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Specific Dynamic Action in Ectothermic Vertebrates: A Review of the Determinants of Postprandial Metabolic Response in Fishes, Amphibians, and Reptiles

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SYNOPSIS

This chapter summarizes current knowledge regarding the postprandial metabolic response in fishes, amphibians, and reptiles. Even though these "lower" vertebrates represent phylogenetically distinct groups, they are all characterized by being ectothermic, which has implications for vitually all aspects of their biology. As some of their morphological, physiological and ecological characteristics are directly influenced by this trait, it is possible to draw broad generalizations for some of these features. An attempt is made here to bring together one such characteristic, the postprandial increase in metabolism (herein referred to as specific dynamic action, SDA). As the nomenclature associated with SDA differs appreciably among studies, an attempt to standardize these diverse nomenclatures comes first. Next the proximate factors that affect the SDA response and its consequences for the energy budget of ecothermic vertebrates are reviewed. Lastly the mechanistic causes of SDA are briefly described.

INTRODUCTION

All animals must eat to match energy expenditure associated with resting metabolism and activities. Procuration and subdual of suitable prey items and their subsequent ingestion and digestion are therefore fundamental for all animals and it seems obvious that a cost-effective digestive system would increase fitness and have been favored through evolution. Given that the demands exerted by digestion have a number of biological consequences, it is not surprising that the mechanisms of feeding and digestion and their physiological implications remain the subject of numerous studies. Hence, for example, digestion exerts profound effects on behavior (e.g. Huey, 1982; Dorcas et al., 1997; Blouin-Demers and Weatherhead, 2001) and triggers rapid and dramatic morphological changes (e.g. Piersma and Lindström, 1997; Starck, 1999a,b; Konarzewski and Starck, 2000; Starck and Beese, 2001). Among the major physiological effects, metabolism increases during digestion. This postprandial increment of metabolic rate, is often referred to as the specific dynamic action of food and abbreviated SDA (e.g. Kleiber, 1961). The processes underlying the SDA response involve mechanical and biochemical degradation along with de novo synthesis. The SDA response is particularly profound in ectothermic vertebrates because of their low basal metabolic rate and because they often ingest meals that are very large compared to their own body mass. Ectothermic animals have accordingly proven convenient for studies on the mechanisms that underlie the SDA response. Nevertheless, even though the metabolic stimulation of food has been studied since the time of Lavoisier, many aspects remain uncertain and there has been considerable controversy about the respective metabolic costs of intestinal growth, protein synthesis, gastric acid secretion, etc. (Secor, 2001, 2003; Starck and Beese, 2001, 2002; Starck et al. 2004). Given that the metabolic costs associated with feeding and digestion are an integral part of organismal function and permeate virtually all aspects of an organism's physiology and ecology, it is important to understand these mechanisms.

SDA accounts for a considerable portion of the energy budget in ectothermic animals. The SDA coefficient, with few upper or lower exceptions, usually accounts for 10% to 20% of the energy obtained from the meal (Jobling, 1981; Pandian, 1987; Secor, 2001). In snakes, two studies have projected the contribution of the postprandial metabolic response to the whole energy budget of free-ranging animals. Secor and Nagy (1994) estimated that 43% and 19% of field metabolic rate of *Crotalus cerastes* and *Masticophis flagellum* respectively is due to the costs associated with SDA during the active season. In the cottonmouth, *Agkistrodon piscivorus*, McCue and Lillywhite (2002) estimated that SDA accounts for almost 40% of the annual energy budget. Considering all the other energy-consuming activities that animals engage in during their life cycle and the "sustained" cost of maintenance of the

physiological systems, the amount of energy allocated for digestion per se is truly amazing. The high cost also stresses the importance SDA may have for the energetic and ecological relationships of ectothermic vertebrates. Perhaps this pattern arises from the "low energy" approach of living typical of ectothermic vertebrates, which allows them to maintain low levels of metabolic activity (Pough, 1983).

A review is given here of the metabolic consequences of feeding in ectothermic vertebrates. Ectothermic vertebrates rely on behavioral adjustments to control their body temperature and their metabolic rates are an order of magnitude lower than that of birds and mammals.

