# The influence of temperature, sexual condition, and season on the metabolic rate of the lizard *Psammodromus hispanicus*

J.W. Patterson* and P.M.C. Davies
Department of Zoology, University of Nottingham, Nottingham NG7 2RD, United Kingdom

**Summary.** Male and female *Psammodromus hispanicus* from southern Europe were acclimated to four seasonal conditions of photoperiod and night time temperature. During the dark period, the lizards' body temperatures fell to ambient air temperature but during the light period the lizards were allowed to thermoregulate behaviourally, and at such times the lizards' mean body temperature varied from 29.0 °C to 32.6 °C. The resting metabolic rate of these lizards was measured in 5 °C steps from 5 °C to 30 °C or 35 °C. Sexual condition had little effect on resting metabolic rate, but at low temperatures lizards acclimated to winter or spring seasonal conditions had lower resting metabolic rates than those acclimated to summer or autumn conditions. At temperatures above 20 °C, seasonal acclimation had no effect on resting metabolic rate. It is considered that the reduction in low temperature metabolic rate in spring and winter is induced by low night time temperatures and serves to conserve energy during those seasons when lizards must spend long periods at low temperature without being able to feed.

## Introduction

Most of the early work on thermal acclimation in ectotherms consisted of acclimating groups of animals to different but constant temperatures and then measuring metabolic rates of the different groups at various temperatures (Precht 1958; Prosser 1958, 1973). This approach was justified

*Abbreviations: G♀* gravid females; *NG♀* nongravid females

\* Present address: Department of Biology, Chancellor College, University of Malawi, P.O. Box 280, Zomba, Malawi

because most of the animals used were aquatic; in aquatic habitats the temperature of the water, and therefore the body temperature of the aquatic ectotherm, changes slowly with season. Most aquatic organisms investigated in this way show a pattern of Precht type 2 (perfect) or type 3 (partial) acclimation (see Fry and Hochachka 1970; Vernberg and Vernberg 1970; Hazel and Prosser 1974). Thus, following a temperature change in the environment, most aquatic animals respond by adjusting their metabolic rate so that it is brought back to or near its original level. In these circumstances, thermal acclimation serves to maintain metabolic rate moderately constant over a range of slowly-changing body temperatures. Exposure to constant temperatures followed by measurements of metabolic rate at different temperatures has also been used as a method to determine the acclimatory responses of terrestrial ectotherms, including reptiles (Gelineo 1965; Murrish and Vance 1968; Dutton and Fitzpatrick 1975). Unfortunately, this is not a close simulation of the thermal conditions which reptiles encounter under natural conditions. Although small reptiles are ectothermic, during the day they utilise solar radiation and various behavioural devices to maintain body temperature well above ambient, while during the night body temperature drops to or near ambient (Stebbins and Barwick 1968; Avery 1971). Thus under natural conditions many reptiles experience considerable fluctuation in body temperature over a 24 h period. Therefore, although results from metabolic rate studies on reptiles acclimated to constant temperatures demonstrate the acclimatory responses of animals to these specific conditions, their usefulness in predicting the responses of reptiles to seasonal temperature changes in the field must be questioned.

We report here on the acclimatory responses of *Psammodromus hispanicus*, a small Spanish lizard. In this study, the lizards were acclimated to four different night time temperatures but were able to raise their body temperatures by basking during the day. In addition, data are presented on the effect of sexual condition on metabolic rate.

## Materials and methods

*Origin and laboratory maintenance of animals.* Adult *Psammodromus hispanicus* were collected in the vicinity of Calpe on the Mediterranean coast of Spain (latitude 38°20′N, longitude 0°5′E) between 1st and 11th April 1975.

In the laboratory, the lizards were housed in glass aquaria 92 × 31 × 31 cm high in a constant temperature room with facilities for the automatic control of photoperiod. Each aquarium was covered with a wooden lid. A 100 W light bulb which was attached to the underside of the lid was turned on for the whole of the light period so that the lizards were able to raise their body temperatures by behavioural thermoregulation during this period. During the dark period, the lizards' body temperatures fell to the temperature of the constant temperature room. Food (small larvae of *Tenebrio molitor* and second instar larvae of *Locusta migratoria*) and water were constantly available, and were supplemented once a week with calcium and multivitamin preparations.

