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METABOLIC RECOVERY FROM EXHAUSTIVE ACTIVITY BY A SMALL LIZARD

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Abstract—1. Whole-body lactate production during intense activity was insensitive to body temperature T_b from 25 to 35°C in the lizard *Podarcis taurica*.
2. Whole-body lactate removal during recovery was more sensitive to T_b from 15 to 35°C and was two orders of magnitude slower than production.
3. At 30°C a significant oxygen debt persisted for a similar period to elevated lactate.
4. Lizards recovering in refuges at 25 or 35°C emerged later than unexercised lizards, while, at 15°C they emerged after a short period and speeded recovery by basking.

INTRODUCTION

Anaerobic glycolysis is a major source of energy for activity in reptiles (reviews in Bennett, 1978, 1982; Gatten, 1985). Although this can rapidly produce ATP in the muscles, it is not sustainable as it leads to glycogen depletion and lactate accumulation with resulting acid–base imbalance. A period of recovery is therefore needed after intense activity, during which the animal is to some degree incapacitated. Lactate removal during recovery may be measured as a fall in blood levels or as total lactate in whole body homogenates, usually depending on the size of the animal. These measures may not be equivalent (Bennett and Licht, 1972; Gratz and Hutchison, 1977). The former can be related to the problem of acid–base imbalance and the mechanism of blood buffering (Gleeson and Bennett, 1982), but the latter is more useful in discussion of the overall rate of recovery. Previous studies of total lactate removal have involved either few samples (Bennett and Licht, 1972; Gratz and Hutchison, 1977) or single temperatures (Coulson, 1980; Gleeson, 1982). The time-course and temperature-dependence of this process are therefore poorly understood. The main aim of this paper is to provide these data for a small lacertid lizard, *Podarcis taurica*, which was available in large numbers.

The rate of lactate production during intense exercise was also investigated in detail at a wide range of body temperature (T_b): 15–35°C. Lactate production is usually described by two parameters, the anaerobic scope (rate over the first 30 sec of activity) and the anaerobic capacity (difference between levels at rest and at exhaustion). These were originally based on the timing of qualitative running performance (Bennett and Licht, 1972) and are now standard. The only reptile for which a comprehensive curve for glycolysis is available (*Anolis carolinensis*—Coulson, 1980) was exercised at a single T_b, as this subtropical lizard could not be stimulated to activity at low T_b.

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Closely related reptiles often show differences in aerobic metabolism correlated with their behaviour or thermal experience (e.g. Hailey and Davies, 1986), while anaerobic glycolysis seems to be rather invariable (Bennett and Licht, 1972; Bennett and Ruben, 1975). A possible reason for this lack of variation is that anaerobic glycolysis is most useful in intense exercise such as escaping predators, which usually involves similar behaviour in related animals, although some lactate does accumulate in less intense activities (Pough and Andrews, 1985). The sympatric lizards *P. taurica* and *P. erhardii* are examples of the two major ecological types of the genus *Podarcis*, inhabiting scrub or grassland and cliffs or walls, respectively. They have similar foraging behaviour, and an equivalent species pair in Italy (*P. sicula* and *P. muralis*) have identical thermal preferences and food consumption (Avery, 1978). Their escape behaviour differs markedly, however; burrow refuges are scarce in open scrub and *P. taurica* must often make long runs to them, while *P. erhardii* is usually near a suitable crevice. The final aim of this paper is to quantify the escape behaviour of these lizards and compare their lactate production during intense activity.

METHODS

Animals

Podarcis taurica (Balkan wall lizard) and *P. erhardii* of 3–8 g were caught at Alyki, Greece (40°N, 22°E), mostly in spring and autumn. Some lizards of each species were chased until they escaped into a refuge, and the distance run and their escape behaviour were noted using the scheme developed by Schall and Pianka (1980) for ecologically-similar Teiid lizards in scrub. Lizards were chased away from cover when possible, and so the escape distances are worst case measures rather than the distance to the nearest refuge.

Lizards were kept in 1 × 0.5 m cages with grass, water, a bulb for thermoregulation for 10 hr per day, and fed *Tenebrio* larvae. Most were used within 3 weeks of capture, though some were kept up to 2 months; such a period of confinement does not affect the anaerobic capability of lizards (Gleeson, 1979). Those kept for long periods did not

have excessively fat bodies when analysed. T_b during normal activity in the cages was measured with a quick-reading mercury thermometer.

