THE EFFECTS OF INTENSITY ON THE ENERGETICS OF BRIEF LOCOMOTOR ACTIVITY

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Summary

The energetic costs associated with locomotion are often estimated only from the energy expended during activity and do not include the costs incurred during recovery. For some types of locomotion, this method overlooks important aspects of the metabolic costs incurred as a result of the activity. These estimates for energetic cost have also been predicted from long-duration, low-intensity activities that do not necessarily reflect all the behavior patterns utilized by animals in nature. We have investigated the effects of different activity intensities on the metabolic expenditure (per unit distance traveled) associated with brief exercise, and offer a more inclusive analysis of how the energetics of short-duration activities might be analyzed to estimate the costs to the animal. Mice ran on a treadmill for 15 or 60 s at 25%, 50% or 100% of maximum aerobic speed (MAS) while enclosed in an open-flow respirometry system. Following the run, each mouse was allowed to recover while remaining enclosed in the respirometry chamber. Excess exercise oxygen consumption (EEOC), the excess volume of oxygen consumed during the exercise period, increased with the duration and increased linearly with the intensity of exercise. In contrast, the volume of oxygen consumed during the recovery period, or excess post-exercise oxygen consumption (EPOC), was independent of exercise intensity and duration and accounted for more than 90% of the total metabolic cost. The net cost of activity (C_{act}), calculated by summing EEOC and EPOC and then dividing by the distance run, increased as both activity duration and intensity decreased. The values for C_{act} ranged from 553 ml O_2 g^{-1} km^{-1} for a 15 s run at 25% MAS to 43 ml O_2 g^{-1} km^{-1} for a 60 s run at 100% MAS. Combining these data with data from a companion paper, we conclude (1) that EPOC is independent of both the duration and intensity of activity when exercise duration is brief in mice, (2) that EPOC accounts for a majority of the oxygen consumed as a result of the activity when exercise durations are short, and (3) that animals can minimize their energy expenditure per unit distance by running faster for a longer period.

Key words: exercise, locomotion, activity, oxygen consumption, energetics, cost of activity, mouse.

Introduction

Understanding the energy expenditure associated with locomotion is important because these costs create boundaries within which animals must live. In the past, estimates for the cost of moving between two points have often been calculated in two different ways. In humans, the oxygen consumed during the exercise and/or recovery period was measured and used to determine the metabolic costs associated with activity (Hagberg et al., 1980; Gore and Withers, 1990; Zanconato et al., 1991; Bahr, 1992). In other animals, the costs were calculated by exercising them at low intensities until a steady-state rate of oxygen consumption was achieved. Then, only a portion of the oxygen consumed during the run was divided by the distance the animals ran during that period to give an energetic cost per unit distance (Margaria et al., 1963; Taylor et al., 1970, 1982; Tucker, 1970; Schmidt-Nielsen, 1972; Fernando et al., 1993; Mueller et al., 1994). This second approach has been used to estimate the costs of several activities varying in duration and intensity because no-one has investigated whether activities of different durations all result in the same energetic cost per unit distance. Recent research in mice has shown that activities of short duration do not result in the same energetic cost per unit distance as activities of longer duration when recovery costs are included in the calculation (Baker and Gleeson, 1998). Duration is an important consideration since most animals utilize behavior patterns of both long and short duration (Garland, 1983; Madison, 1985; Kenagy and Hoyt, 1989). Therefore, it is important to understand how the energetics of brief exercise differs from the energetics of prolonged exercise.

In a previous paper, Baker and Gleeson (1998) examined the
effects of short activity durations on energetic cost by combining the methods used by human physiologists with those of comparative animal physiology. The costs incurred during recovery were included, and these were divided by the distance the animals ran. Mice were run at maximum sprint speed for periods of a minute or less, and we concluded that short-duration activity is much more costly than originally thought when the cost of activity ($C_{\text{act}}; \text{mLO}_2 \text{g}^{-1} \text{km}^{-1}$) was calculated. The principal cause of this difference is the significance of post-exercise oxygen consumption to an energetic analysis of short-duration activities. The volume of oxygen consumed during this recovery period has been termed the excess post-exercise oxygen consumption (EPOC) and is defined as the elevated metabolism occurring after vigorous exercise (Gaesser and Brooks, 1984). Our recent study (Baker and Gleeson, 1998) showed that EPOC accounted for more than 90% of the total energetic expenditure when mice were run for 60 s or less. Therefore, the cost of activity associated with brief bouts of activity are high because a majority of the oxygen consumption resulting from the exercise occurs during the recovery period.

