J. exp. Biol. (1978), 77, 33–56
With 9 figures
Printed in Great Britain

OXYGEN CONSUMPTION IN THE LIZARD GENUS *LACERTA* IN RELATION TO DIEL VARIATION, MAXIMUM ACTIVITY AND BODY WEIGHT

BY PATRICIA A. CRAGG

*Research Unit for Comparative Animal Respiration, The University Woodland Road, Bristol BS8 1UG, England**

(*Received* 17 *January* 1978)

SUMMARY

1. Diel recordings of $\dot{V}_{O_2}$ under a 12 h Light/12 h Dark regime, constant light or constant dark reveal a strong endogeneous diurnal rhythm in *L. sicula*. *L. vivipara* show an exogeneous rhythm with activity occurring only in the light whilst *L. viridis* have a weak endogeneous rhythm that is modified by behavioural factors and inhibited by dark.

2. Standard (or basal) $\dot{V}_{O_2}$ can only be attained after several hours in an 'indifferent' environment, shielded from extraneous stimuli. Measurements must be at night (light or dark) for unrestrained *L. sicula* and in the dark (day or night, restrained or unrestrained) for *L. vivipara* and *L. viridis*. Intrageneric std $\dot{V}_{O_2}$ (ml h^{-1} STPD) = 0·328 $W^{0.76}$ or 0·216 $W^{0.77}$ for 1- or 3-days starvation at 30 °C for 0·2 to 34 g *Lacerta*.

3. Intrageneric maximum $\dot{V}_{O_2}$ (determined for 30 to 60 s of provoked activity during the day) = 2·66 $W^{0.747}$ at 30 °C for 1-days starvation.

4. Respiratory exchange ratio, R = 0·75 or 0·85 for std $\dot{V}_{O_2}$ after 1 or 3 days starvation and 0·95 and 1·45 for mean daily and max $\dot{V}_{O_2}$. High R values are considered a result of anaerobic metabolism and hyperventilation during activity.

INTRODUCTION

It is generally accepted that in mammals, birds and many poikilotherms oxygen consumption under standard or basal conditions (std $\dot{V}_{O_2}$) is related to body weight (W) by an exponent of approximately 0·75 (e.g. Kleiber, 1947; Hemmingsen, 1960; Lasiewski & Dawson, 1967; Schmidt-Nielsen, 1970). This exponent is a compromise between weight dependency, i.e. $\dot{V}_{O_2} \propto W^{1.0}$, and surface area dependency, i.e. $\dot{V}_{O_2} \propto W^{0.67}$ (Hemmingsen, 1960; Gould, 1971) and has recently been explained by an elastic rather than a geometric similarity theory (McMahon, 1973). Despite earlier evidence that reptiles and amphibians also obeyed an approximate $W^{0.75}$ proportionality (Hemmingsen, 1960; Kayser & Heusner, 1964), exponents to the contrary appeared in later literature (reptiles, see review by Bennett & Dawson, 1976; amphibians, Whitford, 1973; Ultsch, 1974). Recently, adherence to an approximate 0·75

* Present address: Department of Physiology, University of Otago Medical School, Dunedin, New Zealand.

exponent has been re-established interspecificially for reptiles (Bennett & Dawson, 1976) and for amphibians when in air (Feder, 1976), because care was taken to ensure that the experimental animals were in a resting or even standard condition. The latter is defined as the minimum metabolism of a fasting individual at a specified temperature (Bartholomew, 1972). Only a few reptilian studies (e.g. Roberts, 1968*a*; Ruben, 1976*a*; Jameson, Heusner & Arbogast, 1976) have been performed under such standard conditions. It is also becoming increasingly apparent that reptiles have a marked circadian $\dot{V}_{O_2}$ rhythm (Roberts, 1968*a*; Songdahl & Hutchison, 1972; Mautz & Case, 1974; Jameson *et al.* 1976; Gratz & Hutchison, 1977) and thus std $\dot{V}_{O_2}$ can only be obtained in the dark whilst in the quiescent phase of the circadian cycle (Bennett & Dawson, 1976). Also, the animal must be untethered (McDonald, 1976) and in an 'indifferent' environment (Aschoff & Pohl, 1970) and without thermal stress (Bartholomew, 1972), which, for a reptile, is most likely to be attained near its preferred body temperature (PBT).

This paper reports an intrageneric study for *Lacerta* in which std $\dot{V}_{O_2}$ was determined for a body weight range of 0·2 to 34 g. The purpose was two-fold. Firstly, Bennett & Dawson (1976) had rejected most of the available data for *Lacerta* on the grounds that they were not even resting, let alone standard, measurements and thus it seemed desirable to investigate thoroughly the procedure necessary to attain std $\dot{V}_{O_2}$ in a number of *Lacerta* species. Secondly, intraspecific or intrageneric studies of resting $\dot{V}_{O_2}$ in lizards and other reptiles (see review by Bennett & Dawson, 1976) had yielded exponents ranging from 0·4 to 1·09 in marked contrast to the accepted interspecific 0·75 exponent. Although some departures from 0·75 have been attributed to an insufficient size range or a lack of measurement standardization (Kleiber, 1947; Schmidt-Nielsen, 1970) some genuine departures have been documented in non-reptiles (Hemmingsen, 1960; Hughes, 1977; Wilkie, 1977) and thus the intrageneric exponent for *Lacerta* has been examined.

Maximum oxygen consumption (max $\dot{V}_{O_2}$) scaling has received far less attention than std $\dot{V}_{O_2}$ but it appears that the approximate 0·75 exponent still applies to mammals and birds (Hemmingsen, 1960; Pasquis, Lacaisse & Dejours, 1970; Berger & Hart, 1974; Taylor *et al.* 1978). In 14 reptilian species, max $\dot{V}_{O_2}$ yielded an exponent of 0·82 although there was considerably more interspecific variability in max $\dot{V}_{O_2}$ than in std $\dot{V}_{O_2}$ indicating different capactities for exercise or inaccurate max $\dot{V}_{O_2}$ measurement (Bennett & Dawson, 1976). On the latter point, lizard max $\dot{V}_{O_2}$ can only be maintained for 30 s to perhaps 2 min (Bennett, 1972; Bennett, Dawson & Bartholomew, 1975) whereas many of the reported max $\dot{V}_{O_2}$ measurements were from periods of 5 min or more. Furthermore, the best exercise performance can only occur during the normal activity period (Gratz & Hutchison, 1977) and the highest max $\dot{V}_{O_2}$ usually occurs near PBT (Bennett & Dawson, 1976). With these conditions satisfied, max $\dot{V}_{O_2}$ has been determined intragenerically in *Lacerta*. Other reptilian intrageneric studies are not available and Hughes *et al.* (1971) and Prange & Jackson (1976) report the only intraspecific studies finding exponents of 0·97 and 0·94, respectively, for two species of chelonian in submaximal activity.

METHODS

Animal maintenance

L. vivipara were collected locally between late March and August with the viviparous young being born in captivity in July/August. *L. sicula* and *L. viridus* were obtained from various importers between April and September. Each species, including the recently-hatched *L. vivipara*, were kept in separate vivaria containing sand, gravel and straw/hay terrains, rocky shelters, a constant supply of water and plastic netting providing extensive climbing areas. *Tenebrio* larvae and blowfly maggots were provided in excess three times a week, occasionally being supplemented by other insects and earthworms. Liquid multi-vitamins were frequently given with either food or the water. Recently-hatched *L. vivipara* were continuously supplied with green and black flies because if starved for more than 2 days they would not begin re-feeding. All lizards were kept under a 12 h Light (06.00 to 18.00 h) and 12 h Dark regime with the over-head lighting giving an incident temperature of 35 °C. Environmental temperatures were kept constant at 30 ± 1 °C, except for *L. vivipara*, where it was approximately 20 °C, since higher background temperatures in this species caused a premature death.

Diel and std $\dot{V}_{O_2}$ *measurements*

Lizards, except for recently-hatched *L. vivipara*, were entrained to the 12 h L/12 h D regime for at least one month before studies commenced during the ensuing summer months. 8 recently-hatched *L. vivipara* (a few days old, body weight 0·2 g), 8 adult *L. vivipara* (1·5 to 4·1 g), 8 *L. sicula* (6·0 to 9·8 g) and 8 *L. viridis* (14 to 34 g) were used and all were in a healthy condition. *L. vivipara* were housed at 30 °C for 24 h and all lizards were starved for 1 or 3 days (2 days in recently-hatched) prior to the experiment. Each unrestrained lizard was placed in an appropriate sized cylindrical respirometer (7 ml for recently-hatched, 225 ml for adult *L. vivipara* and *L. sicula*, 510 ml for *L. virdis*) which was shielded from all visual disturbances by a surrounding black box containing an overhead 12 cm strip light. This light gave no incident heat but followed the normal 12 h L/12 h D regime. The respirometer was shielded from vibration by being placed on a 5 cm thick sponge base, and laboratory noise was kept to a minimum. All experiments were conducted at 30 ± 1 °C, this being close to the PBT of 30–33 °C for *L. vivipara*, 34 °C for *L. sicula* and 33 °C for *L. viridis* (Pough, 1977), and begun between 12.00 and 15.00 h and continued for 28 h. Lizards were weighed before and after the experiment to give a mean weight. Weight loss was approximately 5% due mainly to dehydration since a lizard, on return to its vivarium, drank copious quantities of water and virtually replaced all the loss.

$\dot{V}_{CO_2}$ and $\dot{V}_{O_2}$ were measured using a Beckman LB1 infra-red CO_2 analyser and Servomex Industrial paramagnetic O_2 analyser whose outputs were displayed on a three channel Rikadenki pen recorder together with a simultaneous thermistor recording. O_2 and CO_2 analysers were calibrated before and checked for drifts and recalibrated if necessary during and after each 28 h experiment, calibration gases being made with an H. Wosthoff gas mixing pump and checked by Scholander analysis. All gases were dried with silica gel before entering the respirometer and with $CaCl_2$ before entering the analysers. Initially the analysers and respirometer were contained

in a closed circuit system with air circulating at 450 ml min^{-1}, but later an open circuit with a flow rate of 100 ml min^{-1} was used since this was more accurate. With closed circuits, the system had to be opened every time the % O_2 or % CO_2 had changed by 1 % (during the night a 2 % change was allowed), flushed with fresh air and then sealed again to continue the experiment. The lizards were always totally unaware of this opening and closing but the procedure was tedious especially at night. The other disadvantage of the closed circuit is that it was prone to CO_2 leakage. In contrast, the open circuit involved gas changes of no more than 0·5 %, CO_2 leakage was unimportant, it required less attention and was more sensitive to small or short changes in $\dot{V}_{O_2}$. The details of the closed and open circuit respirometry, the type of records obtained, the derivation of suitable equations for calculating $\dot{V}_{O_2}$ and $\dot{V}_{CO_2}$ and the errors involved are reported by Cragg (in prep.).