CHARACTERIZATION OF METABOLIC RESPONSE TO FEEDING: SPECIFIC DYNAMIC ACTION

Rubner (1902) coined the German term "spezifisch dynamischer Effekt" to describe the increased metabolism during digestion, which was later somewhat inappropriately translated to "specific dynamic action" (SDA). Originally, SDA only included up to postabsorptive processes while "apparent SDA" included the entire postprandial response (Beamish, 1974). Given the difficulties of separating SDA and apparent SDA, SDA has become the most commonly used term to describe the metabolic increment after feeding. The metabolic response to feeding is commonly measured as the increase in the rate of oxygen consumption, although some studies have also characterized changes in heat production by calorimetry or measured the rate of CO_2 excretion. When only the calorigenic effect is measured, SDA is sometimes referred to as "heat increment" (Kleiber, 1961). While CO_2 excretion is often easier to measure than oxygen uptake, its usage to adequately estimate energy expenditure requires assumptions regarding a respiratory quotient.

As discussed below, the SDA response differs among and within species according to meal size and composition, temperature and other factors. However, in general, the SDA response is characterized by a relatively rapid metabolic increment followed by a slow` sm, the maximal rate of metabolism attained during the SDA, or lastly as the integrated SDA response, which represent the total energetic costs of digestion relative to energetic content of the meal. While each of these expressions may be adequate to characterize a given facet of the SDA response, it should be emphasized that some expression can be misleading. For example, the factorial increase in oxygen uptake can be very large if the preceding fasting is low. In that case, usage of the factorial increase may serve to overemphasize the effects of metabolic stimulation by feeding compared to expressing the maximal rate of oxygen consumption or the integrated SDA response.
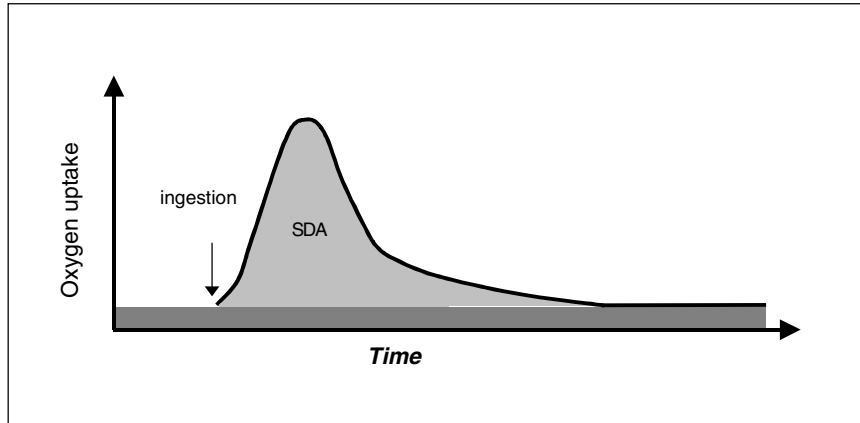
Fig. 12.1. Schematic representation of the metabolic response to feeding and the calculation of the SDA response (SDA — Specific Dynamic Action). Standard metabolic rate is illustrated in dark grey, while the increase in oxygen consumption caused by digestion (SDA) is shown by light grey.

The SDA response may include some of the metabolic costs incurred during the preingestive handling of the meal (foraging, capture, ingestion, mastication, etc.). In *Boa*, constriction and ingestion of the prey are largely anaerobic (Canjani et. al., 2003) and pythons experience a large increase in metabolism after prey constriction even if the prey is not ingested (Secor and Diamond, 1997). Thus, some of the initial cost of digestion, at least in constricting snakes, may include an oxygen debt generated before ingestion (see Cruz-Neto et al., 2001).

FACTORS AFFECTING POSTPRANDIAL METABOLISM

Most studies on the postprandial stimulation of metabolism in fishes, amphibians, and reptiles have merely characterized metabolic rate after feeding, while fewer studies have explicitly focused on the factors that affect and/or determine the SDA response. Furthermore, while some determinants, such as temperature and meal size, have consistent and largely intuitive effects, the actual causes of SDA remain an area with conflicting conclusions and unresolved issues. Within each phylogenetic group, different species are separated to various degrees and present features may, at least in part, reflect historical constraints or persistence of ancestral traits, rather than adaptation toward a present-day situation (Harvey and Pagel, 1993). Aware of this possibility, we adopted a mechanistic/causal approach in this review, rather than an evolutionary historical perspective hindered by lack of data.