Animals not only utilize behavior patterns of varying durations in nature, but their activities also vary in intensity (Madison, 1985; Kenagy and Hoyt, 1989; T. V. Hancock, S. C. Adolph and T. T. Gleeson, in preparation). The present study was designed to determine the effects of activity intensity upon EPOC and the energetic cost when the duration of activity is held constant. Data showing the effects of activity intensity on the energetic cost of locomotion suggest that, as activity intensity decreases, the energetic costs (in units of ml O$_2$ g$^{-1}$ body mass km$^{-1}$; Taylor et al., 1970; Marconi et al., 1982; Kenagy and Hoyt, 1989) increase. However, these values have been estimated from long-duration activity, and recovery metabolism was not included in the estimate. Since it has been shown that the energetics of brief activity differ from the energetics of long-duration exercise, we wanted to examine the effects of activity intensity on the energetics of brief activity.

In this study, laboratory mice were run on a motor-driven treadmill at intensities of 25%, 50% and 100% of maximum aerobic speed (MAS) while activity duration was held constant at either 15 or 60 s. These data were used to determine the effects of activity intensity on oxygen consumption and how this influences the energetic cost of activity. We found that EPOC is independent of activity intensity in mice, but accounts for a majority of the oxygen consumed as a result of the exercise. This relationship explains why the cost of activity increases as activity intensity decreases. The data from this research, when combined with our previous data showing that energetic costs increase with decreasing activity duration, indicate that mice can minimize their energy expenditure by running faster for a longer period of time.

**Materials and methods**

**Animals**

Fifteen female white laboratory mice from an outbred stock (CF-1; Sasco, Inc.) were used for this study. The animals were ear-punched for identification. They were kept five per cage, and food and water were available *ad libitum*. They did not have access to a running wheel or any other form of exercise, were maintained on a 12 h:12 h light:dark photoperiod and all experiments were performed during the light phase. The ten mice used for the 15 s data weighed 23±1.7 g (mean ± s.d.) at the start of the study and had significantly increased in mass to 30±4.2 g ($P<0.05$) after 6 months. The five mice used for the 60 s exercise treatments also gained a significant amount of weight (20±0.3 g *versus* 28.1±0.4 g, $P<0.05$) during the 3 month experiment. An analysis of variance (ANOVA) confirmed that the increase in body mass did not significantly affect the rate of oxygen consumption of these mice. The experimental protocol was reviewed and approved by the University of Colorado’s Animal Care and Use Committee.

**Protocol**

Activity intensities were defined relative to an animal’s maximum aerobic speed (MAS). MAS is the speed at which the animal’s rate of oxygen consumption ($V_O_2$) begins to plateau despite further increases in running speed. At this point, the animal is producing the maximum amount of energy by aerobic means, and any further increases in work output must be fueled by anaerobic metabolism. To determine MAS, five mice were run in an open-flow respirometry chamber at speeds ranging from 1.0 to 2.5 km h$^{-1}$ while oxygen consumption was measured. Each animal was run for 3 min or longer at each speed until a steady-state $V_O_2$ was achieved. The animals ran at each speed three times, on non-consecutive days, and the lowest $V_O_2$ at each speed was used for analysis. The lowest steady-state $V_O_2$ at each speed was plotted against speed to determine the maximum aerobic speed (see Fig. 1). $V_O_2$ increased linearly with speed to a maximum level ($V_O_2_{\text{max}}$), at which point maximum aerobic speed was reached. The point at which $V_O_2$ began to plateau was determined by finding the best-fitting pair of linear equations using bivariate regression analysis. The two regression lines that minimized the residual sums of squares were considered to be the best-fitting lines, and the intersection of the two lines defined the maximum aerobic speed.