Since it took 2 to 3 h for the lizards to become accustomed to the respirometer, the first 3 to 4 h of recordings were discarded and the next 24 h analysed in 20 min blocks. $\dot{V}_{O_2}$ and $\dot{V}_{CO_2}$ were measured in ml h^{-1} at ATPD and corrected to STPD. As well as investigating the diel rhythm of $\dot{V}_{O_2}$ under a 12 h L/12 h D regime, the effect of total dark and total light, the effect of randomly switching the light on or off for an hour and the effect of restraining the lizard or giving shelter within the respirometer were also tested.

Max $\dot{V}_{O_2}$ measurements

32 lizards that had been starved for 1 day only were used: 2 recently-hatched *L. vivipara*, 9 adult *L. vivipara*, 12 *L. sicula* and 9 *L. viridis* with body weights similar to those used in the diel studies. *L. vivipara* were housed at 30 °C for 24 h prior to the experiment. All experiments were conducted at 30 ± 1 °C between the hours of 06.00 and 18.00 and in the light.

Nose masks with an inlet and outlet tube of 2 mm diameter were constructed from cannibalized syringes and stuck to adult lizards with neoprene glue and a small latex rubber ring as previously described for a pneumotachograph nose mask (Cragg, 1978). With the lizard's nose inside, the volume of the mask was 0·05 ml (*L. sicula* and *L. vivipara*) or 0·3 ml (*L. viridis*) and weighed 0·4 g or 1·0 g. The nose mask was incorporated into an open circuit system similar to that used for the diel studies and air was metered through at 100 ml min^{-1}. This flow rate caused a slight negative pressure of −3·0 mm H_2O but such a pressure does not affect the normal breathing pattern of *Lacerta* (Cragg, 1978). Further details of the mask open circuit are reported by Cragg (in prep.) Lizards (23 animals) wearing such masks were either taped to wooden blocks or allowed to run free in an enclosed area with the weight of the mask's tubing being supported. The lizard was provoked into vigorous struggles by continual prodding or feet and tail pinching, and $\dot{V}_{O_2}$ and $\dot{V}_{CO_2}$ were analysed at 15 s intervals, maximum $\dot{V}_{O_2}$ levels being reached rapidly (~ 30 s) and maintained for 30 to 60 s. Stimulation beyond this time was ineffective and was stopped after a total of 2 min. At least one hour was allowed to elaspse before the next provocation. The average of 3 max $\dot{V}_{O_2}$ measurements was taken for each animal. (Electric shocking was less effective than prodding.)

Another source (7 lizards) for max $\dot{V}_{O_2}$ was from 30 to 60 s bouts of frantic activity occurring over the first 5 min after placing the lizards into an open circuit respiro-

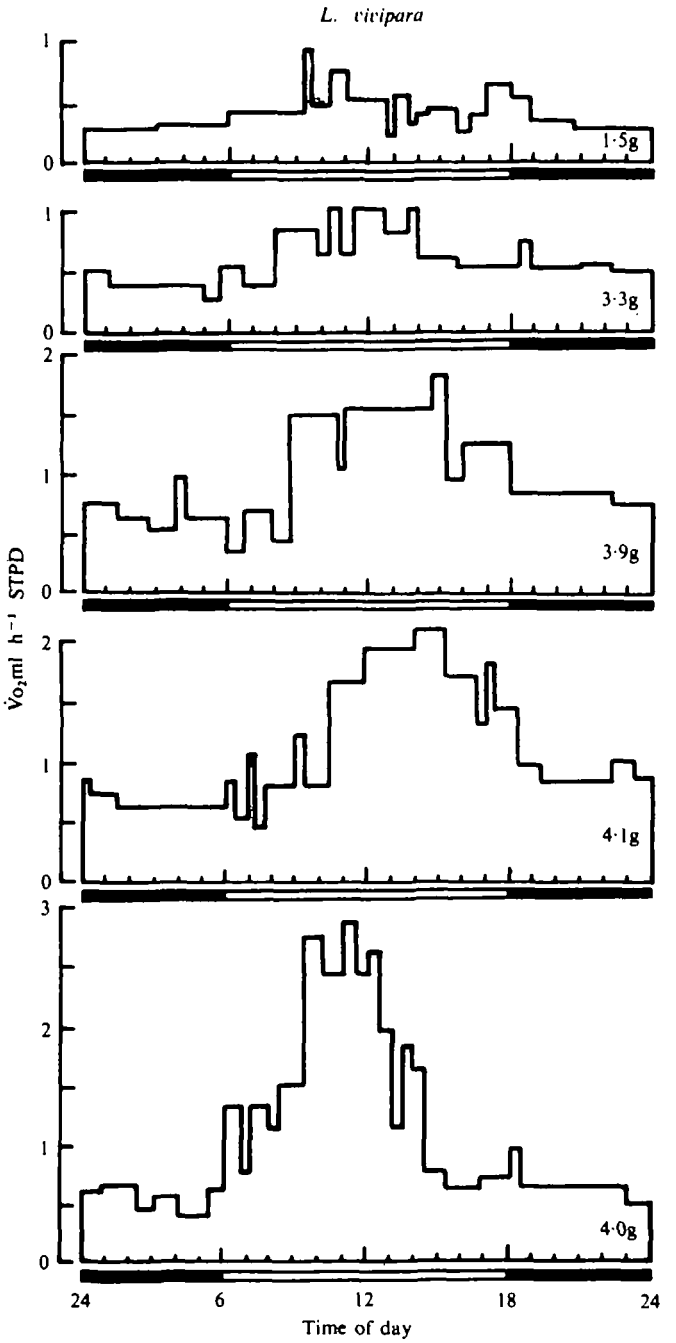

Fig. 1. Histograms of diel $\dot{V}_{O_2}$ under a 12 h L/12 h D regime in 5 adult *L. vivipara* determined by closed circuit respirometry. Note hyper-activity of 4·0 g lizard due to sloughing. (In all histograms $\dot{V}_{O_2}$ is in ml h^{-1} STPD at 30 °C, solid and open bars denote dark and light periods, respectively, and the number in the right hand corner of each histogram is the body weight in g.)

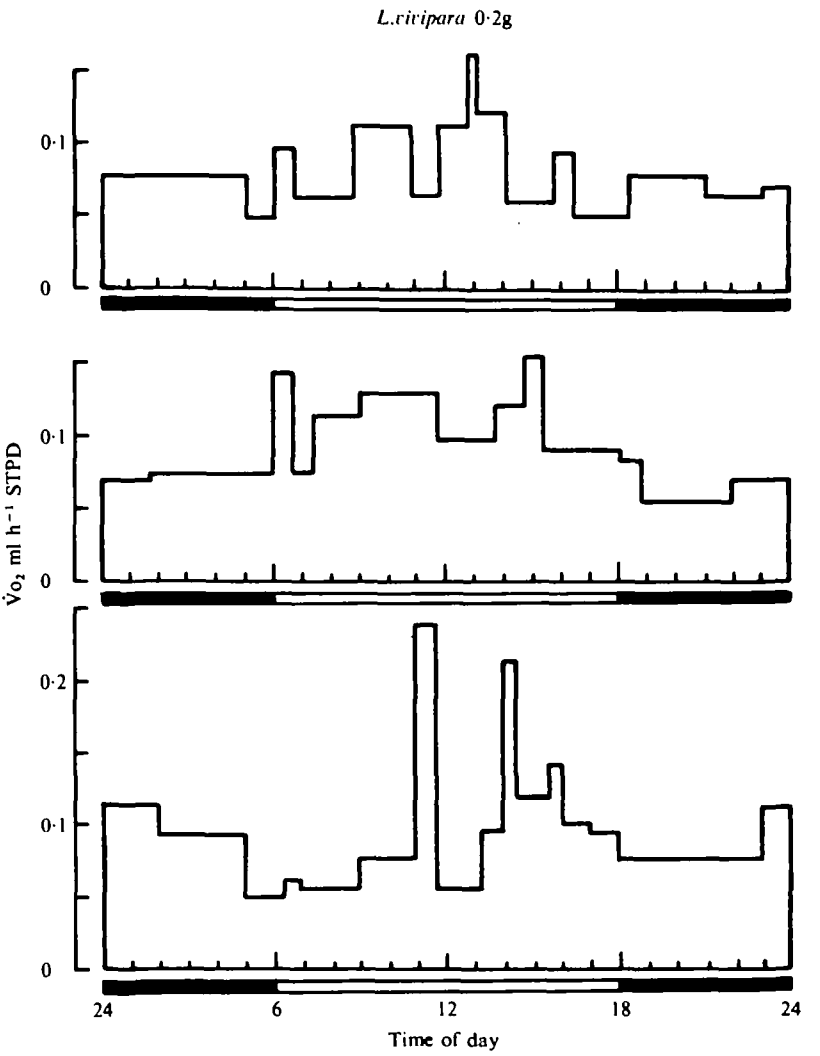

Fig. 2. Histograms of diel $\dot{V}_{O_2}$ under a 12 h L/12 h D regime in 3 recently-hatched *L. vivipara*. Closed circuit respirometry.

meter. This was the only method available for recently-hatched *L. vivipara*. The final source (5 lizards) of max $\dot{V}_{O_2}$ data was from one minute periods of very severe exercise on a respirometer treadmill (Cragg, in prep.). $\dot{V}_{O_2}$ and $\dot{V}_{CO_2}$ were measured in ml h^{-1} at ATPD and corrected to STPD.

RESULTS

Diel rhythms of $\dot{V}_{O_2}$

(i) *L. vivipara*

Figs 1 and 2 illustrate the $\dot{V}_{O_2}$ diel rhythm of 20-min periods in adults and recently-hatched young under a 12 h L/12 h D regime. During the dark hours, $\dot{V}_{O_2}$ was never completely constant but fluctuated about a mean with the rare occurrence of small

peaks. The lizards were curled up with their eyes closed and if disturbed (by opening the respirometer and then handling), were slow to respond. When the light switched on at 06.00 h, there was nearly always an immediate increase in $\dot{V}_{O_2}$ which then was often minimal for the next 2 h. During the rest of the light period the activity peaks were of variable amplitude and their distribution showed no consistent pattern relative to time of day. One individual (Fig. 1, lowest trace) was in the process of sloughing and this increased the day's activity considerably, presumably becasue the lizard was trying to assist the removal of dead skin. The beginning of the dark period at 18.00 h was marked by an immediate lowering of $\dot{V}_{O_2}$ or by a small, short-lived increase. There appeared to be no difference in the diurnal rhythm of 1-day or 3-day starved animals (this applied to the other two species) nor between adults and recently-hatched young.

Observations on behavioural activity of *L. vivipara* in their vivarium showed that the lizards would emerge from their rocky shelters as soon as the light came on or up to 2 h later. During the light period, their time was spent basking, sheltering and foraging (an exploratory activity not necessarily connected with feeding). Basking and sheltering periods often last for 20 min or more whereas foraging periods were always less than 5 min. Periods of activity appeared to be spread throughout the 'day' although some lizards were rather inactive in the 'afternoon'. Some lizards were still basking when the light was switched off at 18.00 h but within a few minutes they took shelter and remained there. *L. vivipara* showed no obvious social interactions or dominance and were not easily distrubed by observers. Presumably increased $\dot{V}_{O_2}$ in the respirometer reflects a modified form of foraging behaviour in an 'indifferent' environment.