What contributes to the cost of digestion? The causal processes for SDA response are complex but can be grouped into 1) catabolic processes, which include enzymatic and mechanical digestion, intestinal transport, peristalsis,

Table 12.1. Definition of the metabolic change during the SDA response

SDA duration	:	The period between ingestion and the return of metabolism to fasting level.
Peak rate	:	Maximal rate of oxygen consumption during SDA.
Time to Peak	:	The period between ingestion and *Peak Rate*.
Factorial Scope during Digestion	:	The relative increase in metabolism during digestion, calculated as *Peak Rate* divided by *Fasting Rate*.
Mean SDA Rate	:	The mean rate measured over the duration of the SDA.
SDA Total Cost	:	The total energy expended during the SDA.
SDA Net Cost	:	The *SDA Total Cost* discounted for maintenance cost (usually estimated from the *Fasting Rate*).
Meal Energy Content	:	The caloric content of the meal.
Assimilation Efficiency	:	The amount of energy that is assimilated from the meal (usually expressed in relative terms).
Energy Assimilated from the Meal	:	The energy actually assimilated from the ingested meal. Calculated from the *Meal Energy Content* and the *Assimilation Efficiency*.
SDA coefficient	:	The *SDA Net Cost* expressed relative to *Energy Assimilated from the Meal*. If assimilation efficiency is not determined, the SDA coefficient can be calculated relative to *Meal Energy Content*.
Fasting rate	:	The rate of the parameter examined (O_2 uptake, heat production, etc.) of post-absorptive animals. Ideally, this should be measured in animals fasting sufficiently long to avoid influence from a previous meal. Fasting animals should, nevertheless, be healthy and in good condition.
Meal Energy Content	:	The caloric content of meal.

absorption and nutrient storage, and 2) anabolic processes, including the costs of amino acid deamination, synthesis of excretory products, increased synthesis and deposition of proteins (Jobling, 1981, 1983; Peck, 1998; Peck and Veal, 2001; McCue et al., 2005).

Meal Size Effects

Meal mass is probably the singlemost influential determinant of the SDA response. In general, increased meal size is accompanied by a proportional rise in SDA response, which is manifested as higher maximal rates of oxygen consumption and larger factorial increments. Increased meal size also prolongs SDA response and maximal rates of oxygen consumption tend to occur later with larger meals. These effects of meal size are well characterized in fishes (e.g. Beamish, 1974; Jobling and Davies, 1980; Soofiani and Hawkins, 1982; Billerbeck et al., 2000). For example, the SDA scope of the SDA increases linearly with meal size in juvenile cod and the Atlantic silverside (*Gadus morhua* and *Menidia menidia* respectively; Soofiani and Hawkins, 1982;

Billerbeck et al., 2000), while the duration of the SDA curve increases linearly with meal size in largemouth bass (*Micropterus salmoides*; Beamish, 1974).

An increased SDA response with elevated meal size has also been documented in reptiles and some amphibians (e.g. Andrade et al., 1997; Secor and Diamond, 1997; Secor and Faulkner, 2002). In snakes, able to ingest very large prey, there seems to be no plateau for the metabolic response to feeding in response to meal size increment. For example, in pythons, boas, and rattlesnakes fed a broad range of meal mass, the pattern of metabolic change during digestion was always characterized by an initial rapid increase that peaked 1 or 2 days after meal ingestion, followed by the slower return to fasting metabolism level in the course of days (e.g. Andrade et al., 1997; Secor and Diamond, 1997; McCue and Lillywhite, 2002; Toledo et al., 2003). Maximal O_2 uptake increased progressively with meal mass and in an extreme case of *Python* ingesting 100% of its own body mass (Secor and Diamond, 1995), has been reported to increase 44 times above fasting levels. Smaller, yet still impressive factorial increments between 5-to 15-fold are more commonly reported (Andrade et al., 1997; Secor, 2001; McCue and Lillywhite, 2002). As in fishes, the peak in the postprandial metabolic response is delayed as meal size increases, which together with the prolonged SDA response, may, at least in part, reflect the fact that snakes ingest their prey without mastication.

As would seem intuitive the costs associated with digestion increase with meal size, but because the energetic content of the food also increases proportionally, the SDA coefficient of pythons, boas, and rattlesnakes tends to be rather unaffected by meal size (e.g Andrade et al., 1997; Secor and Diamond, 1997; Toledo et al., 2003). However, in some species, such as the cottonmouth, the SDA coefficient increases with meal size indicating that large meals are proportionally more energetically expensive to digest (McCue and Lillywhite, 2002). In fishes, the effects of meal size on the SDA coefficient are more variable and somewhat controversial. It has been argued that meal size and the SDA coefficient are inversely related in Antarctic fishes (Peck, 1998). For example, in the Antarctic plunderfish, *Harpagifer antarcticus*, the SDA coefficient varied from 9 to 55% as meal size decreased (Boyce and Clarke, 1997). On the other hand, Soofiani and Hawkins (1982) and Billerbeck et al. (2000) found that the SDA coefficient increased with meal size in cods and the Atlantic silverside (*Gadus morhua* and *Menidia menidia* respectively). Finally, there was no effect of meal size on the SDA coefficient in largemouth bass, *Micropterus salmoides* (Beamish, 1974). It is possible that these differences reflect variation in feeding ecology, different functional and/or physiological constraints or adaptations to specific environments. However, how these factors interact to affect the costs of digestion remains an open question for future studies.