Activity and recovery

Lizards were fasted for 3 or 4 days before use. For recovery, they were rested in a chamber at 35°C for 2 hr and then exercised in a plastic bowl over a hot plate for 2 min. At first they ran rapidly around the bowl in response to tapping the hind legs or tail, and later they were repeatedly overturned and made to right themselves. Lizards were then left to recover in small plastic bottles for various periods, in darkness in chambers at 15, 25 or 35°C (±1°C). This was designed to simulate a lizard exercising at normal activity T_b and escaping to a cold or warm refuge. The rate of cooling under similar conditions was measured with a YSI telethermometer probe inserted 1 cm into the cloaca and taped to the tail, and recorded on a chart recorder. After the recovery period a lizard was immediately frozen in ethanol equilibrated over dry ice (−55°C; Bennett *et al.*, 1981), blotted dry and stored at −20°C. For lactate production, lizards were rested at the test temperature for 5 hr (35°C) or overnight (15 and 25°C), and exercised for various periods before freezing. At 15 and 35°C the plastic exercise arena was over cold water or a hot plate, respectively.

Tissue metabolites

Frozen lizards were stored for up to 2 weeks before lactate analysis. They were manipulated on a marble slab at −20°C. After being cut along the midline with scissors, one half including the tail tip was diced in 3–4 mm sections into 30 ml chilled 10% perchloric acid in a cold pestle on ice, and homogenised until only skin remained (5–8 min). Ten ml of the homogenate was centrifuged at 5000 rpm and 4°C for 10 min; 1 ml of the supernate was neutralised with 0.6 ml 3 M $KHCO_3$ and centrifuged at 10 000 rpm and 2°C for 15 min. A 50 or 100 µl sample was incubated in a cuvette with NAD, LDH (Serva) and a glycine-hydrazine buffer pH 9.5, two samples per lizard, the complete reaction taking 3–6 hr.

Lizards were stored for an additional 1–3 weeks before analysis of hind limb muscle for glycogen. Many of those exercised or recovered at 25 and 35°C were stored for several months; these were found to have deteriorated, and were abandoned. Small muscle samples thawed rapidly, and so the whole thigh was excised, quickly skinned, and boiled in 5 ml 30% KOH for 20 min. Two 0.1 or 0.2 ml samples from each lizard were analysed for glycogen with the anthrone reagent (Seifter *et al.*, 1950) using a saturated Na_2SO_4 co-precipitate (Zwaan and Zandee, 1972) against multiple glucose standards. Dissection of the abandoned lizards showed that the bone accounted for 9 ± 1% of the skinned thigh weight, and muscle glycogen was calculated accordingly.

Oxygen debt

A previously unreported measurement of oxygen debt in *P. taurica* was available for comparison. Five large lizards (7.2 ± 1.5 g) fasted for 3 days were rested overnight at 30°C in a constant temperature room, exercised for 2 min, and placed in a 15 × 2 cm diameter tube in one stream of a Servomex OA 184 oxygen analyser in the same room, after the analyser base line had stabilised. Flow rate was 170 ± 15 ml min^{-1}, and the animal and control streams passed along similar tube systems, each with a 50 ml desiccant tube. The difference of % O_2 between the two streams was followed by 2 hr on a servoscribe 2_S pen recorder, and $\dot{V}O_2$ was calculated over 3 or 10 min intervals as a rate (ml g^{-1} h^{-1}) corrected to standard temperature (0°C) and pressure (760 Torr). These measurements were made in the Biological Laboratory, University of Kent at Canterbury, UK.

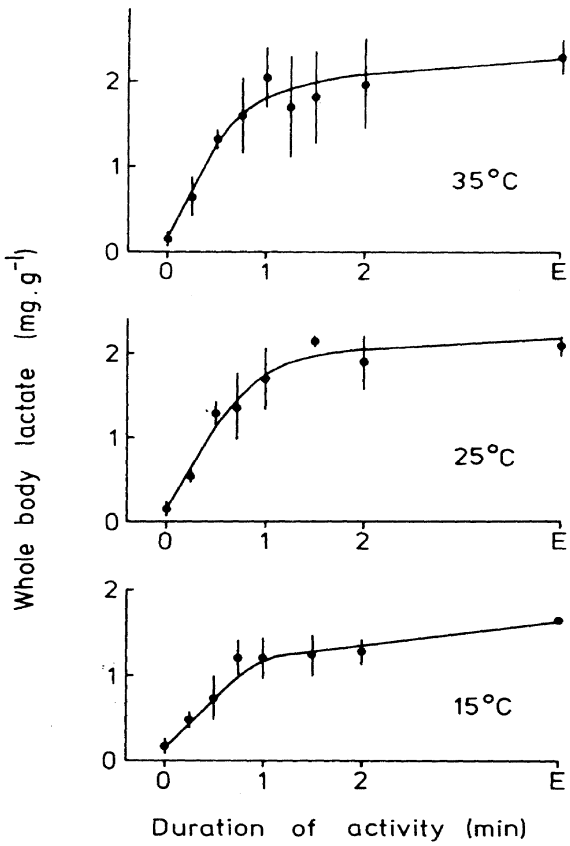

Fig. 1. Total lactate production in *P. taurica* exercised at different body temperatures. Each point is 4 or more lizards ± 1 SD is the level at exhaustion; endurance in Table 1. Curves fitted by eye.

