J. Thermal Biology. Vol. 3. pp. 203 to 205.

0306-4565/78/0710-0203$02.00/0

# METABOLISM AND ACTIVITY OF THE SPANISH FRINGE-TOED LIZARD (LACERTIDAE: *ACANTHODACTYLUS ERYTHRURUS*)

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(*Received* 1 *February* 1978, *in revised form* 24 *April* 1978; *accepted* 12 *May* 1978)

**Abstract**—1. In the field, adult fringe-toed lizards (*Acanthodactylus erythrurus*) had a mean body temperature of 38.8 ± 0.2 (S.E.) °C while subadults maintained a significantly lower temperature ($\bar{x} = 35.4 \pm 0.5$°C).

2. Laboratory measurements of oxygen consumption, ventilation frequency, and heart rate indicate that temperatures above 38°C are stressful to subadults.

3. Activity periods of subadults are curtailed by high temperatures for 3 months in summer while the activity of the more thermophilic adults is curtailed only during July and August.

4. Some lizards maintained a high metabolic rate by achieving a low $Q_{10}$ ($\bar{x} = 1.3$) between 13 and 25°C.

5. Because these lizards initiate activity at black body temperatures of 13°C in their natural habitat, the ability to sustain high rates of aerobic metabolism at low temperatures is probably valuable.

## INTRODUCTION

THE Old World lizard family Lacertidae includes a diverse array of forms demonstrating numerous apparent morphological and ecological parallels with iguanids and teiids of the New World. Information about lacertid physiology could be valuable in testing hypotheses about physiological adaptations of lizards to particular habitats because these hypotheses are based largely on studies of New World forms.

Unfortunately, we have insufficient data about the environmental physiology of lacertids to serve as a basis for such tests (see Avery, 1976 for a review). Physiological information that can be integrated with ecological information is particularly valuable and we took advantage of the opportunity provided by a field study of *Acanthodactylus erythrurus* (Busack, 1976) to collect physiological data as well.

## MATERIALS AND METHODS

Fringe-toed lizards collected in Cádiz Province, Spain, were sent to Cornell University by airmail and housed in groups of 5–10 in 1.2 × 0.6 m sand-floored cages for at least one month before testing. A heat lamp at one end of the cage allowed the lizards to thermoregulate during the photophase of a 14L:10D photoperiod. The photophase was centered on 0800 h EST and was maintained in controlled-temperature chambers during the measurement of physiological functions. This schedule kept the lizards on the same diel cycle they had known in Spain while ensuring that light–dark transitions for the lizards in the laboratory did not coincide with daily cycles of human activity in the building.

Heart rate and ventilation frequency were recorded simultaneously with a Physiograph 4A multichannel recorder from 38 ga stainless steel wires sewn beneath the skin of the chest and back. Five lizards (9.0–10.5 g, $\bar{x} = 9.8$ g) were placed individually in 25 × 50 mm aquaria containing several cm of sand, and transferred to constant-temperature chambers at least one full day before the first recordings. Sand temperature, which was the same as lizard body temperature, was monitored continuously by a Leeds & Northrup Speedomax recorder and varied only ±0.1°C during period of measurement.

Oxygen consumption of nine lizards (6.4–13.4 g, $\bar{x} = 9.4$ g) was measured with an electrolytic cell apparatus described by Hutchison and Kohl (1971) at temperatures from 12.8 to 42.0°C. A recording microbarograph (Belfort Instruments) allowed correction for changes in barometric pressure; records were discarded if pressure changed >0.2 mm Hg/h.

## RESULTS

Heart rate and ventilation frequency increased with increasing temperature. Regressions were calculated using the average value of each lizard × temperature combination. The best fits were given by the following allometric equations:

Heart rate:

$$\text{beats/min} = 0{\cdot}04\,T^{2.40} \quad (n = 32,\ r = 0.98,\ P < 0.01).$$

Ventilation frequency:

$$\text{breaths/min} = 0.08\,T^{1.75} \quad (n = 33,\ r = 0.94,\ P < 0.01)$$

where T is temperature in °C.

