

Eat and run: prioritization of oxygen delivery during elevated metabolic states

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Abstract

The principal function of the cardiopulmonary system is the matching of oxygen and carbon dioxide transport to the metabolic requirements of different tissues. Increased oxygen demands (\dot{V}_{O_2}), for example during physical activity, result in a rapid compensatory increase in cardiac output and redistribution of blood flow to the appropriate skeletal muscles. These cardiovascular changes are matched by suitable ventilatory increments. This matching of cardiopulmonary performance and metabolism during activity has been demonstrated in a number of different taxa, and is universal among vertebrates. In some animals, large increments in aerobic metabolism may also be associated with physiological states other than activity. In particular, \dot{V}_{O_2} may increase following feeding due to the energy requiring processes associated with prey handling, digestion and ensuing protein synthesis. This large increase in \dot{V}_{O_2} is termed “specific dynamic action” (SDA). In reptiles, the increase in \dot{V}_{O_2} during SDA may be 3–40-fold above resting values, peaking 24–36 h following ingestion, and remaining elevated for up to 7 days. In addition to the increased metabolic demands, digestion is associated with secretion of H^+ into the stomach, resulting in a large metabolic alkalosis (alkaline tide) and a near doubling in plasma $[HCO_3^-]$. During digestion then, the cardiopulmonary system must meet the simultaneous challenges of an elevated oxygen demand and a pronounced metabolic alkalosis. This paper will compare and contrast the patterns of cardiopulmonary response to similar metabolic increments in these different physiological states (exercise and/or digestion) in a variety of reptiles, including the Burmese python, *Python morulus*, savannah monitor lizard, *Varanus exanthematicus*, and American alligator *Alligator mississippiensis*.

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1. Introduction

Increased metabolic demand in different regions of the body quickly results in a compensatory increase in cardiac output, redistribution of blood flow to the appropriate tissues, and suitable ventilatory increments. These increments and their physiological basis have

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been particularly well investigated during exercise, and the matching of cardiopulmonary performance and metabolism during activity may be universal among vertebrates (see Jones, 1994 for reviews). However, there are other situations besides physical activity in which the increase in the metabolic demands from multiple organs and tissues may approach or even exceed the O_2 transport capacity of the cardiopulmonary system. These may also pose additional physiological challenges unrelated to O_2 transport, and sometimes they may occur simultaneously with activity. Under the latter conditions, understanding the integrative processes of prioritization during conflicting physiological stresses remains an important challenge in physiology (Jackson, 1987).

In carnivorous reptiles, large increments in aerobic metabolism are associated with physiological states other than activity. In particular, $\dot{V}O_2$ increases following feeding due to the energy requiring processes associated with prey handling, digestion and the ensuing protein synthesis (Andrade et al., 1997; Benedict, 1932; Cruz-Neto et al., 2001; Houlihan, 1991; Overgaard et al., 2002; Secor and Diamond, 1995, 1997a,b; Wang et al., 2002). This large increase in $\dot{V}O_2$ is referred to as “specific dynamic action” (SDA) (Rubner, 1902). In terms of relative metabolic rates, SDA is far more pronounced in ectothermic vertebrates than in endothermic birds and mammals because of the substantially greater maintenance metabolic costs of the latter. The increase in $\dot{V}O_2$ during SDA in some reptiles may resemble or even exceed that during physical activity. For example, in the Burmese python, *Python molurus*,

Table 1

Similarities and differences of two elevated metabolic states: physical activity vs. digestion

	Physical activity	Digestion
Metabolic increment	5–10 × resting	Graded (meal size dependent)
Site of metabolic activity	Skeletal muscle	Gastrointestinal
Metabolic pattern	Catabolism	Anabolism
Acid–base disturbance	Acidosis	Alkalosis
Activating system	Somatic motor and sympathetic	Parasympathetic NS
Activation time	1–5 min	Hours to days

$\dot{V}O_2$ reaches $8 \text{ ml kg}^{-1} \text{ min}^{-1}$, 32 h postfeeding, which is equivalent to the values measured while crawling at 0.4 km h^{-1} (Secor et al., 2000) (Fig. 1). Furthermore, in contrast to the relatively short duration (minutes) of physical activity in this animal, the elevated metabolic rates during SDA are sustained for several days (Secor and Diamond, 1997a,b) (Fig. 1).