Emergence after recovery

One cage was modified to include a controlled temperature refuge. The base of this refuge was a 15 × 7 × 1 cm deep metal box with an internal baffle, through which water at 15, 25 or 35°C from a water bath was fed by gravity at a rate of about 1 l/min^{-1}. The refuge had a cardboard top and sides so that the lizard was in a crevice 7 mm high with an open front along the long side. A lizard was warmed to 35°C in a dark chamber for 1 hr, then exercised for 2 min as above, and placed in the refuge, from which it could see a basking site, food, and a conspecific "scapegoat" engaged in normal activity. A few initial experiments without the latter gave very irregular pre-emergence periods, some over 90 min. The recovering lizard was observed at 2 min intervals through a hidden peephole, and its time to emergence and subsequent behaviour were noted. Control measurements were made on similarly treated but unexercised lizards.

Statistical analysis followed (Sokal and Rohlf, 1981). Unless stated otherwise, P values are for small or equal sample t-tests. Values in the text are ±1 SD.

RESULTS

Lactate production

Resting lactate levels did not differ between the three T_b ($P > 0.1$) and the pooled value 0.15 ± 0.09 ($N = 12$) is therefore used. Lactate accumulated rapidly at an almost constant rate over the first 45–60 sec of activity at all T_b (Fig. 1). This corresponds to the observed period of intense running activity. The initial rate of production may thus be

Table 1. Whole body lactate levels during activity and rate of lactate production and removal, with Q_{10} values

T_b (°C)	35		25		15
Total lactate, 30 sec (mg g^{-1})	1.33 ± 0.12		1.29 ± 0.14		0.74 ± 0.27
Anaerobic scope (mg g^{-1} 30 sec^{-1})	1.18		1.14		0.59
Q_{10}		1.04		1.93	
Total lactate, 2 min (mg g^{-1})	1.96 ± 0.52*		1.89 ± 0.33		1.28 ± 0.14
Total lactate exhausted (mg g^{-1})	2.28 ± 0.21		2.08 ± 0.12		1.64 ± 0.05
Anaerobic capacity (mg g^{-1})	2.13		1.93		1.49
Q_{10}		1.10		1.30	
Lactate removal (mg g^{-1} hr^{-1})	3.6		1.2		0.4
Q_{10}		3.0		3.0	
Time to resting lactate (hr)	0.75		1.55		4.2
Q_{10}		2.1		2.7	
Lactate production/removal	39		110		180
Endurance (min)	8.0 ± 2.0		7.2 ± 1.3		4.2 ± 0.4

*$N = 8$, otherwise $N = 4$. Means ± SD.

calculated over any interval within this period, and anaerobic scope over 30 sec is used in further analysis for historical reasons (Bennett and Licht, 1972). Lactate levels after 30 sec were similar at 25 and 35°C ($P > 0.5$), but were significantly lower at 15°C ($P < 0.02$) (Table 1). Q_{10} for anaerobic scope was thus low (1.04) from 25 to 35°C, and higher (1.93) from 15 to 25°C.

The rate of lactate production decreased sharply after 60 sec (Fig. 1), corresponding to the observed period of reduced activity (slow righting response) up to exhaustion. Curves for 25 and 35°C were very similar, but peak lactate levels were lower at 15°C. Total lactate was not significantly different between 25 and 35°C either after 2 min ($P > 0.5$) or at exhaustion ($P > 0.1$). Total lactate was significantly lower at 15°C than at 25°C at both times ($P < 0.02$ and $P < 0.001$ respectively).

Lactate production effectively ceased after 2 min at 25 and 35°C; levels at 2 min and at exhaustion were not significantly different at either T_b (both $P > 0.2$). Lactate levels increased significantly ($P < 0.01$) between 2 min and exhaustion at 15°C. This contrasts with endurance at different T_b. Time to exhaustion was similar at 25 and 35°C ($P > 0.5$) but shorter at 15 than at 25°C ($P < 0.01$) (Table 1). These endurance measurements were partly subjective, since activity was spasmodic after the initial intense period (Bennett and Licht, 1972). They are, however, for the same occasions as the exhausted lactate data. It is thus clear that the increased lactate between 2 min and exhaustion at 15°C, but not at higher T_b, does not result from greater duration of activity at 15°C.