To determine the effect of activity intensity on the energetic cost of activity, each mouse was fasted for 12 h and then transferred to an open-flow respirometry chamber. The acrylic open-bottomed respirometry chamber (4 cm x 4.5 cm x 15.5 cm) was placed on the treadmill surface. Air was drawn from around the bottom of the chamber and through an opening at the back of the chamber at 700 ml min$^{-1}$ (STPD) during rest and recovery or at 1400 ml min$^{-1}$ (STPD) during and immediately following exercise. Animals were rested in the respirometry chamber for 1–2 h before being run. Before one of the runs, the animal rested for 3 h so that a resting metabolic rate for each mouse could be determined. Once the animal was rested, treadmill speed was increased gradually to one of three intensities: 25% MAS, 50% MAS or 100% MAS, for either 15 or 60 s. After the run, the mouse rested in the respirometry chamber for 60 min to
determine the oxygen consumed during recovery. Both the 25% and 50% MAS exercise treatments were repeated three times so that the lowest $V_{O_2}$ during each run could be used to calculate the metabolic response to the activity. During the rest and recovery periods, the chamber was covered so that visual and auditory disturbances were minimized.

**Measurement of oxygen consumption**

The technique used to sample excurrent air from the respirometry chamber has been described previously (Baker and Gleeson, 1998). Room air was pumped through the respirometry chamber and past the animal throughout the exercise treatment. At these high flow rates, there was an 8 s delay in $V_{O_2}$ response from the respirometry chamber to the time when the value was recorded by the computer. Data were adjusted for this delay before any computations were begun. At high flow rates, the response time for a full-scale deflection in oxygen consumption occurring in the chamber by the analysis system was 1.5 s. Carbon dioxide was not sampled, so Ascarite was used to remove CO$_2$ from the excurrent air before gas analysis. Rates of oxygen consumption were calculated using equation 4a in Withers (1977), following a correction for gas mixing within the respiratory chamber; i.e. ‘instantaneous $V_{O_2}$ correction’, as described by Bartholomew et al. (1981).

The resting rate of oxygen consumption ($\bar{V}_{O_2\text{rest}}$) was defined as the lowest $V_{O_2}$ occurring for 15 min during a 3 h period when the animal was inactive. To determine when recovery was complete following a run, a 3 min running average of $V_{O_2}$ beginning at the start of the recovery period was calculated. Recovery was considered to be complete when the first 3 min average was equal to, or less than, 1.5 times the value of $\bar{V}_{O_2\text{rest}}$ for each individual animal. To find the ‘excess’ oxygen consumed as a consequence of the activity, the volume of oxygen consumed as a result of resting metabolism was subtracted from the volumes of oxygen consumed during the run and recovery. Values for $V_{O_2}$, EEOC, EPOC and energetic cost have been expressed in units of ml $O_2$ consumed rather than an energy equivalent to avoid any assumptions regarding substrate utilization because respiratory quotient cannot be measured during non-steady-state activity. This error is estimated to be less than ±3%.

**Statistical analyses**

EPOC was analyzed as a function of body mass, exercise intensity and distance traveled. A repeated-measure ANOVA was used to determine differences across treatments. Paired and unpaired post-hoc tests were used to examine differences between treatments. Experiment-wise error was adjusted to 5%. Volumes are expressed at STPD. Results are expressed as means ± s.e.m.; N=10 when activity duration was 15 s, and N=5 when duration was 60 s.

**Results**

**Maximum aerobic speed**

Fig. 1 shows how the rate of oxygen consumption ($V_{O_2}$) increased as speed increased, until maximum aerobic speed (MAS) was reached. MAS was reached at a speed of 2.0 km h$^{-1}$, at which point $V_{O_2}$ plateaued at 7.98 ml $O_2$ g$^{-1}$ h$^{-1}$. The equation describing the relationship between $V_{O_2}$ and speed at speeds equal to or less than MAS was $V_{O_2} = 3.99 + 1.94v$ ($r^2=0.68, P<0.0001$). Open squares represent the average $V_{O_2}$ during the 15 s exercise period at 25%, 50% and 100% of maximum aerobic speed (MAS). The open squares are plotted as means ± S.E.M. (N=10).

