endotherms that with a decrease in environmental temperatures below the thermoneutral zone, there would be a corresponding decrease in observed SDA as the heat of SDA is increasingly being used to maintain body temperature. Rubner observed a 50% increase in heat production for a dog fed meat at 30°C, but no increase in heat production when the fed dog was maintained at 7°C. This substitution of SDA for thermogenesis would reduce thermoregulatory costs, allowing the saved energy to be used for other functions (e.g., activities, growth, and reproduction). This adaptive thermal substitution would be most beneficial to endotherms living in cold environments as an energy-conserving mechanism (Campbell et al. 2000). The testing of Rubner's theory, referred to as his "compensation theory", became the aim of many of the SDA studies involving birds and mammals. The findings of these studies have been mixed, whereas several have observed SDA to

decline with ambient temperature, other studies found no evidence of substitution (Rosen and Trites 2003).

Partial substitution of SDA for thermogenesis has been reported for the birds *Coturnix coturnix* and *Falco tinnunculus*, and the mammals *Blarina brevicauda*, *Mesocricetus auratus*, and *Odocoileus virginianus* (Hindle et al. 2003; Jensen et al. 1999; Marjoniemi 2000; Masman et al. 1989; Šimek 1976). Kaseloo and Lovvorn (2006) found that when swimming in 8°C water and diving 2 m to feed on high-protein mussels, the lesser scaup, *Aythya affinis*, experiences an 80% decrease in SDA compared to when swimming and feeding in 23°C water. In observing an absence of an SDA response below thermoneutrality (22°C) for *Troglodytes aedon* chicks, Chappell et al. (1997) concluded that SDA can completely substitute for thermostatic heat production for these chicks at low ambient temperatures.

In contrast are those studies that failed to find any indication that SDA offsets thermoregulatory costs at low temperatures. For Steller sea lions, *Eumetopias jubatus*, swimming in 2°C water and mallard ducks, *Anas platyrhynchos*, swimming on water at 8°C, there were no changes in SDA compared to when exposed to higher water temperatures, 8°C for the sea lions and 23°C for the ducks (Kaseloo and Lovvorn 2003; Rosen and Trites 2003). Decreasing air temperature from 11 to 3°C and from 24 to 9°C likewise had no impact on SDA for the arctic tern chick, *Sterna paradisaea*, and the star-nosed mole, *Condylura cristata*, respectively (Klaassen et al. 1989; Campbell et al. 2000). Rosen and Trites (2003) presented both theoretical and experimental reasons for the absence of SDA substituting for thermoregulatory costs and the explanations for why results differ among studies. These explanations include the possession of alternative physiological, anatomical, and behavioral mechanisms to reduce heat loss, the variation among study organisms in their ecology, taxonomy, and age, and differences in experimental design. For example, the aforementioned lesser scaup does not experience temperature-dependent differences in SDA when consuming a low-protein meal (Kaseloo and Lovvorn 2006). Rosen and Trites (2003) also hypothesized that a decrease in SDA with ambient temperature may stem from the ceasing of digestive activities at low temperatures, rather than reflect thermal substitution.

Gas concentration and salinity

For both aquatic and terrestrial organisms, a decrease in P_{O_2} significantly impacts the SDA response. When exposed to hypoxic water (3 kPa), the green crab, *Carcinus maenas*, experiences a greatly reduced SDA response, as postprandial peak $\dot{V}O_2$ is only 1.27-fold of fasting rates compared to 2.43-fold for crabs in normoxic (21 kPa) water (Mente et al. 2003). For this crab, the hypoxic-induced decline in SDA may in part be due to the concurrent reduction in protein synthesis (Mente et al. 2003). Cod maintained in moderate hypoxic (6.3 kPa) water experience a lower postprandial peak in $\dot{V}O_2$, a longer metabolic response (212 vs. 95 h), and a larger SDA compared to fish maintained in normoxic (19.8 kPa) water (Jordan and Steffensen 2007). In that study it was suggested that hypoxia lowers the ceiling of aerobic capacity thereby digestive performance is limited and hence it takes longer to digest a meal (Jordan and Steffensen 2007). For the lizard *Tupinambis merianae* digesting rodent meals, a decrease in oxygen concentration of inspired air to below 10% generates a significant increase in $\dot{V}O_2$ (Skovgaard and Wang 2004). Interestingly, while digesting, these lizards did not vary their $\dot{V}O_2$ when exposed to increasing levels (up to 6%) of inspired CO_2 (Skovgaard and Wang 2004).

In testing the effects of salinity on the SDA of the grass shrimp, *Penaeus monodon*, Du Preez et al. (1992) found no difference when shrimp were fed shrimp and maintained under three different salinities (5, 15, and 45‰). However, when fed a commercial pellet diet, shrimp maintained at 5‰ had significantly greater SDA compared to when maintained at 45‰. For the crab, *Cancer gracilis*, an acute exposure to lower salinity (32–21‰) at 3 h after feeding triggered a 75% decrease in $\dot{V}O_2$ (McGaw 2006). Metabolic rate of these crabs were restored 3 h later at 21‰ salinity and then increased by 50% when placed back into 100% seawater (McGaw 2006).

Mechanism of SDA

> "The hypotheses which have been presented on specific dynamic action transcend one's power to coordinate them." Graham Lusk (Brody 1945).

