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Effect of Temperature on the Oxygen Consumption of Lizards from different Climatic Regions

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Abstract. Oxygen consumption levels and metabolic rate temperature curves of various lizard species from three different climatic regions were examined in relation to ambient temperature. The species used in this research were as follows: *Anguis fragilis, Lacerta vivipara, Lacerta agilis* (cool temperate species); *Blanus cinereus, Podarcis hispanica, Podarcis lilfordi brauni, Podarcis lilfordi lilfordi, Podarcis muralis, Psammodromus algirus, Tarentola mauritanica* (warm temperate species); *Chalcides ocellatus, Acanthodactylus opheodurus, Acanthodactylus schmidti* (desert species). A double chamber volumetric closed system was used to measure the resting oxygen consumption of the lizards. Acute oxygen consumption determinations were made, that is the lizards were not allowed to acclimate to the test temperatures. Interspecific differences in levels of resting oxygen consumption and in the characteristics of the metabolic rate temperature curves were examined in relation to methods of thermoregulation and in relation to the ecology of the respective species. Evidence for "temperature dependent shifts" and "low thermal dependence" was found in the metabolic rate temperature curves of some species. A diminishing Q_{10} at or below the voluntary body temperatures suggests some degree of metabolic homeostatsis and energy conservation.

Introduction

Oxidative metabolism of multicellular ectothermic animals may, for comparative purposes, be measured indirectly by determining oxygen consumption at different temperature levels. Oxygen consumption is then expressed as the amount consumed per unit body weight per unit time. When mean values of oxygen consumption at each temperature are plotted in semi-logarithmic form, a metabolic rate temperature or M-T curve is obtained. M-T curves provide data which are useful in making comparisons of metabolic rates between species from different climatic regions.

It would be expected that, being ectotherms, the rate of oxygen consumption of lizards will show a steady increase with ambient temperature, in a manner according to Van't Hoff's generalisation (Gordon et al., 1982). However, recent research has shown that when the body temperatures of reptiles change, there are corresponding alterations in oxygen consumption but the relationship may not always be of a linear nature.

Results from recent research suggests that reptiles are capable of adjusting levels of resting oxygen consumption and that there seem to be at least two kinds of adjustments to be found in the M-T curves. One adjustment is associated with lower temperatures and is well below the voluntary (preferred) body temperatures (Spellerberg, 1982) of the reptile species. That is, the lower part of the M-T curve may be elevated or shifted upwards with respect to the rest of the curve. This kind of adjustment has previously been referred to as a ''temperature dependent shift'. Another kind of adjustment is normally associated with body temperatures which are just below or close to the mean voluntary body temperature of the particular species and is seen in the form of a diminished Q_{10}. That is, at temperatures just below the mean voluntary body temperature, the rate of increase in the M-T curve may be found to be less than expected. This kind of adjustment has previously been referred to as ''low thermal dependence'' or ''high temperature compensation''.

Aleksiuk (1971a, 1971b) observed a temperature dependent shift in the M-T curve of the cool temperate snake sub-species *Thamnophis sirtalis parietalis* at between 10° and 15°C, but it was not found in the sub-tropical sub-species *T. s. sirtalis*. This shift in the M-T curve of the cool temperate sub-species may represent an instantaneous adaptation to cold conditions and there is evidence to suggest that variation in isoenzyme activity at different temperatures is the basis for this temperaure dependent compensation (Hoskins and Aleksiuk, 1973). Brown and Loveridge (1980) noted a temperature dependent shift between 20° and 30°C in *Crocodylus niloticus*. They interpreted their results as being a mechanism for energy conservation at the mean voluntary body temperature (about 30°C). Buikema and Armitage (1969) reported a shift in the M-T curve of *Diadophis punctatus* at 15°-20°C (negative Q_{10}) and low thermal dependence-between 25° and 30°C ($Q_{10} < 1.6$). Several examples of low thermal dependence or high temperature compensation have been observed in many species of lizards. Moberly (1963) for example has reported a low thermal dependence at 25°-30°C for brummating (''hibernating'') *Dipsosaurus dorsalis*. This adjustment was not apparent in the warm acclimated *D. dorsalis* during summer. Dawson and Bartholomew (1956) described a low thermal dependence in the M-T curve of *Uta stansburiana* between 30° and 35°C ($Q_{10} < 1.4$) and in *Sceloporus accidentalis* between 30° and 35°C ($Q_{10} < 1.5$).

The aim of this research was to examine the metabolic rate temperature curves of different species of lizards from different climatic regions and to assess the ecological implications of various characteristics of the M-T curves.

Materials and Methods

Lizard species used in the research

Lizard species used in this research were grouped into three categories according to the climatic region in which they were collected (Table 1). The three species collected from cool temperate climatic regions were *Anguis fragilis* (slow-worm), *Lacerta vivipara* (common or viviparous lizard) and *Lacerta agilis* (sand lizard). The legless lizard *A. fragilis* (specimens weighed between 15 and 20 gm) was collected in southern England where it is found in grassland habitats and favours moist conditions. It is a thighmothermic species (Spellerberg, 1976) and tends to be fossorial in its behaviour. A more detailed account of methods of thermoregulation is given in the discussion. The diet of *A. fragilis* consists of slugs and earthworms. Like other cool temperate climatic lizard species, *A. fragilis* undergoes brummation or ''hibernation'' (Spellerberg, 1982) from about October until about the end of March.

Adult specimens of *L. vivipara* were collected from localities in southern England and specimens of *L. agilis* were collected from the Netherlands. Both these species are small diurnal lizards and in terms of their thermoregulation they are shuttling heliotherms. The lizard *L. vivipara* (3-4 gm) is found in cool moist meadows, heathland, field edges and amongst woodlands of alpine regions. It occurs up to altitudes of 2,500 m and as far north in the sub-arctic tundra as latitude 70°. The diet of this species includes adult insects, insect larvae, spiders and earthworms. It brummates for a period of about five months (November to March). The lizard *L. agilis* (8-12 gm) occurs on grassland, amongst sand dunes and on heatlands. Its diet includes adult insects, insect larvae and spiders. The period of brummation of this species is from about early October to March.

Six species of lizards from three different families were collected from warm temperate climatic regions (including parts of the Mediterranean region). These six species were as follows. *Blanus cinereus* (an amphisbaenian); *Podarcis hispanica* (Iberian wall lizard); *Podarcis lilfordi brauni* and *Podarcis lilfordi lilfordi* (Lilford's wall lizard); *Podarcis muralis* (common wall lizard); *Psammodromus algirus* (large psammodromus); *Tarentola mauritanica* (Moorish gecko).