Composition of Diet

Secor and Phillips (1997) compared the SDA of *Varanus albigularis* fed young rats, hard-boiled eggs, ground turkey, and snail mixture. Peak $\dot{V}O_2$ and the integrated SDA response was largest with turkey, snail or rat compared to hard-boiled eggs, but when the SDA response was expressed relative to caloric content of the meal, there were no differences among meal types (Secor and Phillips, 1997). For sharks, Ferry-Graham and Gibb (2001) attributed differences in SDA response between squid and fish diets (Sims and Davies, 1994) to differences in caloric content.

The finding that the SDA response increases proportional to energy content is consistent with the increased SDA response with meal size of a given food item. However, to establish whether some components of the food elicits larger metabolic effects than others, several older and recent studies have manipulated food composition or have given artificial diets (amino acids solutions, gelatine peptone, or others). Early studies on reptiles showed that protein-rich meals elicit larger metabolic changes than diets composed of fat or carbohydrates (e.g. Benedict, 1932) and these findings were later verified. Thus, force-feeding snakes with fat elicits almost no metabolic response (Benedict, 1932; McCue et al., 2005); there are some indications that the SDA response is affected by the amount of fat in the diet in the salt water crocodile, *Crocodylus porosus* (Garnett, 1988). Carbohydrates, in general, fail to stimulate metabolism. Coulson and Hernandez (1983) force-fed alligators with vegetable proteins and noticed that it would appear virtually unchanged in the feces after a few days, indicating that alligators are incapable of digesting this material. Using a stomach tube, they also infused ground rice, wheat flour, corn meal, and potato flour and subsequently followed the changes in carbohydrate levels in plasma. Glucose was the only carbohydrate that was elevated after feeding and it was concluded that crocodilians, as true carnivores with no requirement for dietary carbohydrate, are unable to digest polysaccharides.

In the turtle *Kinixys spekii*, Hailey (1998) found that the cost of digestion varied with diet from 16%, 21%, and 30% of the absorbed energy when fed on fungi, leaves, and millipedes respectively. When expressed relative to protein content, the costs of digestion were strikingly similar (Hailey, 1998). In fishes, the SDA response and its duration also increased with elevated protein content in the diet (Jobling and Davies, 1980; Somanath et al., 2000).

There is ample evidence in ectothermic vertebrates that anabolic processes, and in particular protein metabolism, constitute a dominating factor in SDA response (Ashworth, 1969; Coulson and Hernandez, 1979). In alligators and catfishes, amino acid levels are increased shortly after feeding (Herbert and Coulson, 1976; Brown and Cameron, 1991a) and, if fasting animals are infused with a mixture of amino acids, metabolism will increase to levels comparable to those observed in fed individuals (Coulson and Hernandez,

1979; Brown and Cameron, 1991b). In catfish, it has even been shown that inhibition of protein synthesis completely abolishes the metabolic response to feeding (Brown and Cameron, 1991a,b; see also McCue et al., 2005 for similar data in snakes).

The metabolic and energetic implications of intraspecific differences in food types clearly need more investigation since widespread dietary variation occurs in natural populations and ontogenetically. Species that are omnivorous and generalists may offer suitable models to explore the effects of food type on the postprandial response by characterizing the effects of prey items that differ in composition or digestibility. The effect of prey composition and energetic content on energetic return is an ecologically important relationship and should be taken into account when assessing energy flux from prey to predators. The many facets included in this simple question could be explored in future studies using the natural variation in diet, determined by geographical differences or ontogenetic changes.

