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Review

Metabolic implications of a ‘run now, pay later’ strategy in lizards: an analysis of post-exercise oxygen consumption[☆]

Todd T. Gleeson*, Thomas V. Hancock

Environmental, Population and Organismic Biology, University of Colorado, Boulder, CO 80309, USA

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Abstract

Lizards and many other animals often engage in locomotor behaviors that are of such short duration that physiological steady-state conditions are not attained. It is sometimes difficult to estimate the energetic costs of this type of locomotor activity. This difficulty is addressed by considering as reflective of the metabolic cost of activity (C_{act}) not only the oxygen consumed during the activity itself, but also the excess post-exercise oxygen consumption (EPOC) and any excess metabolites persisting at the end of EPOC. Data from both lizards and mammals demonstrate that EPOC is the major energetic cost when activity is short and intense. This paper evaluates the major metabolic components of EPOC in lizards. We then examine how behavioral variables associated with locomotion (duration, intensity, frequency) can influence EPOC and C_{act} . Short and intense activity is much more expensive by this measure than is steady-state locomotion. Evidence is provided that intermittent activity of short duration can be more economical relative to single bouts of the same activity. Metabolic savings appear greatest when the pause period between behaviors is short. In contrast, endurance is enhanced by short activity periods and longer pause periods, suggesting a tradeoff between endurance and EPOC-related metabolic costs.

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1. Introduction

A major focus of study of animal locomotion in the most recent quarter century has been the energetic costs experienced by animals as they locomote. Through study of oxygen consumption of animals under steady-state conditions, we have come to understand the basic patterns of metabolic expenditure as animals run, fly or swim, and we have developed generalizations of locomotor costs, most frequently expressed as metabolic cost per

unit distance traveled (Taylor et al., 1970; Tucker, 1970; Schmidt-Nielsen, 1972). These approaches have and continue to provide important insights into animal behavioral ecology, locomotor biomechanics, and even muscle function during activity (Kram and Taylor, 1990). Steady-state locomotion comprises only a small segment of many animals' repertoire, however. Many activities of animals in their natural environments are brief in duration and from a physiological perspective, non-steady-state. Examples include the territorial defense and foraging behaviors of many lizards (Huey and Pianka, 1981), birds (McLaughlin, 1989), rodents (Madison, 1985), and migratory locomotion in ghost crabs (Weinstein, 1995). O'Brien et al. (1990) has characterized this type of foraging behavior as saltatory behavior, and classifies most

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*Corresponding author. Tel.: +1-303-492-3106; fax: +1-303-492-6402.

E-mail address: gleeson@colorado.edu (T.T. Gleeson).

animal behaviors in that category. Our modeling of animal locomotion as a steady-state activity fails to reveal fully the metabolic response and energetic consequences of these brief or intermittent behaviors.

In the last few years we have begun to investigate the metabolic consequences of brief activity in lizards and in small mammals. These animals are noted for their brief and furtive behaviors. Lizards are particularly interesting in this regard because not only do the majority of them exhibit a preference for intermittent locomotion, they have aerobic scopes that are less relative to the scope of intensity of their locomotor behaviors. For example, rodents, dogs and horses alike are capable of sprint running speeds that are only 2–3 times the speed that they can sustain using only aerobic pathways of energy production (VO_{2max}), while lizards may exceed this by 20 times (Garland, 1982). As a consequence, brief activities in this latter group of vertebrates are often accompanied by a proportionally larger energy production supplied by lactate production and muscle phosphagen depletion, which may have secondary stimulatory effects on metabolism during the recovery period immediately following activity.

This metabolic recovery from locomotor activity has been an area of interest to exercise physiologists for 100 years. Hill and Lupton (1923) were among the first to attempt quantification of recovery metabolism, and they coined the term 'O₂ debt' to refer to that period of elevated metabolism immediately following activity. The term O₂ debt was meant to imply repayment of some oxygen or aerobic deficit, but this implied relationship has been shown under numerous circumstances in both ectothermic and endothermic vertebrates to be weak or non-existent. In 1984, Gaesser and Brooks proposed to replace the term O₂ debt with an acronym, EPOC, which stands for excess post-exercise oxygen consumption. This newer terminology's primary attribute is that it does not imply causality. The term has been widely accepted, as indicated by over 40 papers in the last 4 years that utilize the term in their title or abstract.