The amphisbaenian *B. cinereus* is for convenience considered together with other lizard species although it is now classified in a separate suborder. Sub-adult specimens (2-3 gm) were collected from southern Spain and all were found under stones and logs. It is a thigmothermic and fossorial species.

The two species *P. hispanica* (3-4 gm) and *P. algirus* (5-9 gm) were collected from southern Spain. Both are small shuttling heliotherms and occur in dry habitats and tend to be associated with coastal chaparral vegetation. Their geographical distribution includes north-west Africa, Iberia and France (Arnold et al., 1978).

The two sub-species *P. lilfordi brauni* (7-12 gm) and *P. lilfordi lilfordi* (6-12 gm) were collected from islands near Majorca and Minorca. It is a species which seems to be confined to small islands which are rocky but without much vegetation. The diet of this

Table 1. Lizard species used in the research and their temperature relations.

	Number of Specimens	Mean Weight (grams)	Locality	Method of Thermoregulation	Voluntary Body Temperature	
					Mean	Range
Cool temperate climatic species						
Anguis fragilis	5	13.3	Southern England	Thigmotherm	23.0	14.0-29.0
Lacerta vivipara	10	3.9	Southern England	Shuttling heliotherm	30.7	28.2-33.3
Lacerta agilis	3	8.4	Netherlands	Shuttling heliotherm	31.0	23.0-38.0
Warm temperate climatic species						
Blanus cinereus	4	2.4	Southern Spain	Thigmotherm	23.4	14.5-31.5
Podarcis hispanica	4	3.6	Southern Spain	Shuttling heliotherm	30.9	28.6-33.0
Podarcis lilfordi brauni	6	7.4	Majorca, Minorca	Shuttling heliotherm	—	—
Podarcis lilfordi lilfordi	6	8.3	Majorca, Minorca	Shuttling heliotherm	—	—
Podarcis muralis	7	5.5	Pyrenees	Shuttling heliotherm	—	—
Psammodromus algirus	4	5.2	Southern Spain	Shuttling heliotherm	—	—
Tarentola mauritanica	10	6.6	Southern Spain	Shuttling heliotherm	—	—
Desert species						
Chalcides ocellatus	103	18.7	Egypt	Shuttling heliotherm and thigmotherm	34.0	28.0-37.0
Acanthodactylus opheodurus	3	3.8	Saudi Arabia	Shuttling-posturing heliotherm	—	—
Acanthodactylus schmidti	4	14.5	Saudi Arabia	Shuttling-posturing heliotherm	—	—

species is reported to include a relatively high proportion of plants (Arnold et al., 1978).

The lizard species *P. muralis* (4-7 gm) was collected from the Pyrenees. It is a shuttling heliotherm and is found in dry habitats where it often basks amongst rocky areas. It has a widespread geographical distribution and ranges from northern France to central Spain and southern Italy.

The Moorish gecko (*T. mauritanica*) was collected from southern Spain. The specimens collected weighed between five and eight grams. It occurs in warm and rocky coastal areas and tends to be nocturnal during the summer but diurnal in the spring.

Three species representing two families were collected from desert regions. The skink *C. ocellatus* (13-32 gm) was collected from desert habitats in Egypt. This species has a very wide distribution (Mediterranean, north and north-east Africa and south-west Asia) and can not be considered to be a desert species throughout its entire range. However, as the specimens used in this research came from desert habitats, it is grouped with other strictly desert species. This diurnal lizard is found burrowing in sandy places, often hiding under stones and ground vegetation in the desert (Al-Sadoon, personal observation). It is also found in arid regions in which a scrub vegetation still flourishes. Ocellated skinks spend a few hours basking in the morning sun. Later in the day, this species avoids the high temperatures of the desert by remaining below the ground or under rocks, emerging later at the end of the day. In terms of thermoregulation it is both a thigmotherm and a shuttling heliotherm. The ocellated skink's diet consists of adult insects and their larvae.

The two species, *Acanthodactylus schmidti* and *Acanthodactylus opheodurus*, were collected from Saudi Arabia. The lizard, *A. schmidti* (10-18 gm) inhabits dry sandy areas, in contrast to *A. opheodurus* (4-5 gm) which is found in hard sandy substrata. The diet of both species consists of adult insects and insect larvae. These two species exhibit both shuttling and posturing forms of thermoregulatory behaviour.

Maintenance of Animals

All cool-temperate species were kept in an outdoor vivarium, 20 sq. m. in area. Water was always available and there was a food supplement of *Tenebrio molitor* larvae. Other insects were regularly provided. The lizards remained in good condition and all appeared to adjust to these outdoor conditions in the vivarium. When oxygen consumption measurements were required, a number of lizards were caught from the vivarium and then housed in a large tank in the laboratory. Additional illumination was provided above the tank for a daily period of 8-9 hours. The lizards were fed on *T. molitor* larvae up until a few days prior to the experiments.

Species from the warm temperate climatic region were kept in an animal house. This facility had a temperature controlled room and a controlled photoperiod cycle of 10 hours light and 14 hours dark. Lizards of the same species were kept in a large tank and provided with conditions similar to those which they would experience in their natural habitat. The lizards were fed on *T. molitor* larvae, fruit, boiled eggs and meat. Water was available at all times. Additional illumination from a lamp was provided in each tank for a daily period of 8-9 hours.

Desert species were also kept in an animal house. All lizards were maintained in large tanks measuring 100 x 50 x 45 cm, each of which contained a substratum of sand. Vegetation and stones were added to the sand to simulate a natural habitat. Heat was provided from an infrared lamp for a daily period of 10 hours. The soil temperature gradient available to the lizards was from 20 to 45°C. The lizards' diet included meal worms and meat. They were also given, when available, live insects, boiled eggs and fruit. Water was always available.