Thus, in certain animals, both activity and digestion can result in metabolic rates five or more times above resting levels and require similar levels of O_2 consumption and carbon dioxide excretion. This equivalence in gas exchange during these two physiological conditions might suggest that similar patterns of cardiopulmonary response would be appropriate for both hypermetabolic states. However, other aspects of these metabolic states differ profoundly (Table 1). Skeletal muscle activity is catabolic and acidotic and is regulated by an increase sympathetic tone. Digestion may involve considerable synthesis and is thus primarily an

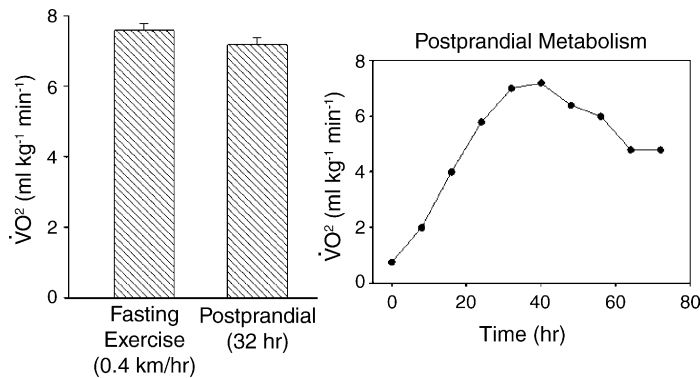


Fig. 1. Oxygen consumption during maximal activity and 32 h postfeeding in the python (mean \pm 1 S.E.). Note: maximal activity is sustained for only several minutes, in contrast to postprandial $\dot{V}O_2$, which is sustained for days (right panel). Redrawn from Secor et al. (2000).

anabolic process. The secretion of large quantities of protons into the stomach results in profound “alkaline tides” in the blood, and the entire digestion process is largely controlled by the parasympathetic nervous system. Further, the time course of the activity response involves much more rapid activation, achieving maximal levels within 1–2 min and its duration is only several minutes to an hour. Maximal metabolic rates during digestion by contrast do not occur until 1–2 days after ingestion and may be profoundly elevated for a week (Secor and Diamond, 1998; Wang et al., 2001a).

The cardiopulmonary response to similar metabolic demands during these different physiological states could be either *stereotyped* or *flexible*. In the former case, equal metabolic increments (e.g., ml O₂ or J) in either the skeletal muscle or the gastrointestinal track would elicit an equal increment in the cardiac response (heart rate and stroke volume, with appropriate redistribution of blood flow) and ventilatory response (breathing frequency and tidal volume), regardless of the physiological state generating the demand. In the latter case, the cardiopulmonary system might have a variety of state-dependent and -appropriate responses that result in the same level of gas exchange. In such a flexible system, the convective components (either cardiac output or lung ventilation) might be markedly state-dependent, appropriate to matching more subtle regulatory factors other than simple energetic demands.

Here we review what is known about the patterns of gas exchange, ventilation and systemic blood flow following voluntarily feeding and treadmill exercise in several reptiles, including the monitor lizard, *Varanus exanthematicus*, the Burmese python, *Python morulus*, and the American alligator, *Alligator mississippiensis*. In addition, we compare the patterns of these cardiopulmonary responses to treadmill exercise in both fasted and fed animals.

2. Postprandial metabolic response: specific dynamic action

It has been known for over 200 years (Lavoisier and Laplace, 1780) that metabolic rate increases after feeding. The first quantitative investigations of this phenomenon were undertaken by Rubner (1902), who termed the relationship the specific dynamic action (or effect) of feeding (SDA). SDA is expressed either as

excess (above resting levels) energy expenditure during digestion or as the ratio of this value to total energy in the meal. In addition, the factorial metabolic increment, the ratio of peak to preingestion metabolic rate, is also frequently measured. SDA is very dependent on food composition, being approximately 30% for protein, 13% for fat, and 10% for carbohydrate (Rubner, 1902; Brody, 1945; Secor et al., 1994; Secor and Diamond, 1997a,b). Thus, in particular, protein requires a major energetic investment prior to acquisition of energy within the food consumed (designated “pay before pumping” by Secor and Diamond, 1995).