2. Physiological components of EPOC in a lizard

The factors contributing to EPOC have only been systematically characterized in mammals, particularly humans, dogs, horses and rats. Phos-

phagen replenishment in skeletal muscle and resaturation of hemoglobin and myoglobin stores in muscle and blood are thought to be major contributors to EPOC in the early minutes post-exercise (Gaesser and Brooks, 1984; Bahr, 1992). The period of EPOC can extend 15–30 min in many mammals, and 45 min to several hours in many ectotherms (Gleeson, 1991, 1996). The physiological explanations for this prolonged period of elevated metabolism are more varied than for the early phase of recovery, and may be more tax-specific. In mammals, body temperature is often elevated following vigorous activity, consequently increasing metabolism (Brooks et al., 1971; Bahr, 1992). A similar Q₁₀ effect is not thought to be a factor in the EPOC of ectothermic vertebrates, only the largest of which are thought capable of elevating body temperature via metabolic heat production. Elevated cardiac and ventilatory work are considered factors, as are fluctuations in levels of circulating catecholamines (Barnard and Foss, 1969; Gladden et al., 1982; Gaesser and Brooks, 1984). Other suggested avenues of excess energy consumption during and after activity include the conversion of accumulated lactate to restore depleted glycogen stores (Rose et al., 1988), ion redistribution and tissue repair (Stainsby and Barclay, 1970), mitochondrial uncoupling and a consequent decrease in the P:O ratio (Brooks et al., 1971), pH depression (Hermansen et al., 1984), and substrate cycling within both the gluconeogenic–glycolytic and triglyceride–fatty acid cycles (Newsholme, 1978; Bahr et al., 1990). Bahr has also suggested that a proportional increase in the oxidation of fatty acids post-activity in humans contributes to EPOC (Bahr et al., 1990).

The causal basis for the prolonged component of EPOC is more complex and less uniform among other vertebrates. Work by Bahr (1992) and Bangsbo et al. (1991, 1997; Bangsbo and Hellsten 1998) have quantified the contributions of these individual components to EPOC in humans. Less is known about how EPOC is partitioned in other taxa. In an attempt to model the components of EPOC in an ectothermic vertebrate, the desert iguana (*Dipsosaurus dorsalis*) was subjected to a 15 s bout of maximal intensity activity (Hancock et al., 2001a). Subsequent analysis was carried out analyzing many of the known components contributing to EPOC in mammals. These individual costs were quantified relative to the observed EPOC following this activity. The majority of EPOC was

Table 1

Contribution of each component as a percentage of total EPOC^a in the desert iguana (*Dipsosaurus dorsalis*) following 15 s of maximum intensity locomotion (Hancock et al., 2001a)

Component	% Contribution
Lactate glycogenesis	33–46 ^b
PCr repletion	19–25 ^b
Catecholamine	~17 ^c
Hb resaturation	<5 ^d
Cardioventilatory	<6
ATP repletion	<5 ^b

^a EPOC = 0.116 ml O₂ g⁻¹.

^b Range of P:O = 2.0–2.5 and percentage of active muscle mass = 50–67%.

^c Nedrow et al. (2001).

^d Gleeson et al. (1980).

accounted for by lactate glycogenesis, PCr repletion, and catecholamine stimulation.

Lactate accumulation was quantified in the gastrocnemius and extrapolated to the whole body (Hancock et al., 2001b). Glycogenic removal of 50% of the accumulated lactate (Gleeson and Dalessio, 1989) accounted for 33–46% of EPOC. This estimate, and those below, vary according to assumptions of the actual active muscle mass, the ATP produced per oxygen molecule consumed (P:O ratio), and compartmental distribution of lactate at different stages of activity and recovery. Summary estimates are presented in Table 1. PCr was depleted extensively in muscle (78%), while ATP was depleted to a lesser extent (13%), a pattern typical in both endotherms (Söderlund and Holtmann, 1991) and ectotherms (Milligan, 1996; Curtin et al., 1997). The contribution of PCr repletion to EPOC was high (19–25% of EPOC), while ATP repletion was a smaller component (< 5% of EPOC). Catecholamine stimulation also contributes to an elevated metabolism post-exercise. Adrenergic receptor blockade decreased EPOC by 17% below control values (Nedrow et al., 2001).