Oxygen consumption measurements

A double chamber volumetric system was used for measurements of oxygen consumption. Animals were not allowed to acclimate to the test temperature i.e. acute M-T curves were obtained. Eight small respirometers were used and each respirometer consisted of two 500 ml flasks joined by a vertical glass manometer filled with manometer fluid. One of the flasks served as the animal chamber and the other as a compensating chamber (thermobarometer). Small bags of soda lime (carbon dioxide absorbent) and silica-gel (water absorbent) were placed in each flask. Each respirometer was placed in a water bath where a constant experimental temperature ($\pm$ 0.5°C) could be obtained. The animals were fasted for two days then placed in the flasks at a given temperature (experimental temperature) for between one and four hours. During this time no readings were taken in order to ensure that the effects of handling were reduced and that the respiration reached standard levels. After this resting period, the animal's oxygen consumption was measured by closing the animal chamber to the atmosphere and then adjusting the thermobarometer so that it was also closed to the atmosphere. The manometer fluid would rise as oxygen is consumed in the animal chamber. A syringe (1 ml) of pure oxygen was attached to the animal chamber and direct readings from the syringe could then be taken, indicating the volume of oxygen necessary to re-adjust the manometer fluid to its previous level.

Standard levels of oxygen consumption are obtained when the animal is not active and is completely at rest. Prior to this state, the levels of oxygen consumption are comparatively high but then slowly diminish as the animal becomes adjusted to the conditions in the respirometer. One example showing the levels of oxygen consumption for *C. ocellatus* and obtained during the animal's adjustment period is given in Figure 1. The measurements of oxygen consumption used in the calculations are also shown in this Figure. The higher levels of oxygen consumption (during the adjustment period) can not be used because they would not be standard levels or would not represent resting levels. The same procedure was adopted for all other species used in this research. That is, the lowest and consistent levels of oxygen consumption at each test temperature have been used in the investigations

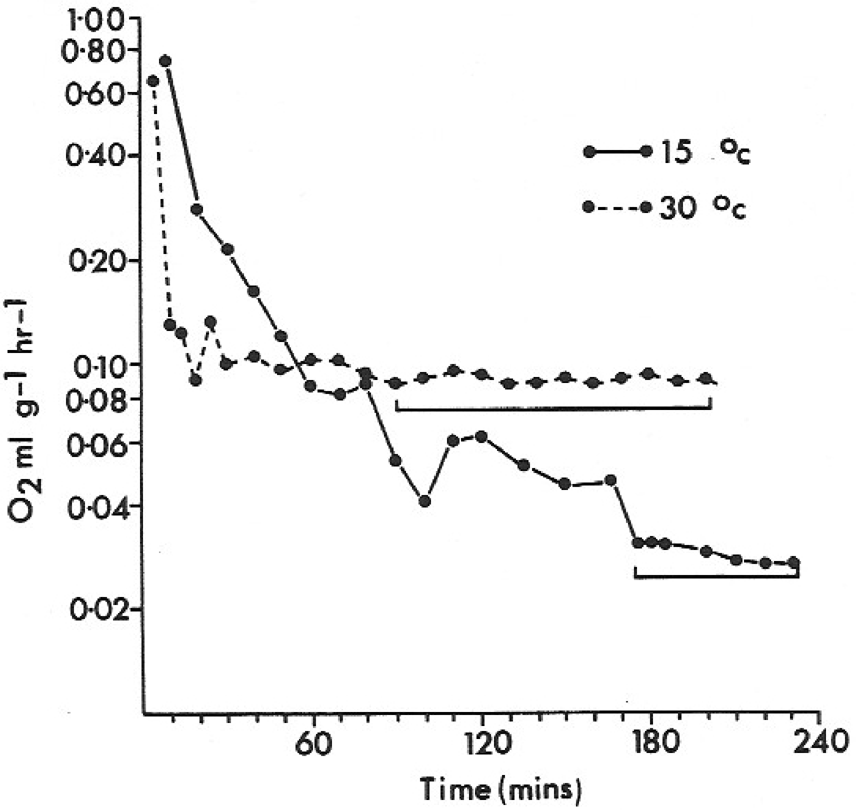


Fig. 1. Oxygen consumption values for *C. ocellatus* obtained over four hours at two test temperatures. These results were obtained from the time the animal was first introduced to the respirometer until a standard level of oxygen consumption was obtained. The standard levels of oxygen consumption are indicated by the horizontal lines.

The test temperatures used were 5°C, 10°C, 15°C, 20°C, 25°C, 30°C and 35°C. The resting oxygen consumption values obtained in the experiments were then converted to standard conditions and, as in previous research on reptiles, are expressed as ml oxygen consumed per gm body weight per hour. All measurements of resting oxygen consumption were made over a period of time when the lizard would normally be active.

Results

Resting oxygen consumption

A summary of the mean resting oxygen consumption values measured at three of the test temperatures (20°C, 30°C, 35°C) is presented in Table 2. As would be expected, the values obtained for each of the 12 species increase with increasing temperature. It is useful to compare these results with those which would be predicted from previous research on other lizard species. Predicted levels of resting oxygen consumption were calculated using regression equations derived by Bennett and Dawson

Table 2. Observed and predicted mean resting oxygen consumption values (0_2 ml $g^{-1}hr^{-1}$) at three temperatures for 13 species. Predicted values calculated using regression equations derived by Bennett and Dawson (1976) and Bennett (1982).

Species	20°C			30°C			35°C		
	Observed	Predicted	Ratio(o/p)	Observed	Predicted	Ratio(o/p)	Observed	Predicted	Ratio(o/p)
A. fragilis	0.110	0.057	1.92	0.175	0.155	1.13	0.223	0.254	0.88
L. agilis	0.181	0.063	2.87	0.360	0.167	2.15	0.487	0.281	1.73
L. vivipara	0.135	0.074	1.82	0.293	0.192	1.52	0.560	0.337	1.66
B. cinereus	0.120	0.080	1.50	0.176	0.207	0.85	0.331	0.387	0.85
P. hispanica	0.160	0.074	2.16	0.370	0.193	1.91	0.585	0.339	1.72
P. l. brauni	0.073	0.064	1.14	0.340	0.170	2.00	—	—	—
P. l. lilfordi	0.085	0.063	1.35	0.205	0.167	1.22	—	—	—
P. muralis	0.172	0.068	2.53	0.469	0.180	2.60	0.427	0.309	1.38
P. algirus	0.123	0.069	1.78	0.344	0.181	1.90	0.505	0.313	1.61
T. mauritanica	0.067	0.066	1.01	0.126	0.174	0.72	0.182	0.297	0.61
C. ocellatus	0.058	0.053	1.09	0.097	0.146	0.66	0.159	0.236	0.67
A. opheodurus	0.100	0.073	1.37	0.208	0.190	1.09	0.363	0.190	1.91
A. schmidti	0.070	0.056	1.25	0.151	0.150	1.00	0.222	0.249	0.89

(1976) for lizards kept at 20°C and 30°C and from equations derived by Bennett (1982) for lizards kept at 35°C (Table 2). The most similar values between the observed and the predicted levels were for the two species *T. mauritanica* and *C. ocellatus*. All of the other observed values were notably different from the predicted values and in most cases the observed values are higher than the predicted values. It is worth noting that most of the lizards studied in the present study were small species (2-18 gms) compared to the large species studied by Bennett and Dawson (1976). This variation in weight could effect the weightspecific resting metabolic rate relationship in lizards.

