

ACTIVITY BEFORE EXERCISE INFLUENCES RECOVERY METABOLISM IN THE LIZARD *DIPSOSAURUS DORSALIS*

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Summary

During recovery from even a brief period of exercise, metabolic rate remains elevated above resting levels for extended periods. The intensity and duration of exercise as well as body temperature and hormone levels can influence this excess post-exercise oxygen consumption (EPOC). We examined the influence of activity before exercise (ABE), commonly termed warm-up in endotherms, on EPOC in the desert iguana *Dipsosaurus dorsalis*. The rate of oxygen consumption and blood lactate levels were measured in 11 female *D. dorsalis* (mass 41.1±3.0 g; mean ± S.E.M.) during rest, after two types of ABE and after 5 min of exhaustive exercise followed by 60 min of recovery. ABE was either single (15 s of maximal activity followed by a 27 min pause) or intermittent (twelve 15 s periods of exercise separated by 2 min pauses). Our results indicate that both single and

intermittent ABE reduced recovery metabolic rate. EPOC volumes decreased from 0.261 to 0.156 ml of oxygen consumed during 60 min of recovery when lizards were subjected to intermittent ABE. The average cost of activity (net \dot{V}_{O_2} during exercise and 60 min of recovery per distance traveled) was almost 40 % greater in lizards that exercised without any prior activity than in lizards that underwent ABE. Blood lactate levels and removal rates were greatest in animals that underwent ABE. These findings may be of particular importance for terrestrial ectotherms that typically use burst locomotion and have a small aerobic scope and a long recovery period.

Key words: activity before exercise, exercise, recovery metabolism, post-exercise oxygen consumption, iguana, *Dipsosaurus dorsalis*.

Introduction

Metabolic rate remains elevated above resting levels for prolonged periods after exercise in both ectotherms and endotherms, a phenomenon that was termed excess post-exercise oxygen consumption (EPOC) by Gaesser and Brooks (1984). When exercise periods are short, EPOC can account for the majority of the cost of activity: EPOC accounts for over 90 % of the total metabolic cost of activity in mice that exercise for less than 1 min (Baker and Gleeson, 1998). Thus, factors that influence recovery metabolic rate following even brief activity may have a large impact on the metabolic cost of activity. Brief activity prior to an exercise bout, commonly termed warm-up in endotherms, is known to influence recovery metabolic rate in mammals (Robergs et al., 1991; Gerbino et al., 1996), but its impact on recovery in ectotherms that typically move using burst locomotion and have extended recovery periods is unclear.

When exercise periods are brief, less than 1 min, EPOC can persist for long periods (Zanconato et al., 1991; Baker and Gleeson, 1998). In the lizard *Dipsosaurus dorsalis*, \dot{V}_{O_2} remains elevated for over 30 min after only 5 s of activity (J. M. Nedrow, D. A. Scholnick and T. T. Gleeson, in preparation). The consequence of an extended recovery time

following progressively shorter activity periods is that EPOC will account for a larger proportion of the metabolic cost of burst locomotion. Thus, in lizards in which locomotion is often characterized by short-duration high-intensity activities (burst locomotion; Hertz et al., 1988) and long recovery periods (Gleeson, 1996), changes in recovery metabolic rate, measured as EPOC volumes, should have a large impact on the total cost of brief activities and could influence locomotor behavior in nature.

EPOC does not appear to be regulated by a single factor. Exercise duration (Gore and Withers, 1990a,b), exercise intensity (Hagberg et al., 1980), body temperature (Wagner and Gleeson, 1996) and hormone concentrations (Borsheim et al., 1994) have all been reported to influence EPOC. There is also evidence that activity before exercise (ABE), commonly termed warm-up in endotherms, can influence recovery metabolic rate in humans (Robergs et al., 1991; Gerbino et al., 1996). In the present study, we examine the possibility that ABE will also influence recovery metabolic rate in a terrestrial ectotherm that exhibits long recovery periods following burst activity.