*Seasonal acclimation.* Climatic data for the different seasons were obtained from Meteorological Office (1964) and List (1968). For the purposes of this study, spring is defined as March to May, summer as June to August, autumn as September to November and winter as December to February. The mean night time temperature for each season was assumed to be the mean of the daily minimum temperatures for each of the months which make up that season. For each seasonal acclimation regime, the temperature of the constant temperature room was set at the mean night time temperature for that season and lights were turned on in the room every day for a period corresponding to the mean photoperiod of that season. Photoperiodic and night time temperature data for the four seasons are shown in Table 1. *Psammodromus hispanicus* were allowed to acclimate to these seasonal regimes for at least four weeks before any measurements were made. Since it is likely that lizards show circannual rhythmicity (Licht 1972; Cuellar and Cuellar 1977a, b) and since this might affect metabolic rate, it was considered desirable to study lizards under different seasonal acclimation regimes at the time of year when those seasons actually occur. Therefore spring acclimated lizards were studied from March to May, summer acclimated lizards from June to August, and so on.

**Table 1.** Photoperiod and night time temperature acclimation regimes for the four seasons

| Season | Photoperiod Light: Dark (h) | Night time temperature (°C) |
|---|---|---|
| Spring | 13:11 | 10 |
| Summer | 14:10 | 20 |
| Autumn | 11:13 | 15 |
| Winter | 10:14 | 5 |

*Temperature relations during the light period.* In order to set an upper limit to the temperature at which metabolic rate was to be measured, body temperatures of *Psammodromus hispanicus* allowed access to a source of heat were measured in a 41 × 26 × 26 cm high glass aquarium kept in a room maintained at the night time temperature of the season under study. Cover, food and water were constantly available, and a 100 W light bulb attached to the underside of the lid served as a source of both light and heat. For testing, lizards were placed in the aquarium in the evening. The light bulb was switched on at 10.00 h the following day and left on until 18.00 h. The body temperature of each lizard was measured five or six times at regular intervals, from one hour after the light bulb was turned on, by inserting the bulb of a Schultheis fast-registering mercury thermometer into the lizard's cloaca. The mean body temperature of individual lizards was computed as the mean of these readings.

These tests were run with three or four lizards in the aquarium at the same time. At no time did there appear to be competition for basking sites, nor were any aggressive interactions observed between the lizards. Therefore it is considered that the mean $T_b$ of individual lizards was unaffected by the presence of other lizards (see also Patterson and Davies 1978 b).

*Measurement of metabolic rate.* In order to study the effect of sexual condition on metabolic rate, lizards were classified as either males ($\male$), nongravid females (NG$\female$) or gravid gemales (G$\female$). G$\female$ were those in which the posterior part of the abdomen was much distended and which were therefore in the terminal phases of egg maturation; G$\female$ were present only in spring and summer because only at these seasons are eggs produced. NG$\female$ were those females in which the posterior part of the abdomen was not distended; in spring they were in the early stages of egg maturation whereas at other seasons they were not maturing eggs.

Metabolic rate was measured as the rate of oxygen consumption. All measurements of oxygen consumption were performed in constant pressure respirometers, having both animal and compensation chambers, immersed in a constant temperature water bath in which temperature was regulated by both a heating and a cooling unit.

Prior to being used for respirometry, *Psammodromus hispanicus* were fasted for three to seven days. After this fast, experimental lizards were held overnight at the temperature of the constant temperature room and then, in the morning, placed in the animal chambers of the respirometers which were then fully assembled and placed in the water bath. Small bags of soda lime were present in both animal and compensation chambers to absorb carbon dioxide. After the apparatus was set up, a period of at least one hour was allowed to elapse before any measurements were made; this is adequate time for equilibration and for animals to recover from the effects of handling. After this period, the taps were closed and five or six measurements of oxygen consumption were made. A close watch was kept on animals in the respirometers both during the period of equilibration and after the taps were closed, and the results were used only if the animals did not move. Similarly, where successive readings from the same animal were erratic, the results were discarded. Since it was necessary to watch the animals during the course of the experiments, respirometry was conducted with animals at a low level of illumination rather than in darkness. At the end of the experiment, the taps were opened, the respirometers taken out of the water bath and the lizards removed and weighed. Oxygen consumption rates were calculated in $\mu l \ g^{-1} \ h^{-1}$ and converted to standard conditions by the method of Scholander et al. (1952). Oxygen consumption rates were measured in this way on five lizards of each sexual

condition and at each season and temperature. The rates in all cases can be assumed to approximate resting metabolic rate.