Anaerobic capacity at exhaustion is shown in Table 1. The low Q_{10} (1.10) from 25 to 35°C was similar to the Q_{10} for anaerobic scope over this T_b interval. From 15 to 25°C anaerobic capacity was less temperature-sensitive than scope (Q_{10} 1.3 and 1.9 respectively).

Lactate removal

Active lizards selected T_b of 34.7 ± 1.8°C ($N = 15$), similar to the 35°C exercise T_b used experimentally. At all three recovery T_b there was a period of constant lactate removal, i.e. a linear decrease with time (Fig. 2). The rate of removal was much more sensitive to T_b than was the rate of production, with Q_{10} of 3.0 over both 15–25°C and 25–35°C intervals. Removal rates were lower than production rates by an average two orders of magnitude, though this varied with T_b due to the different Q_{10} for production and removal (Table 1).

There was a 10 min delay before rapid lactate removal at 35°C (Fig. 2). Extrapolating from the period of linear removal to a resting level of 0.15 mg g^{-1} shows the time for complete recovery from activity in terms of total lactate (Table 1). This had lower Q_{10} than did the peak rate of removal, and Q_{10} was lower from 25 to 35°C than from 15 to 25°C.

Glycogen depletion and replacement

Resting lizards had 8.2 ± 2.7 mg g^{-1} hind limb muscle glycogen, falling to about 3 mg g^{-1} after activity at 15°C (Fig. 3a). The time-course of glycogen depletion was similar to that of lactate production, being greatest over the initial 45–60 sec of activity. After 2 min of activity at 35°C muscle glycogen was reduced to 0.44 ± 0.05 mg g^{-1} (Fig. 3b, 0 hr recovery). Glycogen depletion at 15°C was thus only 66% of that at 35°C; overall depletion, 63% and 95%, respectively. This agrees well with lactate production, since anaerobic capacity at 15°C was only 70% of that at 35°C (Table 1). Glycogen replacement in the hind limb muscle occurred at a constant rate of 15 °C (Fig. 3b), reaching 7.7 ± 2.7 mg g^{-1} after 4 hr. This was not significantly different from the resting level ($P > 0.5$). The rate of replacement at 15°C was 1.81 mg g^{-1} hr^{-1}.

Oxygen debt

Oxygen consumption after activity at 30°C decreased rapidly for 10 min, then at a lower rate up to 60 min, and reached a stable level between 100 and 120 min (Fig. 4). At 60 min or later, $\dot{V}O_2$ was not significantly different from the stable level ($P > 0.05$); it was significantly different at 50 min and earlier ($P < 0.05$ or better).

Resting $\dot{V}O_2$ was not measured, and so is estimated to allow the oxygen debt to be calculated. Cragg (1978) measured $\dot{V}O_2$ at 30°C in the similar Italian *Podarcis sicula* (7–9 g), and resting levels have been estimated from Figs 4 and 5 in this article. Stable night-time $\dot{V}O_2$ was 0.13 ± 0.01 ml g^{-1} hr^{-1} ($N = 3$) under normal photoperiod conditions, and 0.21 ± 0.04 ml g^{-1} hr^{-1} ($N = 4$) in constant light or darkness. These are similar to the value after 2 hr recovery, 0.16 ± 0.07 ml g^{-1} hr^{-1} (Fig. 4), which is thus taken as a truly resting value. Total $\dot{V}O_2$ during