- $V_{O_2}$ (ml $O_2$ g$^{-1}$ h$^{-1}$)
- Speed, $v$ (km h$^{-1}$)

![Fig. 1. Rates of oxygen consumption ($V_{O_2}$) during running at various speeds ($v$). Diamonds represent steady-state values of oxygen consumption for each mouse (N=5). The equation describing the relationship between $V_{O_2}$ as a function of speed below maximum aerobic speed is $V_{O_2}=3.99+1.94v$ ($r^2=0.68, P<0.0001$). Open squares represent the average $V_{O_2}$ during the 15 s exercise period at 25%, 50% and 100% of maximum aerobic speed (MAS). The open squares are plotted as means ± S.E.M. (N=10).](image)

**Responses of $V_{O_2}$ to activity**

The average metabolic response to running at 50% MAS for 15 s is shown in Fig. 2. Once the animal had rested, treadmill speed was increased and the animal began to run. $V_{O_2}$ increased rapidly at this point, stayed elevated during the run and declined to resting levels within 10–40 min after running stopped. Resting $V_{O_2}$ ($V_{O_2\text{rest}}$), determined after the mice had rested quietly for 3 h prior to any exercise, averaged 2.55±0.10 ml $O_2$ g$^{-1}$ h$^{-1}$ (range 2.02–3.24 ml $O_2$ g$^{-1}$ h$^{-1}$).

The excess volume of oxygen consumed during the exercise period, or excess exercise oxygen consumption (EEOC), increased as activity intensity and duration increased (Fig. 3; Table 1). EEOC was 0.009 ml $O_2$ g$^{-1}$ during the 15 s 25% MAS run and increased significantly to 0.022 ml $O_2$ g$^{-1}$ during the 15 s 100% MAS run (ANOVA; $P<0.02$). The values for EEOC during the 60 s runs did not increase significantly (0.069 ml $O_2$ g$^{-1}$ at 25% MAS and 0.098 ml $O_2$ g$^{-1}$ at 100% MAS; ANOVA; $P>0.05$). When activity duration was increased from 15 to 60 s at each intensity, there was a significant increase in EEOC (ANOVA; $P<0.0001$, Table 1). Average $V_{O_2}$ during the 15 s runs was 4.57 ml $O_2$ g$^{-1}$ h$^{-1}$ at 25% MAS, 5.25 ml $O_2$ g$^{-1}$ h$^{-1}$ at 50% MAS and 7.75 ml $O_2$ g$^{-1}$ h$^{-1}$ at 100% MAS. These rates are also plotted in Fig. 1 and lie
near the line describing the relationship between $V_O$ and speed during steady-state activity. The same trend was shown during the 60 s runs. The average $V_O$ during the 25 % MAS run was 6.87 ml O$_2$ g$^{-1}$ h$^{-1}$, and this increased to 8.60 ml O$_2$ g$^{-1}$ h$^{-1}$ during the 100 % MAS run.

As activity intensity and duration increased, the mice covered a significantly greater distance (Fig. 3). Since the intensity of the run was controlled by treadmill speed, the mice ran 2 m (15 s) and 8 m (60 s) during the 25 % MAS runs, 4 m (15 s) and 16 m (60 s) during the 50 % MAS runs, and 8 m (15 s) and 32 m (60 s) during the 100 % MAS runs.

Once exercise ended, $V_O$ gradually declined to resting levels. The time it took for $V_O$ to reach resting values was not significantly different among the different exercise treatments (ANOVA; $P>0.05$). On average, it took the mice 21±2.1 min to recover (Table 1).

The excess volume of oxygen consumed during the recovery period, or excess post-exercise oxygen consumption (EPOC), was not significantly different following the six runs of varying intensities and durations (ANOVA; $P>0.05$). EPOC averaged 0.96±0.10 ml O$_2$ g$^{-1}$ (Fig. 3; Table 1). This volume accounted for more than 91 % of the total excess oxygen consumed as a result of running at each of the three different intensities.

The cost of activity ($C_{act}$) was defined by Baker and Gleeson (1998) as the sum of EEOC and EPOC divided by the distance run. As activity intensity increased, $C_{act}$ decreased (Table 2; Fig. 4). For 15 s runs, $C_{act}$ at 25 % MAS was significantly different from the values for 50 % and 100 % MAS runs ($P=0.003$). $C_{act}$ also tended to decrease with increasing intensity.