Since its discovery, scientists have attempted to explain the source and mechanisms of the postprandial increase in metabolism. From von Mering and Zuntz's "work of digestion" and Voit's "plethora theory", to Rubner's specific dynamic effect of protein, fat, and carbohydrate and Krebs' theories of amino acid oxidation, the contributing processes of SDA have been hypothesized, experimentally explored, and debated (Ashworth 1969; Garrow 1973; James 1992; Kleiber 1961; Lusk 1928). To simplify and possibly clarify the sources of the SDA response, researchers have in the past partitioned SDA into separate components. Tittelbach and Mattes (2002) described two phases of SDA; first a cephalic phase that represents the energy expended due to the cognitive, olfactory, and gustatory stimulation of feeding and which

accounts for 30–53% of overall SDA; and second, a gastrointestinal phase that includes the energy expended on the digestion, absorption, metabolism, and storage of nutrients. James (1992) explained that SDA includes an obligatory component that represents the cost of digestion, absorption, assimilation, and synthesis of proteins and fats, and a facultative component that is the energy expended beyond the obligatory component and results from meal stimulation of the autonomic nervous system and the inherent cycling of substrates (e.g., proteins). Tandler and Beamish (1979) portioned SDA into mechanical SDA, which represents the cost of grasping, chewing, swallowing, and peristalsis, and biochemical SDA, the expenditure associated with active nutrient transport, increase in blood circulation, catabolism of assimilated nutrients, and synthesis of macromolecules (e.g., proteins and urea).

As alluded to by the opening quote of this section, the source of SDA cannot be easily identified or partitioned. It represents the accumulation of many different energy consuming processes that occurs with the digestion and assimilation of a meal. Rather than summarizing the different theories for the source of SDA, a description of how each component of the ingestion, digestion, and assimilation pathway can contribute to SDA is presented. These components have been divided between those that occur prior to the passage of ingested nutrients into circulation (preabsorptive) and those events that occur after (postabsorptive).

Preabsorptive contributions to SDA

Eating and swallowing

It is debatable whether eating and swallowing constitutes a postprandial event and hence would contribute to SDA (Tandler and Beamish 1979). Because animals can simultaneously chew, swallow, and digest their meals, and because mastication, salivary secretion, and swallowing are energy consuming events that are a prerequisite to digestion, they are included in this discussion. Most SDA studies initiate metabolic measurements after food has been swallowed and has entered the stomach, therefore little is known of the cost of mastication and swallowing. Two groups of organisms for which the cost of eating has been examined are reptiles and ruminants (Adam et al. 1984; Cruz-Neto et al. 2001). For the scincid lizards, *Chalcides ocellatus* and *Scincella lateralis*, the cost of subduing and swallowing their insect prey was less than 1% (0.1–0.8%) of meal energy, and increase with meal size and the toughness of the insect's exoskeleton (Grimmond et al. 1994; Pough and Andrews 1985; Prest 1991). Swallowing alone (prey passing only into the

esophagus) is relatively inexpensive for the snakes, *Crotalus durissus* and *Boa constrictor*, equivalent to just 0.003–0.051% of meal energy (Canjani et al. 2003; Cruz-Neto et al. 1999). Interestingly, the constriction and subsequent inspection of the dead prey (an additional cost of feeding) for *Boa constrictor* are equal to a modest 0.048–0.16 and 0.017–0.036% of meal energy, respectively (Canjani et al. 2003).

For domesticated and bighorn sheep, the eating (chewing and swallowing) of hay results in 32–75% increase in resting metabolic rate (Chappel and Hudson 1978; Christopherson and Webster 1972; Osuji et al. 1975; Young 1966). Susenbeth et al. (2004) calculated that steers expend 100–240 J per chew when feeding on straw, grass, silage, or hay. The accumulative cost of eating for cattle was equivalent to 0.44% of meal energy when feeding on pressed pellets, and 1.3–1.9% of meal energy for cattle and sheep feeding on either hay or grass (Adam et al. 1984; Christopherson and Webster 1972; Webster 1972; Young 1966). Similar findings arose from a study of the Amazonian manatee, *Trichechus inunguis*, including a 50–75% increase in metabolism while feeding and a total cost of feeding equal to 3.4–5.4% of gross energy intake (Gallivan and Best 1986).

For reptiles, at least, the chewing and/or swallowing of a meal contribute little to their SDA. The cost of these activities represents 1–4% of the projected SDA for scincid lizards, and 0.02–0.43% of the SDA for *B. constrictor* and *C. durissus* (SDA data from Table 7). For animals that chew more heavily (e.g., ruminants and the manatee), mastication and swallowing constitute a larger fraction (>10%) of their SDA. The movement of food through the esophagus to the stomach would incur a cost stemming from the contractions of longitudinal, circular, and sphincter smooth muscles (Uriona et al. 2005). Although no study has accessed the cost of esophageal passage, it is probably safe to assume that it is an insignificant component of SDA, especially for animals with a very short esophagus (e.g., fishes, amphibians, and lizards).