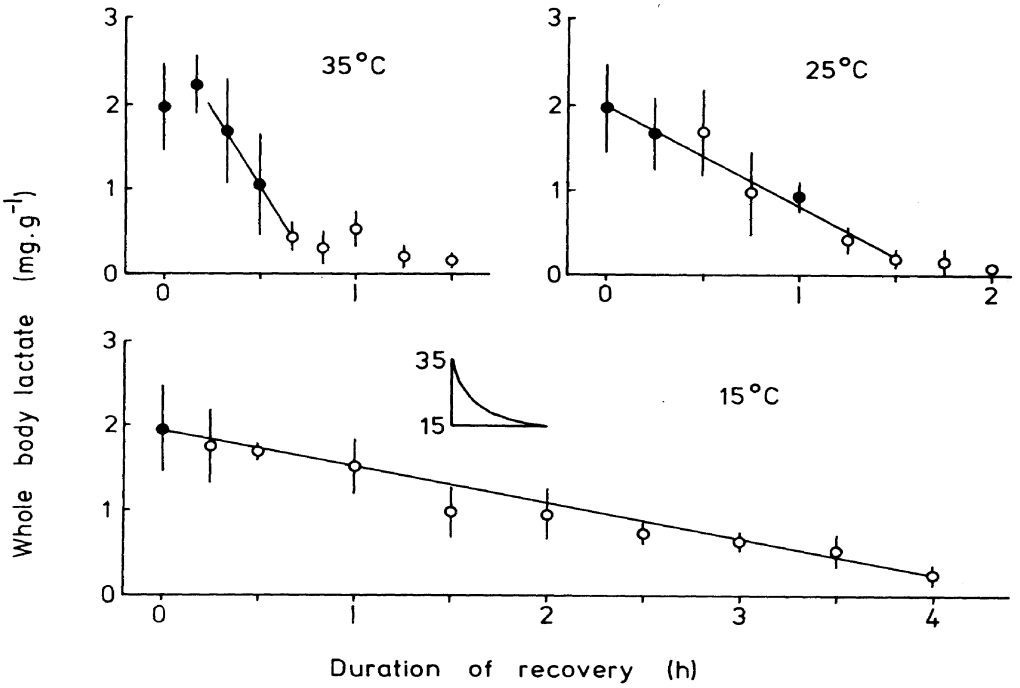

Fig. 2. Total lactate removal in *P. taurica* exercised for 2 min at 35°C and recovering at different T_b. Each point is 4(○) or 8 (●) lizards ± 1 SD. The inset shows the fall of T_b at 15°C, to the same time scale, showing that thermal equilibration was rapid compared to lactate removal. Curves fitted by eye.

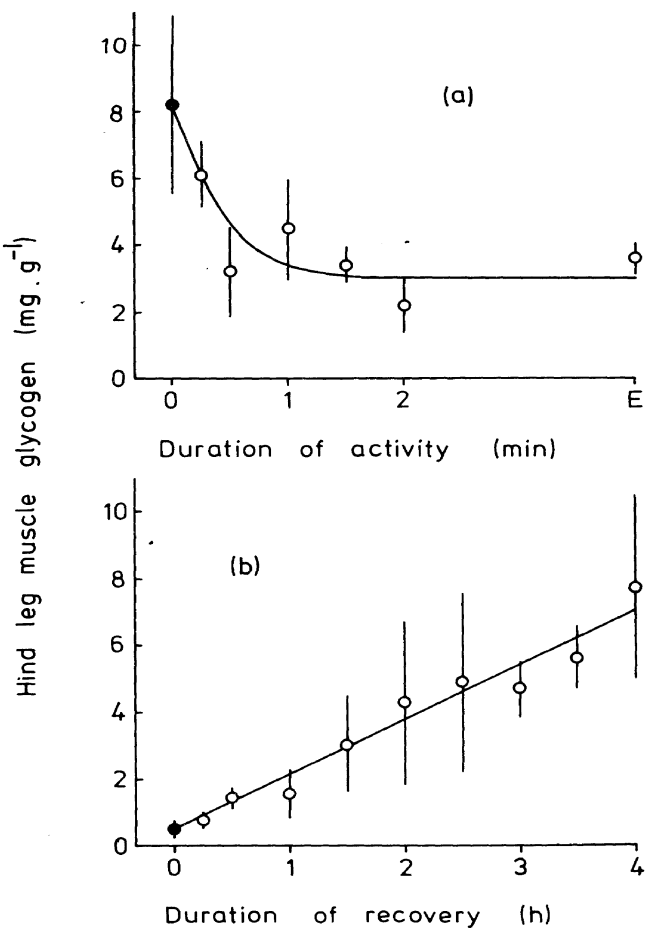

Fig. 3. Muscle glycogen in *P. taurica*. (a) Depletion during activity at 15°C, E = exhausted. (b) Restoration at 15°C after 2 min activity at 35°C. Each point is 4 (○) or 8 (●) lizards ± 1 SD. Curves fitted by eye.

2 hr of recovery was 0.65 ml g^{-1}, of which resting $\dot{V}O_2$ would account for about half (0.32 ml g^{-1}), leaving an oxygen debt of 0.33 ml g^{-1}.

Emergence after recovery

Lizards which had been rested in the dark for 1 hr emerged almost immediately after being placed in the refuge at all three T_b. Those exercised for 2 min remained in the refuge for much longer. Recovery times before emergence (in min, with range, $N = 10$ per group) were:

35°C	29 ± 12 (13–50)
25°C	24 ± 9 (14–45)
15°C	10 ± 8 (2–27).