*Statistical analysis.* Statistical analysis of the results was conducted using methods in Steele and Torrie (1960) and Sokal and Rohlf (1969). Differences between treatment means were considered significant when $P \leq 0.05$.

## Results

### Temperature relations during the light period

Mean $T_b$ maintained by *Psammodromus hispanicus* during the four seasons are shown in Table 2. Analysis of variance (ANOVA) demonstrated a significant effect of season on mean $T_b$ ($P < 0.001$). Further analysis with Duncan's 5% New Multiple Range Test demonstrated that there was no signifi-

**Table 2.** Mean $T_b$ maintained by *Psammodromus hispanicus* allowed access to heat lamps at different seasons

| Season | N | Mean $T_b$ (°C) $\bar{x} \pm SD$ |
|---|---|---|
| Spring | 12 | 30.6 ± 1.0 |
| Summer | 5 | 32.6 ± 1.2 |
| Autumn | 6 | 32.3 ± 0.7 |
| Winter | 6 | 29.0 ± 1.5 |

cant difference in mean $T_b$ between summer and autumn or between spring and winter but both spring and winter were significantly lower than either summer or autumn mean $T_b$. In view of this, it was decided to measure rates of oxygen consumption in all four seasonal acclimation groups in 5 °C steps from 5 °C to 30 °C; 5 °C approximates the lowest temperature to which this species is exposed at any season while 30 °C approximates the maximum to which the lizards raise their body temperatures during winter and spring. In addition, rates of oxygen consumption were measured at 35 °C in the summer and autumn groups since these animals maintained slightly higher body temperatures.

### Metabolic rate

Rates of oxygen consumption for lizards of different sexual condition determined under conditions of different seasonal acclimation and at different measuring temperatures are shown in Table 3. It is evident that, as with other ectotherms, in general metabolic rate increases with temperature although in most cases the magnitude of these increases (expressed by $Q_{10}$) is greater at low temperatures than at high temperatures. Therefore it is likely that also the resting metabolic rate of *Psammodromus*

**Table 3.** Rates of oxygen consumption for *Psammodromus hispanicus*. $\bar{x} \pm SD$

| Season | Sexual condition | Weight (g) | Oxygen consumption rate ($\mu l\ O_2\ g^{-1}\ h^{-1}$) at temperature (°C) | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | 5 | 10 | 15 | 20 | 25 | 30 | 35 |
| *Spring* | ♂ | 1.734 ± 0.197 | 21.40 ± 2.84 | 31.56 ± 11.29 | 84.48 ± 16.06 | 127.8 ± 30.6 | 250.3 ± 47.2 | 398.5 ± 62.8 | – |
| | NG♀ | 1.265 ± 0.174 | 25.21 ± 3.99 | 31.43 ± 7.47 | 97.65 ± 43.08 | 117.0 ± 13.5 | 168.3 ± 27.9 | 363.2 ± 133.1 | – |
| | G♀ | 1.426 ± 0.152 | 22.10 ± 4.77 | 36.99 ± 8.48 | 102.7 ± 52.1 | 174.9 ± 54.8 | 231.6 ± 85.9 | 328.8 ± 50.7 | – |
| *Summer* | ♂ | 1.804 ± 0.233 | 37.11 ± 3.09 | 48.05 ± 7.22 | 66.75 ± 11.09 | 114.4 ± 34.1 | 211.9 ± 38.4 | 366.9 ± 69.1 | 465.8 ± 127.3 |
| | NG♀ | 1.161 ± 0.146 | 26.64 ± 4.11 | 40.58 ± 4.62 | 72.25 ± 10.86 | 151.9 ± 19.2 | 262.5 ± 88.0 | 404.2 ± 111.9 | 442.9 ± 70.0 |
| | G♀ | 1.591 ± 0.345 | 31.52 ± 5.24 | 40.44 ± 11.09 | 60.30 ± 18.42 | 118.3 ± 22.3 | 240.8 ± 73.9 | 424.6 ± 85.1 | 382.1 ± 57.8 |
| *Autumn* | ♂ | 1.861 ± 0.174 | 27.89 ± 4.49 | 43.85 ± 10.14 | 68.50 ± 7.90 | 124.5 ± 27.0 | 235.2 ± 41.9 | 346.2 ± 60.1 | 390.1 ± 72.1 |
| | NG♀ | 1.318 ± 0.180 | 26.67 ± 6.61 | 45.31 ± 5.74 | 51.27 ± 6.11 | 135.3 ± 27.8 | 250.6 ± 30.1 | 287.3 ± 52.2 | 418.2 ± 24.4 |
| *Winter* | ♂ | 1.906 ± 0.203 | 15.55 ± 2.02 | 34.62 ± 3.03 | 74.17 ± 13.20 | 122.8 ± 29.1 | 234.8 ± 36.2 | 338.4 ± 47.4 | – |
| | NG♀ | 1.400 ± 0.195 | 14.52 ± 1.33 | 32.99 ± 2.65 | 59.30 ± 9.06 | 129.9 ± 21.8 | 212.4 ± 10.0 | 314.5 ± 39.7 | – |