The relationship between ABE and overall performance and

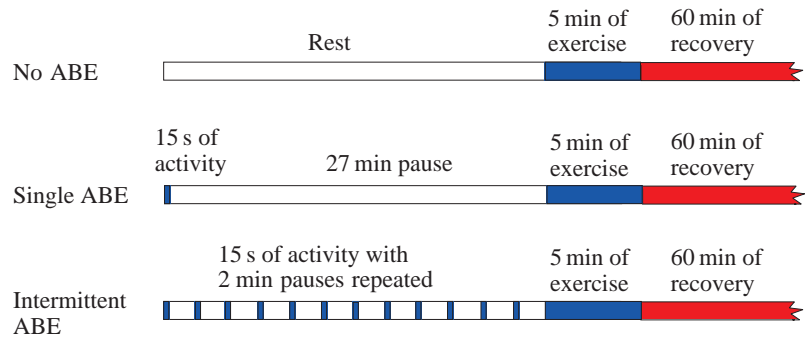


Fig. 1. Exercise protocols. Blue bars represent activity, open bars represent pause or rest, and red bars represent recovery. All activity was preceded by 2 h of rest to ensure that resting $\dot{V}O_2$ was achieved before activity. ABE, activity before exercise.

recovery in ectotherms remains unclear. In humans, ABE has been associated with a variety of physiological changes during and after exercise. Among the changes associated with brief ABE are stimulation of the circulatory system, vasodilatation of tissue blood vessels, enhanced muscle perfusion, increased core and muscle temperatures, increased elasticity of tendons and connective tissues, and changes in inorganic phosphate levels (De Bruyn-Prevost, 1980; Robergs et al., 1991; Gerbino et al., 1996). There is also evidence that skeletal muscle force generation *in vitro* is enhanced during vigorous exercise by ABE in both ectotherms and endotherms (Bruton et al., 1996, 1997).

The aims of the present study were to determine whether either short bursts of activity or brief intermittent activity prior to exhaustive exercise would influence subsequent recovery metabolic rate and blood lactate levels and removal rates in an ectotherm. The lizard *Dipsosaurus dorsalis* was used for these studies because recovery times are typically long, greater than 60 min after 5 min of exercise (Wagner and Gleeson, 1996), and metabolism during recovery has been well-studied (Gleeson, 1985; Gleeson and Dalessio, 1989, 1990; Scholnick and Gleeson, 1996).

Materials and methods

Animal care

Adult female desert iguanas (*Dipsosaurus dorsalis*) weighing 30.9–46.5 g ($N=11$, mass 41.1 ± 3.0 g, mean \pm S.E.M.) were collected from Riverside County, California (California Fish and Game Permit 0024). Lizards were maintained in the laboratory in photothermal cages with a temperature range of 30–45 °C. They were fed a mixture of lettuce and ground rat chow twice a week.

Rest and exercise protocol

Each lizard was fitted with a lightweight clear acetate mask at least 2 h before exercise. The lizard was then placed on the surface of a motor-driven treadmill (maximum speed 1.2 m s^{-1}) equipped with a thermostat and maintained at 40 ± 1 °C and left undisturbed. Resting $\dot{V}O_2$ was measured for the last 20 min of rest and was averaged to determine a resting $\dot{V}O_2$ before each experiment for each animal.

Activity before exercise (ABE) consisted of either a single short burst of activity or multiple intermittent bursts of activity

separated by 2 min pause periods. Single ABE involved one 15 s bout of maximal activity followed by a 27 min pause and then 5 min of exhaustive exercise. Intermittent ABE consisted of twelve 15 s periods of maximal activity separated by 2 min pause periods. The final 2 min pause period was followed by 5 min of exhaustive exercise. The time between the first bout of ABE and the final 5 min of exercise was identical in the two protocols (Fig. 1). In experiments in which there was no ABE, animals exercised for 5 min after 147 min (2 h plus 27 min) of rest. The exercise sequence for each of the 11 lizards was determined randomly.