Metabolic rate temperature curves

Data obtained for resting oxygen consumption values at the seven test temperatures from 5°C to 35°C are presented in the form of M-T curves in Figures 2, 3 and 4. Lizard species were collected from three different climatic regions and so therefore these data have been presented on the basis of the climatic regions from which the

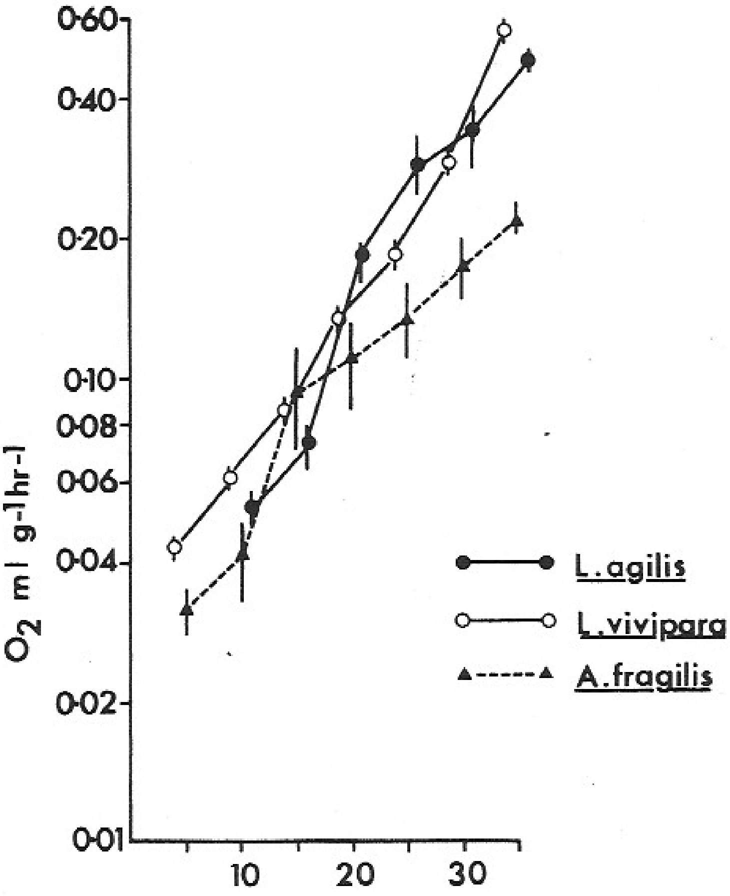
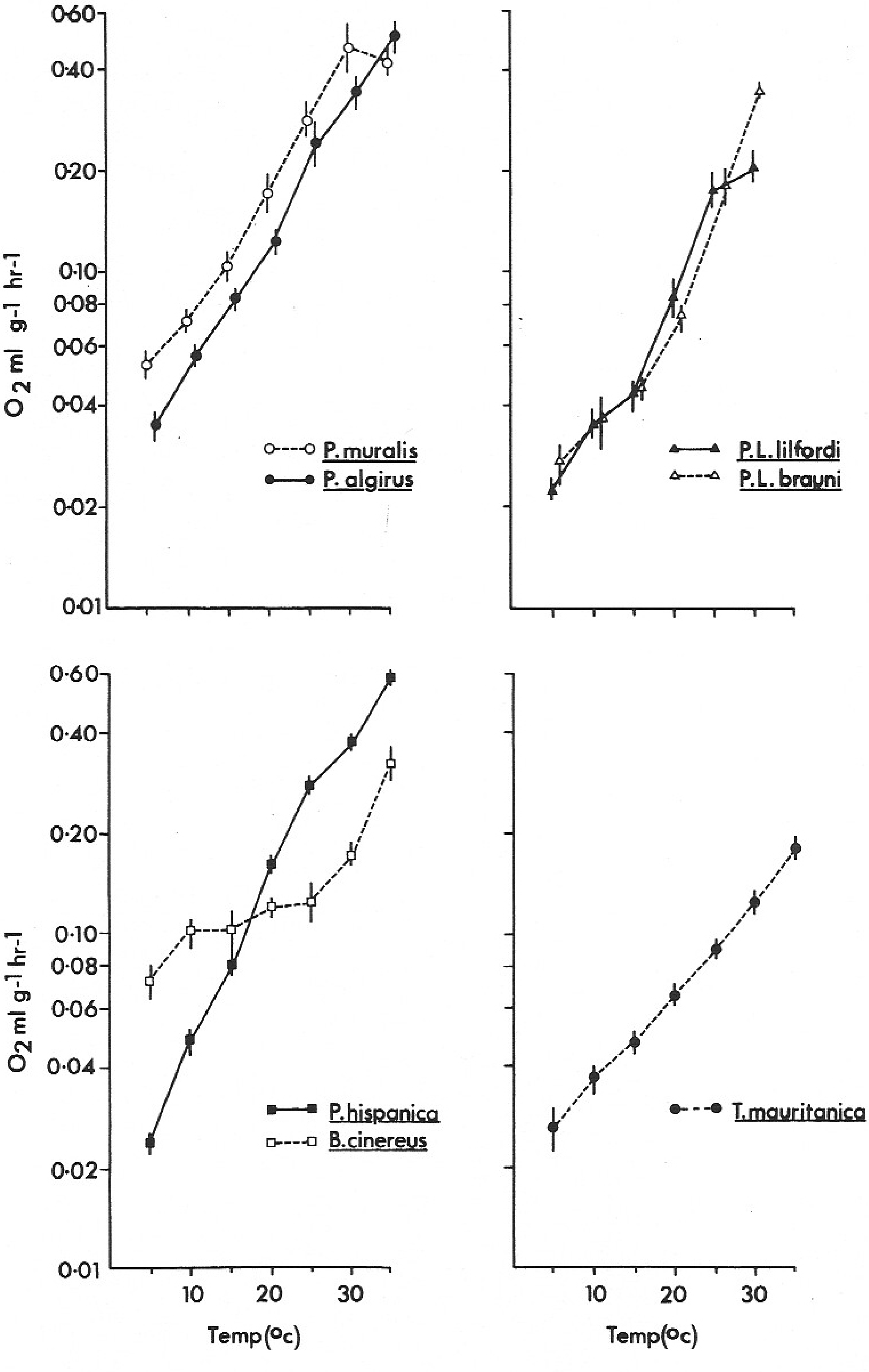


Fig. 2. The influence of temperature on resting oxygen consumption in three species of cool-temperate lizards. Each point represents the mean of different individual lizards. Vertical lines represent ± standard errors. Some of symbols have been displaced slightly from experimental temperatures in the interest of clarity.