There was significant variation between these groups

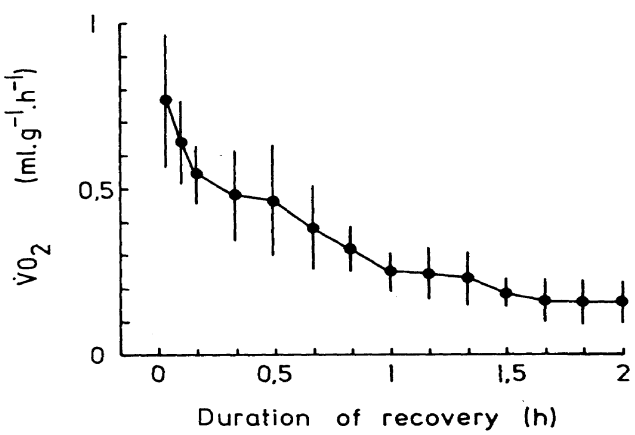

Fig. 4. Oxygen debt in *P. taurica* recovering at 30°C after 2 min activity at the same T_b. $N = 5$, ± 1 SD.

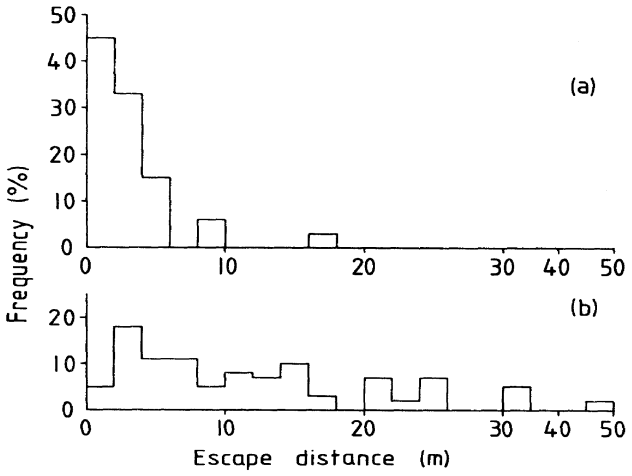

Fig. 5. The distance which lizards ran before reaching a refuge in the field. (a) *P. erhardii*, $N = 34$; (b) *P. taurica*, $N = 61$.

(Kruskal–Wallis test, $P < 0.005$). Wilcoxon two-sample tests showed that recovery periods at 25 and 35°C were not significantly different ($P > 0.1$), but these were significantly longer than at 15°C (both $P < 0.001$).

Lactate levels after the observed periods of recovery may be estimated from the slopes in Fig. 2. At the mean time of emergence, about 50, 30 and 4% of the lactate (above resting) would be removed at 35, 25 and 15°C, respectively. After emergence lizards always moved to the lamp and basked; those from the 15°C refuge remained under the lamp for at least 15 min.

Interspecific differences

Podarcis erhardii usually escaped directly into a hole or crevice, while *P. taurica* had more diverse escape behaviour involving long runs, zig-zag runs and dashes between cover, and seldom escaped directly to a hole (Table 2). Escape behaviour differed significantly between these species; χ^2-tests of "directly to hole" vs other categories, $P < 0.001$. This difference is largely due to habitat. *P. erhardii* was usually close to a suitable hole and could make a short dash to it (Fig. 5a, mean escape distance 3.1 m), while *P. taurica* could often be chased for a long distance before finding cover (mean 11.9 m). Escape distance was significantly different in the two species; χ^2-test of 0–4 vs $\geqslant 5$ m, $P < 0.001$.

Lactate levels during exercise at 35°C did not differ significantly between the two species at any time (Table 2), $P > 0.05$ or greater. There was no trend to the differences, and so further comparison by analysis of variance or combined probability has not been attempted. There was, however, a significant difference in endurance; *P. erhardii* became exhausted more quickly (Table 2). $P < 0.05$.

DISCUSSION

Substrate availability, activity and fatigue

A resting *P. taurica* has about 8 mg g^{-1} glycogen in its hind limb muscles, more than reported for other lizards: 3–5 mg g^{-1} in the related *Lacerta vivipara* (Patterson *et al.*, 1978), 5.7 mg g^{-1} in *Sceloporus occidentalis* (Gleeson, 1982), 3.7 mg g^{-1} in *Agama stellio* (Loumbourdis and Hailey, 1985) and 6.4 mg g^{-1} in an unidentified desert lizard (Haggag *et al.*, 1966), but lower than the 11 mg g^{-1} for the snake *Nerodia rhombifera* (Gratz and Hutchinson, 1977). Resting body lactate, 0.15 mg^{-1}, was low compared to other values for squamate reptiles (Table 3 of Loumbourdis and Hailey, 1985); together, glycogen and lactate levels indicate that true resting conditions were achieved.