Effects of Venom

Many snakes use venom to kill the prey and since the venom often contains digestive enzymes, it has been speculated that the venom may aid degradation of the prey and reduce the ensuing costs of digestion. The effects are largely unexplored, however. Thomas and Pough (1979) observed that digestion in some species of snakes was accelerated if the prey were envenomated. Rodriguez-Robles and Thomas (1992) likewise showed that the venom of the Puerto Rican racer, *Alsophis portoricensis*, also accelerated digestion. M. McCue and S. P. Brito (unpubl. data), working independently, recently showed that envenomation increased the postprandial peak in metabolism, while both duration and the SDA coefficient reduced. This response holds for species possessing proteolytic and miotoxic venom and is more pronounced at low temperatures (M. McCue and S. P. Brito, unpubl. data). Clearly, the physiological and biochemical reasons for these effects deserve to be studied in more detail.

Scaling Effects

Body mass affects metabolic rate and although this scaling effect has long been known and demonstrated to be universal, it remains one of the complex issues in comparative physiology (e.g. Somero, and Childress, 1980; Heusner, 1982; Withers, 1992; Coulson, 1997; Gillooly et al., 2001). In ectotherms, metabolism normally scales by the 0.8 power of body mass (Hemmingsen, 1969; Gillooly et al., 2001), but there are considerable differences (e.g. Thompson and Withers, 1994; Chappell and Ellis, 1987). The scaling effects persist when metabolic rate is increased during exercise or digestion but the scaling exponents may be state dependent. In Burmese pythons, for example, SMR scaled with a power of 0.68, while maximal oxygen uptake during digestion scaled with a power of 0.9 (Secor and

Diamond, 1997). Also, in sharks (*Cephaloscyllum ventriosum*), there is a tendency toward higher maximal rates of oxygen consumption during digestion in large vs small individuals (Ferry-Graham and Gibb, 2001) and a similar pattern was observed in largemouth bass (Beamish, 1974). However, body mass did not affect maximal rates of oxygen consumption during SDA response in dogfish or Antarctic plunderfish, although the SDA responses were prolonged in large animals (Sims and Davies, 1994; Boyce and Clarke, 1997). In turtles and the Atlantic silverside, the duration of SDA response decreased with body mass (Sievert et al., 1988; Billerbeck et al., 2000).

Although body mass often affects the timing and metabolic profile of the SDA response, the SDA coefficient is generally independent of body mass. This has been shown over a very large range of body mass in pythons (Secor and Diamond, 1997), toads (Secor and Faulkner, 2002), and several species of fish (Beamish, 1974; Boyce and Clark, 1997; Billerbeck et al., 2000). In the rattlesnake (*Crotalus horridus*), however, the SDA coefficient appears to increase with body mass (Zaidan and Beaupre, 2003). This would mean that large snakes spend more energy on the digestion of a given prey than smaller snakes. The biological and physiological reasons for this pattern were not studied. Nevertheless, in general, the energetic costs associated with digestion are independent of body mass. As discussed earlier in this section, mass specific metabolic rate is smaller in large compared to small animals. Therefore, if the absolute change in metabolism associated with digestion of a given absolute meal size is independent of body mass, large animals would be expected to have a larger factorial increase in postprandial metabolism. This may also explain why maximal rates of postprandial oxygen consumption scaled with a higher component than resting metabolic rate, although kinetic factors may have to be considered. A similar reasoning has been used to explain the differences in scaling factors between rest and exercise metabolism in amphibians and reptiles (Garland, 1984; Pough and Andrews, 1984; Garland and Else, 1987; Gatten et al., 1992).

Feeding Frequency Effects

Many vertebrates experience long fasting periods that can be caused by seasonal fluctuations in food abundance or by rare encounter with suitable prey. Seasonal fluctuation in food abundance is well known in temperate areas where many endothermic and ectothermic vertebrates survive the cold periods in dormancy without eating for many months (e.g. Carey, 1993; McWilliams and Karasov, 2001; Hume et al., 2002). In tropical areas, seasonal variations in prey abundance are often linked with rainfall and many vertebrates enter aestivation during dry periods in which they fast until rainfall resumes. Many tropical and subtropical reptiles, especially larger snakes, appear to undergo long periods of fasting that last for many months even in the absence of seasonal variations (Greene, 1997; Shine et al., 1998). In snakes, the long fasting periods are partially compensated by an impressive

ability to ingest very large meals. Digestion of large meals after a long fasting period exerts considerable demands on the flexibility of the gastro-intestinal function.

The gastrointestinal (GI) organs are normally considered metabolically very active and it is generally believed that these organs contribute significantly to resting metabolism. Thus it seems advantageous to reduce the energetic costs of maintaining the GI organs during fasting periods, as long as it is possible to regain their digestive functions immediately after ingestion of prey. A number of recent studies on snakes have documented large and very rapid changes in intestinal mass and brush border transport rates after feeding (e.g. Secor and Diamond, 1995, 1998, 2000; Starck and Beese, 2001, 2002). The phenotypic flexibility of the GI system of snakes provides an interesting example of adaptation to an intermittent feeding regime (Piersma and Lindström, 1997; Secor and Diamond, 1998).