All animals were induced to sprint on the treadmill by gently prodding their hind limbs and tail. Treadmill speed was continuously adjusted to match animal effort. After exercise, lizards were left undisturbed on the treadmill surface, and the rate of oxygen consumption and behavior were monitored during recovery. If an animal was active or tried to remove the mask during the recovery period, the experiment was discontinued and repeated after 5 days. The oxygen content of expired gases was measured continuously during rest, ABE, exercise and 60 min of recovery. A previous study found that 60 min was sufficient to account for the majority of EPOC (J. M. Nedrow, D. A. Scholnick and T. T. Gleeson, in preparation). No animal was exercised more than once every 2 days.

Measurements of $\dot{V}O_2$

The rate of oxygen consumption was measured from expired gases drawn through an Applied Electrochemistry S-3/A oxygen analyzer from the lizard's mask. Airflow from the mask was controlled and monitored using a Tylan RO-32 mass flow controller (rate $180\text{--}650 \text{ ml STPD min}^{-1}$). The oxygen analyzer was calibrated with reference gases before the beginning and at regular intervals during each measurement period. Expired gases were drawn from the mask and passed through Drierite and soda lime to remove water vapor and CO_2 . Data were collected from a flow controller, gas analyzer and treadmill by a Lab-NB data-acquisition board (National Instruments, Austin, TX, USA) connected to a Powermac 7100 computer. Instantaneous measurements of $\dot{V}O_2$, speed and distance were computed with LabView programs (v3.1.1, National Instruments) using equations provided by Bartholomew et al. (1981) and Withers (1977). The delay between mask and oxygen analyzer was 7 s at a flow rate of

Table 1. Excess volume of oxygen consumed during 5 min of exercise and during early and late phases of recovery with and without activity before exercise

Type of ABE	Excess volume of oxygen consumed (ml g ⁻¹)					
	During exercise	0–10 min of recovery	11–60 min of recovery	EPOC	Total	Total including lactate
None	0.069±0.004	0.072±0.006	0.189±0.018	0.261±0.020	0.330±0.020	0.387±0.020
Single	0.063±0.004	0.076±0.003	0.102±0.022*	0.178±0.018*	0.241±0.019*	0.311±0.019*
Intermittent	0.059±0.003	0.047±0.009*	0.109±0.030*	0.156±0.039*	0.215±0.041*	0.295±0.041*

Estimates of the additional energy contributed by the lactate remaining at the end of 60 min of excess post-exercise oxygen consumption (EPOC) are also included.

Values are means ± S.E.M. for 11 *Dipsosaurus dorsalis*.

*Indicates a value significantly different from that for lizards that did not undergo activity before exercise (ABE; repeated-measures ANOVA, $P < 0.05$).

See Materials and methods and Fig. 1 for exercise protocols.

650 ml min⁻¹; the response time to an instantaneous full-scale signal at the mask was 1–1.5 s. Excess oxygen consumed during exercise (excess exercise oxygen consumption or EEOC) was calculated as the volume of oxygen consumed above resting levels during the exercise period, and EPOC was determined as the oxygen consumed above resting levels over the 60 min recovery period.

Blood sampling and analysis

In a separate set of experiments, blood lactate concentrations were determined from approximately 25 µl of blood collected from the orbital sinus into heparinized microcapillary tubes. All samples that took longer than 20 s to collect because the animal struggled were discarded. For animals that exercised from rest, blood was collected (i) at rest, (ii) after 5 min of exercise, (iii) after 20 min of recovery, and (iv) after 40 min of recovery. For single ABE, blood was collected from animals as above and, in addition, after 15 s of ABE. For intermittent ABE, blood was collected from animals as in the single ABE protocol and, in addition, after 90 s of ABE (six 15 s bursts of activity) and after 180 s of ABE (twelve 15 s bursts of activity). In a preliminary study, it was determined that blood collection and brief handling did not influence subsequent recovery lactate levels. Blood was immediately deproteinized with cold 6% perchloric acid, centrifuged and frozen at -70 °C for lactate determination as described by Gleeson (1985).