Under conditions of constant dark (Fig. 3), all *L. vivipara* lost their diel rhythm and remained inactive throughout the 'day maintaining the mean dark $\dot{V}_{O_2}$. Constant light also obliterated the diel rhythm as well as stimulating continual elevated activity throughout the 24 h with a mean $\dot{V}_{O_2}$ much higher than the normal mean light $\dot{V}_{O_2}$. Constant light was so disturbing that one, apparently healthy, individual actually died. If shelter was provided within the respirometer, activity still occurred throughout the constant light but it was interspersed with bouts of sheltering and thus mean $\dot{V}_{O_2}$ was reduced to normal light values. Provision of shelter during constant or 12 h dark periods did not reduce mean dark $\dot{V}_{O_2}$ any further. In short experiments in which the light was switched on and off for one hour periods, *L. vivipara* responded immediately by becoming active in the light and quiescent in the dark. Restraining to a wooden block within the respirometer did not alter mean dark $\dot{V}_{O_2}$, but during the light, struggling often occurred and thus mean day $\dot{V}_{O_2}$ was elevated.

(ii) *L. sicula*

Fig. 4 illustrates the diel rhythm under a 12 h L/12 h D regime. During the dark hours, the lizards were curled up asleep and their $\dot{V}_{O_2}$ fluctuated slightly as in *L. vivipara* but, in contrast, if handled they were much quicker to respond. Although the light was switched on at 06.00 h, a consistent increase in $\dot{V}_{O_2}$ did not occur until 07.00 h. During the light phase, there was a very clear cut pattern of two very active periods between 07.00 and 11.00 and between 13.00 and 15.00 h although individual variation is also obvious. Around mid-day, i.e. 11.00 to 13.00 h activity was subdued. $\dot{V}_{O_2}$ declined just before or just after the light was switched off at 18.00 h.

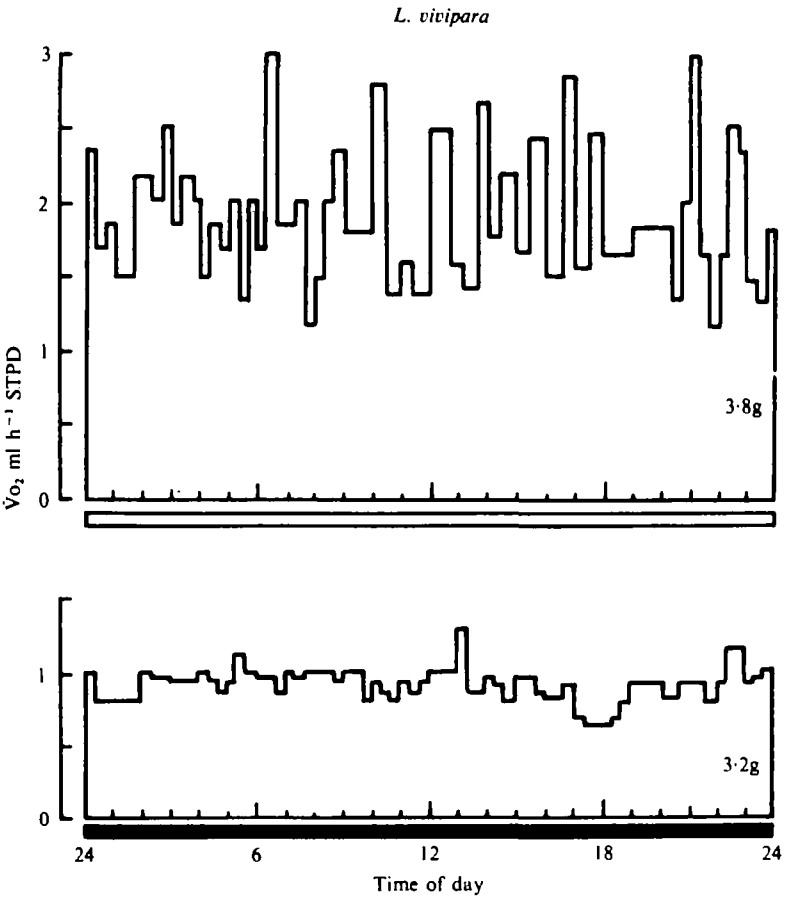

Fig. 3. Effect of constant light or constant dark on diel $\dot{V}_{O_2}$ in a adult *L. vivipara* determined by open circuit respirometry. Note the greater sensitivity of open circuit as compared with closed circuit analysis.

In the vivarium, *L. sicula* did not emerge until 07.00 h although the light came on at 06.00 h. During the light phase, they were active from 07.00 to 18.00 h but were always sheltering around mid-day. They were very active, restless creatures only basking for short periods (5 min maximum) and spending much more time foraging (10 min maximum) and less time sheltering than *L. vivipara*. When the light went out at 18.00 h the lizards, if they had not already anticipated it, quickly retired. *L. sicula*, being inquistive, were very easily distrubed by observers and showed obvious social interactions within a group with the largest lizard always being dominant and occasionally fighting. The non-dominant lizards always spent more time sheltering and were not often allowed to bask directly under the light. The *L. sicula* used were actually from two sub-species, *L. s. sicula* and *L. s. compestris* but no difference in diel rhythm or their behavioural activity could be seen except that the latter were often the larger and hence the more dominant.

Constant dark and constant light for one day (Fig. 5) in no way altered the diel rhythm or the pattern of 'day activity in *L. sicula* in marked contrast to *L. vivipara*. However, sometimes activity did start at 06.00 instead of 07.00 and finish at 19.00

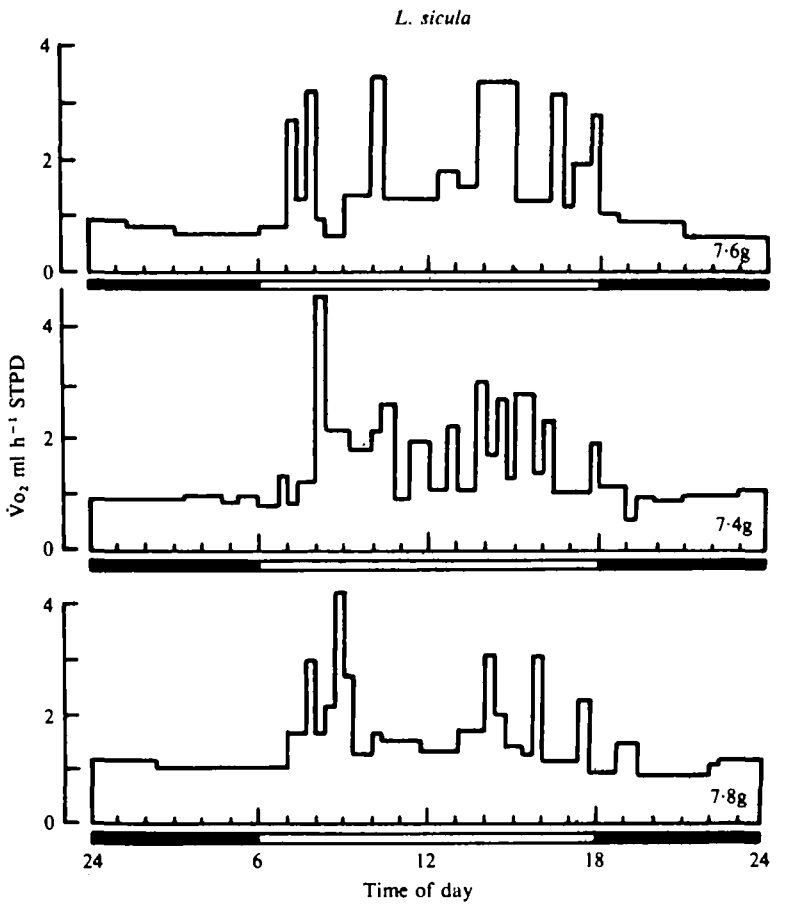

Fig. 4. Histograms of diel $\dot{V}_{O_2}$ under a 12 h L/12 h D regime in 3 *L. sicula*. Closed circuit respirometry.

instead of 18.00 h. Thus, as would be expected, switching the light on or off for an hour did not cause stimulation or inhibition of activity. Provision of shelter within the respirometer did not lower the mean dark or night $\dot{V}_{O_2}$. Restraining the lizard caused some struggling activity even during the dark and hence elevated mean dark $\dot{V}_{O_2}$.

(iii) *L. viridis*

Fig. 6 illustrates the diel rhythm of *L. viridis* under a 12 h L/12 h D regime. As with the other two species, $\dot{V}_{O_2}$ fluctuated slightly about a mean during the dark phase whilst the lizard slept. The response to handling at night was variable ranging from docile to very aggressive. There was no consistent time at which activity was initiated nor was there a consistent pattern of activity during the light phase: peak activity would occur at any time or be evenly distributed throughout the light phase or be virtually absent, and activity could cease at 18.00 h or many hours before.

In the vivarium, *L. viridis* were active between 06.00 and 18.00 h, but there was considerable variation in how early they emerged or retired and when they were most active. Periods of basking could be as long as 45 min and they would also forage for

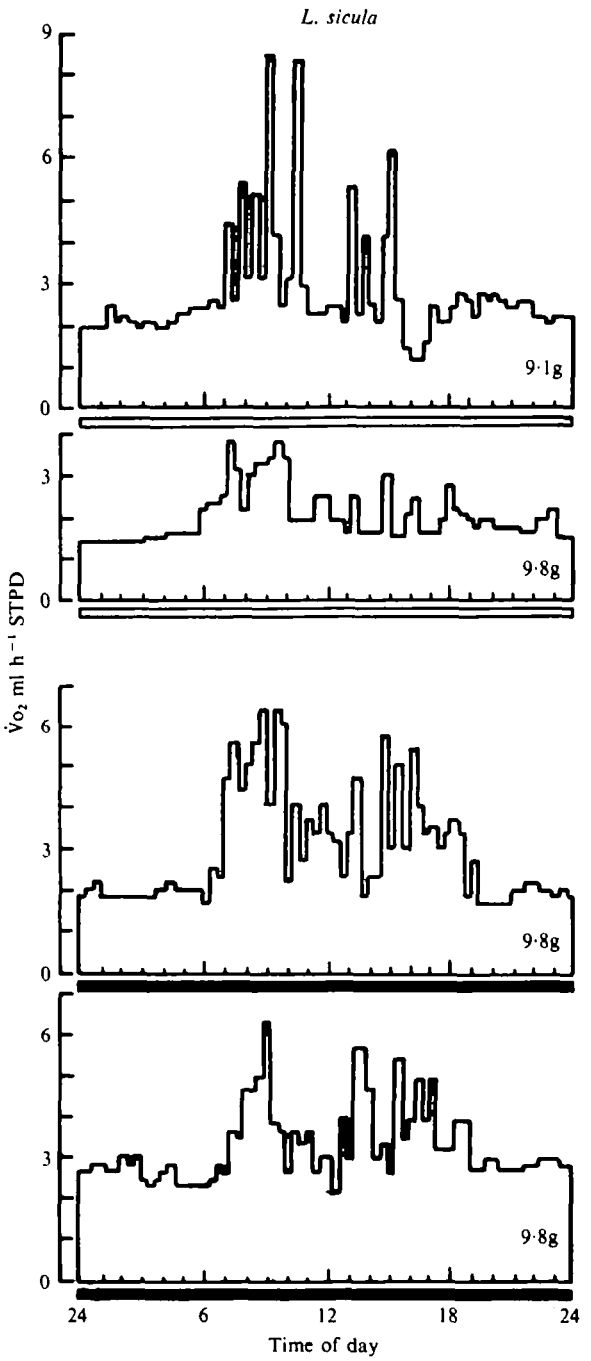

Fig. 5. Effect of constant light or constant dark on diel $\dot{V}_{O_2}$ in 4 *L. sicula*. Open circuit respirometry.