Lesser contributions to EPOC in *Dipsosaurus* are due to elevated cardiac work lasting 28 min into recovery and elevated ventilatory work lasting 10 min into recovery (Hancock et al., 2001a), although these costs together accounted for less than 6% of EPOC. Estimated costs for resaturation of hemoglobin O₂ stores also account for less than 5% of EPOC using data from other iguanids (Gleeson et al., 1980).

3. Defining cost of activity

While EPOC is a well-documented and accepted consequence of activity, it is not routinely incorporated into a calculation of locomotor costs because standard locomotor costs are assessed when steady-state conditions are reached under aerobic conditions. Our standard treatment of locomotor costs considers the metabolic expenditure during the period of locomotion, and expresses that as a function of the distance covered during that same period. These estimates of locomotor costs (e.g. cost of transport, cost of locomotion; Taylor et al., 1970; Tucker, 1970; Schmidt-Nielsen, 1972; Full et al., 1990) accurately reflect the cost while locomoting, and are clearly the appropriate metric for those interested in the muscular economy or biomechanical efficiency of locomotion. If one is interested in understanding the energetic cost to the animal of a particular locomotor behavior, or if one is interested in the total energetic investment in moving from point A to B, a consideration of the costs reflected in EPOC as well as the costs incurred during the behavior itself may be a more appropriate approach.

Baker and Gleeson (1998) coined the term cost of activity (C_{act}) to reflect the combined costs of elevated O₂ consumption during both activity and recovery in mice. Inclusion of recovery costs has also been used to estimate locomotor costs in the lizard *Dipsosaurus dorsalis* (Wagner and Gleeson, 1996), and in several invertebrates where EPOC is large and steady-state conditions are not met (Denny, 1980; Herreid, 1981; Full and Herreid, 1984). The cost of activity (C_{act} , energy expended per unit distance traveled) can be expressed as

$$C_{act} = \frac{EEOC + EPOC + \Delta[X]}{\text{distance traveled}}$$

where EEOC and EPOC represent the energetic equivalence of the mass-specific oxygen consumption elevated above resting levels during exercise and post-exercise, respectively, $\Delta[X]$ represents the energetic contribution reflected in any difference in concentration of metabolite X between the pre-exercise state and the state of the animal at the end of EPOC, and distance traveled is the distance moved during the locomotor behavior under consideration. We have defined the end of EPOC as the time point where VO₂ equals 1.5 × standard

metabolic rate (SMR). The SMR for each individual was measured for 3 h and the lowest mean metabolic rate measured over a 20-min period was used as our estimate of daytime SMR, thus it was rarely reached during recovery. Because $1.5\times$ SMR is indistinguishable from the pre-activity metabolic rate for a quiet, masked animal on the treadmill (Hancock et al., 2001b), it was used as a baseline resting measure. In vertebrates, metabolite X almost always refers to accumulated lactate. Cost of activity can have different units of energy utilization and distance ($\text{kcal g}^{-1} \text{m}^{-1}$, $\text{kJ g}^{-1} \text{km}^{-1}$, etc.), however, the more familiar term cost of locomotion is generally expressed as $\text{ml O}_2 \text{g}^{-1} \text{km}^{-1}$ and that convention is continued here.

C_{act} is distinct from estimates of transport costs in that it incorporates standard transport costs of an activity plus the additional consequent costs associated with recovery. Combining these costs more closely reflects the net energetic cost of activity to the animal. When locomotor activity is prolonged and steady-state conditions are generally met, EEOC is much greater than EPOC and as a consequence C_{act} approaches standard estimates of locomotor costs. When activity is short, however, EPOC is much greater than EEOC and C_{act}

becomes greater than standard estimates of locomotor costs. As an example, maximal running for 60 s results in EPOC volumes that can be more than $9\times$ larger than EEOC in humans, mice, and in lizards (Zanconato et al., 1991; Baker and Gleeson, 1998, 1999; Edwards and Gleeson, 2001; Hancock et al., 2001a; Nedrow et al., 2001). In lizards, this leads to an estimate of the cost of activity that is $3\text{--}7\times$ greater than the estimate based on locomotor costs alone (Hancock et al., 2001a). Even following activity of longer durations, EPOC can be of significant magnitude. EPOC accounted for 75% of total activity related oxygen consumption in alligators after 8 min of exercise (Emshwiller and Gleeson, 1997), 68% in snakes after 10 min (Gratz and Hutchison, 1977), and greater than 50% in some crabs after 15 min of vigorous activity (Full and Herreid, 1984). These observations point to the significance of this component of energetic expenditure associated with activity.