Statistical analyses

Comparisons among exercise groups were made by repeated-measures one-way analysis of variance (ANOVA) followed by a paired *post-hoc* test adjusted to an experiment-wise error of 5% to compare treatment groups. All data are expressed as means ± S.E.M. unless noted otherwise.

Results

The mean metabolic cost of 1 h of recovery, measured as the excess amount of oxygen consumed (EPOC volume), was significantly greater (repeated-measures ANOVA) in lizards

Table 2. Excess volume of oxygen consumed during activity before exercise

Type of ABE	Excess volume of oxygen consumed (ml g ⁻¹)		
	During ABE	Following ABE	Total
Single	0.0041±0.00032	0.0673±0.0139	0.0716
Intermittent			
Average	0.0037±0.0084	0.0200±0.0005	
Sum	0.0443±0.0021	0.2403±0.0151	0.2846

Values are means ± S.E.M. for 11 *Dipsosaurus dorsalis*.

Intermittent activity before exercise (ABE) values are averages for twelve 15 s bouts of activity and the sum is the total excess oxygen consumed during activity and pause periods.

See Materials and methods and Fig. 1 for exercise protocols.

that exercised directly from rest ($P=0.019$) than in lizards that underwent either single or intermittent ABE ($P=0.017$) (Fig. 2). ABE of 15 s decreased EPOC volumes by approximately 32% compared with that of lizards that underwent no ABE (Fig. 2; from 0.261 to 0.178 ml O₂ g⁻¹). Lizards that underwent intermittent ABE had EPOC volumes approximately 40% lower than lizards that underwent no ABE (0.156 compared with 0.261 ml O₂ g⁻¹). ABE did not significantly alter EEOC volume (Table 1; $P > 0.05$, repeated-measures ANOVA). Dividing EPOC into early (0–10 min) and late (11–60 min) phases indicates that single ABE influences recovery oxygen consumption only during the late period (Table 1), while intermittent ABE decreased recovery metabolic rates during both early and late recovery periods. The excess oxygen consumed during ABE was approximately four times higher for intermittent ABE than for single ABE (Table 2).

ABE had no influence on distance traveled during 5 min of exhaustive exercise (Table 3; $P=0.2$, repeated-measures ANOVA). However, the power of this statistical test was low ($\beta-1=0.198$, $\alpha=0.05$), and no significant difference should be interpreted cautiously. Animals subjected to intermittent ABE ran nearly 100 m prior to the 5 min exhaustive run while single