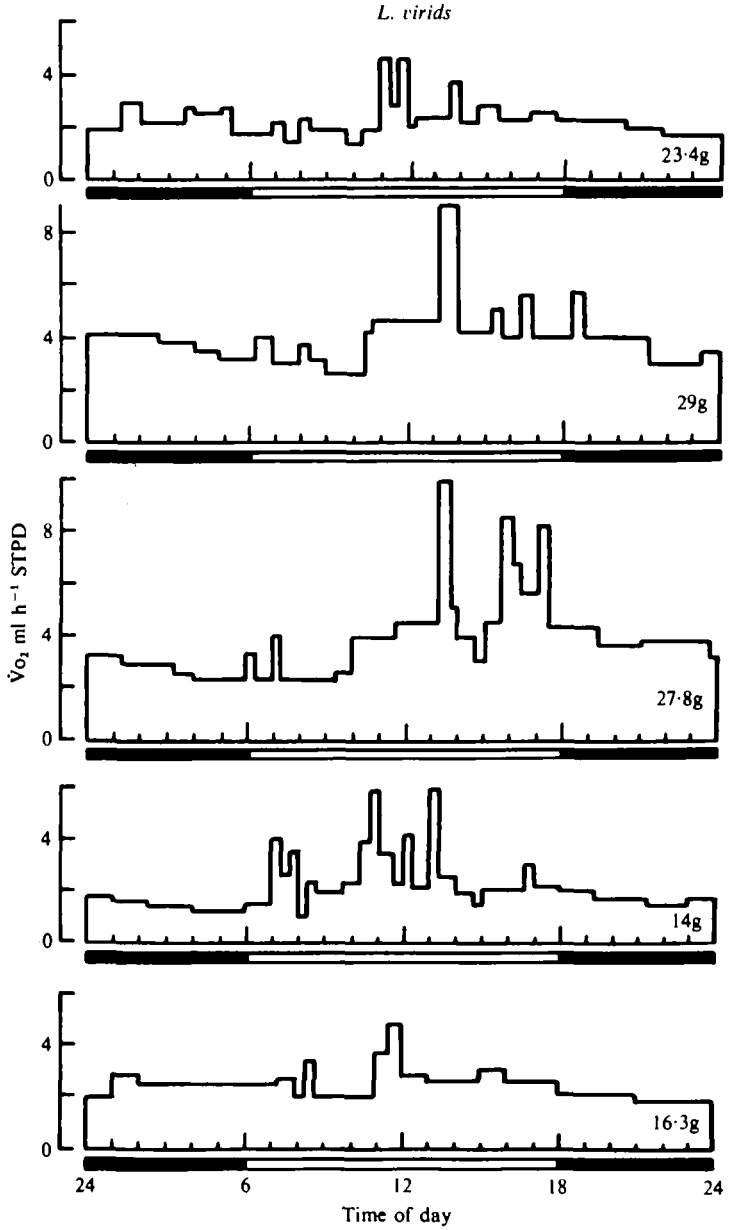

Fig. 6. Histograms of diel $\dot{V}_{O_2}$ under a 12 h L/12 h D regime in 5 *L. viridis*. Closed circuit respirometry.

long periods (30 min or more) without a basking or sheltering interruption. *L. viridis* showed marked social interactions and would spend much of their time guarding their own territory, often fighting, especially over food. Overcrowding could lead to mutilation of the weaker, smaller lizards, The largest lizard was always the more dominant and would often show threatening behaviour to both the other lizards and to observers intent on handling. In contrast to the other two *Lacerta* species, if

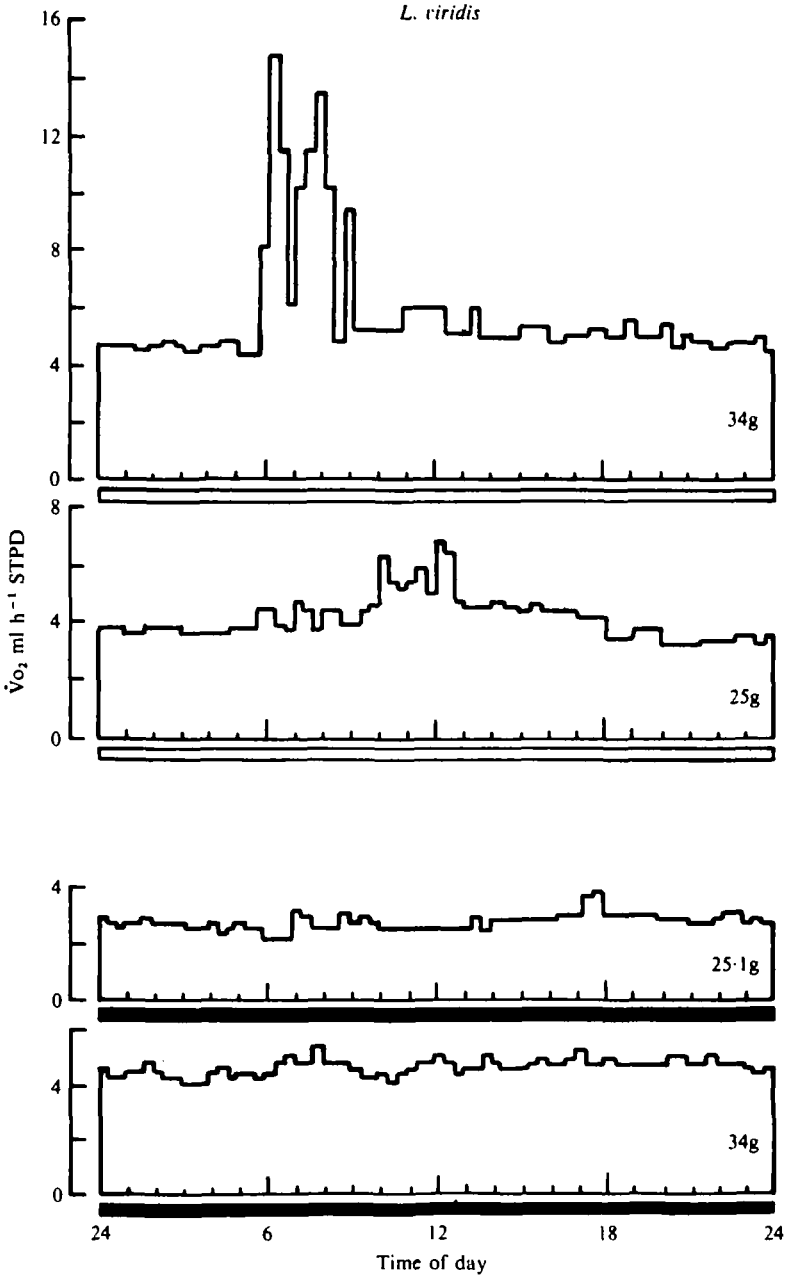

Fig. 7. Effect of constant light or constant dark on diel $\dot{V}_{O_2}$ in 4 *L. viridis*. Open circuit respirometry.

a *L. viridis* was placed in isolation in a vivarium, there was a marked reduction in foraging behaviour and if the vivarium contained only a shelter with straw/hay and no climbing area, foraging behaviour was virtually non-existent.

In constant dark (Fig. 7), *L. viridis* showed no diel rhythm remaining inactive throughout the 'day' as well as 'night' as was the case with *L. vivipara*. Under constant light, activity occurred within the normal day, i.e. 06.00 to 18.00 h but it

Table 1. *Comparison of unrestrained activity in a respirometer under 12 h L/12 h D regime. Values reported as* ± S.D.

Species	*N*	mean light $\dot{V}_{O_2}$/mean dark $\dot{V}_{O_2}$	peak $\dot{V}_{O_2}$/minimum $\dot{V}_{O_2}$
L. vivipara (recently-hatched)	8	1·35 ± 0·22	3·77 ± 0·8
L. vivipara adult	8	1·6 ± 0·15	4·44 ± 0·35
L. sicula	8	1·83 ± 0·38	5·25 ± 2·02
L. viridis	8	1·24 ± 0·2	3·6 ± 0·84

was as variable in pattern as in the 12 h L/12 h D regime. This was similar to *L. sicula*. However, the 'night' $\dot{V}_{O_2}$ during constant light was in some cases normal but in others elevated – presumably sleep was not possible in the latter. This response was in some respects similar to that of *L. vivipara*, except that bouts of high activity did not occur. Switching the light on tended to stimulate activity and switching off tended to inhibit activity but on many occasions there was no change in $\dot{V}_{O_2}$ in response to these stimuli. Provision of shelter within the respirometer did not alter mean dark $\dot{V}_{O_2}$ but did allow sleep at 'night' in constant light. Restraining the lizard made no difference to mean dark $\dot{V}_{O_2}$ values and tended to lower mean light $\dot{V}_{O_2}$ indicating that it seemed to 'accept' the restriction.

(iv) *Comparison of the* 3 *species*

An indication of the differences between the 3 species in unrestrained behaviour in a respirometer whilst under a 12 h L/12 h D regime can be obtained by comparing mean light $\dot{V}_{O_2}$/mean dark $\dot{V}_{O_2}$ ratios and peak $\dot{V}_{O_2}$/minimum $\dot{V}_{O_2}$ ratios (Table 1). It is apparent that the recently-hatched *L. vivipara* and *L. viridis* were less active in terms of both these ratios than the adult *L. vivipara* and *L. sicula*, the latter being the most active. The same trend also occurred after 3 days of starvation.

(v) *Respiratory exchange ratio, R*

For 1-day starved and 3-day starved conditions, the respiratory exchange ratio (or respiratory quotient, $R = \dot{V}_{CO_2}/\dot{V}_{O_2}$) was 0·95 ± 0·05 and 0·94 ± 0·06 respectively, during the light phase of the 12 hL/12 h D regime. In contrast, R was 0·85 ± 0·05 and 0·75 ± 0·04 respectively, during the dark phase. All R values are obtained from open not closed circuit respirometry.

