

## POSTPRANDIAL EXERCISE: PRIORITIZATION OR ADDITIVITY OF THE METABOLIC RESPONSES?

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*Accepted 28 March 2001*

### Summary

Monitor lizards (*Varanus exanthematicus*) were used to examine the prioritization or additivity of the metabolic responses associated with exercise and digestion, either of which can elevate metabolic rate independently. Rates of oxygen consumption ( $\dot{V}_{O_2}$ ) and ventilation ( $\dot{V}_E$ ) were measured in lizards during fasting exercise, postprandial rest and postprandial exercise. In fasting animals,  $\dot{V}_{O_2}$  increased with walking speed to a maximal value of  $15.9 \text{ ml O}_2 \text{ kg}^{-1} \text{ min}^{-1}$  at  $1.25 \text{ km h}^{-1}$ . Postprandial resting metabolic rate was elevated significantly above fasting levels ( $4.1$  versus  $2.0 \text{ ml O}_2 \text{ kg}^{-1} \text{ min}^{-1}$ ). During postprandial exercise,  $\dot{V}_{O_2}$  increased to a maximal value of  $18.8 \text{ ml O}_2 \text{ kg}^{-1} \text{ min}^{-1}$  at  $1.25 \text{ km h}^{-1}$ . At every level of exercise,  $\dot{V}_{O_2}$  was significantly higher in postprandial animals by a similar increment; the maximal rate of oxygen consumption was significantly increased by 18% in postprandial individuals. Maximal  $\dot{V}_E$  did not differ in fasting and postprandial animals and, therefore, the greater  $\dot{V}_{O_{2\max}}$  of postprandial animals cannot be attributed to a higher ventilation rate. Air convection

requirement ( $\dot{V}_E/\dot{V}_{O_2}$ ) is significantly lower in postprandial animals at rest and at all levels of exercise, indicating a relative hypoventilation and increased pulmonary oxygen extraction efficiency. We suggest that this increased oxygen extraction may be due to decreased cardiopulmonary shunts and/or to lower mixed venous oxygen content. The data unequivocally support an additivity model rather than prioritization models for the allocation of elevated metabolic rate: the postprandial metabolic increment is not suspended during exercise, but rather is added onto the cost of exercise. It is clear that fasting exercise did not elicit truly maximal levels of cardiopulmonary oxygen transport in these animals, indicating problems for design models that make this assumption.

Key words: activity, digestion, exercise, lizard, maximal aerobic speed, maximal rate of oxygen consumption, oxygen consumption, postprandial, prioritization, reptile, specific dynamic action, symmorphosis, *Varanus exanthematicus*, ventilation.

### Introduction

Organisms in nature must undertake many different kinds of activities and sometimes do several simultaneously. Their physiological design must accommodate these simultaneous demands either by according priority to one of them or by somehow sharing common support systems. Historically, physiological studies have concentrated on the analysis of mechanisms underlying function in a single performance state. While this mode of investigation has been enormously productive, it has ignored the physiological problems imposed by simultaneously competing systems. Technical and conceptual advances in physiology have now made it both possible and desirable to undertake the analysis of prioritization and resolution of conflicting demands (Jackson, 1987). In this study, we investigate the response of the oxygen uptake and transport systems to simultaneously increased functional demand in two different performance states: exercise and digestion.

Both exercise and digestion independently increase rates of oxygen consumption ( $\dot{V}_{O_2}$ ). In many organisms, the magnitude of  $\dot{V}_{O_2}$  during strenuous exercise greatly exceeds

the specific dynamic action observed during digestion (Kleiber, 1975). However, in others, particularly in infrequently feeding reptiles, the metabolic scopes of exercise and digestion can be similar (Benedict, 1932; Secor and Diamond, 1995; Secor and Diamond, 1997). In *Python molurus*, for example, postprandial  $\dot{V}_{O_2}$  values are equal to those of snakes engaging in maximal sustainable exercise (Secor et al., 2000). Reptiles therefore provide an ideal organismal system in which to study physiological prioritization because of the major energetic commitments, and potential conflicts, caused by exercise and digestion. What happens to oxygen consumption and transport when postprandial animals exercise? Is priority of oxygen transport accorded to exercise or to digestion, is it shared or is the capacity for  $\dot{V}_{O_2}$  somehow increased to accommodate both (additivity)? Here, we study the pattern of oxygen transport during fasting exercise and postprandial exercise in the monitor lizard *Varanus exanthematicus*. This study is an extension of earlier observations (Hicks et al., 2000) on the

cardiopulmonary physiology of this species during fasting exercise and during digestion at rest.