Gastric breakdown

Among animals and their wide array of meals, there is tremendous variation in the state of the ingested meal as it enters the stomach. Yet regardless of its state on arrival, the meal must be broken down into a soup-like chyme before it is allowed passage into the small intestine. Thus, the variation in the effort exerted by the stomach contributes to the variation in SDA. Intuitively, meals that have been heavily masticated, have a small particulate size, or have a high fluid content are predictably processed in the stomach with less effort and more rapidly than meals that are completely intact and/or possess components that are tough

to digest (e.g., chitinous exoskeleton or bone). Less energy would therefore be expended by the stomachs of hummingbirds and African egg-eating snakes digesting their liquid diets compared to that of pythons digesting an intact porcupine, wild boar, deer, or pangolin (Shine et al. 1998).

Gastric breakdown of food is achieved by mechanical and chemical mechanisms. The former entails alternating contractions of circular, longitudinal, and diagonal smooth muscle fibers that churns the food within the stomach, thereby increasing the food's exposure to gastric secretions. In response to feeding and the entry of food into the stomach, gastric oxyntopeptic cells (parietal cells in mammals) release H^+ and Cl^-, the former ion being actively pumped via H^+/K^+ ATPase transporters, into the lumen where they form HCl (Forte et al. 1980). Simultaneously, these cells (chief cells in mammals) release pepsinogen which when exposed to a pH of 4 or less is activated into the proteolytic enzyme, pepsin. Therefore, the larger the meal, the tougher the meal, and the more intact the meal is, the more pepsinogen and HCl that will need to be produced. With the stochiometry of the H^+/K^+ ATPase of one ATP utilized for each H^+ pumped, maintaining a highly acidic (pH 1–2) gastric lumen against the buffering capacity of a large meal possibly for days suggest a potentially high cost of gastric breakdown for some animals (Reenstra and Forte 1981).

The reported contribution of gastric function to SDA has ranged from nonexistent to highly significant, although few studies have attempted to ascertain experimentally the cost of gastric performance (Andrade et al. 2004; Secor 2003). Those reports that have largely discounted the contribution of gastric function and other preabsorptive activities to SDA cite studies that have observed similar increases in postprandial metabolism whether the meal (typically a protein solution) was orally ingested or administered intravenously (Borsook 1936; Coulson and Hernandez 1979). Three groups of animals for which an appreciable cost of gastric performance may be expected are ruminants, birds that use their muscular gizzard (caudal to the acid-producing proventriculus) to pulverize hard food items (e.g., seeds and bivalves), and animals that ingest large intact prey items (e.g., snakes). The cost of rumination, which includes contractions of the rumen, esophageal peristalsis, and chewing is estimated to be equivalent to 0.2–0.4% of ingested energy, roughly 2–4% of SDA for sheep (Osuji et al. 1975; Toutain et al. 1977). For a 600-kg steer, the daily cost of rumination is estimated to be 2,240 kJ, assuming it spends 7 h a day ruminating at a cost of 8.9 J/min per kg (Susenbeth et al. 1998, 2004). The heat produced by anaerobic fermentation within the sheep's rumen is estimated to be between 64 and 68 J/kJ of energy fermented and thus be equivalent to 13% of their SDA (Webster et al. 1976).

For red knots (*Calidris canutus*) digesting shelled bivalves, the cost of gizzard activity was found to be immeasurable, possibly owing to the rapid crushing action of their gizzards and the quick passage of prey remains into the intestine (Piersma et al. 2003). Predictably, the cost of gizzard activity would be higher for birds that require more effort to grind their hard food. The high cost of gastric performance for snakes is illustrated in a study using the Burmese python. Experimentally reducing the work load of the python's stomach by infusing into their stomach homogenized rat or mixed nutrient liquid diet, or infusing homogenized rat directly into their small intestine reduced SDA (compared to that from a intact rat meal) by an average of 26, 57, and 67%, respectively (Fig. 18; Secor 2003). McCue et al. (2005) also reported for the Burmese python a decrease in SDA generated from a liquid meal compared to an intact meal. Others have suggested that the contribution of gastric acid secretion to SDA is minimal for snakes given that the administration of an acid secretion inhibitor, omeprazole, did not significantly reduce SDA for the boa constrictor (Andrade et al. 2004). However, the authors acknowledged that acid secretion was possibly later restored allowing the snakes
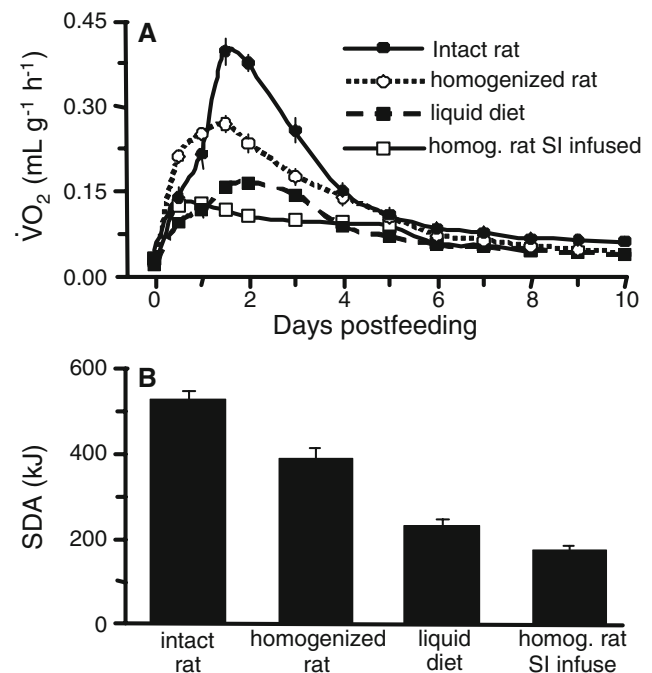
Fig. 18 a Postprandial metabolic profile of *Python molurus*, following the ingestion of an intact rat, the gastric infusion of homogenized rat and liquid diet, and small intestinal infusion of homogenized rat. All meals equal in mass to 25% of snake body mass. **b** SDA generated from each of these meal treatments. Magnitude and duration of elevated postprandial metabolism decline with a decrease in the structural integrity of the diet and the bypassing of gastric digestion. Figures were drawn from data presented in Secor (2003)