Standard and diel $\dot{V}_{O_2}$ scaling

From the data obtained in the 12 h L/12 h D experiments, four categories of $\dot{V}_{O_2}$ were considered for the 1- and 3-day starved conditions: mean dark $\dot{V}_{O_2}$, mean light $\dot{V}_{O_2}$, peak $\dot{V}_{O_2}$ and minimum $\dot{V}_{O_2}$. Peak values only occurred in the light and minimum values usually in the dark. Logarithmic plots of $\dot{V}_{O_2}$ versus body weight are reported in Table 2 and one is illustrated in Fig. 8. Initially $\dot{V}_{O_2}$ data from recently-hatched animals were not incorporated with the adult data in case development factors obscured metabolic scaling. However, after examination of total and adult-only exponents, this precaution does not appear to be necessary although inclusion of

Table 2. *Logarithmic relationship between* $\dot{V}_{O_2}$ *and body weight* (0·2 *to* 34 *g*).

$\dot{V}_{O_2} = a\ W^b$ where $\dot{V}_{O_2}$ is in ml h^{-1} STPD, W in g, a is the intercept in ml h^{-1} and b the logarithmic regression coefficient (or exponent). No exponent had a S.D. greater than ±0·05. Number of lizards = 12 to 15 for each regression (N = 9 to 12 for adult only). CC = correlation coefficient. (All correlations significant at $P < 0{\cdot}001$ level.)

Category		Intercept	Exponent	CC	Exponent (adults only)	CC (adults only)
Minimum $\dot{V}_{O_2}$	1-day starved	0·208	0·83	0·97	0·78	0·93
	3-day starved	0·147	0·77	0·97	0·94	0·93
Dark $\dot{V}_{O_2}$ (12 h mean)	1-day starved	0·328	0·76	0·98	0·74	0·95
	3-day starved	0·216	0·77	0·99	0·80	0·96
Light $\dot{V}_{O_2}$ (12 h mean)	1-day starved	0·547	0·77	0·92	0·57	0·8
	3-day starved	0·355	0·76	0·98	0·63	0·89
Peak $\dot{V}_{O_2}$	1-day starved	0·975	0·8	0·96	0·74	0·9
	3-day starved	0·608	0·78	0·98	0·69	0·89
			0·779 ± 0·022		0·737 ± 0·1	

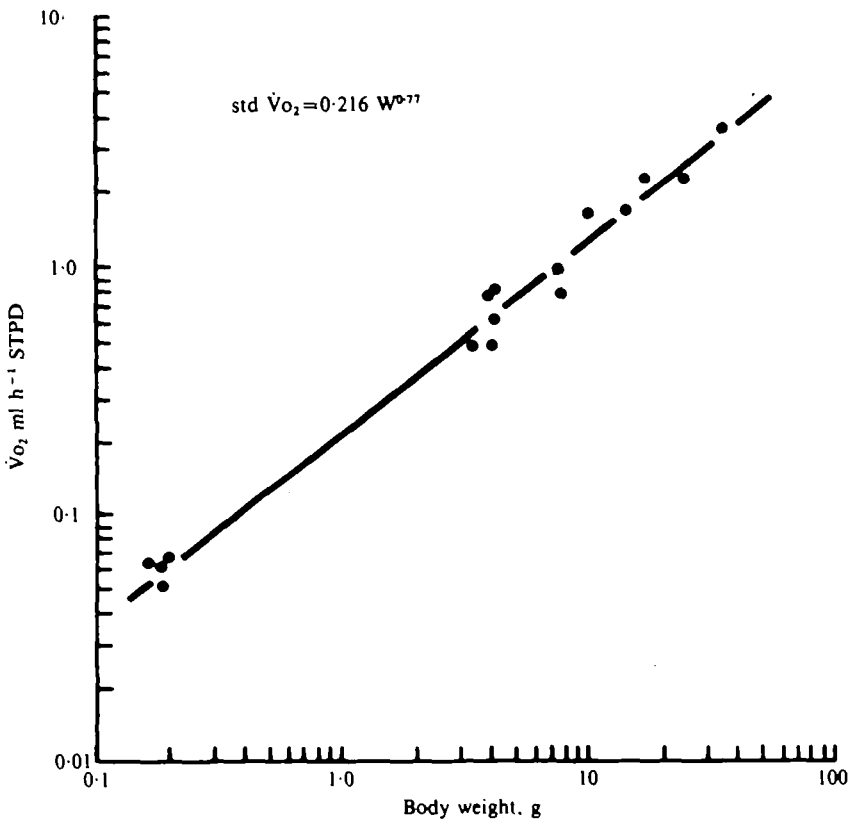

Fig. 8. Log/log. plot of std $\dot{V}_{O_2}$ (ml h^{-1} STPD) and the body weight (g) at 30 °C after 3-days starvation. Std $\dot{V}_{O_2}$ determined from mean dark $\dot{V}_{O_2}$ under 12 h L/12 h D regime. For further details see Table 2.

recently-hatched data does improve the correlation coefficient. There are two reasons for this: (*a*) the size range is increased from 1·25 to 2·25 log. cycles and (*b*) *L. viridis* and 0·2 g *L. vivipara* both gave the lower behavioural $\dot{V}_{O_2}$ ratios (Table 1) and since they occupy the two extremes of the body weight range they are both needed to provide an even balance to the log/log plot.

Better correlation coefficients were obtained for 3- than for 1-day starved conditions and the best was found in the mean dark $\dot{V}_{O_2}$ after 3 days starvation. Despite the fact that the minimum and peak $\dot{V}_{O_2}$ recordings were each taken from one 20 min period per 24 h, they gave surprisingly clear cut regressions. Standard metabolism is considered to be measured most accurately by mean dark $\dot{V}_{O_2}$ regressions and thus std $\dot{V}_{O_2} = 0{\cdot}328\ W^{0{\cdot}76}$ for 1-day starved or std $\dot{V}_{O_2} = 0{\cdot}216\ W^{0{\cdot}77}$ for 3-days starved. Likewise, routine day activity is best measured as mean light $\dot{V}_{O_2}$ and thus day $\dot{V}_{O_2} = 0{\cdot}547^{0{\cdot}77}$ (1-day starved) or day $\dot{V}_{O_2} = 0{\cdot}355\ W^{0{\cdot}76}$ (3-days starved).

Max $\dot{V}_{O_2}$ scaling and max R

Max $\dot{V}_{O_2}$ was related to body weight as max $\dot{V}_{O_2} = 2{\cdot}57\ W^{0{\cdot}78}$ (correlation coefficient 0·95, significant at $P < 0{\cdot}001$ level) for 1-day starved adult lizards and with inclusion of 0·2 g *L. vivipara* data, the relationship became max $\dot{V}_{O_2} = 2{\cdot}66\ W^{0{\cdot}747}$ (correlation coefficient 0·975, significant at $P < 0{\cdot}001$ level). These intercepts were approximately 8 times greater than std $\dot{V}_{O_2}$ for 1 days starvation (Fig. 9). During maximum activity, the respiratory exchange ratio was high and variable being $1{\cdot}45 \pm 0{\cdot}25$. Further details concerning the speed of attainment of max $\dot{V}_{O_2}$ and $\dot{V}_{CO_2}$ and their decline during recovery are the subject of another paper (Cragg, in preparation).

DISCUSSION

Diel activity rhythms

These experiments were designed primarily to determine the best procedure for recording standard metabolism rather than to study circadian rhythms *per se* in *Lacerta*. Although, it is appreciated that in circadian studies an acktograph is preferable to $\dot{V}_{O_2}$ measurements (Aschoff & Pohl, 1970), recent work has shown a good correlation of diel activity and $\dot{V}_{O_2}$ in the lizard, *Xantusia*, and snake, *Natrix*, albeit only at higher temperatures in the latter (Mautz & Case, 1974; Gratz & Hutchison, 1977). Thus the diel $\dot{V}_{O_2}$ of *Lacerta* is probably a reasonable reflection of diel activity and since circadian rhythms can only be demonstrated in constant light or dark in an 'indifferent' environment (Aschoff & Pohl, 1970), it is considered that this study can contribute to reptilian circadian data.

Some reptiles are diurnal and some nocturnal or crepuscular but all have a periodicity of approximately 24 h with either one or two periods of activity (Cloudsley-Thompson, 1961; Saint-Girons, 1971). If the rhythm is endogenous (or circadian), the 24 h periodicity persists for many days when under constant light or dark. Endogenous rhythms can, however, still be adjusted to seasonal changes using cues from light and/or temperature fluctuations, the latter often being the more dominant (Evans, 1966). The pineal organ is one of the detectors of light cues and may even be one of the circadian oscillators (Songdahl & Hutchison, 1972; Underwood, 1977). Reversal

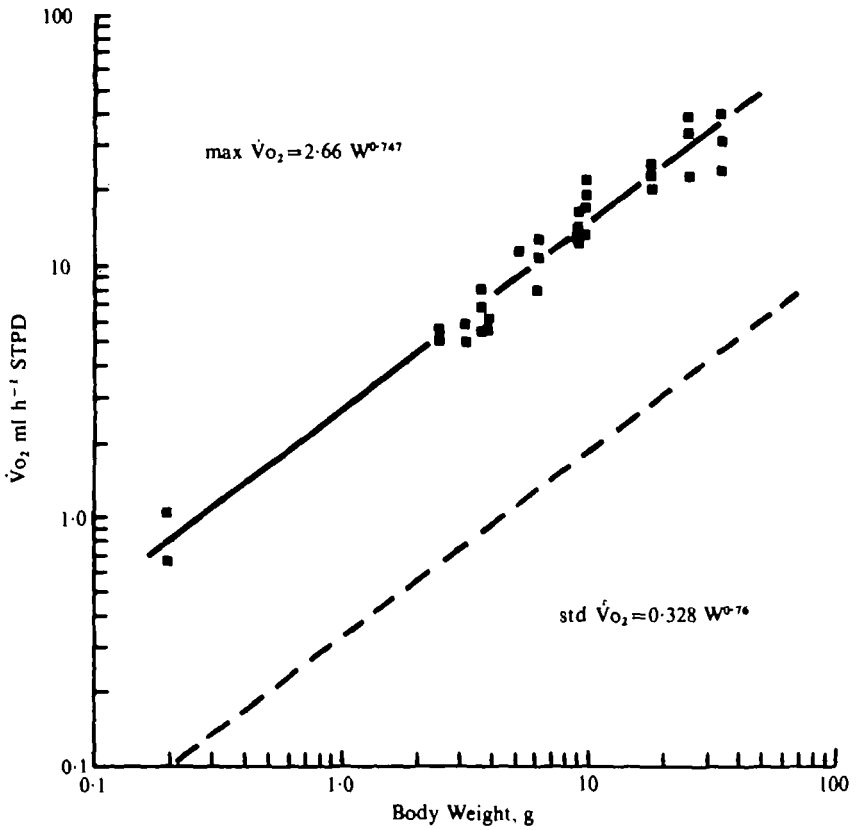

Fig. 9. Log/log plot of max $\dot{V}_{O_2}$ (ml h^{-1} STPD) and body weight (g) at 30 °C after 1-days starvation. Dashed line is for std $\dot{V}_{O_2}$ at 30 °C after 1-days starvation with an intercept 8 times less than max $\dot{V}_{O_2}$.

of the light/dark phases causes constant activity in endogeneously rhythmic reptiles with entrainment to the reverse lighting taking many days to become established (Cloudsley-Thompson, 1961).