#### Graphical models of prioritization and additivity

We present graphical hypotheses concerning potential patterns of oxygen transport during postprandial exercise (Fig. 1). These will be tested directly in the ensuing experiments. These hypotheses are each compared with known patterns (see Hicks et al., 2000) of  $\dot{V}_{O_2}$  during fasting rest, fasting exercise and postprandial rest (Fig. 1A). As in most other animals during fasting exercise,  $\dot{V}_{O_2}$  increases approximately linearly with exertion (in this case, speed of walking on a treadmill) to the maximal aerobic speed (MAS), the speed at which the maximal rate of oxygen consumption ( $\dot{V}_{O_{2max}}$ ) is attained. Walking at speeds faster than MAS does not increase  $\dot{V}_{O_{2max}}$  and entails rapid exhaustion associated with extensive supplemental anaerobic metabolism. At rest, postprandial animals have a  $\dot{V}_{O_2}$  elevated above fasting levels. The following are some potential outcomes for  $\dot{V}_{O_2}$  during postprandial exercise which are compared with the pattern described above.

**Priority to exercise** (Fig. 1B). During postprandial exercise, all metabolism associated with digestion is curtailed and all elevated  $\dot{V}_{O_2}$  is attributable to exercise. The pattern of  $\dot{V}_{O_2}$  as a function of speed is indistinguishable from that during fasting exercise. The MAS and  $\dot{V}_{O_{2max}}$  are the same as in fasting animals and endurance is not curtailed.

**Priority to digestion** (Fig. 1C). During postprandial exercise, digestive metabolism continues unabated, leaving less aerobic metabolic scope for exercise.  $\dot{V}_{O_{2max}}$  is the same as in fasting animals, but it is attained at a lower MAS with an attendant decrease in endurance.

**Additivity** (Fig. 1D). The resting postprandial metabolic increment is maintained during exercise, increasing  $\dot{V}_{O_2}$  by a similar amount at all levels of exertion.  $\dot{V}_{O_{2max}}$  is also increased by this increment, resulting in the same MAS and endurance as in fasting animals.

There are obviously also possible intermediate conditions among these three hypotheses, such as a shared prioritization between exercise and digestion. However, we believe that these hypotheses, with their clear and contrasting predictions concerning metabolic rates of exercising animals, MAS,  $\dot{V}_{O_{2max}}$  and endurance, form a useful framework for data analysis, and one turns out to describe the experimental results precisely.

## Materials and methods

### Animals

Thirteen savannah monitor lizards (*Varanus exanthematicus*) with body masses ranging from 145 to 900 g were purchased from a licensed supplier (California Zoological Supply, Santa Ana, CA, USA). Upon arrival, the lizards were kept in large terraria with free access to heating lamps and other heat sources allowing behavioral thermoregulation. A 12h:12h light:dark cycle was maintained, and water was

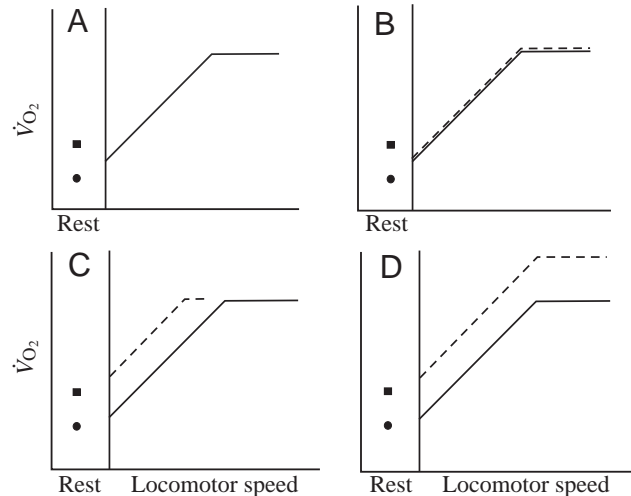


Fig. 1. Hypothetical patterns of rates of oxygen consumption ( $\dot{V}_{O_2}$ ) during rest and treadmill exercise in fasting and postprandial animals. Circle, fasting rest; square, postprandial rest; solid line, fasting exercise; dashed line, postprandial exercise. (A) Previously documented patterns 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  $\dot{V}_{O_{2max}}$  is increased. See text for a more detailed explanation.

always available *ad libitum*. Food was withheld for 3 weeks prior to experiments.