to fully digest their meals (Andrade et al. 2004). Therefore, gastric effort, a function of ingested meal structure, should be considered for some animals a significant contributor to SDA.

Intestinal peristalsis and absorption

Energy consuming activities of the intestine during digestion would include peristalsis (i.e., smooth muscle contraction), the production and actions of enzymes (e.g., disaccharidases and aminopeptidases), the production and secretion of regulatory peptides (e.g., CCK, GIP, and secretin), the transmembrane transport of nutrients (requiring ATP-driven maintenance of a sodium gradient), and any post-transport synthesis within intestinal cells (e.g., proteins, triglycerides, and chylomicrons). Regardless of these activities, it has been assumed for many organisms that the intestine contributes modestly (if at all) to SDA. Benedict and Emmes (1912) found that violent intestinal peristalsis of the human GI tract, following the ingestion of sodium sulphate or agar, resulted in negligible increases in heat production. Similarly for the fish *Pleuronectes platessa*, when fed an indigestible meal of kaolin there was no detectable increase in oxygen consumption (Jobling and Davies 1980). The lack of any differences in the metabolic response of a complete amino acid mixture administered orally or intraperitoneally lead Coulson and Hernandez (1979) to remark for the alligator that the cost of amino acid absorption and transport is low enough to be undetectable. Blaxter (1989) calculated for man that the cost of enzymatic hydrolysis of lipids, polysaccharides, and proteins in the intestinal lumen amounts for only 0.1–0.2% of the energy content of the substrate being hydrolyzed, and that the cost of colonic fermentation equals 1% of meal energy. In contrast, the cost of anaerobic fermentation in herbivores may account for as much as 50% of SDA (Blaxter 1989). Other findings that do suggest a significant expenditure due to intestinal function include a 41% increase in oxygen uptake by the small intestine with a doubling of meal size for sheep (Han et al. 2002), a 70% reduction in SDA following the removal of 80% of the small intestine for rats (Luz et al. 2000), and an eightfold increase in intestinal blood flow after feeding for *P. molurus* (Secor 2005b). Independent of intestinal function, another potential source of postprandial cost resides in intestinal hypertrophy, which is a characteristic response of many animals after an extended period of fasting (Piersma and Lindström 1997; Wang et al. 2006). With feeding, the small intestine may double or even triple in mass, at a cost that represents the energy expended on the synthesis of new cells and/or larger cells (Secor 2003, 2005a).

Postabsorptive contributions to SDA

Substrate catabolism

Historically, investigators viewed SDA largely as a postabsorptive phenomenon. This stems from the noted lack of any increase in metabolic rate when subjects were fed an inert meal which generates gut activity but no nutrient absorption (e.g., kaolin to fish, bones to dogs, agar to humans) and that the intravenous administration of amino acids increases metabolic rates to the same extent as the oral ingestion of those amino acids (Benedict and Emmes 1912; Borsook 1936; Jobling and Davies 1980; Lusk 1912a, b, c; Weiss and Rapport 1924). The postabsorptive contributions to SDA span the numerous cellular activities that are incidental to the processing and assimilation of absorbed biomolecules. Many of these events are not novel to postprandial periods, but occur continuously during periods of fasting. Ingestion thereby triggers an increase in the rates and magnitudes of many of these cellular processes (Blaxter 1989; Reeds et al. 1985).

Of the three nutritive biomolecules, the fate of amino acids is cited as having the largest impact on postabsorptive SDA (Bonnet 1926; Karst et al. 1984; Lusk 1928; Nair et al. 1983; Tandler and Beamish 1980). Whereas the digestion of a high protein meal, characteristic of carnivores, would theoretically increase plasma concentrations of absorbed amino acids by over 100 mmol/L and osmotic pressure by a similar increase, such meals generate only 2–10 mmol/L increase in plasma concentration of those amino acids (Coulson and Hernandez 1983). Thus, absorbed amino acids must be rapidly incorporated into new proteins and/or catabolized. The catabolism of amino acids involves several sources of heat production, including the deamination of the amino acids, the transamination of the amino groups, the fate of the carbon residues which are either oxidized or used to form glucose (gluconeogenesis) or lipids (ketogenesis), and the formation and excretion of the nitrogenous byproducts (ammonia, urea, or uric acid). For more than a century, each of these sources has been implicated in contributing to the SDA response (Blaxter 1989; Borsook 1936; Bradley et al. 2003; Krebs 1964; Lusk 1930; Rubner 1902; Williams et al. 1912).