0·60
0·40
0·20
0·10
0·08
0·06
0·04
0·02
0·01
O$_2$ ml g^{-1} hr^{-1}
P. muralis
P. algirus
P.L. lilfordi
P.L. brauni
P. hispanica
B. cinereus
T. mauritanica
10
20
30
Temp(°c)

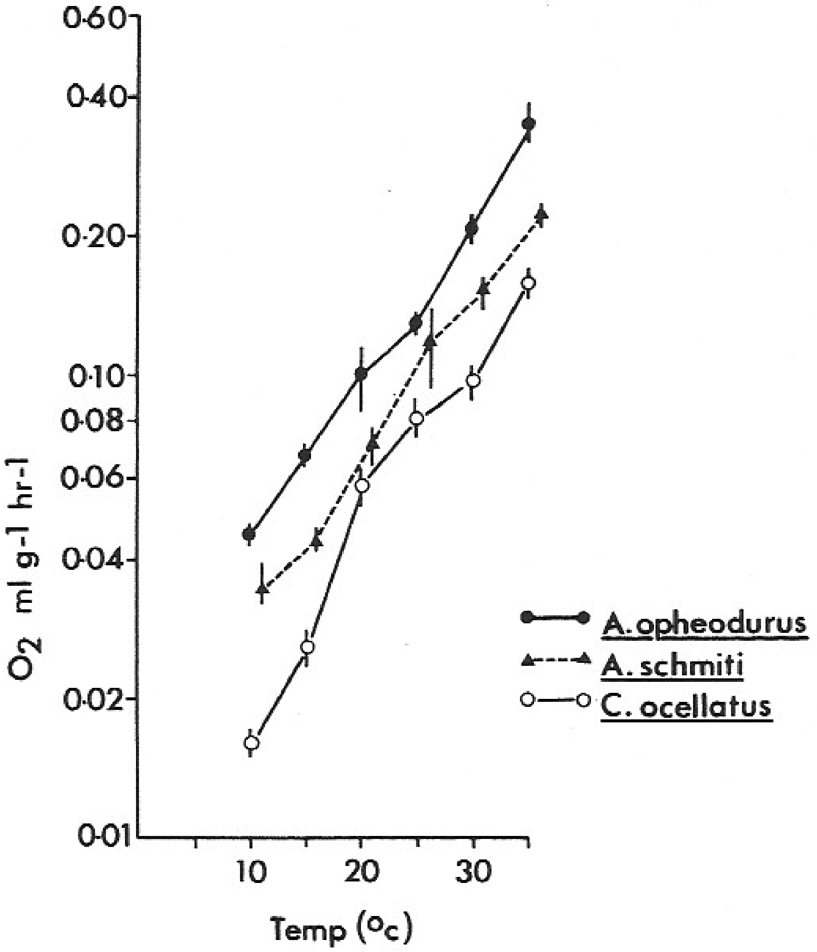


Fig. 4. The influence of temperature on oxygen consumption in three species of desert lizards. Each point represents the mean of different individual lizards. Vertical lines represent ± standard errors. Some of the symbols have been displaced slightly from experimental temperatures in the interest of clarity.

species was obtained. In general there is an increase in oxygen consumption with increasing temperature and only one instance where the level decreased (*P. muralis* between 30°C and 35°C). There are many interspecific differences in both levels of oxygen consumption and in the rates of change of the M-T curves over the temperatures used. The M-T curves of three species (*A. fragilis, B. cinereus, C. ocellatus*) were noticeably different compared to the M-T curves of all the other species. This and other aspects are considered in the discussion.

Fig. 3. The influence of temperature on resting oxygen consumption in seven species of warm-temperate lizards. Each point indicates the mean oxygen consumption of different individuals. Vertical lines represent ± standard errors. Some of symbols have been displaced slightly from experimental temperatures in the interest of clarity.

Q_{10} values

The Q_{10} values for observed resting oxygen consumption values are presented in Table 3. There was no general pattern of increasing Q_{10} values over the temperature range used in this research. That is, there is variation in the Q_{10} values both at low temperatures and at high temperature. All Q_{10} values were found to be positive apart from that obtained for *P. muralis* at temperatures between 30° and 35°C. The lowest "overall" Q_{10} value was that obtained for *B. cinereus* (1.66) and the highest "overal" Q_{10} values were those obtained for the species *P. hispanica* (2.90) and *P. l. brauni* (2.75).

The Q_{10} values which were closest to unity were those obtained for *B. cinereus* (1.04 at 10° to 15°C), *L. agilis* (1.31 at 25° to 30°C) and *P. l. lilfordi* (1.37 at 25° to 30°C). The highest values were those obtained for *L. agilis* (6.32 at 15° to 20°C), *P. l. brauni* (6.08 at 20° to 25°C) and *C. ocellatus* (5.03 at 15° to 20°C).

Table 3. Q_{10} values of resting oxygen consumption rates.