### Measurement of ventilation and gas exchange

In the first set of experiments ( $N=8$ , mass 145–170 g),  $\dot{V}_{O_2}$  was determined using an open mask system (Gleeson et al., 1980; Mitchell et al., 1981a; Mitchell et al., 1981b; Thompson and Withers, 1997). Room air was drawn (at 300–400 ml min<sup>-1</sup>) through a loose-fitting, lightweight acetate mask placed over the head of each animal. The expired air was dried (Drierite) and continuously monitored with an oxygen analyzer (Applied Electrochemistry; model S-3A). In the second set of experiments ( $N=5$ , mass 480–900 g), ventilation and gas exchange were directly measured using an experimental arrangement modified from Wang and Warburton (Wang and Warburton, 1995) and previously described in detail (Hicks et al., 2000). Briefly, short pieces of flexible gas-tight tubing were glued to both nostrils, fused on top of the head of the lizard and connected to a T-piece. This T-piece was, in turn, attached to gas-tight Tygon tubing at both ends. One end led to the oxygen analyzer, connected in series, while the other served as a reservoir. A flow pump (Applied Electrochemistry), connected in series with the gas analyzers, maintained a constant gas flow between the T-piece and the gas analyzer and, thus, provided continuous delivery of room air to the lizard. A pneumotachograph (8421 Series, 0–5 LPM, H. Rudolph, Inc.) was connected ‘upstream’ relative to the T-piece. At this position, airflow decreased during exhalations,

while inhalations caused increases in airflow. A Valendyne (MP-45-1-871) differential pressure transducer continuously monitored the resulting changes in pressure gradients across the pneumotachograph. At any given breath, the signal from the differential pressure transducer preceded that from the gas analyzer by approximately 2 s.

The  $\dot{V}_{O_2}$  of single breaths was determined as the area below the baseline signal for room oxygen. The relationship between this area and gas exchange was determined by simulating exhalations with known gas compositions through the T-piece (which during experiments was connected to the nostrils of the lizard). Similarly, the expired tidal volume of single breaths was determined from the integrated flow signal from the differential pressure transducer. Again, the relationship between this integral and tidal volume (in ml) was quantified by injection of a range of gas volumes through the T-piece. All calibration procedures produced very tight correlations between injected gas volumes and integrated flow signal ( $r^2 > 0.98$ ) and were reproducible within a few per cent before, during and after experiments. In both sets of experiments, experimental variables were recorded on a computer using the Acknowledge (version 3.2.4) data-acquisition system (Biopac Inc., Goleta, CA, USA).

#### Experimental protocol

At least 18 h prior to experimentation, animals were placed within a large climatic chamber maintained at 35 °C, the preferred body temperature of this species (Hicks and Wood, 1985). A few hours before treadmill exercise, the lizard was placed on the treadmill, covered with a cloth and left undisturbed with the mask or tubing connected to the experimental apparatus. Immediately before running, pre-exercise ventilation and/or gas exchange rates were measured over a 60 min period. Although the lizards quickly relaxed and remained quiescent when placed on the treadmill, these pre-exercise values do not represent true standard values. The exercise regime commenced with a walking speed of 0.25 km h<sup>-1</sup>, followed by 0.5, 0.75, 1.0, 1.25 and 1.5 km h<sup>-1</sup> (in that order). Each tread speed was maintained for approximately 5 min. The maximum speed is the highest at which the lizards were able to match the belt speed for at least 2 min.