**Table 4.** ANOVA P-values for rates of oxygen consumption of *Psammodromus hispanicus* (N.S. = non-significant, i.e. $P>0.05$)

| Source of variation | Temperature (°C) | | | | | | |
|---|---|---|---|---|---|---|---|
| | 5 | 10 | 15 | 20 | 25 | 30 | 35 |
| Between seasons | <0.001 | <0.001 | 0.005–0.001 | N.S. | N.S. | N.S. | N.S. |
| Between sexual conditions | N.S. | N.S. | N.S. | N.S. | N.S. | N.S. | N.S. |
| Interaction | 0.025–0.01 | N.S. | N.S. | 0.025–0.01 | 0.025–0.01 | N.S. | N.S. |

**Table 5.** Summary of Duncan's 5% New Multiple Range Test on rates of oxygen consumption of *Psammodromus hispanicus*[a]

| Temperature (°C) | Season and sexual condition | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Spring | | | Summer | | | Autumn | | Winter | |
| | ♂ | NG♀ | G♀ | ♂ | NG♀ | G♀ | ♂ | NG♀ | ♂ | NG♀ |
| 5 | 21.40 | 25.21 | 22.10 | 37.11 | 26.64 | 31.52 | 27.89 | 26.67 | 15.55 | 14.52 |
| 10 | 31.56 | 31.43 | 36.99 | 48.05 | 40.58 | 40.44 | 43.85 | 45.31 | 34.62 | 32.99 |
| 15 | 84.48 | 97.65 | 102.7 | 66.75 | 72.25 | 60.30 | 68.50 | 51.27 | 74.17 | 59.30 |
| 20 | 127.8 | 117.0 | 174.9 | 114.4 | 151.9 | 118.3 | 124.5 | 135.3 | 122.8 | 129.9 |
| 25 | 250.3 | 168.3 | 231.6 | 211.9 | 262.5 | 240.8 | 235.2 | 250.6 | 234.8 | 212.4 |

[a] Each figure in the body of the Table is the mean rate of oxygen consumption for that group. Those means not underscored by a common line or a line at the same level are significantly different from each other (i.e. $P<0.05$).

*hispanicus* is more temperature sensitive at the lower than at the higher temperature ranges.