### Table 1. Summary of EEOC and EPOC, and recovery times following exercise, in mice for 15 or 60 s

<table>
<thead>
<tr>
<th>Exercise intensity (% MAS)</th>
<th>EEOC (ml O$_2$ g$^{-1}$) 15 s</th>
<th>EEOC (ml O$_2$ g$^{-1}$) 60 s</th>
<th>EPOC (ml O$_2$ g$^{-1}$) 15 s</th>
<th>EPOC (ml O$_2$ g$^{-1}$) 60 s</th>
<th>Recovery time (min) 15 s</th>
<th>Recovery time (min) 60 s</th>
</tr>
</thead>
<tbody>
<tr>
<td>25</td>
<td>0.009±0.0012$^a$</td>
<td>0.069±0.0079$^*$</td>
<td>1.01±0.230</td>
<td>1.12±0.398</td>
<td>24±5.1</td>
<td>23±7.5</td>
</tr>
<tr>
<td>50</td>
<td>0.012±0.0009$^b$</td>
<td>0.090±0.0088$^*$</td>
<td>0.65±0.173</td>
<td>1.39±0.377</td>
<td>16±4.8</td>
<td>27±8.0</td>
</tr>
<tr>
<td>100</td>
<td>0.022±0.0033$^c$</td>
<td>0.098±0.0075$^*$</td>
<td>0.85±0.199</td>
<td>1.15±0.188</td>
<td>17±3.1</td>
<td>23±3.8</td>
</tr>
<tr>
<td>ANOVA</td>
<td>$P=0.017$</td>
<td>$P=0.216$</td>
<td>$P=0.482$</td>
<td>$P=0.922$</td>
<td>$P=0.886$</td>
<td>$P=0.888$</td>
</tr>
</tbody>
</table>

$^1$Values are means ± S.E.M; (N=10 for 15 s exercise; N=5 for 60 s exercise).

Different superscripts within columns denote significant differences with exercise intensity ($P<0.05$).

$^a$Significant difference with exercise duration.

EEOC, excess exercise oxygen consumption; EPOC, excess post-exercise oxygen consumption; MAS, maximum aerobic speed.
when activity duration was 60 s but, because of the limited sample size, the data failed to show statistical significance among different groups (ANOVA; $P>0.06$). A linear regression analysis showed the slope of the line to be significantly different from zero ($P=0.046$). When $C_{\text{act}}$ was compared between activity durations at the same exercise intensities, values for 60 s runs were significantly lower than values for 15 s runs at 25 % and 100 % MAS (ANOVA; $P=0.026$).

### Discussion

As activity intensity increased, the animals ran farther per unit time, but the total amount of oxygen consumed during exercise and recovery remained almost constant. This is because the volume of oxygen consumed during the recovery period (EPOC), which was itself independent of exercise intensity, accounted for the majority of the oxygen consumed as a consequence of the activity (Table 1). EPOC may be dependent upon activity intensity only when exercise durations are long and intensity is fairly high. Hagberg et al. (1980) reported that EPOC increased significantly with intensity when human subjects were exercised for 20 min at intensities greater than 65 % $V_{\text{O}_{2\text{max}}}$. At intensities lower than 65 % $V_{\text{O}_{2\text{max}}}$, Hagberg et al. (1980) found that EPOC was independent of intensity. When subjects were exercised for shorter durations (5 min), EPOC increased insignificantly with increasing exercise intensity. Similarly, Zanconato et al. (1991) reported that the pattern of $V_{\text{O}_{2}}$ recovery was independent of exercise intensity when adults and children performed cycle ergometry exercise for 1 min. It is possible that during short activity durations there is not a graded response of the components that influence EPOC. If there is not a graded response, this would cause EPOC to be constant following various activity durations of less than 5 min and would explain why EPOC is independent of activity intensity following exercise lasting a minute or less.

This study re-emphasizes the importance of including EPOC when considering the total metabolic cost of brief activity to an animal. When activity durations are short, EPOC comprises a large percentage of the total oxygen consumed as a result of the activity because the oxygen consumed during the brief exercise period is small. EPOC accounted for more than 90 % of the total following 15 and 60 s of activity at varying intensities. Baker and Gleeson (1998) reported similar results following 5–60 s of activity in mice exercising at maximum intensity. Following these short activity durations, EPOC was also more than 90 % of the total oxygen consumed. This is in contrast to long activity durations. EPOC only represents 63 % of the total $V_{\text{O}_{2}}$ after 5 min of running in mice (E. J. Baker, unpublished data), and following 20–80 min of activity in humans, EPOC only accounted for 1–10 % of the total metabolic costs (Sedlock et al., 1989; Gore and Withers, 1990). Similar trends showing the effect of duration on EPOC have also been reported in *Dipsosaurus dorsalis*, an ectothermic vertebrate (J. M. Nedrow, D. A. Scholnick and T. T. Gleeson, in preparation; T. V. Hancock, S. C. Adolph and T. T. Gleeson in preparation).