In the first experiment ( $N=8$ ), only  $\dot{V}_{O_2}$  was measured, because the animals were too small for simultaneous measurements of ventilation with this apparatus. The second experiment ( $N=5$ ) was identical in protocol except that ventilation was also monitored in these larger animals. In all animals, gas exchange and minute ventilation were measured and averaged during the last 2–3 min of each level of exercise. Following exercise, gas-exchange rates and minute ventilation were measured for an additional 3–4 min. On the following day, lizards were fed a mixture of Tegu and Monitor Food (Zoomenu, San Luis Obispo, CA, USA) and raw eggs equal to 20% of their body mass. The size of the postprandial metabolic increment is a direct function of meal size in this species (Hicks et al., 2000). This ration was previously shown

to generate a maximal postprandial metabolic increment of approximately 2.5 ml O<sub>2</sub> kg<sup>-1</sup> min<sup>-1</sup> (Bennett et al., 2000). The animals were left undisturbed for 24 h, and the exercise protocol was then repeated; the maximal postprandial metabolic increment occurs at 24 h post feeding in this species (Hicks et al., 2000).

#### Data analysis

Oxygen consumption measurements are corrected to STPD conditions; ventilation volumes are corrected to BTPS conditions. Except as noted, data are analyzed using paired (by individual, fasting *versus* postprandial) *t*-tests. Data are reported as means  $\pm$  1 S.E.M. Significance is judged as  $P \leq 0.05$ .

#### Results

Rates of oxygen consumption at rest and during progressive treadmill exercise in both fasting and 24 h postprandial lizards in the first experimental series are reported in Fig. 2. In fasting animals,  $\dot{V}_{O_2}$  increased linearly with walking speed up to a maximal value of 15.9  $\pm$  0.92 ml O<sub>2</sub> kg<sup>-1</sup> min<sup>-1</sup> at 1.25 km h<sup>-1</sup>. This is a factorial increment of approximately eight times resting  $\dot{V}_{O_2}$ . Animals could not sustain exercise at 1.5 km h<sup>-1</sup>. Resting metabolic rate was elevated significantly above fasting levels when the animals were 24 h postprandial (4.1  $\pm$  0.36 *versus* 2.0  $\pm$  0.18 ml O<sub>2</sub> kg<sup>-1</sup> min<sup>-1</sup>,  $P=0.0001$ ). These observations are very similar to those we previously reported for this species (Hicks et al., 2000). During postprandial exercise,  $\dot{V}_{O_2}$  again increased linearly up to a maximal value of 18.8  $\pm$  1.15 ml O<sub>2</sub> kg<sup>-1</sup> min<sup>-1</sup> at 1.25 km h<sup>-1</sup>. Animals could not sustain exercise at 1.5 km h<sup>-1</sup>. At every level of exercise, including the MAS of 1.25 km h<sup>-1</sup>,  $\dot{V}_{O_2}$  was significantly higher in postprandial animals ( $P \leq 0.04$ ). The maximal rate of oxygen consumption was therefore significantly increased by 18% in postprandial individuals ( $P=0.04$ ). The postprandial metabolic

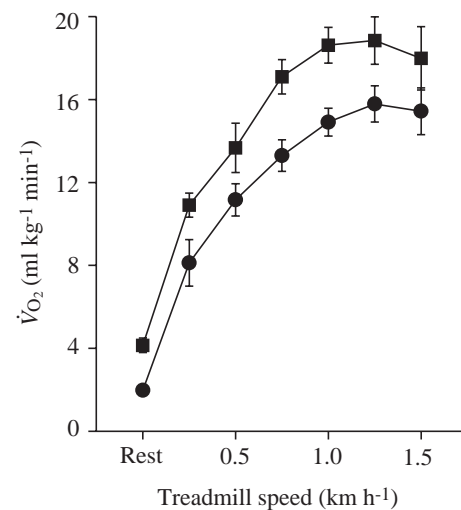


Fig. 2. Rates of oxygen consumption ( $\dot{V}_{O_2}$ ) during rest and treadmill exercise in fasting and postprandial lizards. Circles, mean fasting; squares, 24 h mean postprandial. Values are means  $\pm$  1 S.E.M. ( $N=8$ ).