The largest postprandial metabolic increments have been found in carnivorous reptiles. Benedict (1932) and, more recently and thoroughly, Secor and Diamond and their coworkers have undertaken an extensive series of investigations on the topic in several reptiles, principally in snakes. They have found that the impact on reptilian energetics is very large for two reasons, enormous protein-rich meals and low resting metabolic rates. Many large carnivorous reptiles naturally eat very rarely, sometimes only once a month or less (Secor et al., 1994; Secor and Diamond, 1995). They tolerate long periods of fasting, exceeding one year in large individuals (Benedict, 1932; Secor et al., 1994). During this time, intestinal tissue regresses, curtailing maintenance costs (Secor and Diamond, 1997a,b). These animals are then capable of consuming enormous meals, which are primarily protein, generating a very high SDA. The magnitude of the postingestion metabolic increment is directly proportional to meal size (Preest, 1991; Hicks et al., 2000; Secor and Diamond, 1997a; Secor and Phillips, 1997). Peak levels of gas exchange during digestion in reptiles are greater than four-fold preingestion levels (Benedict, 1932; Busk et al., 2000b; Coulson and Hernandez, 1983; Overgaard et al., 2002; Secor and Diamond, 1995; Secor and Phillips, 1997; Secor et al., 1994; Wang et al., 2001a) with a maximal reported value of 44 times fasting metabolic rate (Secor and Diamond, 1997b). The levels of O₂ consumption attained during digestion can equal or exceed maximal rates achieved during strenuous physical activity (Preest, 1991; Secor and Diamond, 1997b; Secor et al., 1994, 2000). Thus, in reptiles, digestion can make demands on gas transport capacities equivalent to those of intense exercise, with the metabolic impact of digestion being greatly extended in comparison to that of activity.

The mechanisms responsible for the pronounced metabolic response in reptiles remain elusive, but three plausible mechanisms have been proposed. First, Secor and Diamond (1998) suggest that a significant portion of the metabolic increment results from the postprandial increase in organ mass and function, specifically intestinal mass and up-regulation of brush-border protein transport capacity. However, recent studies indicate that simple swelling of the enterocytes, a process with low energetic cost, may account for the increase observed in intestinal mass in *Python* (Starck and Beese, 2001). Alternatively, the active pumping of hydrogen ions into the stomach during the postprandial period, is suggested to account for up to 50% of the SDA in *Python* (Secor, 2003). However, recent studies in *Boa constrictor* found that the magnitude of SDA (both postprandial peak in \dot{V}_{O_2} and total duration of the SDA) was not reduced following infusion of omeprazole (a proton pump inhibitor) (Andrade et al., 2004). Finally, several studies have suggested that following the ingestion of a meal, largely composed of protein, a resulting increase in protein synthesis accounts for the majority of the postprandial metabolic response (Brown and Cameron, 1991a,b; Coulson and Hernandez, 1979; Houlihan, 1991; McCue et al., in press).

3. Postprandial alkaline tide

Following the ingestion of a large meal, H^+ is actively pumped into the stomach lumen. Hydrogen ions are generated within the parietal cells from dissociation of water, and the resulting hydroxyl ions combine with carbon dioxide to form bicarbonate ion. The resulting bicarbonate is transported out of the basolateral membrane in exchange for chloride. Consequently, bicarbonate concentration within the blood increases following the ingestion of a meal, an increase referred to as the “alkaline tide”.

The magnitude of the alkaline tide has been measured in a variety of species of reptiles (snakes, lizards and crocodylians) (Busk et al., 2000a,b; Hartzler et al., 2003; Overgaard et al., 1999; Wang et al., 2001a). Despite the phylogenetic distance between these species, all exhibit similar patterns in the magnitude and duration of the alkaline tide following ingestion of similar size meals. Plasma HCO_3^- concentration increases

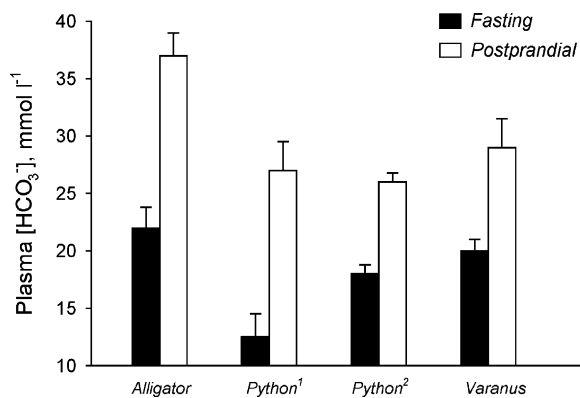


Fig. 2. Plasma bicarbonate ($[HCO_3^-]$) concentrations in the American alligator (Coulson et al., 1950), Burmese python¹ (Secor and Diamond, 1995), Burmese python² (Overgaard et al., 1999) and Savanah monitor lizard, *Varanus* (Hartzler et al., 2003), during fasting and 24–30 h after ingesting a meal.