Given the large structural and functional changes in GI morphology that occur soon after ingestion, it was logical to propose that this growth accounts for a large portion of the SDA response (e.g. Secor and Diamond, 1995, 1997). To investigate this possibility, Secor and Diamond (2000) compared metabolic and morphological changes during the postprandial period of four frequently feeding species of snakes with four species that feed infrequently. They concluded that infrequent feeders digest slower but have a more pronounced metabolic response, which reflects the larger functional and morphological gastrointestinal changes. Thus it was concluded that the relatively high SDA coefficient of infrequently feeding species reflects energetic costs associated with rebuilding form and function. However, other digestive processes, such as secretion, production of enzymes and acid, and up-regulation of brush-border transporters could also contribute (see also Secor, 2003).

To test the contribution of intestinal remodeling in pythons, Overgaard et al. (2002) studied the effects of the previous fasting duration on SDA response. Upon feeding, intestinal mass and function remain elevated for many days. Thus, if intestinal remodeling is energetically expensive, then a second meal, ingested while intestinal function is still elevated, should elicit a smaller SDA response. Overgaard et al. (2002) showed that the SDA coefficient does not change with a fasting duration between 60 to 3 days, and it was concluded that intestinal growth does not constitute a major contributor to SDA response. In a similar experiment, Iglesias et al. (2003) found that the SDA coefficient of the skink, *Eulamprus quoyii*, feeding frequently (8.8%) did not differ from that of lizards fed with the same amount of food infrequently (9.4%). These findings are consistent with the proposal that intestinal expansion is structurally simple and energetically cheap (Starck and Beese, 2001). Indeed, Secor (2003) estimated that gastrointestinal up-regulation contributes with only 5% of python SDA overall cost. On the other hand, the production of HCl (and enzymes) and protein synthesis were the processes that responded

for the largest portion of the postprandial metabolic response of pythons (55% and 26% respectively; Secor, 2003). A small contribution of intestinal growth was also suggested for turtles (Hailey, 1998).

Ideally, size changes in GI organs should be measured concomitant with metabolic rate to test for the existence of a causal relationship between morphological change and energetic expenditure. Isolated evaluation of the metabolic changes experienced by the different tissues/organs involved in digestion is also a promising approach.

Temperature Effects

Temperature affects virtually all physiological processes of ectothermic vertebrates and the postprandial metabolic response is no exception. Many studies have addressed behavioral selection of higher body temperatures during digestion, i.e., "the postprandial thermophilic response", but there continues to be considerable controversy about the magnitude and functional importance of this response (e.g. Huey 1982; Dorcas et al. 1997; Sievert and Andreadis 1999; Peterson et al., 1993; Regal 1966; McGinnis and Moore 1969; Touzeau and Sievert, 1993; Witters and Sievert, 2001). This may, at least in part, reflect that some studies have investigated relatively few animals and that laboratory studies may yield results that differ from studies in natural settings. For example, the colubrid snake, *Elaphe obsolete*, exhibited a postprandial thermophilic response in laboratory but not in the field (Blouin-Demers and Weatherhead, 2001). Nevertheless, as documented in many other species of ectothermic vertebrates, body temperature is less variable during digestion of free-ranging *Elaphe* (see also Dorcas et al., 1997). This is accomplished through altered behavior as digesting *Elaphe* were more likely to be found at the edges rather than within the forest compared to fasting individuals (Blouin-Demers and Weatherhead, 2001). Thus, due to complex interactions with the environment, more field studies are highly desirable.

There are plenty of reports regarding upper and lower limits outside which animals are unable to complete digestion (Dorcas et al., 1997; Du et al., 2000; Wang et al., 2003). The ultimate consequences of failure to attain adequate body temperatures during digestion include regurgitation and/or death. On the other hand, the benefits in selecting warmer temperatures during digestion include an elevated rate of digestion and/or enhanced efficiency of digestion (Stevenson et al., 1985; Lillywhite, 1987; Hailey and Davies, 1987; Reinert, 1993; Sievert and Andreadis, 1999; Wang et al., 2003). An optimal rate of digestion has been modeled as the ratio between enzyme breakdown and rate of intestinal absorption (Logan et al., 2002). In accordance with this model, the rate of gastrointestinal motility, secretion, and absorption increase with elevated temperature (e.g. Dandrifosse, 1974; Skoczylas, 1978; Stevenson et al., 1985; Lillywhite, 1987; Hailey and Davies, 1987; Reinert, 1993; Sievert and Andreadis, 1999; Wang et al., 2003) and some digestive enzymes have maximal activity at rather high temperatures