Each amino acid is unique in structure, therefore, each has been hypothesized to generate its own characteristic SDA when catabolized (Brody 1945). Lusk (1928) reported significant variation in the SDA of dogs generated by different amino acids; glycine and alanine each produced a large SDA, leucine and tyrosine produced moderate responses, and glutamic and aspartic acids generated no SDA response. In contrast, others at that time found tyrosine, glutamic acid, and phenylalaine to exert a greater SDA than either glycine or alanine (Rapport and Beard

1927; Terroine and Bonnet 1926; Wilhelmj et al. 1928). Coulson and Hernandez (1979) fed 2 mmol of each amino acid to 200 g alligators and observed increases in metabolic rate for only arginine, aspartate, glutamate, lysine, and methionine. Borsook and Keighley (1933) proposed that the SDA of each amino acid is the result of two components; the first is constant among amino acids and is the cost of oxidative deamination and urea synthesis and excretion ($\sim$34 kJ/g of N), whereas the second is amino acid-specific and is the cost associated with the fate (e.g., oxidation or glucose synthesis) of the carbon residue. More recently, Blaxter (1989) reported that the heat produced from the oxidation of an amino acid to carbon dioxide, water, and urea varies between 650 and 5,000 kJ/mol.

The primary site of amino acid catabolism and urea production is the liver, which, therefore, has been considered a significant source of the SDA response (Wilhelmj et al. 1928). Dogs whose livers had been removed were found to experience no SDA response when given intravenously alanine or glycine (Wilhelmj et al. 1928). The cost of producing and excreting the nitrogenous byproducts of amino acid catabolism varies considerably depending on its endpoint. It is generally assumed for fish that the combined cost of producing and secreting ammonia is insignificant, given that ammonia readily diffuses into the surrounding water (Jobling 1981). The cost of urea synthesis from NH_3 is estimated to be about 16 kJ/g N or 360 kJ/mol of urea, representing approximately 20% of total protein SDA (Borsook 1936; Borsook and Keighley 1933; Buttery and Boorman 1976). Excretion of urea by the kidney adds another 4–8 kJ/g N (Borsook 1936). The production of uric acid is even more expensive, estimated at 1,400 kJ/mol (Buttery and Boorman 1976).

Biosynthesis of body constituents

Absorbed amino acids, glucose, and lipid molecules that are not immediately catabolized are directed into synthesis pathways, requiring the input of energy. The synthesis of glycogen from glucose requires first the transformation of glucose to glucose-6-phosphate which forms a α-1,4 linkage with an existing glycogen molecule resulting in the release of one molecule of uridine diphosphate and the formation of one molecule of water at an estimate cost of 2.1 molecules of ATP (Blaxter 1989). Absorbed fatty acids can be incorporated into different kinds of lipids, though the predominant form is triglycerides which are stored in fat bodies or adipose tissue. The synthesis of fat from absorbed lipids is considered to be relatively inexpensive (480 kJ/mol synthesized or 0.015 kJ expended per kJ synthesized), whereas the formation of fat from either carbohydrates (6,100 kJ/mol synthesized) or amino acids

(12,800 kJ/mol synthesized) is more costly (Reeds et al. 1982; Blaxter 1989).

For much of the twentieth century, the focus was largely on amino acid catabolism and the fate of amino acid residues as the source of SDA (Brody 1945; Krebs 1964; LeGrow and Beamish 1986; Lusk 1928). With Ashworth (1969) and more recent studies (Brown and Cameron 1991b; Carter and Brafield 1992; Houlihan et al. 1990; Lyndon et al. 1992), that attention has shifted to protein synthesis as the dominant postabsorptive source of heat production. As suggested by the rapid disappearance from circulation of absorbed amino acids, any amino acid not immediately catabolized is channeled into protein synthesis pathways. This has been demonstrated by the postprandial increases in rates of protein synthesis for a variety of different organisms, in particular, invertebrates (Houlihan et al. 1990; Mente et al. 2003; Robertson et al. 2001a, b) and fishes (Lied et al. 1983; McMillan and Houlihan 1988; Fig. 19). Rates of protein synthesis are estimated from the relative incorporation of injected labeled phenylalanine or leucine into selected tissues (Fauconneau et al. 1989; Houlihan et al. 1990; Robertson et al. 2001a, b). The overall
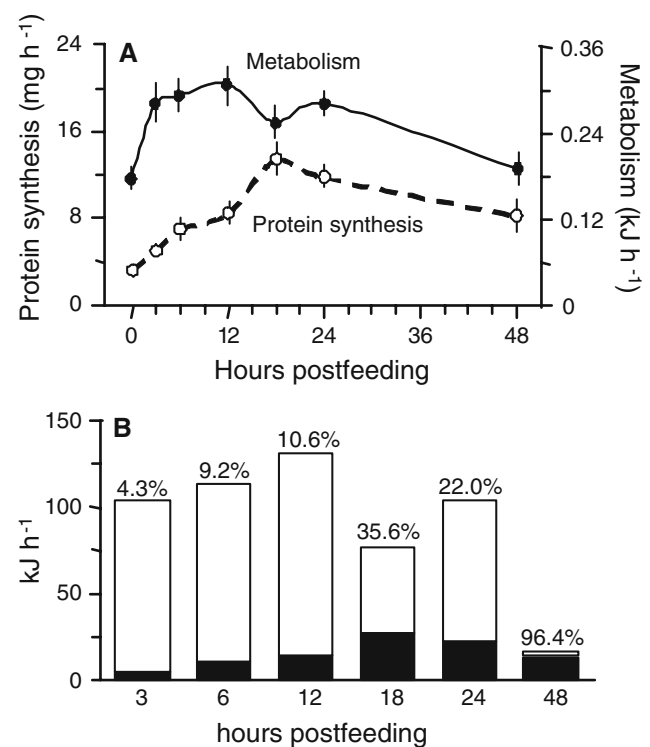
Fig. 19 a Profile of postprandial metabolism (kJ/h, *solid symbols*) and protein synthesis rates (mg/h, *open symbols*) for the fish, *Gadus morhua*, following the consumption of a fish meal weighing 6.4% of body mass. b The contribution of protein synthesis (*solid bars*) to the SDA response (*open bars*) at six time points after feeding for *G. morhua*. The percentages at the *top of the bars* represent the relative contribution of protein synthesis to SDA. Figures were drawn from data presented in Lyndon et al. (1992)