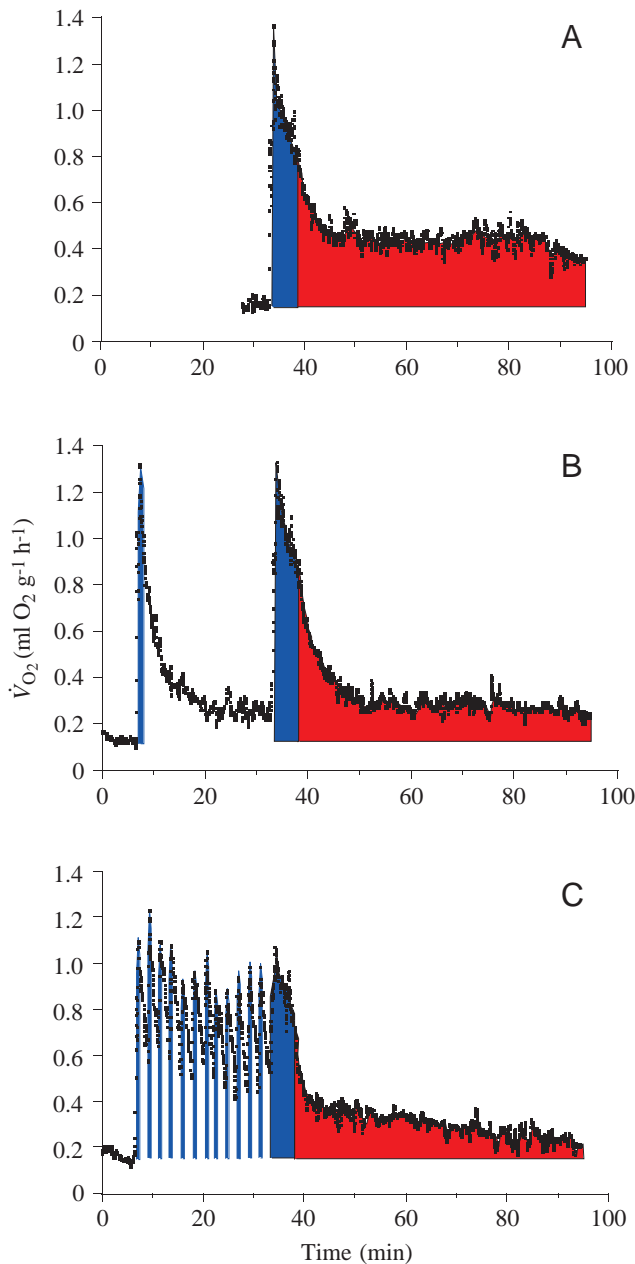


Fig. 2. $\dot{V}O_2$ values with no activity before exercise (ABE) (A), single ABE (B) and intermittent ABE (C). Excess oxygen consumption ($\text{ml g}^{-1} \text{h}^{-1}$) during ABE and 5 min of maximal exercise is represented in blue, and that during 60 min post-exercise oxygen is represented in red. Data in A are offset by 27 min for easier comparison with B and C. $\dot{V}O_2$ values are means for 11 *Dipsosaurus dorsalis*. The exercise protocol is described in Fig. 1.

ABE animals ran approximately 12 m in 15 s. Single ABE did not appear to influence distance run during 5 min of activity compared with animals that exercised without any prior activity ($P=0.63$). The total distance run was almost twice as great when animals were subjected to intermittent ABE compared with single ABE.

The average cost of activity (EEOC plus EPOC per distance traveled) was more than 30% larger in lizards without any

Table 3. Mean distance lizards traveled for different exercise protocols

Type of ABE	Distance traveled (m)		
	During ABE	During 5 min of exercise	Total distance
None	0	54.3±6.7	54.3±6.7
Single	12.3±0.5	57.0±7.1	69.3±7.1
Intermittent	95.7±6.2	37.4±8.4	132.7±14.2***

Values are means ± s.e.m. for 11 *Dipsosaurus dorsalis*.

ANOVA: *** $P<0.001$ compared with lizards that did not undergo activity before exercise.

See Materials and methods and Fig. 1 for exercise protocols.

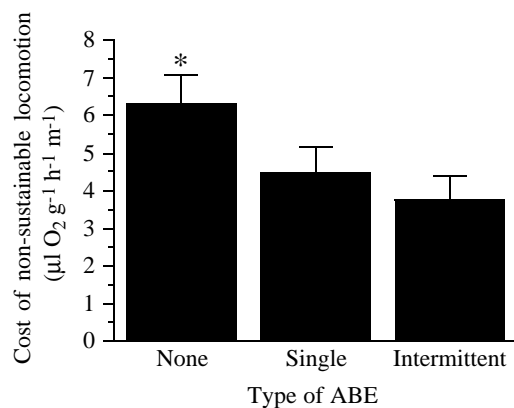


Fig. 3. Cost of non-sustainable locomotion (total oxygen consumed during ABE, exhaustive exercise and 60 min of recovery per gram of animal per hour per distance traveled). Lizards that exercised from rest had a significantly higher cost of non-sustainable locomotion than did lizards that underwent single or intermittent activity before exercise (ABE) (repeated-measures ANOVA, $P<0.05$). Values are means + s.e.m. for 11 *Dipsosaurus dorsalis*. The exercise protocol is described in Fig. 1.