in lizards (Licht, 1964). As examples of the direct effects of temperature, gut motility increases with temperature in vivo in the lizards *Varanus* and *Ctenosaura* (Mackay, 1968) as well as in *Caiman* (Diefenbach, 1975a). Also, secretion rate of gastric acid increases with temperature in *Caiman* (Diefenbach, 1975a,b) and similar effects have been documented in the snake *Natrix*, which also increase the secretion of digestive enzymes at high temperatures (Skoczylas, 1970a,b). Temperature effects on the dynamics of intestinal transporters have not been investigated.

In almost all studies to date, elevated temperature led to shortening of SDA response while the maximal rates of oxygen consumption were higher (Hailey and Davies, 1987; Wang et al., 2003; Toledo et al., 2003). However, in the plaice (*Pleuronectes platessa*), maximal oxygen consumption following a meal does not change with temperature (Jobling and Davies, 1980). As the higher rate of oxygen consumption is balanced by a shorter duration of SDA response, the energy expenditure associated with digestion, the SDA coefficient, does not change markedly with temperature (Wang et al., 2003). Thus, in *Python* the SDA coefficient was virtually unaffected between 20 and 35ºC (Wang et al., 2003) while it decreased somewhat when temperature was increased from 25 to 30ºC in *Boa* (Toledo et al., 2003). On the other hand, Powell et al. (1999) noted a trend toward increasing SDA coefficient with higher body temperatures in the horned frog, *Ceratophrys cranwelli*. In the Atlantic silverside, *Menidia menidia,* Billerbeck et al. (2000) found that the fish spent 23% more energy when digesting at 28ºC vs 17ºC.

The postprandial peak in metabolism and its magnitude are usually delayed at low temperatures (Hailey and Davies, 1987; Wang et al., 2003; Toledo et al., 2003). However, as prefeeding metabolism is also affected by temperature, the SDA factorial scope is, in general, not affected by temperature (Jobling and Davies, 1980; Toledo et al., 2003). However, if the metabolic machinery is working close to maximal capacity, the factorial scope may be reduced. For example, in *Boa* the factorial scope was temperature independent during digestion of small meals while the metabolic increment following large meals was larger at 25ºC vs to 30ºC (Toledo et al., 2003). This may indicate that metabolic demand imposed by the digestion of exceedingly large meals (40%) in combination with elevated body temperature (30ºC) approached the maximal oxygen transport capacity of the *Boa´*s cardiorespiratory system (Toledo et al., 2003).

Animals that ingest large meals, such as many snakes, may have their locomotor and defensive abilities temporarily impaired during digestion (Garland and Arnold, 1983; Ford and Shuttlesworth, 1986). In that case, a faster digestion at elevated temperature may serve to reduce predation risks and allow for better mobility (Pauly and Benard, 2002). In addition, a faster rate of digestion may enable larger food intake, which would enhance body condition, facilitate growth and, possibly, increase fitness (e.g. Du et al., 2000).

INTERACTION OF SDA AND OTHER METABOLICALLY DEMANDING ACTIVITIES

Under natural conditions, animals often need to perform multiple tasks at the same time. When the metabolic demands arising from different activities, such as exercise, digestion, and thermoregulation, occur simultaneously, it may be important to exert priorities so that one activity can be emphasized at the expense of an other activity. However, in some cases the demands placed by the concurrent activities may be additive so that both tasks can be performed simultaneously.