Unlike estimates of the cost of locomotion, EPOC and the consequent C_{act} are influenced by behavioral variables such as the duration of activity, the intensity with which it is undertaken, and the frequency at which the behavior is repeated. Below, we address these variables.

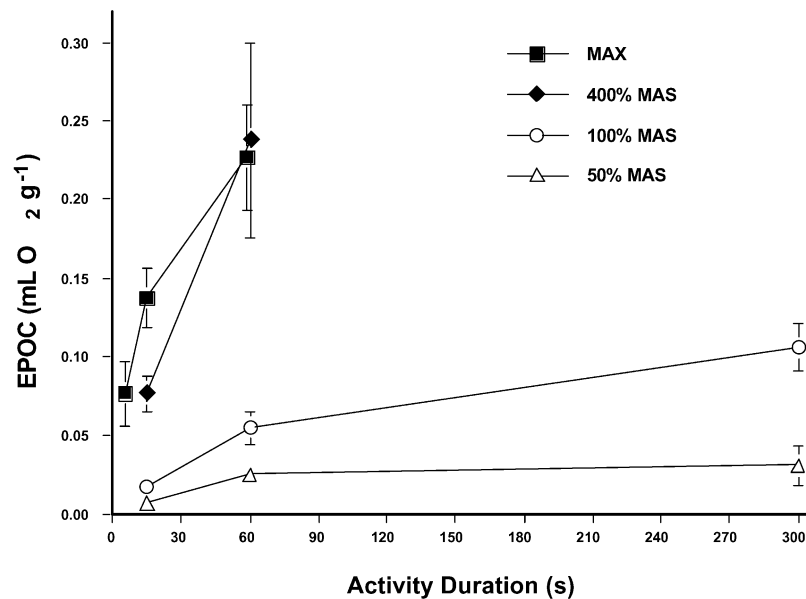


Fig. 1. The excess post-exercise oxygen consumption (EPOC; $\text{ml O}_2 \text{g}^{-1} \pm \text{S.E.M.}$) for multiple locomotor regimens in the desert iguana (*Dipsosaurus dorsalis*) where the recovery costs are included in addition to costs incurred during the activity itself. Regimens spanned activity durations of 5–300 s and activity intensities including a low and highly sustainable intensity of 50% of the maximal aerobic speed (MAS) up to maximal intensity (MAX) activities.

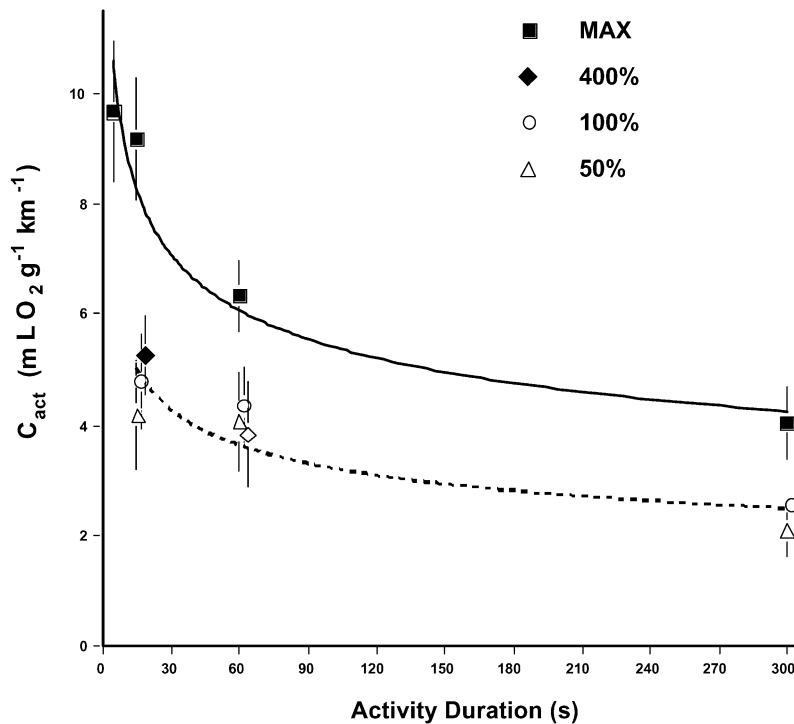


Fig. 2. The cost of activity (C_{act} ; ml O₂ g⁻¹ km⁻¹ ± S.E.M.) for multiple locomotor regimens in the desert iguana (*Dipsosaurus dorsalis*) where the recovery costs are included in addition to costs incurred during the activity itself. Regimens spanned activity durations of 5–300 s and activity intensities including a low and highly sustainable intensity of 50% of the maximum aerobic speed (MAS) up to maximal intensity (MAX) activities (from Hancock and Gleeson, in preparation).