	Q_{10} values for oxygen consumption for temperature range indicated						
	5-10°C	10-15°C	15-20°C	20-25°C	25-30°C	30-35°C	"Overall" Q_{10}
A. fragilis	1.83	4.90	1.40	1.53	1.65	—	1.99
L. agilis	—	1.92	6.32	2.62	1.31	2.15	2.46
L. vivipara	2.01	1.98	2.46	1.86	2.53	3.65	2.35
B. cinereus	1.93	1.04	1.38	1.10	1.95	3.54	1.66
P. hispanica	4.00	2.77	4.00	3.08	1.73	2.50	2.90
P. l. brauni	1.78	1.56	2.63	6.08	3.56	—	2.75
P. l. lilfordi	2.68	1.43	3.91	4.24	1.37	—	2.44
P. muralis	1.78	2.09	2.73	2.72	2.73	0.83	1.99
P. algiris	2.56	2.25	2.14	3.87	2.02	2.15	2.43
T. mauritanica	2.02	1.61	2.03	1.84	1.92	2.09	1.91
C. ocellatus	—	2.59	5.03	1.91	1.43	2.66	2.50
A. opheodurus	—	2.17	2.13	1.66	2.60	3.04	2.24
A. schmidti	—	1.43	2.65	2.84	1.64	2.16	2.07

Discussion

M-T curves and method of thermoregulation

The wealth of literature on reptile thermoregulation has established the use of the terms thigmotherm and heliotherm. Lizard species which use the former kind of behaviour usually obtain most of their body heat by contact with their immediate surroundings. Heliothermic lizards obtain most of their body heat by basking in the sunlight. Some heliothermic species tend to spend much of their basking behaviour by adopting specialized basking postures so as to control the rate of heat uptake. Other heliothermic species adopt a form of behaviour which consists of shuttling between sunlit areas and shaded ares. This shuttling behaviour is an alternative way of controlling the rate of heat uptake. In many cases it is not possible to classify a lizard species as being either entirely a shuttling heliotherm or a posturing heliotherm, but in most species one form of behaviour is predominant.

Two of the species examined in this research are distinctly thigmothermic. Both *A. fragilis* and *B. cinereus* only rarely bask in the open and for most of the time they obtain body heat by way of contact with the ground and their immediate surroundings. The M-T curves of these two species are distinct from the M-T curves obtained for the other species and are particularly characteristic at those temperatures which represent the voluntary body temperatures of the respective species (Table 1). The voluntary body temperature for *B. cinereus* determined in a temperature gradient chamber has been found to be between 14.5° and 31.5°C with a mean of 23.4°C (Spellerberg, personal observation). The voluntary body temperature of *A. fragilis* has been reported to be between 14°, 29°C with a mean of 23°C (Spellerberg, 1977). The results obtained here show that at the voluntary temperatures levels of these two species, the Q_{10} values are low (*A. fragilis*, 1.53; *B. cinereus*, 1.10) compared to the Q_{10} values for other species obtained at 20°-25°C.

Although voluntary body temperatures are known for only a few of the heliothermic species used in this research, there seems to be a slight decrease in the Q_{10} values just below the voluntary body temperatures, preceded by an increase in the Q_{10} values. This aspect is particularly noticeable in the desert species *C. ocellatus* which has a voluntary temperature of 34.0°C (Sadoon, personal observation). In the case of this species, the Q_{10} between 30° and 35°C was found to be 2.66 but between 25° and 30°C the Q_{10} was found to be 1.43 than between 20° and 25°C and Q_{10} was 1.91. Similarly, and in the case of the warm temperate species *P. hispanica*, there was a Q_{10} of 2.5 between 30° and 35°C but between 25° and 30° the Q_{10} was 1.73 which is preceded by a higher Q_{10} value of 3.08 between 20° and 25°C.

These low Q_{10} values which occur at or just below the lizards' voluntary temperatures have previously been reported as a mechanism which assists metabolic homeostasis (see review by Bennett and Dawson, 1976). Davies and Bennett (1981) have discussed the implications of declining Q_{10} values at high temperatures in the cool temperate snake species *Natrix natrix* and have suggested that this is a mechanism which reduces basic energetic costs. Such adjustments in the M-T curves of reptiles indicate that some species do have some degree of metabolic homeostatis.

Comparison of species from within climatic regions

Of the three M-T curves for the cool temperate lizard species (Figure 2) those for *L. agilis* and *L. vivipara* are similar but the upper part of the M-T curve for *A. fragilis* is comparatively low. That is and above 15°C the resting oxygen consumption for *A. fragilis* is less than that for the other two cool temperate species. These levels of resting oxygen consumption and the characteristics of the M-T curves would seem to be explained in part by the differences in behaviour and ecology of the respective species.

The lizard *A. fragilis*, as mentioned before, is a thigmothermic species, which only rarely basks and it has a comparatively slow form of locomotion. The other two species are shuttling heliotherms and in comparison to *A. fragilis* they frequently move about their habitat while foraging and basking. They have a rapid form of locomotion which is characteristic of a shuttling heliotherm. The comparatively high "overall" Q_{10} values for *L. agilis* and *L. vivipara* (Table 3) would therefore seem to be a prerequisite for this kind of day-to-day activity, so typical of many small, diurnal, heliothermic lizards.

Apart from the M-T curve for *B. cinereus*, the shape of the M-T curves for the remaining five species of warm temperate lizards is fairly consistent (Figure 3). The Q_{10} values for *B. cinereus* are comparatively low throughout the temperature range of 10° to 25°C and this characteristic would seem to be linked to both the thigmothermic and fossorial behaviour of this species. Comparison of the M-T curves of the other five warm temperate species reveals some interesting differences particularly in the levels of resting oxygen consumption. For example the "overall" M-T curve obtained for *T. mauritanica* is lower than for the other species and at temperatures of 20°C and above, the level of resting oxygen consumption is clearly lower than that obtained for any of the other warm temperate species, including the fossorial *B. cinereus*. Being the only geck species, it is tempting to suggest that the M-T curve obtained here is characteristic of a warm temperate gecko which is mainly nocturnal during the summer. Further comparative research is necessary before a full explanation for this low M-T curve can be offered.

The upper part of the M-T curves (20°-30°C) for *P. algirus, P. muralis, P. l. brauni*, and *P. hispanica* are similar but some differences in the levels of resting oxygen consumption occur at temperatures betwen 5°C and 20°C. Such differences may be interpreted as being indicative of temperature dependent shifts and this aspect is discussed below.

The M-T curves obtained for the three lizard species collected from desert regions are all different with respect to the levels of resting oxygen consumption (Figure 4). Both *A. opheodurus* and *A. schmidti* are heliothermic lizards and both are capable of rapid locomotion. By way of contrast *C. ocellatus* burrows in the sand and often remains hidden below the sand or beneath the vegetation. It would seem that the low levels of resting oxygen consumption for this species are suited for this kind of behaviour whereas the higher levels obtained for the two species of *Acanthodactylus* are a prerequisite for rapid locomotion. The ecology of the latter two species has not been well researched and so therefore it is not possible to offer an explanation for the difference between the two M-T curves.