within 6–12 h, reaches a maximum at 24–48 h following ingestion and remains elevated above fasting levels for up to 7 days. The increase in plasma HCO_3^- concentration range from 5 to 20 $mmol\ l^{-1}$ above fasting values, but rarely increases by more than 20 $mmol\ l^{-1}$ (Fig. 2).

4. Cardiopulmonary response during SDA

The postprandial period presents two, rather conflicting, physiological challenges to the cardiopulmonary system in reptiles. The elevated demands for oxygen must be met with appropriate elevations in lung ventilation and cardiac output, while the system must simultaneously responding to the challenges of a significant acid–base disturbance. Lung ventilation increases during the postprandial period. However, studies in snakes, lizards and alligators all show that the postprandial increments in metabolic rate are associated with a relative hypoventilation, indicated by significant reductions in \dot{V}_E/\dot{V}_{CO_2} and a rise in arterial P_{CO_2} (Busk et al., 2000b; Glass et al., 1979; Hicks et al., 2000; Overgaard et al., 1999; Secor et al., 2000; Wang et al., 2001a). The resulting respiratory acidosis partially compensates for the postprandial metabolic alkalosis and dampens the increase in pH. Although effective lung ventilation does not rise proportionally to increased metabolic production of CO_2 , it should be noted that overall lung ventila-

tion does increase substantially during the postprandial period and this increase is achieved by different mechanisms among reptiles. For example in *V. exanthematicus*, the increased ventilation is predominantly accomplished through a doubling of tidal volume, whereas breathing frequency only increased slightly (Hicks et al., 2000). In contrast, in the Burmese python, *P. morulus*, the increased ventilation is caused by a six-fold increase in breathing frequency (Secor et al., 2000), while tidal volume actually decreases within the initial 24 h after feeding. Thus even the means by which relative hypoventilation is achieved appears to be flexible, at least among taxa. The mechanisms responsible for the relative hypoventilation may include overall changes in ventilatory control and/or mechanical constraint imposed by the prey on the lungs and/or the respiratory muscles.

The general pattern of a postprandial hypoventilation occurs despite the significant increases in tissue oxygen demands that approach or even exceed those during maximal activity (Fig. 3). Interestingly, although the respiratory acidosis can partially compensate for the metabolic alkalosis, this physiological strategy could potentially come at the expense of corresponding reductions in lung P_{O_2} and the potential impairment of oxygen transfer from lung to blood. However, several studies have indicated a rather paradoxical response in arterial blood gas composition during the postprandial period. For example, in the Burmese

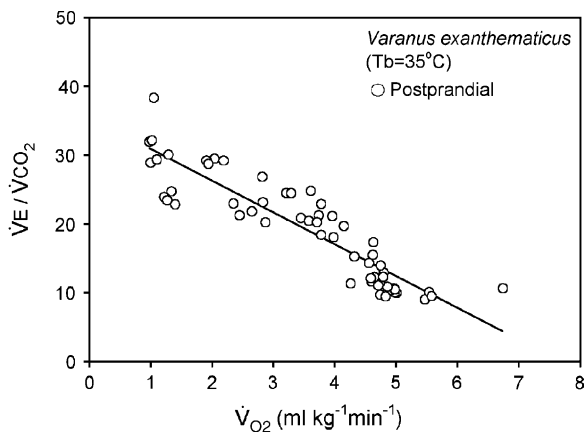


Fig. 3. The effects of an increase in postprandial metabolic rate (\dot{V}_{O_2}) on air convection requirements for CO_2 \dot{V}_E/\dot{V}_{CO_2} in *V. exanthematicus* at 35°C. Redrawn from Hicks et al. (2000).