In contrast, a few reptiles (agamid lizards) have weak or no endogeneous rhythms, and their rhythmic behaviour is strongly controlled by exogeneous stimuli, light so far being the only stimulus tested (Toye, 1972; Rao & Rajabai, 1973). During 12 h L/12 h D regimes these lizards are active throughout the light phase and will entrain immediately, or at least by the second day, to reversed lighting. Under constant light they become arrhythmic and under constant dark they become either arrhythmic (*Sitana*; Rao & Rajabai, 1973) or maintain some of the normal 'day' activity (*Agama*; Toye, 1972 and skink, *Tiliqua*, Firth, Webb & Johnson, 1972).

Diel activity rhythms have been studied previously in *Lacerta* by Kayser & Marx (1951), Hoffman (1955, 1959, 1960) and to some extent by Avery (1976). Fischer (e.g. 1961) has shown that *L. sicula*, *L. muralis* and *L. viridis* are able to use orientation of the sun to judge the time of day. In *L. sicula*, it is apparent that the diel rhythm is endogenous because it persists during constant light or dark (Hoffman, 1955, 1960; this study) and because activity is consistently delayed for an hour after the onset of light

and consistently reduced around mid-day (this study). However, the rhythm can be entrained to cycles of fluctuating temperature (Hoffman, 1969) with the active period reduced at lower temperatures (Hoffman, 1969; Avery, 1976). Data for *L. agilis* and *L. muralis* (Kayser & Marx, 1951) show many similarities to *L. sicula*.

L. vivipara, on the other hand, had no endogenous rhythm, activity being continually stimulated by light and inhibited by dark – a phenomenon which has not been reported for any other reptile. However, some endogeneous control must be present since (*a*) in constant light there was obviously a need for intermittent shelter, i.e. voluntary semi-darkness, and (*b*) Avery (1976) found two consistent peaks in basking activity which could be reduced to just the early peak at lower temperatures of radiation intensities. In contrast to basking activity, no distinct pattern could be discerned for foraging activity in *L. vivipara* either at ~20 °C (vivarium) or 30 °C (respirometer) although there was a consistent tendency to be less active in the first 2 h particularly at ~ 20 °C. Avery & McArdle (1973) have shown that this delay in *L. vivipara* emergence or activity is governed by the amount of incident solar radiation, in contrast to other lizards (Heath, 1962; Evans, 1967).

L. viridis showed a diel rhythm which was similar in some respects to *L. vivipara* and in other respects to *L. sicula*. In constant dark, *L. viridis* were totally inactive and appeared to have no endogeneous rhythm but in constant light, a normal diurnal rhythm persisted. This may indicate that *L. viridis* has an endogeneous rhythm which is completely inhibited by the dark. However, the situation is complicated by the fact that *L. viridis* are often inactive when there is nothing to investigate and this may explain (*a*) the activity inhibition in constant dark and (*b*) the lack of a consistent activity pattern in the 'day'. Using an acktograph with a simulated natural environment, Hoffman (1959) found no difference between the diurnal rhythm of *L. sicula* and *L. viridis*. One must conclude that behavioural factors are a very strong modifier of any endogeneous rhythm in *L. viridis*.

Apart from the different balance of factors controlling their diel rhythms, the three *Lacerta* species also had different amplitudes of diurnal activity both in the vivarium and respirometer as well as different proportions of foraging, sheltering and basking (for more detailed behavioural comparisons between *L. sicula* and *L. vivipara*, see Avery, 1976). Jameson *et al.* (1976) found distinct male and female activity patterns in *Sceloporus occidentalis* although the mean 'day' $\dot{V}_{O_2}$ levels were the same (at sea level), but an obvious male/female difference was not apparent in *Lacerta*, apart from the dominant lizard of a group being male. Even in *L. sicula* which had a clear pattern of diurnal activity, there was obvious variation from one animal to another but such variations from individual to individual and within the same animal from day to day are the rule rather than the exception (Songdahl & Hutchison, 1972; Mautz & Case, 1974; Jameson *et al.* 1976). During the abrupt transition from light to dark, *Sceloporus cyanogenys* gave a final activity peak (Songdahl & Hutchison, 1972) and such a phenomenon was occasionally seen at the onset and offset of light in *Lacerta*. In constant light, *S. occidentalis* required sand in which to bury before a clear diel rhythm and std $\dot{V}_{O_2}$ could be recorded (Jameson *et al.* 1976). Such shelter was immaterial to *L. sicula*, useful for *L. viridis* and vital to *L. vivipara* but in the latter a clear diel rhythm still could not be established.

Determination of std $\dot{V}_{O_2}$

As Bartholomew (1972) has pointed out, the environmental circumstances for minimum stress differ from species to species and the accuracy of the standard metabolic determination will depend largely on how well the investigator knows his experimental animal. It is apparent that std $\dot{V}_{O_2}$ can be measured in unrestrained *L. sicula* only at night but either in the dark or light. In contrast for *L. vivipara* and *L. viridis* restrained or unrestrained measurements during the day or night can be made providing the animal is in the dark. Shelter is not necessary in any of these conditions. Thus, although Kramer's (1934) statement that std $\dot{V}_{O_2}$ could not be recorded in the dark if it was daytime was made for both *L. sicula* and *L. viridis*, I find it applicable to *L. sicula* only. Roberts (1968*a*) also found that dark during the day would not yield std $\dot{V}_{O_2}$ in *Uta stansburiana*. Further criteria for std $\dot{V}_{O_2}$ are that the lizards must be in an 'indifferent' environment, shielded from extraneous stimuli, and allowed at least 2 to 4 h to settle down.

Factors that can modify std $\dot{V}_{O_2}$, e.g. circadian rhythms, behavioural aggregation, temperature, thermal acclimation, season or hibernation, age, sex and feeding/starvation, have been discussed extensively by Bennett & Dawson (1976). Most metabolic studies have not considered the possibility of sex differences but females are considered to have a lower (about 75%) metabolic rate than males (e.g. *Uta*, Roberts, 1968*a*). However, Jameson *et al.* (1976) only found this difference at high elevations and not at sea level. Sample size in this *Lacerta* study did not allow a sex separation but a preliminary analysis did not reveal any sex influence on std $\dot{V}_{O_2}$. Finally, starvation for only one day was required to render *Uta* in the post-absorptive state and std $\dot{V}_{O_2}$ then remained unchanged for the next two weeks (Roberts, 1968*a*). In contrast, *Lacerta* gave a 30% reduction in std $\dot{V}_{O_2}$ from 1 to 3 days starvation which might be explained by the fact that *Tenebrio* larvae take two days to be cleared from the stomach of *Anolis* (Gist, 1972), although Avery (1973) reports one day for clearance in *L. vivipara*.

Table 3 lists the standard, resting or semi-active $\dot{V}_{O_2}$ determinations previously measured in *Lacerta* and shows conclusively that Bennett & Dawson (1976) were correct in their selection of only Kramer's (1935) data for their interspecific scaling studies. They also rejected Krehl & Soetbeer's (1899) 30 °C data but retained the 37 °C data. Recently, Jammes & Grimaud (1976) reported a resting $\dot{V}_{O_2}$ of 0·145 ml h^{-1} g^{-1}, 10% of which was due to cutaneous oxygen exchange, for restrained *L. viridis* (31·8 g) at 20 °C which again is considerably above the 0·046 ml h^{-1} g^{-1} predicted for the same size lizard at 20 °C by Bennett & Dawson (1976).

Determination of max $\dot{V}_{O_2}$

Criteria for the measurement of a genuine max $\dot{V}_{O_2}$ were outlined earlier but use of a mask (20 out of 32 experiments) rather than a whole animal respiratory prevents the inclusion of any cutaneous respiration. Although there was no obvious trend of $\dot{V}_{O_2}$ values from the respirometer being higher than from the mask, the possible error involved must be considered. It has only recently been appreciated that reptilian scales do allow both gas exchange and water loss (e.g. Heatwole & Seymour, 1975; Jammes & Grimaud, 1976). There is considerable species variability but, to some

Table 3. *Standard, resting or semi-active* $\dot{V}_{O_2}$ *measurements in ml* h^{-1} g^{-1} *STPD for* Lacerta *at* 30 °C.

(Last column is std $\dot{V}_{O_2}$ in ml h^{-1} g^{-1} STPD at 30 °C as predicted from the equation $\dot{V}_{O_2} = 0{\cdot}328\ W^{0{\cdot}77}$ for 1-day starved *Lacerta* at night and in the dark.)

Source	Animal	Body weight, g	Measured $\dot{V}_{O_2}$	Predicted std $\dot{V}_{O_2}$
Kramer, 1935	*L. trilineata*	54	0·124	0·126
Krehl & Soetbeer, 1899	*Lacerta* spp	110	0·22	0·105
	L. muralis	5·0	0·408	0·224
	L. sicula	5·5	0·425	0·218
Gelineo & Gelineo, 1955	*L. melisellensis*	6·8	0·323	0·210
	L. viridis	19·2	0·436	0·159
Nielsen, 1961	*L. sicula* and *L. viridis*	~ 19·0	~ 0·6	0·160
Avery, 1971	*L. vivipara*	~ 4·0	~ 0·75	0·325
Tromp & Avery, 1977	*L. vivipara*	2·0	0·38	0·28

extent, the more aquatic the reptile, the greater is its proportion of cutaneous gas exchange. In resting *L. viridis* (Jammes & Grimaud, 1976), cutaneous respiration accounts for 16% of the $\dot{V}_{CO_2}$ and 10% $\dot{V}_{O_2}$. The only data during activity is for sea snakes in which cutaneous proportions for $\dot{V}_{CO_2}$ and $\dot{V}_{O_2}$ did not alter from those at rest (Heatwole & Seymour, 1975) and therefore with no further evidence available, it has to be assumed that active *Lacerta* consume 10% more O_2 and produce 16% more CO_2 than is measured with the mask. Thus max $\dot{V}_{O_2}$ might be 2·93 instead of 2·66 m h^{-1} for a 1 g *Lacerta* whilst the respiratory exchange ratio might be 1·53 instead of 1·45

Respiratory exchange ratio, R

According to Bennett & Dawson (1976) a resting, fasting reptile should have an R of approximately 0·7 with higher or lower values being found in reptiles equilibrating (over several weeks) to high or low temperatures, respectively. This equilibration is necessary because blood bicarbonate concentration (i.e. CO_2 retention) is inversely proportional to temperature. However, many of the R values previously reported (see Bennett & Dawson, 1976) range from 0·65 to 1·46 under what often appear to be acclimated conditions and with no clear correlation between increasing R and temperature increases. It has been suggested (Cragg, 1978*b*) that some of the low R values in the literature might be a result of CO_2 leakages in closed circuit respirometry and Table 4 indicates that high R values for *Lacerta* are a result of varying degrees of activity. Table 4 also shows that lack of acclimation to the prevailing temperature does not influence R in *Lacerta* (Nielsen's data) and that an R of 0·7 to 0·75 is only obtained in *Lacerta* during standard metabolism after 3 days starvation.