The relationship of oxygen consumption to temperature is shown in Fig. 1; photophase and scotophase values were calculated separately and did not differ. The best fits were provided by exponential equations:

Photophase:

$$\text{ml}\ O_2/\text{g}\cdot\text{h} = 0.031\,e^{0.070T} \quad (n = 33,\ r = 0.85,\ P < 0.01).$$

Scotophase:

$$\text{ml}\ O_2/\text{g}\cdot\text{h} = 0.034\,e^{0.065T} \quad (n = 12,\ r = 0.79,\ P < 0.01).$$

Combined:

$$\text{ml}\ O_2/\text{g}\cdot\text{h} = 0.034\,e^{0.065T} \quad (n = 45,\ r = 0.80,\ P < 0.01).$$

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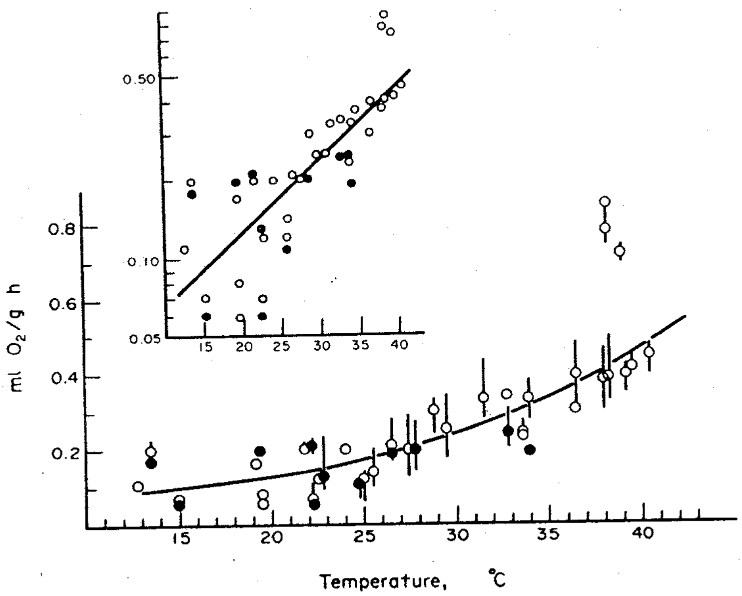

Fig. 1. Relationship between oxygen consumption and temperature in *Acanthodactylus erythrurus*. Each symbol represents the mean value of 1–14 hourly values for an individual lizard at that temperature. Open circles are values during photophase, closed circles represent scotophase. Inset: A semi-logarithmic plot of the same data.

Seven hours of records from three lizards at temperatures above 38°C produced values that were consistently nearly twice those of other lizards at the same temperatures.

## DISCUSSION

Oxygen consumption of *Acanthodactylus erythrurus* showed a constant $Q_{10}$ of 1.9 from 15 to 35°C. Three lizards had $Q_{10}$ values from 3.6 to 4.1 at temperatures above 38°C and one specimen died at 42°C. These observations suggest a physiological sensitivity to high temperature that is also reflected by the behaviour of the lizards in the field. Although the thermometer Busack (1976) used would not record temperatures below 33.9°C, 52 measurements of active lizards during September and October showed only three animals with temperatures below that value. Adult *A. erythrurus* body temperatures averaged 37.8°C (S.E. ± 0.2°C, $n = 41$) while eight subadults had a mean of 35.4 ± 0.5°C and three subadults had temperatures below 33.9°C. Maximum voluntary body temperature was 37°C for subadults and 41°C for adults.

Black body temperatures in shade are a good approximation of the coolest microenvironments available to active fringe-toed lizards. The body temperature of *A. schreiberi*, which is the same size as *A. erythrurus*, was closely tied to soil surface temperatures even when the lizards were in full sun (Duvdevani & Borut, 1974a). At the Cádiz field site, daily black body temperatures in shade exceeded 38°C from June through August and the activity pattern of subadult lizards was bimodal with peaks at 1000–1100 h and 1700–1800 h and little or no midday activity. Adults had bimodal activity patterns only in July and August when maximum black body shade temperatures reached or exceeded 41°C in midafternoon (Busack, 1976). Thus, it appears that the relatively low temperature tolerance of *A. erythrurus* directly limits activity periods under natural conditions during 20–25% of their annual 10–12 month activity season; similar bimodal activity periods during hot weather have been reported for iguanid lizards (Mayhew, 1968).

Duvdevani & Borut (1972a, b) studied four species of *Acanthodactylus* in Israel. *Acanthodactylus pardalis* had the lowest activity temperature of the four species, 37.8 ± 0.2°C, which is identical to that of *A. erythrurus* in Spain. Like *A. erythrurus*, *A. pardalis* appears to be sensitive to high temperatures. Figure 2 in Duvdevani & Borut (1974b) suggests that there was an abrupt increase in oxygen consumption in some *A. pardalis* at 40°C and heat suppression of metabolism at 42.5°C. In our study three subadult *A. erythrurus* showed abrupt increases in oxygen consumption at temperatures between 38.1 and 39.5°C and the single specimen tested at 42°C died.