4. Activity duration influences EPOC and C_{act}

Extending the duration of an activity extends the time and the cost of recovery. As activity increases in duration from 5 to 300 s in *Dipsosaurus*, an increase in EPOC is also seen (Fig. 1). This occurs at maximal intensity (Hancock et al., 2001a), as well as at lower intensities of 100–400% of the maximum aerobic speed (MAS; Hancock and Gleeson, 2002; Nedrow et al., 2001). In humans, significant graded increases in EPOC are also seen at higher intensities as activity duration is extended (Hagberg et al., 1980; Gore and Withers, 1990; Bahr, 1992). In both lizards and humans, low intensity activities do not appear to increase recovery costs as the activity duration is extended (Fig. 1). But, at higher intensities when anaerobic metabolism contributes to energy production, extending activity incurs a cumulative cost during recovery.

The increase in total costs to the animal (EEOC + EPOC + $\Delta[X]$), must be weighed against the increases in distance to evaluate the relative

economy (C_{act}) of different activity regimens. In *Dipsosaurus*, distance traveled increased proportionally more than did EPOC, and also more than total costs when EEOC is included (Hancock et al., 2001a; Hancock and Gleeson, 2002). Thus, C_{act} decreases as activity duration is extended (Fig. 2) because increases in total costs are modest compared to the additional distance gained. This decrease in C_{act} with activity duration is even more exaggerated in mice because EPOC did not increase with activity duration (Baker and Gleeson, 1998), and thus additions in distance come at no additional recovery cost.

5. Activity intensity influences EPOC and C_{act}

As with increases in activity duration, increases in activity intensity cause a prolonged recovery and more costly EPOC in *Dipsosaurus* (Fig. 1). For a common activity duration (15–300 s), EPOC volume increased 9–10-fold as intensity increased from 50 to 100 to 400% MAS. This likely reflects the additional and proportional reliance on anaer-

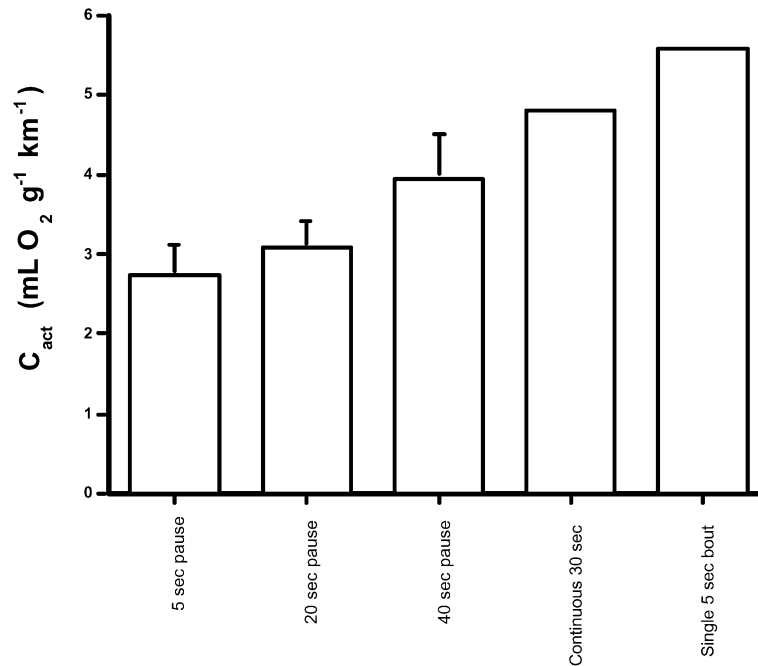


Fig. 3. Cost of activity (C_{act} ; ml O₂ g⁻¹ km⁻¹ ± S.E.M.) for intermittent, 5 s running with variable pause period (5, 20, 40 s pause periods), compared to C_{act} for single bouts of 30 and 5 s running. The latter two are extrapolated from Hancock and Gleeson (2002).

obic resources as intensity is increased. Increases in EPOC are also seen as activity intensity increases in humans (Knuttgen and Saltin, 1972; Hagberg et al., 1980; Gore and Withers, 1990; Zanconato et al., 1991; Bahr, 1992; Laforgia et al., 1997) and in horses (Keng et al., 1999; Langsetmo and Poole, 1999) whether activity duration is long or short (1–80 min).