R values as high as 1·5 or 1·7 occur in exercising man due to mainly hyperventilation but partly anaerobic metabolism (Mountcastle, 1974) and this is probably the explanation for lizards. Anaerobic metabolism may be a greater contributor to the lizard's high R value since it is very predominant in reptilian activity (Bennett & Dawson, 1976). Of course, increasing body temperature during lizard activity may also

Table 4. *Respiratory exchange ratio, R, in* Lacerta

Species	Temperature °C	*R*	Comments	Source
L. trilineata, *L. sicula* and *L. viridis*	20	0·64 to 0·78	Acclimated, std metabolism. Few days starvation	Kramer, 1934
L. sicula and *L. viridis*	10	0·88	Not acclimated, restrained, semi-active, 1-days starvation.	Nielsen, 1961
	20	0·80		
	30	0·81		
	35	0·82		
L. viridis	20	0·89	Acclimated, resting, restrained, ½-days starvation	Jammes & Grimmaud, 1976
L. viridis	20	0·83	Acclimated, semi-active, ½-days starvation	Jammes & Grimmaud, 1976
L. vivipara, *L. sicula* and *L. viridus*	30	0·75	Acclimated, std $\dot{V}_{O_2}$. 3-days starvation	This study
	30	0·85	Acclimated, std $\dot{V}_{O_2}$. 1-days starvation	This study
	30	0·95	Acclimated, daily $\dot{V}_{O_2}$. 1- and 3-days starvation	This study
	30	1·45	Acclimated, max $\dot{V}_{O_2}$. 1-days starvation	This study

drive off CO_2. The only other reptilian study (Gratz & Hutchison, 1977) that has measured *R* during maximum activity found that in the snake, *Natrix*, *R* actually decreased (at 15 and 25 °C) or rose only slightly (35 °C), but they suggest that this was because snakes are not as dependent as other reptiles on the bicarbonate buffer system.

Although in mammals an *R* of 0·7 is indicative of fat metabolism, 0·82 of protein or mixed diet and 1·0 of carbohydrate metabolism (Mountcastle, 1974), Roberts (1968*b*) has pointed out that in uricotelic animals R for protein metabolism also approximates to 0·7. The lizard diet of *Tenebrio* larvae is composed of protein, lipid and carbohydrate in the proportions 2:2:1 (Gist, 1972) and thus R should approximate to a mixed diet/protein value, i.e. 0·7. *R* values around 0·85 for less than 3 days starvation (Table 3) may be indicative of an increased proportion of carbohydrate metabolism.

Scaling of std and max $\dot{V}_{O_2}$

Std $\dot{V}_{O_2}$ of *Lacerta* in the minimum stress period, i.e. at night whilst in the dark, was proportional to $W^{0·74}$ to $W^{0·8}$ (Table 2). Measurements that relied on the spontaneous behavioural actions of the lizards (Table 1) gave a wider range of exponents: 0·77 to 0·94 for minimum $\dot{V}_{O_2}$, 0·57 to 0·77 for mean day $\dot{V}_{O_2}$ and 0·69 to 0·8 for peak $\dot{V}_{O_2}$ (Table 2). It is considered that under true standard conditions at 30 °C in *Lacerta*,

std $\dot{V}_{O_2}$ = 0·328 $W^{0.76}$ or 0·216 $W^{0.77}$ for 1- or 3-days starvation. Kramer's (1934) exponent of 0·694 for *Lacerta* covering a greater species and size range of 1·7 to 71 g is not at variance with the above data especially as further treatment of his data to regression analysis yields an exponent of 0·794 with a correlation coefficient of 0·995 significant at $P < 0{\cdot}001$ level. Interestingly, the exponent relating food consumption to body weight in *L. vivipara* is reported as 0·7 to 0·79 (Avery, 1971). Thus, intragenerically *Lacerta* obey the 0·75 exponent for metabolic scaling in contrast to many other reptiles (see Bennett & Dawson, 1976). The intercept value of this *Lacerta* study is very similar to Bennett & Dawson's (1976) reptilian data: resting $\dot{V}_{O_2}$ = 0·287 $W^{0.77}$ at 30 °C, implying that their resting values were close to standard conditions. Also, in agreement with Bennett & Dawson (1976), it is concluded that very young reptiles do not have a greater or lower weight-specific $\dot{V}_{O_2}$ than would be predicted from adult data (Figs. 8 and 9) in contrast to mammals (Wilkie, 1977) and fishes (Hughes, 1977).

Although the intercept value is similar for all reptilian Orders (Bennett & Dawson, 1976), mammalian and bird Orders each have their own intercept in the sequence monotrene, marsupial, eutherian, non-passerine and passerine (Dawson & Hulbert, 1970). In Table 5, *Lacerta* and eutherian data are compared, eutherians being chosen only because their data are more extensive. Eutherians consume approximately 11 times more O_2 than 1-day starved *Lacerta* (Table 5) and if *Lacerta* data is adjusted from 30 °C to 37 °C by assuming a Q_{10} of 2·12 (Bennett & Dawson, 1976), the eutherian/*Lacerta* ratio becomes approximately 6.

In maximum activity, *Lacerta* continue to obey the 0·75 scaling exponent with a relationship of max $\dot{V}_{O_2}$ = 2·66 $W^{0.747}$. This results in a max $\dot{V}_{O_2}$ increment of ~ 8 times std $\dot{V}_{O_2}$ being identical to small eutherians (Table 5) although increments of 11 to 22 for large eutherians (Pasquis *et al.* 1970) and ~ 10 for all eutherians (Taylor *et al.* 1978) have also been reported. Since Bennett & Dawson (1976) report an interspecific lizard increment of only 5·8 fold, it seems likely that the conditions were sub-maximal. An alternative or contributory explanation is that lizards have differing capacities for exercise (Bennett & Dawson, 1976) as a result of different lung complexities, enzyme activity and muscle myoglobin concentrations (Ruben, 1976*b*).

Even under maximum activity at 30 °C, *Lacerta* cannot reach the std $\dot{V}_{O_2}$ of a eutherian (Table 5) and are not likely to even at 37 °C because all lizards so far examined, except *Varanus*, show a metabolic pleateau or even a decline in max $\dot{V}_{O_2}$ at temperatures above their preferred body temperature (Bennett & Dawson, 1976). Only two reptiles, the lizards, *Cnemidophorus tigris* (Asplund, 1970) and *Varanus gouldii* (Bennett, 1972), have surpassed in maximum activity the eutherian std $\dot{V}_{O_2}$. Explanations for this reptile/eutherian metabolic differential are various (see Bennett & Dawson, 1976).

In conclusion, *Lacerta* data obey the 0·75 metabolic scaling exponent for both std and max $\dot{V}_{O_2}$ but it is considered, in agreement with Schmidt-Nielsen (1970), that a range of 0·7 to 0·8 is an equally acceptable exponent. This is because errors are introduced by the use of linear regression analysis for log/log allometric relationships (e.g. Manaster & Manaster, 1975). Whilst believing in genuine deviations from the 0·75 exponent, the author fells certain criteria must be satisfied before such a departure can be readily accepted, viz: (*a*) an adequate size range of no less than one log cycle, (*b*) rigorous standardization of the degree of starvation, minimum stress for std $\dot{V}_{O_2}$

Table 5. *Comparison of metabolic scaling in* Lacerta *and small Eutherian mammals*

(W in g. $\dot{V}_{O_2}$ in ml h^{-1} STPD. E/L = Eutherian/*Lacerta* ratio)

Variable	*Lacerta* 30 °C	Eutherian 37 °C	E/L ratio	Eutherian source
Std $\dot{V}_{O_2}$ 1-days starvation	$0{\cdot}328\ W^{0{\cdot}756}$	$3{\cdot}42\ W^{0{\cdot}75}$ $3{\cdot}8\ W^{0{\cdot}75}$	$\sim 11{\cdot}0$	Pasquis *et al.* 1970 Schmidt-Nielsen, 1975
Max $\dot{V}_{O_2}$ 1-days starvation	$2{\cdot}66\ W^{0{\cdot}747}$ or $2{\cdot}57\ W^{0{\cdot}75}$	$26{\cdot}16\ W^{0{\cdot}73}$ or $28{\cdot}2\ W^{0{\cdot}8}$	$\sim 10{\cdot}0$	Pasquis *et al.* 1970 Taylor *et al.* 1978
max $\dot{V}_{O_2}$/ std $\dot{V}_{O_2}$	$\sim 8{\cdot}0$	$\sim 7{\cdot}5$	$\sim 0{\cdot}0$	

and true short period maximum activity for max $\dot{V}_{O_2}$ and (*c*) where possible an equal distribution of points along the body weight axis so that regression analysis is not 'weighted' in favour of the larger or smaller animal.

This study was financed by a Medical Research Council Studentship. I would like to express my thanks to my supervisor, Professor G. M. Hughes, and to Dr R. A. Avery for supplying some of the *L. vivipara* and for many discussions on the ecology and behaviour patterns of *Lacerta*.

REFERENCES

ASCHOFF, J. & POHL, H. (1970). Rhythmic variations in energy metabolism. *Fedn. Proc. Fedn. Am. Socs. exp. Biol.* **29**, 1541–1552.

ASPLUND, K. K. (1970). Metabolic scope and body temperature of whiptail lizards (*Cnemidophorus*). *Herpetologica* **26**, 403–411.

AVERY, R. A. (1971). Estimates of food consumption by the lizard *Lacerta vivipara* Jacquin. *J. Anim. Ecol.* **40**, 351–365.

AVERY, R. A. (1973). Morphometric and functional studies on the stomach of the lizard, *Lacerta vivipara*. *J. Zool., Lond.* **169**, 157–167.

AVERY, R. A. (1976). Thermoregulation, metabolism and social behaviour in Lacertidae. In *Morphology and Biology of Reptiles* (ed. A. d'A. Bellairs and C. B. Cox), pp. 245–259. Academic Press.

AVERY, R. A. & MCARDLE, B. H. (1973). The morning emergence of the common lizard *Lacerta vivipara* Jacquin. *Br. J. Herpet.* 5, 363–368.

BARTHOLOMEW, G. A. (1972). Energy metabolism. In *Animal Physiology: Principles and Adaptations*, 2nd edn (ed. M. S. Gordon), pp. 63–72. New York: MacMillan.

BENNETT, A. F. (1972). The effect of activity on oxygen consumtpion, oxygen debt and heart rate in the lizards *Varanus gouldii* and *Sauromalus hispidus*. *J. comp. Physiol.* **79**, 259–280.