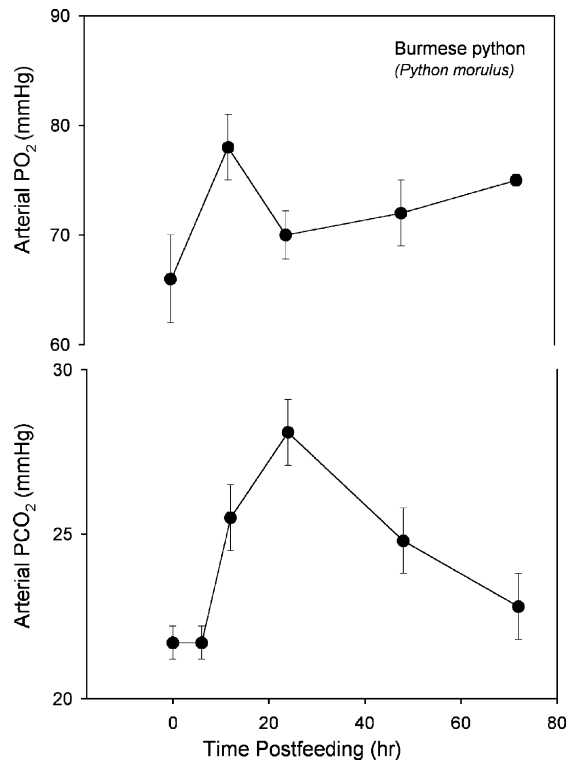


Fig. 4. Arterial blood gases (P_{O_2} and P_{CO_2}), in the Burmese python during fasting and throughout the postprandial period. Data redrawn from Overgaard et al. (1999).

python, *P. morulus*, the increase in arterial P_{CO_2} , resulting from the relative hypoventilation, is also associated with a significant increase in arterial P_{O_2} (Fig. 4). This pattern of blood gas response, a postprandial rise in arterial P_{CO_2} accompanied by significant increase in arterial P_{O_2} , has been measured in lizards, snakes, and in the alligator (Busk et al., 2000b; Hartzler et al., 2003; Overgaard et al., 1999; Wang et al., 2001a). Such a response would not be predicted by the standard respiratory equations; however, this apparent paradox may result from the unique cardiac morphology of reptiles, a morphology that allows for regulation of venous admixture or cardiac shunt (Wang et al., 2004).

The morphology of the reptilian heart results in the potential for cardiac shunts (Hicks, 1998). Cardiac shunts are typically defined by their direction, either as right-to-left (R–L) or left-to-right (L–R). A R–L shunt represents bypass of the pulmonary circulation and the recirculation of systemic (oxygen poor) venous blood

back into the systemic arterial circulation. Since this blood bypasses the lungs, the shunted portion has no chance to be oxygenated. In contrast, a L–R shunt represents the recirculation of pulmonary (oxygen rich) venous blood to the pulmonary circulation via the pulmonary artery. In other reptiles, there is the potential for either R–L or L–R shunts, but the anatomy of the crocodylian heart permits only the potential for R–L shunts. The direction and magnitude of cardiac shunts is largely determined by the vascular resistance of the pulmonary and systemic circulations with the regulation of these vascular circuits resulting from changes in autonomic tone and the release of neurohumoral factors (Hicks, 1998; Wang et al., 2001b). Changes in autonomic tone are partially generated within the central nervous system, but stimulation of pulmonary stretch receptors and vascular chemoreceptors may also be involved (Wang et al., 1997b).

The varying magnitude of cardiac shunts has a direct and pronounced effect on oxygen transport. Shunted systemic venous blood decreases arterial oxygen saturation, resulting in arterial hypoxemia and reduction in tissue oxygen delivery. In contrast, a L–R shunt represents recirculation of pulmonary (oxygen rich) venous blood into the pulmonary circulation. Thus regulation of cardiac shunts allows an alternative mechanism for changing blood gases independent of the respiratory control, a level of blood gas regulation not possible in mammals and birds (Hicks, 1998; Wang et al., 1997b).