Table 1. Ventilation in fasting and 24 h postprandial lizards at rest and walking at maximal aerobic speed

Feeding state	Activity level	Breathing frequency (breaths min <sup>-1</sup> )	Tidal volume (ml kg <sup>-1</sup> )	Minute volume (ml kg <sup>-1</sup> min <sup>-1</sup> )	Air convection requirement (ml air ml <sup>-1</sup> O <sub>2</sub> )
Fasting	Rest	1.5±0.38	40.6±14.0	42.7±4.30	22.2±3.23
	MAS	16.8±3.56	74.0±14.18	1046±68.6	69.1±6.34
Postprandial	Rest	1.4±0.48	93.1±43.28	68.7±13.38	17.0±3.20
	MAS	14.8±2.51	84.6±25.92	952±40.4	57.0±4.03

Values are presented as means ± 1 S.E.M.; *N*=5.  
MAS, maximal aerobic speed (1.5 km h<sup>-1</sup>).

increment was similar at all levels of exercise ( $P=0.41$ , repeated-measures analysis of variance) and thus represents a constant additional cost to exercising animals. (Note that body mass values reported here are all pre-feeding and do not include the mass of the undigested meal.)

Ventilation in the second experimental series is reported in Fig. 3A and Table 1. As in the former experiment,  $\dot{V}_{O_{2max}}$  was significantly higher in postprandial animals ( $P=0.02$ ). Values of  $\dot{V}_{O_{2max}}$ , as measured by the two different methods, were not significantly different (fasting,  $P=0.7$ ; postprandial,  $P=0.2$ ). Therefore, contrary to measurements made previously (Schultz et al., 1999) on other species of *Varanus*, measurements of  $\dot{V}_{O_2}$  during activity made using either metabolic masks or nasal tubes produced equivalent values of  $\dot{V}_{O_{2max}}$  in these animals. Ventilation rate ( $\dot{V}_E$ , ml air kg<sup>-1</sup> min<sup>-1</sup>) increases markedly during exercise in both fasting and postprandial animals, 24-fold in the former and 14-fold in the latter. These increments in ventilation are mostly due to increments in ventilation frequency: in postprandial animals, tidal volume does not even change significantly ( $P=0.7$ ). Maximal  $\dot{V}_E$  did not differ in fasting and postprandial animals ( $P=0.3$ ). Therefore, the greater  $\dot{V}_{O_{2max}}$  of postprandial animals cannot be attributed to a higher ventilation rate. Dividing  $\dot{V}_E$  by  $\dot{V}_{O_2}$  yields the air convection requirement (ml air ml<sup>-1</sup> O<sub>2</sub>), an inverse indication of oxygen extraction efficiency. Air convection requirements in both fasting and postprandial animals at rest and during exercise are reported in Fig. 3B and Table 1. As we found previously (Hicks et al., 2000), fasting animals hyperventilate during exercise (at MAS,  $P=0.002$ ), i.e. a smaller proportion of the oxygen is removed from the ventilated air. Also as shown previously, at rest, postprandial animals hypoventilate in comparison with fasting ones ( $P=0.02$ ). The current data indicate that, as during fasting, postprandial animals also hyperventilate during exercise in comparison with rest (at MAS,  $P=0.003$ ). However, a relative hypoventilation in comparison with the fasting state is maintained during exercise. At every level of exercise, air convection requirement is lower (i.e. oxygen extraction efficiency is higher) in exercising postprandial animals ( $P\leq 0.05$ ). At MAS, air convection requirement in fasting animals is approximately 20% greater than in postprandial ones.