To test for effects of season and sexual condition on metabolic rate, these data were analysed by means of ANOVA. Two way ANOVA was performed on data for each temperature and the P-values are shown in Table 4. At no temperature did sexual condition alone have any significant effect on metabolic rate. However, season showed significant effects at 5 °C, 10 °C and 15 °C, and interaction (season × sexual condition) showed significant effects at 5 °C, 20 °C and 25 °C. No significant effects were demonstrated at 30 °C or 35 °C. For those temperatures at which ANOVA demonstrated significant effects, the data were analysed further with Duncan's 5% New Multiple Range Test to test for significant differences between treatment means. The results are summarised in Table 5. At 5 °C, the metabolic rate in winter is significantly lower than that of animals at any other season, while the metabolic rate of males in summer is significantly higher than all others; in general, spring animals have lower metabolic

rates than summer and autumn animals at 5 °C. At 10 °C winter and spring animals have a lower metabolic rate than summer and autumn animals while at 15 °C animals in spring have significantly higher metabolic rates than at other seasons. At 20 °C gravid females in spring respire at higher rates than any others except NG♀ in summer, and at 25 °C NG♀ in spring have a lower metabolic rate than any others apart from ♂ in summer and NG♀ in winter. It is evident from the above that, apart from temperature, the major effect on metabolic rate is season, and that seasonal effects occur mainly at low temperatures.

### Discussion

There is considerable variation in the temperature sensitivity of reptile metabolic rate. In some species, $Q_{10}$ is constant over a wide range of temperatures (Prieto and Whitford 1971; Snyder 1975), whereas in others the $Q_{10}$ varies, usually having lower values at the higher temperatures (Snyder and Weathers 1976; Fitzpatrick et al. 1978). *Psam-*

*modromus hispanicus* belongs to the latter group. Such a pattern of temperature sensitivity presumably allows the animal to have relative metabolic independence from temperature changes around the preferred temperature (hence the low $Q_{10}$) while allowing energy to be conserved during inactivity at low temperatures (Bennett and Dawson 1976).

Sexual condition had little effect on resting metabolic rate of *Psammodromus hispanicus*. It is known that in some species of amphibians (Dunlap 1969; Fitzpatrick 1971) and reptiles (Dutton and Fitzpatrick 1975), including other species of European lacertid lizards (Patterson and Davies, in preparation), the metabolic rate of G♀ is higher than that of NG♀ and ♂, but no such effects are evident for *Psammodromus hispanicus*.

Apart from temperature, the major influence on metabolic rate is seasonal acclimation, and an examination of Tables 4 and 5 demonstrates that seasonal effects are most evident at low temperatures (5 °C and 10 °C). In general, resting metabolic rate at 5 °C and 10 °C is lower in spring and winter than in summer and autumn acclimated animals. The spring and winter groups were acclimated to lower night time temperatures than the summer and autumn groups, so it is possible that acclimation to low night time temperature reduces low temperature metabolic rate. However, photoperiod as well as night time temperature was varied between the seasonal acclimation groups so it is possible that the difference in metabolic rate between the seasons may have been induced, at least in part, by photoperiodic differences. Photoperiod affects the metabolic rate of some animals (Whitford and Hutchison 1965) but not others (Wood and Orr 1969; Fitzpatrick 1971). However, if the seasonal effects on low temperature metabolism are due to differences in night time temperature, acclimation to low night time temperature reduces low temperature metabolism in *Psammodromus hispanicus* and therefore this species at low temperature appears to exhibit Precht type 5 or inverse acclimation (Precht 1958; Prosser 1958, 1973). Inverse thermal acclimation has been recorded in a number of other animals, including some reptiles (Jacobson and Whitford 1970; Patterson and Davies 1978a, b) and has usually been interpreted as a method of energy conservation at temperatures too low for the animal to be able to gather food effectively (Dunlap 1971; Fitzpatrick et al. 1972; Hazel and Prosser 1974; Patterson and Davies 1978b). A similar explanation will account for the results of this present study since in the area where *Psammodromus hispanicus* occurs, the col-

dest seasons (spring and winter) are also the seasons when there are the longest periods of heavy cloud cover (see Meteorological Office 1964) during which the lizards are unable to raise body temperature by basking and thus must spend long periods at low temperature without being able to feed.

This study demonstrates that in *Psammodromus hispanicus* acclimated to seasonal conditions of night time temperature and photoperiod, differences in metabolic rate between acclimation groups occur only at low temperatures. These temperatures are experienced during the dark period by some acclimation groups but not by others. Thus it appears that the biologically important thermal difference between the seasons is the level to which the temperature drops at night. During the day, providing that the sun shines, the lizards are able to raise body temperature by basking to a level which is relatively independent of season.

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