Reductions in R–L shunt, and subsequent increases in arterial oxygen levels, are associated with elevated metabolic states in reptiles (Wang et al., 2001b) and a similar response may be occurring during the postprandial period. However direct measurements of cardiac shunting during SDA have not been made. The pattern of blood gas changes measured during SDA could, alternatively, result from reductions in \dot{V}_A/Q heterogeneity or improvements in diffusion capacity. In terms of the former, this is unlikely. In *V. exanthematicus*, a four-fold elevation in \dot{V}_{O_2} , during treadmill exercise, is associated with a significant increase in \dot{V}_A/Q heterogeneity (Hopkins and Hicks, 1995). The precise mechanism(s) accounting for the blood gas behavior during elevated metabolic states in reptiles are unknown as comparative studies on \dot{V}_A/Q distributions during exercise are rare (Powell and Hopkins, 2004) and there are no studies on \dot{V}_A/Q distributions during SDA.

5. Cardiopulmonary response to elevated metabolic states: SDA versus exercise

Because the metabolic demands during SDA may approach the values measured during activity, it is of interest to compare the similarities and differences in the cardiopulmonary response to SDA and exercise, within a single species. Recently, Hicks et al. (2000) measured the postprandial cardiopulmonary physiology of the monitor lizard *V. exanthematicus* and compared the results to previously published values for treadmill exercise in the same individual experimental animals. The change in heart rate and stroke volume for a given increment in \dot{V}_{O_2} is not different during exercise and digestion. In other words, the cardiac response appears to be stereotyped in regard to these two elevated metabolic states: equal increments in \dot{V}_{O_2} elicit equal increments in cardiac output, regardless of the nature of the elevated metabolic state (Fig. 5). In contrast, the ventilatory response is very dependent on the nature of the elevated metabolic stimulus. During digestion, an increase in \dot{V}_{O_2} results in a relative hypoventilation in comparison to rest ($\dot{V}_E/\dot{V}_{CO_2} = 76\%$ rest), whereas hyperventilation occurs during exercise ($\dot{V}_E/\dot{V}_{CO_2} = 200\%$ rest) (Fig. 6). During exercise, breathing frequency increased 10–40-fold above resting values, accompanied by large reductions in tidal volume. In contrast, postprandial increases in \dot{V}_{O_2} resulted in relatively minor

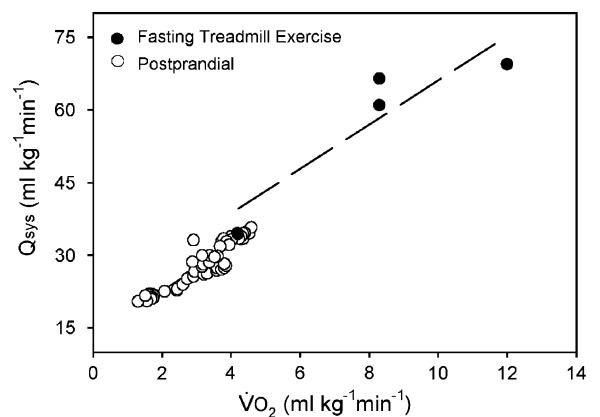


Fig. 5. The effects of an increase in metabolic rate (\dot{V}_{O_2}), either during digestion (open circles) or during fasting treadmill exercise (filled circles) on cardiac output in *V. exanthematicus* at 35 °C. Redrawn from Hicks et al. (2000).

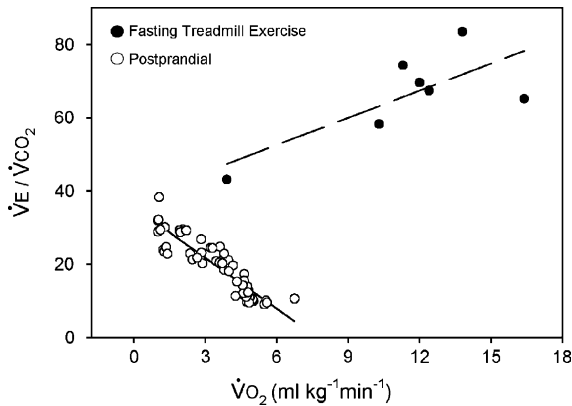


Fig. 6. The effects of an increase in metabolic rate ($\dot{V}O_2$) on air convection requirements for CO_2 (\dot{V}_E/\dot{V}_{CO_2}), either during the postprandial period (open circles) or during fasting treadmill exercise (filled circles). Data from *V. exanthematicus* at 35 °C, redrawn from Hicks et al. (2000).

changes in frequency and almost a doubling of tidal volume.