Lactate production was remarkably insensitive to T_b from 25 to 35°C. The period of intense exercise could be divided into two phases: a rapid lactate increase for about 60 sec corresponding to intense behavioural activity, and a period of non-significant increase thereafter until exhaustion, during which the lizard could only right itself slowly. Muscle glycogen was nearly exhausted at the end of the first phase, for example it was reduced to 5% of resting level after 2 min at 35°C. It is thus probable that the first stage of fatigue results from glycogen depletion. The energy source for the low activity of the second phase, which lasts for about 6 min, may be extra-muscle glucose (Hochachka, 1985). Final exhaustion, at the end of the second phase, probably results from acid–base imbalance (Gleeson and Bennett, 1982). The initial accumulation of lactate was significantly slower at 15°C. Total lactate continued to increase during the second phase at 15°C, but reached lower peak levels than at 25–35°C, and muscle glycogen was only reduced by 63%. It is thus clear that substrate depletion is not responsible for fatigue at 15°C.

It is possible to predict the behaviour of the rate-limiting step of glycolysis in *P. taurica* from these results. Between 25–35°C this step is insensitive to T_b, because anaerobic scope has low Q_{10}, and to pH, because glycolysis is still rapid from 30 to 60 sec when the lactate level is already high. Glycolysis is slower at 15°C, and sensitive to low pH at this T_b; glycolysis stops while substrate is still available, and at a lactate level at which it is still rapid at 25–35°C. The rate-limiting step may be phosphofructokinase (PFK), the regulatory enzyme of glycolysis which is present in relatively large amounts in lizards with high anaerobic performance (Bennett, 1972a). Inhibition of PFK by low pH during exercise has been shown in mammal muscle (Edwards, 1983).

Table 2. Escape behaviour in the field and lactate levels at 35°C in *Podarcis taurica* and *P. erhardii*

	P. taurica	*P. erhardii*
Escape category N	61	34
Open to grass (%)	35	0
Open to shrub	20	0
Open to ground cover	3	6
Zig-zag open	20	0
Shrub to shrub	13	3
Directly to hole	8	91
Lactate, resting (mg g^{-1})	0.15 ± 0.09	0.22 ± 0.14
30 sec	1.33 ± 0.12	1.21 ± 0.16
60 sec	2.04 ± 0.34	1.64 ± 0.14
2 min	1.96 ± 0.52	2.05 ± 0.26
Exhausted	2.28 ± 0.21	2.17 ± 0.43
Endurance (min)	8.0 ± 2.0	4.9 ± 1.5

Variation in glycogen availability

Most animals were used in the autumn, when lizards have greatest capacity to store glycogen (Di Maggio and Dessauer, 1963) and muscle glycogen reaches peak levels. Muscle glycogen is lowest in summer; 3.3 mg g^{-1} in *Sceloporus* (Gleeson, 1982) and 1–2 mg g^{-1} in *Lacerta* (Patterson *et al.*, 1978). Most of the glycogen in the muscle was used up during intense activity at normal T_b, suggesting that lizards have greatly reduced anaerobic capacity during summer. The alternative hypothesis for the seasonal pattern found in *Lacerta* is that summer levels are the normal available for use in exercise, and that additional storage in autumn is for use during hibernation and is unavailable for activity. This alternative can now be rejected; the high level of muscle glycogen in *P. taurica* was fully utilised during exercise.

The implication of low muscle glycogen, and hence anaerobic capacity, in summer, is that lizards should be easier to catch than at other times. In fact *P. taurica* were almost impossible to catch during summer; less than 10% were caught, compared to more than 50% in spring and autumn. Our hypothesis is that *P. taurica* have higher T_b in summer and so aerobic metabolism plays a greater part in energy production during escape.

Interspecific differences in activity

The escape behaviour of *P. taurica* and *P. erhardii* was significantly different, the former having to run much further to reach a refuge. Their anaerobic scope and capacity were, however, indistinguishable. The only significant difference was endurance, *P. erhardii* remaining active for only 61% as long as *P. taurica*. While this difference is in the direction which would be expected from their escape distances, it is difficult to interpret ecologically; the second phase of low activity which is longer in *P. taurica* would not seem to offer good opportunities to escape from predators. These species would be good experimental material for analysing the physiology of final fatigue.

Lactate removal and recovery

There was no significant loss of lactate over the first 10 min of recovery at any T_b, and there was a noticeable delay before lactate removal began at 35°C. One possible reason for this is a delay in transport to the liver. Compartmentalisation studies have shown that lactate does not reach peak levels in the blood and liver until 10–15 min after exercise (Bennett and Licht, 1972; Gleeson, 1980a). Lizard skeletal muscle can resynthesise glycogen, but this only accounts for a small proportion of the total lactate removed (Gleeson, 1985).