Although EPOC and the total costs increased with activity intensity in *Dipsosaurus*, these increases were approximately proportional to the additional distance gained. Thus, C_{act} did not change significantly when intensity was increased from 50 to 100 to 400% MAS for common activity durations (Fig. 2, Hancock and Gleeson, 2002). This suggests that the economy of the activity is independent of intensity over this range. This agrees with results seen in horses for 100 s of activity, where total costs increased proportionally to total distance run such that C_{act} was independent of intensity (Keng et al., 1999), and in humans where cumulative O₂ consumption rose proportionally to 50 s of cycle ergometer work as intensity increased (Zanconato et al., 1991).

6. Activity frequency influences EPOC and C_{act}

Data from small animals suggest that performing locomotion in an intermittent fashion provides an economy not apparent from analysis of single bouts of activity (Gleeson and Hancock, 2001). Essentially, frequently repeated bouts are more economical than would be predicted from the cumulative cost because the animal does not incur the entire recovery cost with each bout. In *Dipsosaurus*, when a 5–40 s pause is allowed between six 5 s bouts of intense activity, the C_{act} decreases as much as 51% relative to the C_{act} associated with a single bout of 5 s activity and by as much as 43% relative to 30 s of continuous running (Fig. 3, Hancock and Gleeson, in preparation). Similar economy was exhibited by mice (Edwards and Gleeson, 2001) and voles (Gleeson and Hancock, 2001), with energetic savings up to 88% below the single activity C_{act} . A full explanation for why multibout activity is more economical than a single bout awaits future study, however, there are some costs of activity that can reasonably be expected to occur the first time an animal is

active, but not during subsequent bouts if bouts are spaced closely enough in time. These first-time costs might include costs associated with an acceleration of cardiopulmonary functions, of catecholamine stimulated substrate mobilization, and of lactate removal. In all cases, the shortest pause periods afforded the greatest energetic savings. As the pause period is extended, the animal incurs an additional cost with no additional gains in distance. Interestingly, although longer pauses increase costs, they also enable an increase in the endurance of the animal (Hancock and Gleeson, in preparation). Similar endurance benefits are reported in geckos by Weinstein and Full (1999). We speculate that both the increased costs and the enhanced endurance seen with longer pause periods is due to partial replenishment of phosphocreatine levels in muscle, as it is in other vertebrates (Saltin and Essen, 1971; Curtin et al., 1997).

7. Summary

The behavioral repertoire of animals include locomotor activities which are often brief in duration, of variable intensity, intermittent in nature, and do not reflect a physiological steady-state. Our energetic modeling of these behaviors often underestimates the actual cost to the animal because of the costly EPOC. Inclusion of EPOC can result in estimates of activity costs that are many times more costly per unit distance traveled than when these costs are not considered. Recent studies in our lab and in others have shown that the energetic expenditure associated with EPOC can be the major cost of brief locomotion in both lizards and in mammals. In lizards, a taxa where locomotor activities are generally brief, EPOC increases as running duration increases over 5–60 s. Because distance traveled increases at a greater rate than do EPOC costs, longer runs are more economical per unit distance. This relationship is also observed in rodents, man, and horses and should be the general case. Although EPOC increases with activity intensity in lizards, it does so in proportion to the additional distance run. Thus, it appears that the economy of the activity is insensitive to the intensity, except for maximal intensity activities that appear to incur additional costs. Performance of locomotor behavior in an intermittent, repetitive fashion also affords some economy to the animal over predictions based on single bouts of activity. EPOC following vigorous activity can be

attributed largely to metabolic costs associated with creatine phosphate replenishment, glycogenic removal of accumulated lactate, and metabolic stimulation by elevated catecholamine titers post-exercise. How these costs are attenuated following intermittent activity, and how these costs are influenced by other behaviors such as thermoregulation, remains the subject for future study.

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