Temperature dependent shifts and low thermal dependence

In the case of both *L. agilis* and *L. vivipara* (Figure 2), characteristics of the lower parts of the M-T curves (that is at 10° to 15°C compared to 15° to 20°C) suggest that there may be some kind of adjustment. That is, at lower body temperatures, these two species may have M-T curves with temperature dependent shifts and so maintain levels of resting oxygen consumption suitable for activity and locomotion, be it slow locomotion. Without such adjustments in the M-T curves, the levels of oxygen consumption at lower body temperatures would be so reduced so as to make it less easy for these lizards to remain active at low temperatures. Living in cool temperate climates as they do, sudden changes in ambient temperature may be experienced both in the autumn and the spring. Temperature dependent shifts would seem therefore to be an adaptation to weather conditions which from day to day may change very rapidly.

The lower part of the M-T curve for *L. vivipara* is clearly higher than the lower parts of the curves for the other two cool temperate species. It is of some interest therefore to find that the geographical distribution of *L. vivipara* is far more widespread than that of the other two species (see note in materials and methods). The seasonal activity of *L. vivipara*, compared to the seasonal activity of *L. agilis* is such that it remains active for a longer period of time in the autumn and emerges from brummation at an earlier time in the year. The daily activity period of *L. vivipara* is also longer than the daily activity period of *L. agilis* (House et al., 1980). Throughout the year *L. vivpara* would therefore be exposed to a lower range of temperatures than experienced by *L. agilis* and the presence of the temperature dependent shift in the curve of *L. vivipara* is clearly linked to the ecology of this species.

Inspection of the M-T curves for the six warm temperate climatic species reveals some evidence of temperature dependent shifts as seen in the M-T curves for *P. l. lilfordi* and *P. l. brauni* (Figure 3). In the case of these two sub-species and at the temperatures below 20°C there seems to be an elevation in the M-T curves with respect to the rest of the curves. It is of interest therefore to note that these two sub-species have a very restricted distribution on small rocky islands and in general are exposed to a "hostile" environment (Arnold et al., 1978). Although in the Mediterranean, the climate of small islands around Majorca and Minorca is characterised by both high day-time temperatures and low night-time temperatures.

Evidence for the presence of low thermal dependence, that is a diminished Q_{10} at or just below the voluntary temperature, is to be found in the M-T curves of *A. fragilis, B. cinereus, P. hispanica* and *C. ocellatus*. Further research is needed on the voluntary (preferred) temperatures of the other species so as to investigate further the presence or absence of low thermal dependende.

Comparison of M-T curves of species from different climatic regions

In order to compare the M-T curves of lizard species from different climatic regions, it was thought useful to compare only those species which were similar in their ecology and behaviour (Table 1). The mean weight of the "matched" pairs are also similar. Using these two criteria, the M-T curves of three pairs of lizard species are compared in Figure 5. It is interesting to note that in each case, the M-T curve of the cool temperate species is always higher than the M-T curve of the other species. A possible

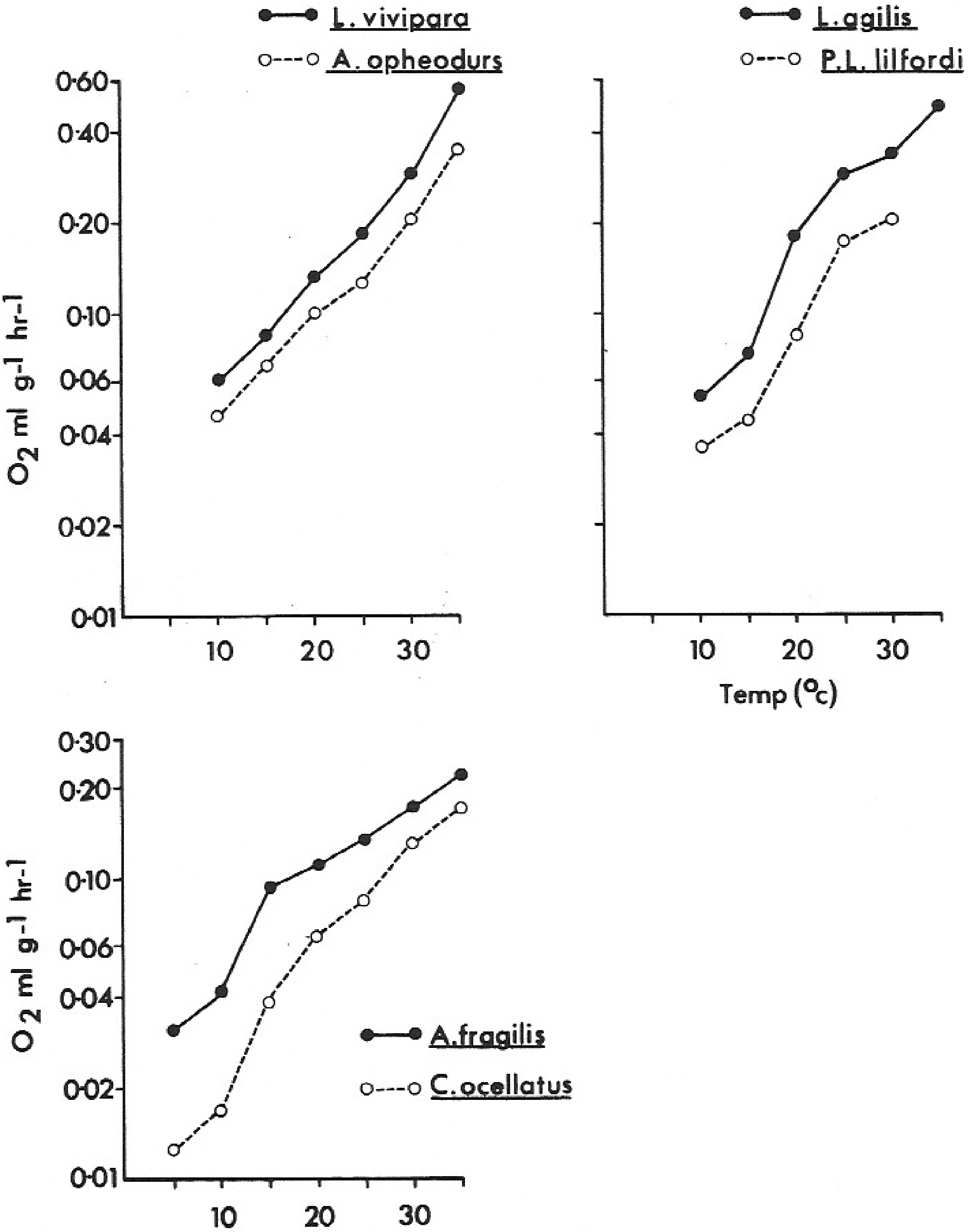


Fig. 5. The metabolic rate-temperature curves of "matched" species from different climatic regions superimposed to facilitate comparison.