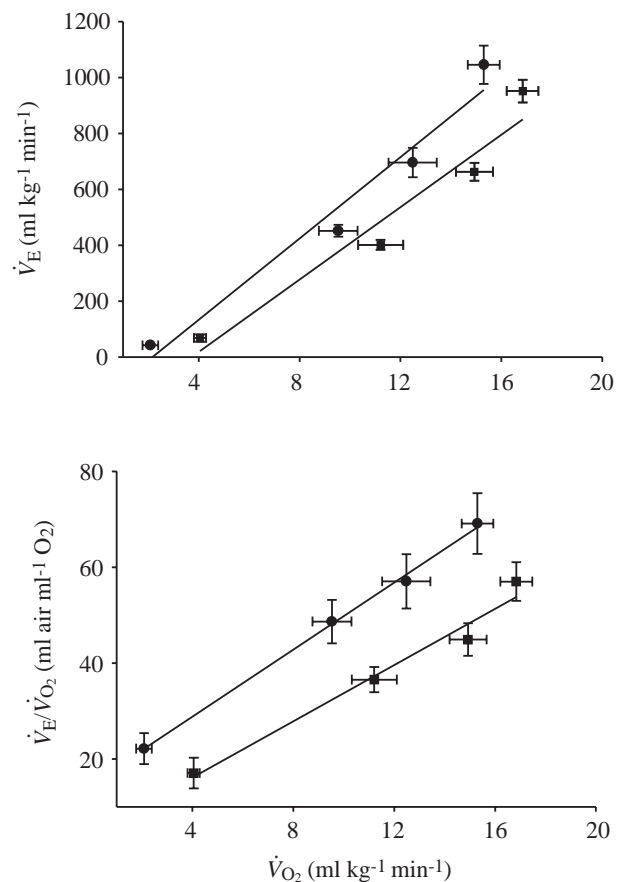


Fig. 3. Ventilation ( $\dot{V}_E$ ) and air convection requirement ( $\dot{V}_E/\dot{V}_{O_2}$ , where  $\dot{V}_{O_2}$  is the rate of oxygen uptake) during rest and treadmill exercise in fasting and postprandial lizards. Circles, mean fasting; squares, 24 h mean postprandial. Values are means ± 1 S.E.M. (*N*=5); lines are least squares linear regressions ( $\dot{V}_E$  fasting  $r^2=0.84$ ,  $P<0.001$ ;  $\dot{V}_E$  postprandial  $r^2=0.86$ ,  $P<0.001$ ;  $\dot{V}_E/\dot{V}_{O_2}$  fasting  $r^2=0.33$ ,  $P<0.01$ ;  $\dot{V}_E/\dot{V}_{O_2}$  postprandial  $r^2=0.23$ ,  $P<0.03$ ).

### Discussion

The major experimental findings are quite clear: the postprandial metabolic increment is not suspended during postprandial exercise and  $\dot{V}_{O_{2max}}$  increases substantially above levels observed in fasting animals. A similar increment in  $\dot{V}_{O_{2max}}$  was previously observed in postprandial pythons (Secor



et al., 2000). These results clearly and unequivocally support the additivity hypothesis (Fig. 1D): the postprandial  $\dot{V}_{O_2}$  increment is sustained at all levels of exercise,  $\dot{V}_{O_{2max}}$  is increased, and MAS and endurance are conserved. In this condition, no functional trade-offs appear to have been made: neither exercise nor digestion appears to have been compromised at the expense of the other. The priority to exercise hypothesis (Fig. 1B) is rejected because  $\dot{V}_{O_2}$  is increased in postprandial animals at all levels of exercise and because  $\dot{V}_{O_{2max}}$  is increased. The priority to digestion hypothesis (Fig. 1C) is rejected because  $\dot{V}_{O_{2max}}$  increases, MAS is not attained at a lower  $\dot{V}_{O_2}$  and endurance is not curtailed in postprandial animals.