Cost of activity ($C_{\text{act}}$; Baker and Gleeson, 1998) varies from the traditional definitions of the energetic cost of traveling between two points because the recovery oxygen, or EPOC, is included. This approach is not novel. The relationship between the oxygen consumed during recovery and exercise in humans has been studied for 90 years (Benedict and Carpenter, 1910; Krogh and Lindhard, 1920). More recently, EPOC has been used to address issues of animal energetics in a variety of other organisms (Brett, 1964; Full and Herreid, 1984; Wagner and Gleeson, 1996). By considering the metabolic costs associated with recovery metabolism, we have assumed that any energetic costs met by anaerobic metabolism during activity are reflected in post-exercise oxygen consumption. This assumption is true as long as lactate concentrations in the body tissues return to resting concentrations by the endpoint of EPOC and stores of high-energy phosphates have been replenished. The time required for the removal of lactate from the blood after brief exercise in mice is comparable with the time required for $V_{\text{O}_{2}}$ to reach resting levels during recovery (Hatta et al., 1994). Following brief activity, blood lactate concentrations rise to

![Fig. 4. Cost of activity ($C_{\text{act}}$) for both 15 s and 60 s runs at different intensities. Circles represent data from 15 s runs and squares represent data from 60 s runs. $C_{\text{act}}$ decreased as activity intensity increased and as activity duration increased. Values are plotted means ± s.e.m. (N=10 for 15 s runs; N=5 for 60 s runs). MAS, maximum aerobic speed.](image)

### Table 2. The cost of activity for exercise at varying intensities for 15 or 60 s

<table>
<thead>
<tr>
<th>Exercise intensity (% MAS)</th>
<th>Cost of activity, $C_{\text{act}}$ (ml O$_2$ g$^{-1}$ km$^{-1}$)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>15 s</td>
</tr>
<tr>
<td>25</td>
<td>553±122.3$^a$</td>
</tr>
<tr>
<td>50</td>
<td>162±42.8$^b$</td>
</tr>
<tr>
<td>100</td>
<td>110±25.5$^b$</td>
</tr>
</tbody>
</table>

Values are means ± s.e.m. ($N=10$ for 15 s exercise; $N=5$ for 60 s exercise).
Different superscripts within a column denote significant differences ($P<0.05$).
MAS, maximum aerobic speed.
relationship between
This equation is also the slope of the line describing the run has the units ml O\textsubscript{2} g\textsuperscript{-1}
1971), so the energy supplied by the remaining excess of duration, or conversely, that \( C \) energetic cost because EPOC has been included in calculating
phosphate concentrations will have returned to resting levels. recovery in mice, it is reasonable to assume that high-energy
muscle (Hultman et al., 1967). Therefore, after 20 min of
regenerated after 5 min of recovery in the quadriceps femoris
7 min. ATP concentrations were not significantly altered
phosphate concentrations following exercise has been shown to occur quickly. Piiper and Spiller (1970) reported that creatine
phosphates following exercise has been shown to occur
\[ \text{Cost of activity (ml O}_2 \text{ g}^{-1} \text{ km}^{-1}) \]