explanation for this elevation in the M-T curves of the cool-temperate species is that these lizards may have a comparatively short time in which to adjust prior to the commencement of winter dormancy. Therefore, it is important that these lizards are able to be as active as possible whenever weather conditions permit. Compared to other species they also have a short seasonal activity in which to forage, grow, reproduce and then to accumulate fat reserves prior to winter dormancy. These cool-temperate species may not partition long periods of time for basking yet as daily temperatures diminish they must be able to remain as active as possible so as to avoid predation and locate sites suitable for nocturnal activity. Indeed greater overall levels of metabolism have obvious advantages and provide benefits in cool environments. In contrast, those lizards from warm-temperate and desert regions are rarely subjected to long winters and normally have a long period of seasonal activity. Therefore, the oxygen consumption is lower than that of cool-temperate species. A lower metabolic rate also prolongs the time an animal can live on a given amount of food (Gordon et al., 1982). Similar results have been reported by Davies and Bennett (1981) who maintained juveniles of the cool-temperate snake *N. natrix* and the warm-temperate *N. maura* under identical and constant photothermal and nutritional conditions prior to hatching, until the end of the oxygen consumption determination. However, despite this rather unusual experimental condition, they found that the M-T curve of the cool-temperate *N. natrix* was above that of the warm-temperature snake *N. maura* at a temperature range between 5-30°C. The authors noted that the shift found in the cool-temperate snake would provide this species with two principal advantages: a temperature benefit and an instantaneous compensation cost.

An alternative interpretation is that the M-T curves of the cool temperate species (*L. vivipara, L. agilis, A. fragilis*) have undergone a shift to the left with respect to the M-T curves of lizards of similar weight and ecology from either warm temperate or desert regions (*A. opheodurus, P. l. lilfordi, C. ocellatus*). One explanation for this apparent shift could involve the temperatures normally experienced by the various species. That is, the range of temperatures experienced by the cool temperate species would be comparatively lower than that experienced by the species from warm temperate climatic regions or desert regions. Taking this aspect into consideration, the resting oxygen levels during normal activity would be similar in each of the pairs of "matched" species. For example, during the normal daily activity period of *L. vivipara* and *A. opheodurus* the former species might often be exposed to a temperature range of about 15°C to 20°C and the latter species might often be exposed to a higher range of temperatures of about 25°C to 30°C. If this were true, then the levels of oxygen consumption associated with normal daily activity would perhaps be not as dissimilar as they appear. Clearly more work is needed on the ecology of these respective species so as to analyse further these apparent differences in the M-T curves.

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References

Aleksiuk, M. (1971a): Temperature-dependent shifts in the metabolism of a cool temperate reptile, *Thamnophis sirtalis parietalis*. Comp. Biochem. Physiol. **39A**, 495-503.

Aleksiuk, M. (1971b): An isoenzymic basis for instantaneous cold compensation in reptiles: Lactate dehydrogenase kinetics in *Thamnophis sirtalis*. Comp. Biochem. Physiol. **40B**, 671-681.

Arnold, E.N., Burton, J.A. (1978): A field Guide to the Reptiles and Amphibians of Europe. Collins, London.

Bennett, A.F. (1982): The energetics of reptilian activity. In: Biology of Reptilia. Vol. 13. p. 155-199. Gans, C. & Pough, F., eds., Academic Press, London.

Bennett, A.F., Dawson, W.R. (1976): Metabolism. In: Biology of the Reptilia. Vol. 5. p. 127-223. Gans, C. & Dawson, W.R., eds., Academic Press, London.

Brown, R., Loveridge, J.P. (1980): The effect of temperature on oxygen consumption and evaporative water loss in *Crocodylus niloticus*. Comp. Biochem. Physiol. **69A**, 51-57.

Buikema, A.L., Armitage, K.B. (1969): The effects of temperature on the metabolism of the prairie ringneck snake, *Diadophis punctatus arnyi* Kennicott. Herpetologica **25**, 194-206.

Davies, P.M.C., Bennett, E.L. (1981): Non-acclimatory Latitude-Dependent Metabolic adaptation to temperature in Juvenile Natricine snakes. J. Comp. Physiol. **142**, 489-494.

Dawson, W.R., Bartholomew, G.A. (1956): Relation of oxygen consumption to body weight, temperature and temperature acclimation in lizards *Uta stansburiana* and *Sceloporus accidentalis*. Physiol. Zool. **29**, 40-51.

Gordon, M.S., Bartholomew, G.A., Grinnell, A.D., Jørgensen, C.B., White, N. (1982): Animal Physiology, 4th Edit. MacMillan Publ. Co., Inc. NY & London.

Hoskins, M.A.H., Aleksiuk, M. (1973): Effects of temperature, photoperiod and season on *in vitro* metabolic rates of tissues from *Thamnophis sirtalis parietalis*, a cold climate reptile. Comp. Biochem. Physiol. **45A**, 737-756.

House, S.M., Taylor, P.J., Spellerberg, I.F. (1980): Patterns of daily behaviour in two lizard species *Lacerta agilis* L. and *Lacerta vivipara* Jacquin. Oecologia **44**, 396-402.

Moberly, W.R. (1963): Hibernation in the desert iguana, *Dipsosaurus dorsalis*. Physiol. Zool. **36**, 152-160.

Spellerberg, I.F. (1976): Adaptations of reptiles to cold. In: Morphology and Biology of Reptiles. p. 261-285. DA Bellairs, A. & Cox, C., eds., Linnean Society Symposium Series No. 3. Academic Press, London & New York.

Spellerberg, I.F. (1977): Reptile body temperatures. The Herptile. Vol. II, (3) 8-37.

Spellerberg, I.F. (1982): Biology of reptiles. Blackie and Son Ltd., London.