The key to sustaining both exercise capacity and the postprandial metabolic increment is the increase in  $\dot{V}_{O_{2max}}$ . The 18% increment was attained not by an increase in  $\dot{V}_E$  but rather by an increase in  $O_2$  extracted from ventilated air; a similar pattern was previously found in exercising postprandial pythons (Secor et al., 2000). This greater extraction efficiency is reflected in hypoventilation during both rest and exercise. How might this increased oxygen extraction efficiency be attained? A variety of factors, singly or in combination, might at least theoretically be responsible for increased extraction. We regard the most likely factors to be decrements in shunts and/or lower mixed venous oxygen content. Shunts, both cardiac and pulmonary, occur extensively in reptiles under a variety of circumstances (for a review, see Hicks, 1998). A right-to-left ventricular shunt diverts an average of 30% of mixed venous blood directly to the systemic arterial circulation in resting *Varanus exanthematicus* (Heisler et al., 1983). Decrement or abolition of this shunt could direct substantially more venous blood into the pulmonary circulation and increase oxygen uptake. Also, a reduction in right-to-left shunt leads to an increased arterial  $P_{O_2}$  and a higher overall  $P_{O_2}$  gradient for diffusion from the blood to the mitochondria. In addition, pronounced ventilation-perfusion ( $V/\dot{Q}$ ) heterogeneity and intrapulmonary shunt exist within the lungs of these animals. These factors contribute to a large gradient between alveolar  $P_{O_2}$  and left atrial  $P_{O_2}$  (a 4 kPa  $P_{O_2}$  gradient at rest and during exercise in *Varanus exanthematicus*; Hopkins et al., 1995). During exercise, a reduction in areas of low  $V/\dot{Q}$  and in the intrapulmonary shunt would further increase oxygen extraction from ventilated air. Simultaneous measurements of  $P_{O_2}$  of blood within the left and right atria and systemic arterial and venous circulation in fasting and postprandial animals, exercising and at rest, would clearly indicate whether shunts were decreasing in active or digesting animals. Additional pulmonary oxygen extraction could occur if mixed venous  $O_2$  content were lowered during postprandial exercise. Such a decrement might occur, depending on the relative flow and oxygen content of blood returning in the splanchnic and skeletal muscle circulation, if both systems were maintaining high metabolic rates. Measurement of mixed venous  $O_2$  content in fasting and postprandial animals, exercising and at rest, would indicate whether this is an additional source of increased pulmonary oxygen extraction. The increase in

$\dot{V}_{O_{2max}}$  may also be partially attributable to additional cardiovascular factors not measured in these experiments. For instance, maximal heart rate in exercising postprandial pythons exceeds that of either resting postprandial or exercising fasting animals (Secor et al., 2000). Only more detailed physiological studies can fully partition the mechanistic basis of the greater  $\dot{V}_{O_{2max}}$ .

The increment in  $\dot{V}_{O_{2max}}$  in postprandial exercising animals (Fig. 2) suggests that exercise alone does not elicit  $\dot{V}_{O_{2max}}$ . This conclusion follows similar observations on exercising postprandial pythons (Secor et al., 2000). These studies suggest that excess oxygen transport capacity in the cardiopulmonary system exists that is not accessed by maximal muscle activity. This result is a significant caveat to the use of exercise alone to define maximum oxygen transport capacities. It is also a significant challenge to the hypothesis of symmorphosis (Taylor and Weibel, 1981; Weibel et al., 1991), which proposes that organisms are efficiently designed without excess capacity. It should be recognized, however, that considerable structural and physiological plasticity exists during the postprandial state in reptiles, including upregulation of transport capacities within the intestine and, in some instances, an increase in organ size (Secor and Diamond, 1995; Secor and Diamond, 1997). It may be possible that, during the 24 h postprandial period, the cardiopulmonary system has been sufficiently remodeled such that its transport capacity has been significantly increased. Only more detailed studies of the kinetics of the postprandial cardiopulmonary response can permit a determination of whether such changes, if they do occur, are sufficient to permit an 18% increment in  $\dot{V}_{O_{2max}}$ .

From a design point of view, then, what accounts for the apparent excess capacity of the cardiopulmonary system to transport oxygen? This is only 'excess' capacity from the point of view of fasting exercise. Animals in nature may well have to exercise while digesting, and cardiopulmonary design may thus naturally have to accommodate postprandial exercise. A closely related species, *Varanus albigularis*, has been observed to be very active during its feeding and growth season, walking an average of 1.5–2 km day<sup>-1</sup> (Phillips, 1995). In *Varanus exanthematicus*, if  $\dot{V}_{O_{2max}}$  had not increased during the postprandial period and metabolic priority was accorded to digestion (Fig. 1C), then MAS and endurance would have decreased. In this instance, assuming the average postprandial metabolic increment of 3.3 ml  $O_2$  kg<sup>-1</sup> min<sup>-1</sup>, MAS would have been reduced to between 0.5 and 0.75 km h<sup>-1</sup>, a value typical for lizards dependent principally on anaerobic metabolism to fuel higher-intensity exercise (Bennett, 1991; Bennett, 1994). Thus, to sustain high levels of aerobic activity, oxygen delivery systems may necessarily have to be designed to accommodate simultaneous elevated metabolic rates in two or more functional systems.

This research was supported by NSF grant IBN-9727762 to the authors. We thank Colleen Farmer and Daniel Warren for assistance with these experiments.

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