prior activity ($6.08 \mu\text{l O}_2 \text{g}^{-1} \text{h}^{-1} \text{m}^{-1}$) as in those that underwent ABE ($4.45 \mu\text{l O}_2 \text{g}^{-1} \text{h}^{-1} \text{m}^{-1}$ for single ABE and $3.74 \mu\text{l O}_2 \text{g}^{-1} \text{h}^{-1} \text{m}^{-1}$ for intermittent ABE; repeated-measures ANOVA, $P<0.05$; Fig. 3). Over 60 min of recovery, almost 80% of the total excess metabolic cost of exercise was due to EPOC. Thus, the average cost of activity is substantially reduced by 30–38% if either intermittent or single ABE occurs before exhaustive exercise (Fig. 3).

Blood lactate levels do not correlate with EPOC volumes (Fig. 4). The lowest post-exercise lactate levels recorded were from lizards that exercised without ABE. Resting levels of blood lactate were $3.5 \pm 1.4 \text{ mmol l}^{-1}$ and increased to more than 30 mmol l^{-1} after single ABE and subsequent exercise. Intermittent ABE did not result in higher lactate values than did single ABE, suggesting that lactate accumulation after a single 15 s bout of activity is not additive when the activity is repeated (Fig. 4). Rates of blood lactate removal during 40 min of recovery from exhaustive exercise were more than six times

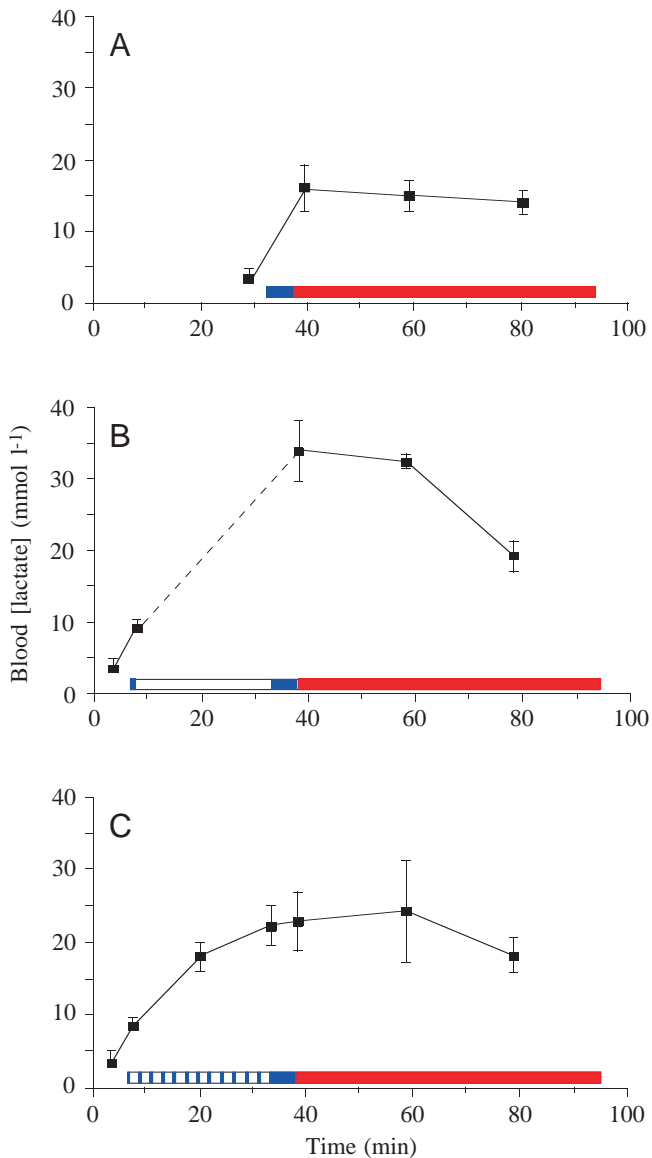


Fig. 4. Blood lactate levels with no activity before exercise (ABE) (A), with single ABE (B) and with intermittent ABE. Colored bars under the graph represent the exercise protocol described in Fig. 1. Blood lactate values are means \pm S.E.M. for 11 *Dipsosaurus dorsalis*. The dashed line in B represents the change from resting levels.

faster in lizards that underwent single ABE as in lizards without any prior activity (Fig. 4), yet no significant lactate recovery ($P=0.13$, $\beta=0.28$, $\alpha=0.05$) occurred following intermittent ABE.