Digestion and exercise are likely to occur at the same time. Jobling (1981) observed that maximal oxygen uptake during swimming was greater in post-prandial fish than in fasting animals and that the difference increased with meal size. He therefore suggested that postprandial metabolism is limited by cellular metabolism rather than the capacity of the cardiorespiratory system to transport oxygen. Nevertheless, this may not be a general pattern as some species of fish do not exhibit this additive effect between exercise and digestion and other fishes appear to attain maximal rates of oxygen consumption even after small meals (Vahl and Davenport, 1979; Boyce and Clarke, 1997). In the largemouth bass, *Micropterus salmoides*, exercise did not affect the SDA coefficient or SDA duration in fishes forced to swim at 1.4 to 2.5 BL^{s-1} after eating 4% of their body mass (Beamish, 1974). In toads, maximal oxygen uptake was not affected by digestive state (Andersen and Wang, 2003). The interaction between exercise and digestion has also been studied in pythons and varanid lizards (Secor et al., 2000; Bennett and Hicks, 2001). In both species the metabolic response to exercise and digestion were virtually additive so that maximal metabolic rates during exercise were larger for post-prandial animals than for fasting animals. Interestingly, when digesting pythons exercised there was a marked increase in total ventilation but not in cardiac output. In V*aranus*, however, total ventilation during exercise was not significantly affected by digestion. The additivity of the responses also indicates that the cardiorespiratory system is unlikely to constrain metabolic rate during exercise of fasting lizards or snakes. It is possible that oxygen diffusion and/or aerobic capacity of muscles are the limiting factors (see Secor et al., 2000). Although the examples from pythons and *Varanus* may suggest that metabolic demand associated to SDA and exercise always occurs additively, it is possible that other proximal factors, e.g. prey size, temperature, may affect this interaction. In the colubrid snake *Natrix maura*, there is an indication that exercise and digestive metabolic demands are not additive (Hailey and Davies, 1987). Finally, the interaction between SDA and other metabolic demands may vary according to the nature of these other demands and/or with SDA duration and magnitude. For example, in tegu lizards, *Tupinambis merianae*, which exhibit a marked cycle of circadian variation in metabolism, the interaction between the metabolic demands

arisen from this circadian changes with that arisen from meal digestion was found to vary as a function of digestion duration. On the two immediate days following feeding, priority was given to digestion and circadian changes in metabolism were abolished. On the third and subsequent days postprandial, the metabolic demands were clearly added to each other and circadian changes in metabolism were resumed. This response seems to be a regulated response of the animal, which becomes less active after food ingestion, rather than an inability of the respiratory system to support simultaneous demands at the first two days (W. Klein, unpublished data).

The conceptual framework proposed by Bennett and Hicks (2001) to describe the interaction of conflicting metabolic demands includes the two most probable modes in which such interaction may occur in ectotherm vertebrates, i. e. priorization and additivity. Nonetheless, an alternative not considered by Bennett and Hicks (2001), and usually not considered for ectotherms, is "substitution", meaning that the heat generated by one activity is transferred to another. The classical example would be use of SDA or exercise heat for thermoregulation by endotherms that might prevent the use of extra energy for this purpose (Costa and Kooyman, 1984). For ectotherms, it is generally assumed that the heat generated during digestion is insufficient for thermal regulation (Hailey and Davies, 1987), However, increased body temperature speeds digestion and may result in ecological and energetic benefits. Is it possible that metabolically derived heat during SDA bears the same effects on the digestive process as those caused by postprandial thermophilic response? In a recent study, Tattersall et al. (2004) documented a significant increase in body temperature in the South American rattlesnake, *Crotalus durissus*, due to thermogenesis. They also found that heat generation during rattlesnake digestion was meal size dependent, and that the amount of heat generated may be ecologically relevant for improvement of the snake´s digestion (see also Benedict, 1932; Van Mierop and Barnard, 1976; Marcellini and Peters, 1982). Bennett et al. (2000) found that metabolic rate of *Varanus* increased three-four times during the digestive process but that body temperature increased less than 1ºC.

Since many activities other than exercise take place while the animals are digesting (pregnancy, thermoregulation, etc.), there is a clear need to study these interactions and interprets their consequences in an ecologically relevant context.

CONCLUDING REMARKS

Considerable advances have been made in recent years regarding the physiological, morphological, and endocrine consequences of feeding in ectothermic vertebrates (Busk et al., 2000; Holmberg et al., 2003; Wang et al., 2001a, b; Overgaard and Wang, 2002; Starck and Beese, 2001, 2002; Conlon et al.,

1997a, b; White et al., 1999; Secor et al., 2000, 2001). However, it seems that further investigations of the metabolic and energetic consequences would be interesting. Many aspects regarding the metabolic consequences of feeding are relatively well known for fishes but very little information is available for amphibians (e.g. Wang et al., 1995; Powell et. al., 1999; Busk et al., 2000). Within reptiles, most attention has been placed on snakes to the neglect of other groups. Matrix filling experiments would thus be very welcome to facilitate correlations of SDA responses with habitats, feeding habits, and taxonomic/phylogenetic groupings. At a more mechanistic level, it is desirable to investigate neural and humoral control mechanisms underlying activation of the postprandial metabolic response.

Acknowledgments

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