A similar pattern of response has been documented in the Burmese python (Secor et al., 2000). In these studies, cardiopulmonary function in pythons was measured during fasting at rest, exercising while fasting, and digesting. Pythons crawling at 0.4 km/h achieved $\dot{V}O_{2\max}$ and incurred significant increases in all measured variables, highlighted by a 24-fold increase in \dot{V}_E and very significant hyperventilation ($\dot{V}_E/\dot{V}_{CO_2} = 244\%$ fasting rest). In response to the digestion of a rat meal (25% of snake body mass), gas exchange and ventilatory and cardiovascular variables significantly increase to peak values between 32 and 56 h postfeeding. $\dot{V}O_2$ and heart rate of pythons reached similar levels during exercise and digestion, but ventilation pattern was considerably different, reflected in a relative hypoventilation during digestion ($\dot{V}_E/\dot{V}_{CO_2} = 62\%$ fasting rest). As in the lizards, heart rate, stroke volume, and cardiac output exhibited very similar changes during similar metabolic increments associated with digestion or exercise (Secor et al., 2000).

These studies demonstrate a stereotyped cardiac response to different elevated metabolic states. Undoubtedly, patterns of blood distribution to different tissues change according to their metabolic demands, but the cardiac output per unit oxygen consumed remains constant. In contrast, pulmonary ventilation exhibits

a more flexible response. Specifically, activity results in hyperventilation and digestion results in hypoventilation in comparison to fasting rest. The pattern of this response is found in widely divergent taxonomic groups, appearing in lizards (Hicks et al., 2000; Wang et al., 1997a), snakes (Secor et al., 2000), crocodylians (Busk et al., 2000b; Farmer and Carrier, 2000) and is even apparent in amphibians (Andersen et al., 2003). What accounts for the state-dependent response of the pulmonary system? The physiological changes associated with activity in reptiles are dominated by a pronounced acidosis, resulting from reliance on anaerobic metabolism (Bennett, 1994). In contrast, digestion is dominated by an alkalosis, resulting from the secretion of H^+ into the stomach and accumulation of $[HCO_3^-]$ in the blood. These differences in acid–base status during activity and digestion are undoubtedly a primary variable responsible for the differential pulmonary response.

6. Cardiopulmonary response to postprandial exercise

It is now clear that either exercise or digestion may significantly challenge the oxygen transport capacities of the cardiopulmonary system in reptiles. The aerobic capacities of these animals are rather low to begin with, at least in comparison to those of mammals and birds, and the aerobic demands of either physical activity or digestion may approach their limits. What happens then when these animals have to both eat and run simultaneously? Does the resulting demand exceed the transport capacity of the cardiopulmonary system? If so, which elevated metabolic state, activity or digestion, gets priority? How is this priority accorded physiologically?

In concept, priority could be accorded to either the exercise state or the digestive state or both could proceed simultaneously and result in an additive response without either giving ground. If priority were accorded to exercise, digestive metabolic processes would be scaled down commensurate with the increase in aerobic exercise demand. Capacity for aerobically sustained activity would be identical to that in a fasting animal (Fig. 7B). Conversely, if priority were given to digestion, aerobic scope for activity would be curtailed according to the magnitude of the digestive metabolic increment, and aerobic exercise capacity would de-