cost of protein synthesis and its contribution to SDA can, therefore, be estimated from the amount of new protein synthesized and assumptions of synthesis cost (Fig. 19).

Alternatively, the contribution of protein synthesis to SDA can be assessed by administering the protein synthesis inhibitor cyclohexamide prior to ingestion and observing the postprandial metabolic response. For the catfish, *Ictalurs punctatus*, the infusion of cyclohexamide prior to the infusion of amino acids abolished the previously observed increase in metabolic rate and doubling of protein synthesis (Brown and Cameron 1991a, b). The administration of cyclohexamide before the ingestion of a complete amino acid mixture (representing the composition of amino acids in a mouse) resulted in a 71% decrease in SDA for the Burmese python, *P. molurus* (McCue et al. 2005). Thor (2000) observed a significantly diminished SDA response with cyclohexamide treatment for both *Acartia tonsa* (SDA decreased by 93%) and *Calanus finmarchicus* (SDA decreased by 88%).

It is estimated that five ATP molecules are required to incorporate an amino acid into a protein, one ATP for the transport of the amino acid and four ATP to form the peptide bond (Reeds et al. 1985). Assuming that each molecule of consumed oxygen is linked to the synthesis of six molecules of ATP (1 L of O_2 consumed results in ~ 250 mmol of ATP produced) and that the formation of 1 mol of ATP requires a mean expenditure of 80 kJ, then theoretically the synthesis of 1 g of protein costs approximately 3.5 kJ (~ 0.2 kJ/kJ of protein synthesized) (Blaxter 1962; Coulson and Hernandez 1979; Reeds et al. 1985). This is a theoretical minimum for the cost of protein synthesis and when rates of protein synthesis are matched against metabolic rates or assessed using cyclohexamide administration, estimates of the cost of protein synthesis are much higher, ranging between 0.4 and 5.4 kJ/kJ synthesized (Aoyagi et al. 1988; Pannevis and Houlihan 1992; Smith and Houlihan 1995; Whiteley et al. 1996).

Even at neutral energy balance, protein synthesis accounts for between 11 and 20% of total energy expenditure (Reeds et al. 1982, 1985). With feeding, protein synthesis costs escalate and account for an estimated 20–40% of SDA (Houlihan et al. 1990; Lyndon et al. 1992). Combined with the less significant costs of glycogen and lipid formation, the cost of biosynthesis (i.e., the cost of growth) is a dominant contributor to SDA (Kiørboe et al. 1985; Wieser and Medgyesy 1990).

SDA in energy budgets

Energy budgets, commonly depicted analytically or graphically, illustrate the balance between ingested meal energy (EI) and the energy excreted as feces (FE) and nitrogenous waste products (UE), the energy used for metabolism [SMR or BMR, SDA, and activity metabolic rate (AMR)], and the energy incorporated into the body as growth, reproduction, and fat stores (Congdon et al. 1982; Elliott 1976)

$$EI = FE + UE + SMR + SDA + AMR + growth \\ + reproduction + fat.$$

Following this general construction, energy budgets serve to tabulate the magnitude of energy flux for an individual or individuals for durations generally ranging from 1 day to 1 year. Given its variation among species with respect to its cost relative to meal energy, SDA constitutes a minor to significant portion of an individual's energy budget. Attention to the contribution of SDA to an energy budget has largely been directed at ectotherms. Stonefly nymphs, *Acroneuria californica*, in July ($T_b = 16$–$17°C$) allocate approximately 20, 45, 10, and 25% of ingested energy to egestion (feces and urate), respiration (SMR and AMR), SDA, and growth, respectively (Heiman and Knight 1975). In aquaculture, energy budgets are constructed to identify components of energy loss (e.g., feces and SDA) that could be reduced by altering meal composition and size and feeding schedules thereby enabling more of the ingested energy to be allocated to somatic growth (Fu and Xie 2004; LeGrow and Beamish 1986; Peres and Oliva-Teles 2001). Practical studies of fish energetics have estimated that SDA contributes to 25–50% of total metabolic expenditure (sum of SMR, SDA, and AMR) and is equivalent to 9–20% of ingested energy (Miura et al. 1976; Owen 2001; Xie et al. 1997).