Discussion

The present study demonstrates that ABE that is similar to warm-up activities in endotherms can alter subsequent recovery metabolic rate in the lizard *Dipsosaurus dorsalis*. A single 15 s burst of activity or multiple 15 s bursts of intermittent activity before exhaustive exercise decreased recovery oxygen consumption volumes by 30–40% (Fig. 2).

In addition, excess volumes of oxygen consumed during 5 min of activity and 60 min of recovery are significantly lower following ABE, suggesting that activities following ABE are energetically cheaper (Table 1). These results suggest that there may be behavioral or physiological means by which animals that move sporadically can reduce the high cost of recovery resulting from a brief period of exercise.

Influence of ABE on recovery metabolic rate

Following a brief period of exercise, oxygen consumption rates remain elevated above resting levels for extended periods in a variety of ectotherms and endotherms such as aquatic crabs (McMahon et al., 1979), land crabs (Full and Herreid, 1983, 1984), lizards (Gleeson and Dalessio, 1989), fish and amphibians (for a review, see Bennett, 1978), mice (Baker and Gleeson, 1998), horses (Lund et al., 1996) and humans (Zanconato et al., 1991). After only 5 s of activity, $\dot{V}O_2$ remains elevated for more than 30 min in the lizard *D. dorsalis* (J. M. Nedrow, D. A. Scholnick and T. T. Gleeson, in preparation) and for almost 20 min in mice (Baker and Gleeson, 1998). Our results indicate that ABE can reduce EPOC volumes following 5 min of exhaustive exercise, suggesting that brief activities prior to exhaustive exercise can partially reduce the high cost of recovery.

There are a number of possible explanations for the reduction in recovery metabolic rate in lizards following ABE. One hypothesis is that, at the onset of exercise when there has been no prior warm-up activity, the circulatory and respiratory systems cannot immediately meet energy demands. There is evidence that altered muscle perfusion during exercise may be associated with brief warm-up activity in humans (Germino et al., 1996). ABE may therefore enhance oxygen and substrate delivery during subsequent exercise, thereby reducing reliance on cellular energy stores and consequently reducing EPOC. ABE may have a dramatic influence on lizard recovery metabolic rate in part because of the relatively low (compared with endotherms) aerobic capacity and longer recovery periods typical of ectotherms (Bennett and Dawson, 1972). Thus, even small enhancements in circulatory or respiratory function prior to exercise may have a large impact on EPOC in lizards.

While factors such as lactate accumulation and endocrine response are known to influence EPOC, the causal mechanism for elevated $\dot{V}O_2$ during recovery remains unclear. Of the many exercise studies conducted on humans, it has been reported that the magnitude and length of EPOC can be influenced by exercise duration (Gore and Withers, 1990a,b) and intensity (Hagberg et al., 1980) and even the type of activity (Laforgia et al., 1997). The results presented in this study suggest that the type of activity prior to exhaustive exercise can also influence EPOC and that as little as 15 s of activity 27 min prior to exercise can decrease subsequent EPOC.

Effect of ABE on lactate metabolism

Single ABE resulted in elevated blood lactate levels and elevated rates of lactate removal during recovery compared with animals that exercised directly from rest (Fig. 4). One

possible mechanism for the altered lactate removal rates may be higher levels of aerobic metabolism during intermittent activity resulting in greater aerobic utilization of lactate during the 2 min pause periods. In addition, it was recently reported that glucagon levels peak during the first 15 min of recovery in *D. dorsalis*, while corticosterone levels are elevated only after 45 min of recovery when lizards are exercised without any prior activity (Scholnick et al., 1997). Thus, the temporal occurrence of different locomotor activities may be a significant factor in determining overall recovery metabolic rate by elevating levels of 'recovery hormones' earlier in the recovery period than in animals that exercise from rest, thereby enhancing lactate removal rates.