22 mmol l\textsuperscript{-1}, and they then fall to 7.2 mmol l\textsuperscript{-1} after 20 min of recovery (Hatta et al., 1991, 1994), which is the time required for \( \text{VO}_2 \) to reach resting levels in mice (Table 1). Resting blood [lactate] in mice is approximately 3.3 mmol l\textsuperscript{-1} (Baile et al., 1971), so the energy supplied by the remaining excess of 3.9 mmol l\textsuperscript{-1} of lactate in the blood that has not been accounted for in our calculation of EPOC would account for a 2.4 % underestimation of the energy required for the mice to run for 15–60 s (assuming, liberally, that whole-body [lactate]=blood [lactate] and that 1 mol lactate=17 mol ATP; Bennett and Licht, 1972). Accounting for high-energy phosphates represents another possible source of error, but resynthesis of high-energy
phosphates following exercise has been shown to occur quickly.
Values for \( C_{\text{act}} \) are higher than traditional estimates of energetic cost because EPOC has been included in calculating \( C_{\text{act}} \). For example, Taylor et al. (1970) reported that the minimum cost of running (\( M_{\text{run}} \)) is dependent upon body mass and can be predicted by the equation \( M_{\text{run}}=8.46W^{0.4} \), where \( M_{\text{run}} \) has the units ml O\textsubscript{2} g\textsuperscript{-1} km\textsuperscript{-1} and \( W \) is body mass in grams. This equation is also the slope of the line describing the relationship between \( \text{VO}_2 \) and speed for each species at speeds below maximum aerobic speed. Using this equation, Taylor et al. (1970) predicted the energetic cost of running for a 30 g mouse to be 2.17 ml O\textsubscript{2} g\textsuperscript{-1} km\textsuperscript{-1}. Likewise, data from Fig. 1 predicts a cost of 1.94 ml O\textsubscript{2} g\textsuperscript{-1} km\textsuperscript{-1} for steady-state activity in mice. Thus, \( M_{\text{run}} \) represents the actual cost of the act of locomoting because the calculation only considers the oxygen consumed during the exercise period. Others have also used only the exercise oxygen consumption to estimate cost (Tucker, 1970; Schmidt-Nielsen, 1972; Gleeson, 1979; John-Alder and Bennett, 1981; Full et al., 1990). In contrast, \( C_{\text{act}} \) takes into account the oxygen consumed both during activity and during recovery, and therefore represents the total energetic cost of the activity. Such an approach can be beneficial in cases where an animal’s \( \text{VO}_2 \) never attains steady-state conditions although exercise duration is long (Full and Herreid, 1984) and in the more common cases where exercise duration is brief and steady-state conditions are assumed not to be met (Baker and Gleeson, 1998).

Another finding of our study was that \( C_{\text{act}} \) was lower for 60 s runs at all intensities than for 15 s of activity (Table 2). This is in agreement with our previous research (Baker and Gleeson, 1998), which showed that \( C_{\text{act}} \) decreased as activity duration increased when mice ran at maximum sprint speed. Taken together, these two studies indicate that, at each exercise intensity, \( C_{\text{act}} \) can be minimized by increasing activity duration, or conversely, that \( C_{\text{act}} \) can be minimized by increasing intensity at any given duration. We predict \( C_{\text{act}} \) to be greater than \( M_{\text{run}} \) for short-duration activity, but \( C_{\text{act}} \) would approach \( M_{\text{run}} \) as exercise duration increased.

On the basis of the present data and data from our companion paper (Baker and Gleeson, 1998), we propose a model that combines both duration and intensity to describe the energetics of a single bout of locomotor activity in mice. The model predicts that the activity costs of mice are minimized when animals run at high intensities or for long periods (Fig. 5). Conversely, animal locomotor activity is most costly per unit distance when the activity is brief and slow. The relationship among these three variables in mice can be described by the equation: \( C_{\text{act}}=573–2.4x–6.2y \), \( r^2=0.58 \), \( P=0.0005 \), where \( x \) is % MAS and \( y \) is activity duration in seconds. Just as \( M_{\text{run}} \) predicts costs beyond the relevant behavioral capacity for small animals, this model also extends the mathematical surface beyond the behaviorally relevant conditions for a mouse. For example, a small mammal cannot run for 10 min or more at its maximum sprint speed. Similarly, when the duration or intensity of activity approach values of zero, we posit that the estimates of cost bear no biological importance because the duration of the behavior is so short as to make the cost unimportant or the activity is so low in intensity that the behavior does not represent ‘locomotion’. The middle surface predicted by the model is, however, of probable behavioral and energetic relevance. This model offers researchers a better description of the energetics associated with a single bout of activity which describes some types of in-field activities. For example, widespread foraging and migration may be described by the part of the model representing long-duration, low-intensity behaviors during which costs are low, while escaping a predator or social interactions among conspecifics may be described by the portion of the model representing intense and brief behaviors.
However, since this model describes the total metabolic cost incurred by a single bout of exercise, it should not be used to describe the energetic cost of intermittent activity until there are data available that examine the relationship between constant and intermittent activity.

In conclusion, EPOC was unaffected by activity intensity when the duration of the behavior was short. EPOC accounted for a majority of the oxygen consumed as a result of the activity (>90%) and, consequently, the values for $C_{act}$ were much higher than traditional estimates of the cost of running. Since EPOC was unaffected by activity intensity but the distance that the animals ran increased with intensity, $C_{act}$ decreased as intensity increased. Taken together with with previous data (Baker and Gleeson, 1998), we have found that locomotor costs are minimized whenever animals run faster and for longer periods.

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References