For free-ranging animals, energy budgets are developed from a combination of laboratory and field measurements. In the laboratory, the energy lost as feces and urate can be determined using bomb calorimetry and indirect calorimetry can be used to measure SMR or BMR, SDA, and the cost of activity. Field data includes observations of food intake and activity patterns, measurements of body temperatures (pertinent to ectotherms), and estimates of field metabolic rates (which encompass SMR/BMR, SDA, and AMR) using the techniques of doubly labeled water (Congdon et al. 1982; Nagy 1989). For three studies on the energetics of free-ranging snakes using doubly labeled water and laboratory SDA measurements, SDA was estimated to be equivalent to 16, 19, 40, and 43% of daily energy expenditure during the activity season for *Acanthophis praelongus*, *Masticophis flagellum*, *Thamnophis sirtalis*, and *Crotalus cerastes*, respectively (Christian et al. 2007; Peterson et al. 1998; Secor and Nagy 1994; Fig. 20). Estimates of SDA equaling 20 and 38% of the annual energy budget were computed from lab-based studies for *Crotalus horridus* and *Agkistrodon piscivorus*, respectively (McCue and Lillywhite 2002; Zaidan and Beaupre 2003).
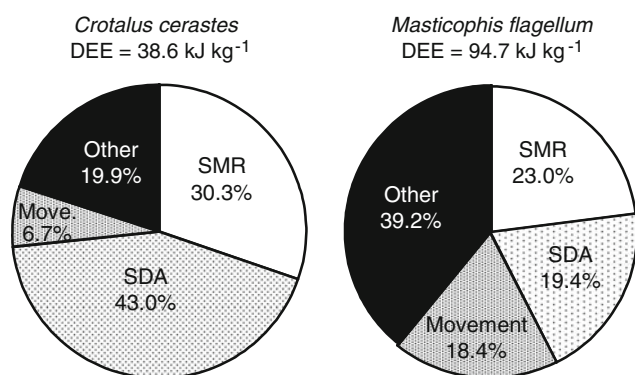
Fig. 20 The partitioning of daily energy expenditure (*DEE*) into standard metabolic rate (*SMR*), specific dynamic action (*SDA*), movement, and other activities for the snakes *Crotalus cerastes* and *Masticophis flagellum* during their activity season (April–October). For *C. cerastes* and *M. flagellum*, 43.0 and 19.4% of their daily energy expenditure is due to SDA, respectively. Figures are drawn from data presented in Secor and Nagy (1994)

For endotherms, the incorporation of SDA into energy budgets has largely been reserved for livestock (Blaxter 1962; Brody 1945). Hall (2006) developed a computational model to study the regulation of body composition in humans and subdivided SDA into expenditures specific to the processing of protein, carbohydrate, and fat.

Future outlook

Characterizing and quantifying the postprandial metabolic response has and will continue to capture the applied and exploratory interest of biologists, nutritionalists, and aquaculturalists. The past two centuries have produced a rich supply of studies, data, and theories regarding SDA. This review serves to collate the available published data on SDA, summarize the various determinants of the SDA response, and identify the preabsorptive and postabsorptive processes that combine to generate the metabolic response. Even with this wealth of information, there is still much to be learned about this metabolic phenomenon. Below are highlighted several topics that would benefit from future attention.

Species diversity

The past few decades have generated a solid foundation in our understanding of the SDA of invertebrates, fishes, and more recently, reptiles. Lagging behind with respect to species numbers are SDA studies on amphibians and wild birds and mammals. The merits of expanding species coverage of SDA, regardless of taxa, include more robust approaches to analyzing body size, phylogenetic, and ecological relationships with SDA. Researchers can use

this review to identify taxonomic gaps in SDA data that can be filled, as well as identify clusters of data that can be analyzed presently or after the addition of more information. Even if the intention of a new study is non-comparative, matching the methodologies (similar meal size, meal type, etc.) of previous studies will allow it to be used comparatively and thus enhance its scientific value. Regardless of rationale and scope (from single species characterization to multi-taxa, multi-determinant analyzes), studies of SDA should be encouraged.

Determinants of SDA

Scientists will undoubtedly continue investigating the effects of various determinants (e.g., meal composition, meal size, meal type, etc.) of the SDA response. Whereas the impact of several determinants (e.g., meal size and meal composition) can be predicted with confidence, understanding the effects of others (e.g., meal type and ambient temperature) would benefit from their study over a wider array of species. For example, we know very little regarding the effects of gas concentrations and salinity on SDA. Terrestrial animals that retreat deep into a burrow after feeding may experience hypoxia, as well as hypercapnia, due to their elevated metabolic rate and inadequate air exchange. Aquatic organism may likewise experience hypoxic conditions due to eutrophication and the lack of mixing of water layers (e.g., Gulf of Mexico Dead Zone). Determining whether a decline in oxygen availability affects the capacity to digest and assimilate a meal would be informative. In aquatic environments, responding to a change in salinity can place additional physiological burden on an organism. For aquatic organisms the metabolic consequence on SDA with a change in salinity has not yet been thoroughly examined.