The peak rate of removal was strongly influenced by T_b, with Q_{10} of about 3. The time to recover to resting total lactate had lower Q_{10}, of 2.1–2.7. This pattern is similar to that in *Anolis carolinensis* (Bennett and Licht, 1972), and blood lactate and oxygen debt duration are also temperature-dependent in the marine iguana (Gleeson, 1980a). The latter study suggested that rapid repayment of oxygen debt could explain basking behaviour by marine iguanas after foraging dives, although it was also shown (Gleeson, 1980b) that these dives were supported aerobically. Prolonged basking (K thermoregulation of Hailey and Davies, in press) in the marine iguana is thus more likely to facilitate digestion of the food obtained (e.g. Greenwald and Kanter, 1979) than recovery from activity. This study has shown that recovery affects thermoregulation in *P. taurica*, which avoid cool refuges where lactate removal would take 4 hr, and bask at normal T_b of about 35°C where it takes less than 1 hr.

Glycogen resynthesis and recovery

Muscle glycogen was restored to pre-exercise level during recovery at 15°C, over a similar time scale to that of lactate removal. This took place in the absence of dietary carbohydrate, which is necessary to mammals but which would impose severe constraints on reptiles with heavy reliance on anaerobic glycolysis (Gleeson, 1982). While most of the lactate produced during exercise is oxidised in mammals, in lower vertebrates it has been suggested that most is reconverted to glucose (Gratz and Hutchison, 1977; Bennett, 1978). The fate of lactate may be predicted by considering the size and time-course of the oxygen debt. This may have alactacid and lactacid components, i.e. resynthesis of high energy phosphates and reoxygenation of respiratory pigments, and gluconeogenesis, respectively.

Dmi'el and Rappeport (1976) and Gleeson (1980) have suggested that oxygen debt in reptiles is primarily alactacid, based on the different time-course to that of lactate removal, while Gratz and Hutchison (1977) suggest that about 50% of the debt is lactacid in the snake *Nerodia*. Bennett (1972b) separated the debt into these components for two large lizards, using the change of slope in the plot of log $\dot{V}O_2$ during recovery as an indicator of a metabolic transition. All of these studies have used large reptiles, in which total lactate levels (and so removal rates) can only be measured with difficulty (Gratz and Hutchison, 1977) if at all; blood lactate is an unreliable indicator of total levels (e.g. Bennett and Licht, 1972). It is therefore of interest to attempt this analysis on the small *P. taurica*.

This discussion uses Gratz and Hutchison's (1977) values for ATP equivalent of oxygen debt (1 μl $O_2 = 0.268$ μmol ATP) and requirement for gluconeogenesis (6 μmol ATP for 2 μmol lactate to glucose). These were based on the mammalian pattern of gluconeogenesis in the liver using the oxidation of fatty acids for energy. Oxygen debt at 30°C was 0.33 ml g^{-1}, producing 88 μmol ATP g^{-1}. The lactate removed is taken as the average of that produced after 2 min at 25 and 35°C, 1.81 and 1.74 mg g^{-1} respectively above resting. This would use 59 μmol ATP g^{-1}. The measured oxygen debt would thus supply about 150% of the energy requirement for total gluconeogenesis.

Lactate removal at 30°C would take about 1 hr by interpolation between recovery at 25 and 35°C. This is also the time which a measurable oxygen debt persisted. The time scale of raised $\dot{V}O_2$, the size of the oxygen debt, and the complete replacement of muscle glycogen, all suggest that most or all of the lactate produced during activity is resynthesised to glycogen in *P. taurica*.

Alactacid oxygen debt

$\dot{V}O_2$ decreased sharply in the first 10 min recovery at 30°C, to a stable rate of decrease during the main period of recovery, 10–60 min. One interpretation of this pattern is that there is an exponential decline of $\dot{V}O_2$ (Bennett, 1972b). Coulson (1980) has suggested an exponential decay for total lactate removal in *Anolis* at 28°C, though his Fig. 1 could as easily be interpreted as a linear decline. While the shape of the recovery curve in *P. taurica* at 35°C is ambiguous, those at 15 and 25°C are clearly linear, i.e. an enzyme-limited rather than substrate-limited process. In that case, why does $\dot{V}O_2$ decline more rapidly in the first 10 min?

The initial 10 min is also the time of a delay before lactate removal begins at 35°C. Oxygen debt during this period must therefore be alactacid. Twenty-four per cent of the total oxygen debt, 0.08 ml g^{-1}, occurred in this period, comparable to the 33% of the total debt calculated to be surplus to lactacid requirements. This measure of alactacid debt is also comparable to that for the amphibian *Amphiuma*, 0.06 ml g^{-1} (Preslar and Hutchison, 1978; Withers and Hillman, 1981) and for the large lizards *Varanus* and *Sauromalus*, 15% of total debt (Bennett, 1972b).

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