Other measures of physiological function can be derived from our data. All show considerable stability between 15 and 35°C and less stability between 35 and 40°C. Oxygen extraction in the lungs was 1.3 to 1.4 × $10^{-4}$ ml $O_2$/g·breath between 15 and 35°C and rose to 1.5 × $10^{-4}$ ml $O_2$/g·breath at 40°C while oxygen pulse (quantity of oxygen transported by each heart beat) declined steadily from 5.1 × $10^{-5}$ ml $O_2$/g·beat at 15°C to 3.8 × $10^{-5}$ ml $O_2$/g·beat at 35°C and rose to 3.9 × $10^{-5}$ ml/g·beat at 40°C. These oxygen pulse values are similar to those reported for a variety of iguanid, anguid, scincid, and varanid lizards (Templeton, 1970). The ventilation frequency of *A. erythrurus* falls within the range recorded or expected for 16 species of lizards in several families (Bennett, 1973). The $Q_{10}$ for ventilation frequency in

*A. erythrurus* from 30 to 37°C was 1.8, and $Q_{10}$ for the other species was 1.9 (range 1.0–3.7).

Oxygen consumption values of *A. erythrurus* fall among the values reported for other species of *Acanthodactylus* (Duvdevani & Borut, 1974b). All of these values are higher than those predicted by the equations relating body size to metabolic rate derived by Bennett & Dawson (1976). *Acanthodactylus erythrurus* exceeds the predicted values by 100% at 20°C and by 50% and 36% at 30 and 37°C respectively. The high values at 30 and 37°C may reflect only the difficulty of obtaining truly resting metabolic rates from these active lizards, but the discrepancy at 20°C may have a more interesting physiological basis. Figure 1 appears to show two groups of metabolic rates at temperatures below 25°C; one group with mean values near 0.2 ml $O_2$/g·h and a second with mean values from 0.05 to 0.15 ml $O_2$/g·h. The separation of the two groups is particularly striking below 20°C. The high $\dot{V}_{O_2}$ values correspond to low $Q_{10}$ values below 25°C ($1.3 \pm 0.1$, $n = 7$) whereas the low $\dot{V}_{O_2}$ values have high $Q_{10}$'s ($\bar{x} = 4.0 \pm 1.2$, $n = 8$). It is the high oxygen consumption values of the first group of measurements that lead to the large divergence from predicted metabolic rate at 20°C.

Tromp & Avery (1977) reported a shift in metabolic rate between 15 and 20°C for *Lacerta vivipara* that increased oxygen consumption below 20°C to nearly twice the values which would have been expected from an extrapolation of the metabolism–temperature curve observed above 20°C. Aleksiuk (1971a) reported a similar temperature-dependent shift in oxygen consumption by garter snakes and associated it with a shift in isoenzymes (1971b); anomalously high oxygen consumption of *A. erythrurus* at low temperatures may reflect this same phenomenon. Alternatively, high oxygen consumption values may indicate activity by the lizards during some periods of measurement and quiescence at others. If this is true, their ability to sustain activity at low body temperatures is impressive; one lizard maintained a metabolic rate between 0.18 and 0.23 ml $O_2$/g·h for seven hours at 13.5°C.

The ability to be active at low temperatures, whether it is sustained by a metabolic shift or not, may be a valuable feature of the lizards' physiological adaptation. Busack (1976) reported that lizards initiated activity in the morning when black body shade temperatures reach 13°C; subadults were active in all months, and adults were active except in December and January. From November through March average monthly air temperatures were 8–12°C and minimum temperatures were below freezing. The ability to initiate and sustain activity even at low body temperatures allows the lizards to emerge from nocturnal retreats and commence basking. As a result they are able to extend their activity season into or through the winter months.

*Acknowledgements*—The authors are grateful to L. T. and W. R. Maxwell and Miguel Moya for assistance in the field and Edward Francolini for assistance in the laboratory. Victor Hutchison kindly provided details of the design of electrolytic cell apparatus. R. A. Avery read the manuscript and made helpful suggestions.

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*Key Word Index*—Reptile; lizard; metabolism; body temperature; environmental physiology; *Acanthodactylus erythrurus*.