Elevated catecholamine levels earlier in the exercise or recovery periods may also affect subsequent metabolism and lactate utilization. Catecholamine levels are known to increase during exercise and to accelerate blood lactate removal in lizards (Gleeson et al., 1993). Stimulation of lactate removal during ABE or earlier in the recovery period may therefore result in lower cellular lactate levels during exercise and reduced EPOC volumes. Warm-up activities are also known to elevate lactate clearance rates during recovery in humans (Houmard et al., 1991).

Implications

The consequences of altered recovery metabolism on ectotherm energetics and locomotion may be important to animal locomotion in nature. Unfortunately, there has been no detailed locomotion study for *D. dorsalis* to determine whether brief exercise or intermittent activity influences performance in the field. As reviewed by Hertz et al. (1988), lizards rarely move continuously, with locomotion in many species being characterized by brief activity followed by pauses. This may be supported by recent field observations that suggest that startled *D. dorsalis* run for less than 15 s (T. Hancock and S. Adolph, personal communication). It has previously been reported that other ectotherms, such as the ghost crab *Ocypode quadrata*, can increase their endurance by moving intermittently but without significant changes in muscle lactate levels or $\dot{V}O_2$ compared with continuous exercise regimens in the laboratory (Weinstein and Full, 1992). *O. quadrata* were also found to locomote intermittently in the field when stressed (Weinstein, 1995), suggesting that brief or intermittent activity may be an important performance and endurance factor in nature for ectotherms. It will be interesting to examine the impact of ABE on EPOC following brief intermittent activity, which may be a more common locomotor pattern in lizards than exhaustive exercise.

If EPOC is included in the metabolic cost of exercise (cost of activity), then even a brief period of activity prior to exercise can greatly reduce the cost of locomotion (Fig. 3). A short burst of activity prior to exercise reduced the cost of activity (net oxygen consumption during and after an exercise bout per distance traveled) from 6.08 to as little as 3.74 $\mu\text{l O}_2 \text{ g}^{-1} \text{ h}^{-1} \text{ m}^{-1}$. The majority of the energetic savings can be attributed to reductions in metabolic rate during recovery.

The lactate produced to power running that is not metabolized before the rate of oxygen consumption returns to resting levels should be accounted for when estimating the total metabolic cost of activity. In the present study, 14–19 mmol l^{-1} of lactate remained after 40 min of recovery (Fig. 4). The additional oxygen needed to convert the remaining lactate to ATP (1.5 mol of ATP generated per 1 mol of lactate; 1 ml of $\text{O}_2 = 0.28 \text{ mmol of ATP}$; T. V. Hancock, S. C. Adolph and T. T. Gleeson, in preparation) will increase the amount of oxygen consumed during the remainder of recovery by between 0.057 and 0.080 ml g^{-1} (Table 1). Because the lactate concentration at the end of recovery was approximately 5 mmol l^{-1} higher in the lizards that underwent ABE, the energy saving due to activity before exercise is reduced to approximately 20–22%. The calculations above are overestimates of the contribution of the remaining lactate to EPOC because lactate values are based on 40 min of recovery rather than lactate remaining after rates of oxygen consumption return to resting levels. However, activity before exercise still reduced recovery metabolic rate by approximately 20% (Table 1).

Our results suggest that brief periods of activity before exhaustive exercise can significantly alter recovery metabolic rate in lizards. Because of the lengthy and costly recovery periods common in ectotherms following even brief exercise, our results suggest that intermittent activity in the field may provide behavioral or physiological means by which animals can partially reduce the high recovery costs suggested from studies of single bouts of exercise. Although the cause of the reduction in EPOC due to ABE remains unclear, post-exercise blood lactate levels and removal rates suggest that ABE may alter hormone levels prior to exercise, thereby decreasing metabolic rate earlier in the recovery period.

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