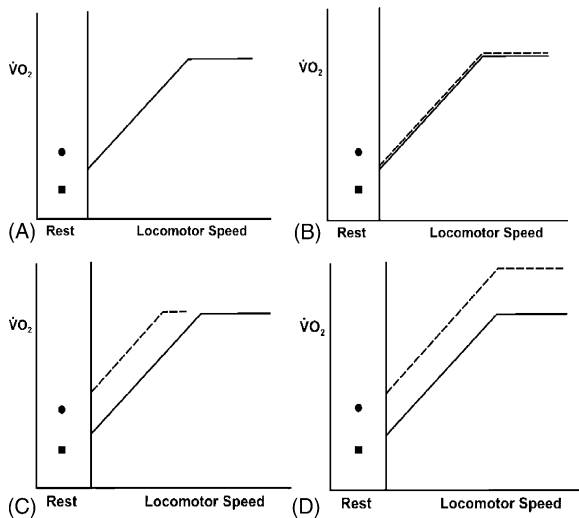


Fig. 7. Hypothetical patterns of rates of oxygen consumption (\dot{V}_{O_2}) during rest and treadmill exercise in fasting and postprandial animals. Circle, fasting rest; square, postprandial rest; solid line, fasting exercise; dashed line, postprandial exercise. (A) Previously documented patterns for fasting and postprandial animals at rest and fasting animals during exercise; (B) priority to exercise. Postprandial exercise \dot{V}_{O_2} is indistinguishable from fasting exercise \dot{V}_{O_2} ; (C) priority to digestion. The postprandial metabolic increment is maintained during exercise, curtailing performance; (D) additivity. The postprandial metabolic increment is maintained and $\dot{V}_{O_2 \max}$ is increased. Redrawn from Bennett and Hicks (2001).

cline (Fig. 7C). In an additive response, the digestive metabolic increment would be added onto the metabolic demand associated with exercise. In this case, no priority would be accorded, and oxygen consumption would be higher at any level of exercise than in a fasting animal, including an increment in apparent maximal oxygen consumption (Fig. 7D).

To investigate cardiopulmonary prioritization, Bennett and Hicks (2001) measured the \dot{V}_{O_2} and pulmonary ventilation during the simultaneous presentation of two elevated metabolic states, intense physical activity and digestion in the lizard, *V. exanthematicus*. In these experiments, \dot{V}_{O_2} was measured after a two-week fast and during incremental treadmill exercise. The \dot{V}_{O_2} during fasting rest was $1.9 \text{ ml kg}^{-1} \text{ min}^{-1}$, increasing eight-fold at $\dot{V}_{O_2 \max}$ (○). Animals were then fed a standardized meal (20% of body mass) and 24 h later, resting and exercise \dot{V}_{O_2} measurements were repeated. The resting postprandial \dot{V}_{O_2} was two-fold

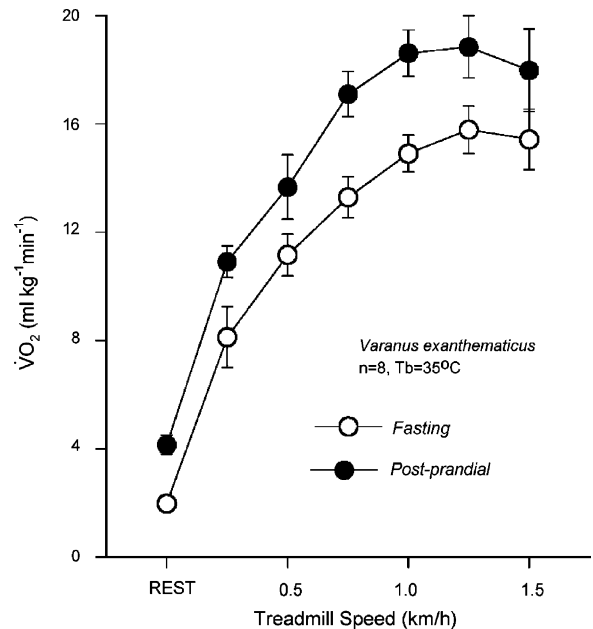


Fig. 8. Oxygen consumption (\dot{V}_{O_2} , mean \pm S.E.M.) during fasting and postprandial exercise on a motorized treadmill, in the lizard *V. exanthematicus* at 35°C from Bennett and Hicks (2001).

greater than fasting levels. This metabolic increment was retained at all levels of exercise and was apparently added on to the costs associated with fasting exercise. Postprandial $\dot{V}_{O_2 \max}$ (●) was 20% greater than fasting $\dot{V}_{O_2 \max}$ (Fig. 8). The \dot{V}_{O_2} measured during the simultaneous presentation of both physical activity and digestion, indicates that $\dot{V}_{O_2 \max}$ is therefore *additive*, with the increase equal to the sum of the two individual metabolic components. Similar measurements on *Python* also revealed additive responses during postprandial exercise (Secor et al., 2000). We conclude that there is excess transport capacity in the cardiopulmonary system of these animals that is not accessed by fasting exercise alone and therefore is available to support additional digestive metabolic costs. The corollary of this observation is that standard methodologies using fasted animals and graded exercise may not determine true maximal oxygen consumption. The cardiovascular and pulmonary systems may have additional capacities for gas transport beyond those accessed during activity alone. These results may therefore have more general implications regarding the determination of gas transport capacity.

Acknowledgements

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