BENNETT, A. F. & DAWSON, W. R. (1976). Metabolism. In *Biology of the Reptilia*, vol. 5 (ed. C. Gans), pp. 127–223. New York: Academic Press.

BENNETT, A. F., DAWSON, W. R. & BARTHOLOMEW, G. A. (1975). Effects of activity and temperature on aerobic and anaerobic metabolism in the Galapagos marine iguana. *J. comp. Physiol.* **100**, 317–329.

BERGER, M. & HART, J. S. (1974). Physiology and energetics of flight. In *Avian Biology* vol. 4 (ed. D. S. Farner and J. R. King), pp. 415–477. Academic Press.

CLOUDSLEY-THOMPSON, J. L. (1961). *Rhythmic activity in animal physiology and behaviour*. New York and London: Academic Press.

CRAGG, P. A. (1978). Ventilatory patterns and variables in rest and activity in the lizard, *Lacerta*. *Comp. Biochem. Physiol.* (in the Press).

DAWSON, T. J. & HULBERT, A. J. (1970). Standard metabolism body temperature and surface areas of Australian marsupials. *Am. J. Physiol.* **218**, 1233–1238.

EVANS, K. J. (1966). Responses of the locomotor activity rhythms of lizards to simultaneous light and temperature cycles. *Comp. Biochem. Physiol.* **19**, 91–103.

EVANS, K. J. (1967). Observations on the daily emergence of *Coleonyx variegatus* and *Uta stansburiana*. *Herpetologica* **23**, 217–222.

FEDER, M. E. (1976). Lunglessness, body-size and metabolic rate in Salamanders. *Physiol. Zoöl.* **49**, 398–406.

FIRTH, B. T., WEBB, G. J. W. & JOHNSON, C. R. (1972). Effect of time of day and photoperiod on heart rate in the scincid lizard, *Tiliqua scincoides*. *Comp. Biochem. Physiol.* **43**A, 805–808.

FISCHER, K. (1961). Untersuchungen zur Sonnenkompassor ientierung und Laufaktivität von Smaragdeidechsen (*Lacerta viridis* Laur.). *Z. Tierpsychol.* **18**, 450–470.

GELINEO, S. & GELINEO, A. (1955). La consommation d'oxygène chez différentes espèces de lézards à habitats différents. *C. r. Séanc. Soc. Biol.* **149**, 565–568.

GIST, D. H. (1972). The effects of starvation and refeeding on carbohydrate and lipid reserves of *Anolis carolinensis*. *Comp. Biochem. Physiol.* **43**A, 771–780.

GOULD, S. J. (1971). Geometric similarity in allometric growth: a contribution to the problem of scaling in the evolution of size. *Am. Nat.* **105**, 113–136.

GRATZ, R. K. & HUTCHINSON, V. H. (1977). Energetics for activity in the diamondback water snake, *Natrix rhombifera*. *Physiol. Zoöl.* **50**, 99–114.

HEATH, J. E. (1962). Temperature – independent morning emergence in lizards of genus *Phrynosoma*. *Science, N.Y.* **138**, 891–892.

HEATWOLE, H. & SEYMOUR, R. (1975). Pulmonary and cutaneous oxygen uptake in sea snakes and a file snake. *Comp. Biochem. Physiol.* **51**A, 399–405.

HEMMINGSEN, A. M. (1960). Energy metabolism as related to body size and respiratory surfaces, and its evolution. *Reports of Steno Memorial Hospital and the Nordisk Insulinlaboratorium*, vol. IX. Copenhagen.

HOFFMAN, K. (1955). Aktivitätsregistrierungen bei frisch geschlüpften Eidelhsen. *Z. vergl. Physiol.* **37**, 253–262.

HOFFMAN, K. (1959). Die Aktivitätsperiodik von im 18 – und 36 – Stunden-tag erbrüteten Eidechsen. *Z. vergl. Physiol.* **42**, 422–432.

HOFFMAN, K. (1960). Versuch zur Analyse der Tagasperiodik – I Der Einfluss der Lichtintensitat. *Z. vergl. Physiol.* **43**, 544–566.

HOFFMAN, K. (1969). Zur Einfluss der Zeitgeberstärke auf die Phasenlarge der synchronisterten circadianew Periodik. *Z. vergl. Physiol.* **62**, 93–110.

HUGHES, G. M. (1977). Dimensions and respiration of lower vertebrates. In *Scale effects in animal locomotion* (ed. T. J. Pedley), pp. 57–81. London: Academic Press.

HUGHES, G. M., GAYMER, R., MOORE, M. & WOAKES, A. J. (1971). Respiratory exchange and body size in the Aldabra giant tortoise. *J. exp. Biol.* **55**, 651–665.

JAMESON, E. W., HEUSNER, A. A. & ARBOGAST, R. (1976). Oxygen consumtpion of *Sceloporus occidentalis* from three different elevations. *Comp. Biochem. Physiol.* **56**A, 73–80.

JAMMES, Y. & GRIMAUD, C. (1976). Ventilation, pulmonary and cutaneous gas exchange in the awake lizard, *Lacerta viridis*. *Comp. Biochem. Physiol.* **55**A, 279–286.

KAYSER, C. & HEUSNER, A. (1964). Étude comparative de metábolisme énergétique dans la série animale. *J. Physiol. (Paris).* **56**, 489–524.

KAYSER, C. & MARX, C. (1951). Le rhythme Nycthémérrl de L'Activité et la mémoire du temps chez le Lézard (*Lacerta agilis* et *Lacerta muralis*). *XX Congr. int. Phil. Sci. (Paris).* 1949, 6, *Biol.* 96–103.

KLEIBER, M. (1947). Body size and metabolic rate. *Physiol. Rev.* **27**, 511–541.

KRAMER, G. (1934). Der Ruheumsatz von Eidechsen und seine quantitative Beziehung zur Individuengrösse. *Z. vergl. Physiol.* **20**, 600–616.

KRAMER, G. (1935). Weitere Untersuchungen über die Umsatzgrösse von Eidechsen, insebsondere ihre Abhängigheit von der temperatur. *Z. vergl. Physiol.* **22**, 39–49.

KREHL, L. & SOETBEER, F. (1899). Untersuchungen über die Wärmfokonomie der poikilothermen Wirbelthiere. *Pflügers Arch. ges. Physiol.* **77**, 611–638.

LASIEWSKI, R. C. & DAWSON, W. R. (1967). A re-examination of the relation between standard metabolic rate and body weight in birds. *Condor* **69**, 13–23.

MCDONALD, H. S. (1976). Methods for the physiological study of reptiles. In *Biology of the Reptilia*, vol. 5 (eds. C. Gans and W. R. Dawson), pp. 19–126. New York: Academic Press.

MCMAHON, T. (1973). Size and shape in biology. *Science, N.Y.* **179**, 1201–1204.

MANASTER, B. J. & MANASTER, S. (1975). Techniques for estimating allometric equations. *J. Morph.* **147**, 299–308.

MAUTZ, W. J. & CASE, T. J. (1974). A diurnal activity cycle in the granite night lizard, *Xantusia henshawi*. *Copeia 1974*, 243–251.

MOUNTCASTLE, V. B. (1974). *Medical Physiology*, vol. 2, 13th edn. C. V. Mosby Company.

NIELSEN, B. (1961). On the regulation of respiration in reptiles. I. The effect of temperature and CO_2 on the respiration of lizards (*Lacerta*). *J. exp. Biol.* **38**, 301–314.

PASQUIS, P., LACAISSE, A. & DEJOURS, P. (1970). Maximal O_2 uptake in 4 species of small mammals. *Respir. Physiol.* **9**, 298–309.

POUGH, F. H. (1977). The relationship of blood oxygen affinity to body size in lizards. *Comp. Biochem. Physiol.* **57**A, 435–442.

PRANGE, H. D. & JACKSON, D. C. (1976). Ventilation, gas exchange and metabolic scaling of a sea turtle. *Respir. Physiol.* **27**, 369–377.

RAO, M. V. S. & RAJABAI, B. S. (1973). Rhythmic activity in ground dwelling Agamid Lizard, *Sitana ponticeriana*. *Br. J. Herpet.* **4**, 328–332.

ROBERTS, L. A. (1968*a*). Oxygen consumption in the lizard, *Uta stansburiana*. *Ecology* **49**, 809–819.

ROBERTS, L. A. (1968*b*). Water loss in the desert lizard *Uta stansburiana*. *Comp. Biochem. Physiol.* **27**, 583–589.

RUBEN, J. A. (1976*a*). Aerobic and anaerobic metabolism during activity in snakes. *J. comp. Physiol.* **109**, 147–158.

RUBEN, J. A. (1976*b*). Correlation of enzymatic activity, muscle myoglobin concentration and lung morphology with activity metabolism in snakes. *J. exp. Zool.* **197**, 313–320.

SAINT-GIRONS, H. (1971). Quelques facteurs du rhythme circadian d'activité chez les lépidosauriens (reptiles). *Bull. Soc. zool. Fr.* **96**, 317–330.

SCHMIDT-NIELSEN, K. (1970). Energy metabolism, body size and problems of scaling. *Fedn. Proc. Fedn. Am. Socs. exp. Biol.* **29**, 1524–1532.

SCHMIDT-NIELSON, K. (1975). *Animal Physiology. Adaptation and environment.* Cambridge University Press.

SONGDAHL, J. H. & HUTCHINSON, H. V. (1972). The effect of photoperiod, parietalectomy and eye enucleation on oxygen consumption in the blue granite lizard, *Sceloporus cyanogenys*. *Herpetologica* **28**, 148–156.

TAYLOR, C. R., SEEHERMAN, H. J., MALOIY, G. M. O., HEGLUND, N. C. & KAMAU, J. M. Z. (1978). Scaling maximum aerobic capacity (V_{O_2} max) to body size in mammals. *Fedn. Proc. Fedn. Am. Socs. exp. Biol.* **37**, 473.

TOYE, S. A. (1972). The locomotory activity of the rainbow lizard, *Agama agama* (L). *Br. J. Herpet.* **4**, 252–257.

TROMP, W. I. & AVERY, R. A. (1977). A temperature-dependent shift in the metabolism of the lizard *Lacerta vivipara*. *J. therm. Biol.* **2**, 53–54.

ULTSCH, G. R. (1974). Gas exchange and metabolism in the Sirenidae (*Amphibia: Caudata*). I. Oxygen consumption of submerged sirenids as a function of body size and respiratory surface area. *Comp. Biochem. Physiol.* **47**A, 485–495.

UNDERWOOD, H. (1977). Circadian organisation in lizards: The role of the pineal organ. *Science, N.Y.* **195**, 587–589.

WHITFORD, W. G. (1973). The effect of temperature on respiration in the Amphibia. *Am. Zool.* **13**, 505–512.

WILKIE, D. R. (1977). Metabolism and body size. In *Scale effects in animal locomotion* (ed. T. J. Pedley), pp. 23–36. London: Academic Press.