Source of SDA

The debate on the relative importance of preabsorptive versus postabsorptive events contributing to the SDA response may best be resolved by measuring tissue and/or organ specific rates of metabolism and protein synthesis prior to and after feeding. Changes in organ metabolism with feeding would provide an estimation of the organ's contribution to SDA. Such a tactic has been applied to estimate the postprandial change in metabolism of the sheep's intestinal tract by measuring arterio-venous differences in O_2 concentration of the intestine (Han et al. 2002; Kelly et al. 1993). Taking a different approach, Rosas et al. (1995) removed the digestive gland from fasted and fed shrimp, *Penaeus setiferus*, and measured in vivo the gland's $\dot{V}O_2$. These studies report that organ metabolism contributes significantly (22–70%) to the SDA

response. Matched with organ-specific measures of protein synthesis (Lyndon et al. 1992), the metabolic compartment of SDA can be more accurately defined.

Central control of SDA

Studies on rodents and humans have described the central role of the autonomic nervous system (ANS) in the control of SDA, specifically the facultative component of SDA which is defined as the energy expended in excess of that required for meal digestion and assimilation (Acheson et al. 1984; Rothwell et al. 1982). Postprandial increases in norepinephrine turnover have been suggested as evidence that SDA is mediated by the sympathetic nervous system (LeBlanc and Brondel 1985; Welle et al. 1981; Young and Landsberg 1977). That the administration of drugs (e.g., propranolol and clonidine) which block adrenergic receptors suppresses the SDA response supports this view (Acheson et al. 1983; Schwartz et al. 1988). This view is not without controversy as other studies have found no effect of acute beta blockade on SDA (Campbell et al. 1987; Nacht et al. 1987; Thörne and Wahren 1989). Adding to the confusion, both epinephrine (rather than norepinephrine) and the parasympathetic autonomic nervous system (rather than the sympathetic) have also been demonstrated to mediate the SDA response (Astrup et al. 1989; Nacht et al. 1987). Besides the ANS, both thyroid (principally T_3) and pancreatic (principally insulin) hormones have been implicated to interact with the ANS to stimulate facultative thermogenesis (Diamond and LeBlanc 1988; Marques-Lopes et al. 2003; Silva 2006). Given the conflicting results and opinions regarding the control of the ANS and the potential stimulatory role of thyroid and pancreatic hormones on SDA, this is a field of SDA investigation that warrants further investigations both for mammals and non-mammals.

SDA and activity

The best model organisms for studying SDA are those that upon ingesting a meal remain literally motionless for the duration of digestion, thereby any energy expended above SMR or BMR is due solely to the SDA response. Whereas we can rely upon some snake species to be motionless for days after feeding, most organisms are active while digesting. With the exception of a few sedentary species of fish (e.g., sharks and catfish, Ferry-Graham and Gibb 2001; Fu et al. 2005c), the vast majority of fish swim while digesting, and most invertebrates, amphibians, reptiles, birds, and mammals likewise experience some degree of activity while digesting. Hence, many species face episodes of two metabolic demands: movement, and digestion. Given that each species possess a finite metabolic capacity, might the demands of one metabolic need (activity) interfere with that of the other (digestion)? For fishes, the conclusions have been mixed and include; (1) the demand for digestive metabolism is sacrificed for activity costs (Blaikie and Kerr 1996; Furnell 1987), (2) the demand for activity cost is sacrificed for SDA (Alsop and Wood 1997), and (3) swimming cost and SDA are independent (Lucas and Priede 1992). The first scenario is applicable to the crab *Cancer gracilis*, and the toad, *Bufo marinus*, neither of which experienced a significant difference in $\dot{V}O_2$ during activity between fasted and digesting states (Andersen and Wang 2003; McGaw 2007). In contrast, the third scenario fits the lizard *Varanus exanthematicus*, the snake *P. molurus*, and the dog *Canis familiaris* that while digesting a protein meal and exercising, $\dot{V}O_2$ reflects the additive components of fasting exercise $\dot{V}O_2$ and resting postprandial $\dot{V}O_2$ (Anderson and Lusk 1917; Bennett and Hicks 2001; Secor et al. 2000). The capacity to "eat and run" and the potential prioritizing of vascular delivery of oxygen and nutrients between two metabolic demands deserve further study (Hicks and Bennett 2004).

Integrative responses of SDA

As showcased in this review, SDA is generated from a series of integrative physiological processes that results in the digestion and assimilation of a meal. Whereas the vast majority of SDA studies has focused on the metabolic output (e.g., heat production or gas exchange) of the response and the actions of the digestive system, there is growing awareness of the interactions of other supportive organ systems (e.g., pulmonary and cardiovascular) during digestion. The lizard *V. exanthematicus* and the snake *P. molurus* both increase ventilation during digestion as a product of increases in breathing frequency and tidal volume (Hicks et al. 2000; Secor et al. 2000). Because the increases in ventilation do not match the increases in $\dot{V}O_2$, both species hypoventilate during digestion leading to an increase in blood P_{CO_2}, which theoretically serves to buffer the accumulation of HCO_3^- generated from gastric acid production (Wang et al. 2001). These two reptile species also experience postprandial increases in cardiac output due to a more than doubling of heart rate and a doubling of stroke volume for *P. molurus* (Hicks et al. 2000; Secor et al. 2000). Future studies that combine measurements of gas exchange, ventilation, cardiac output, blood flow, and the performance of other tissues will be able to demonstrate the functional integration of postprandial metabolism, organ performance, and homeostasis.

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