LOW METABOLIC RATE IN A NOCTURNAL DESERT LIZARD, ANARBYLUS SWITAKI MURPHY (SAURIA: GEKKONIDAE)

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(Received 20 May 1981)

Abstract—1. Metabolic rates were measured in two xeric-adapted gekkonid lizards, Anarbylus switaki and Coleonyx variegatus.
2. Standard metabolic rates (SMR) were 0.074 ml O₂/hr in A. switaki and were 70% of the value predicted on the basis of mass from regression equations. The SMR of 0.146 ml O₂/hr in C. variegatus is similar to the predicted value for a lizard of this mass.
3. During intense activity, metabolic rates of 0.378 and 0.804 ml O₂/hr were measured in A. switaki and C. variegatus, respectively.
4. Various theories to explain reduced SMR in lizards are discussed, and it is concluded that none is entirely satisfactory, and caution should be exercised in interpreting the adaptive significance of reduced SMR.

INTRODUCTION

Standard metabolic rate (SMR) has been measured in a sufficient number and diversity of lizards that SMR can be predicted for a lizard of any given size from standard regression equations (Bennett & Dawson, 1976). These regression equations emphasize the similarities in metabolism among lizards and facilitate a sufficient number and diversity of lizards that SMR comparisons of lizard metabolism with that of other groups of organisms. Despite the high degree of correlation between SMR and body mass in lizards, a few species have SMRs markedly lower than predicted values (Vance, 1959; Snyder, 1971; Mautz, 1979). To date, reduced SMR has been most intensively studied in lizards of the family Xantusiidae (Vance, 1959; Snyder, 1971; Mautz, 1979) although a reduced SMR has also been measured in Aniella pulchra (Vance, 1959).

A preliminary study (Putnam, 1978) indicated that Anarbylus switaki Murphy, a nocturnal, xeric-adapted species of gecko, has a reduced SMR. Since cases of reduced SMR are rare among lizards, we undertook an examination of the metabolism of this species in greater detail. Individuals of this monotypic genus (Murphy, 1974) were collected in Baja California Norte and Baja California del Sur, Mexico. Individuals were collected at night in boleld strewn arroyos with sparse scrub and cardon. Field endeavors failed to locate a permanent supply of fresh water in the immediate vicinity of the collecting sites. The nocturnal, xeric-adapted gecko, Coleonyx variegatus, from the low desert of southern California was studied for comparison since it is closely related to Anarbylus and is similar in size and habitat to this species.

MATERIALS AND METHODS

A. switaki and C. variegatus were maintained in the laboratory on a diet of crickets and mealworms and given free access to water. They were kept at 25 ± 1°C on a L:D 15:9 photoperiod. Animals were tested within 3 weeks of capture. The average mass of A. switaki was 9.46 g (range 8.66-10.37 g) and of C. variegatus was 3.62 g (range 2.97-4.58 g).

In a group of three A. switaki and three C. variegatus, SMR was assessed using an open-flow system described by Bennett and Gleeson (1976). Lizards were fasted for four days and then placed in 500 ml chambers through which dry, CO₂-free air flowed at a rate of approximately 50 ml/min (monitored upstream). Downstream air was dried, the CO₂ removed, and the oxygen content of triplicate 20 ml samples was measured using a Beckman E2 Paramagnetic Oxygen Analyzer. The animal chambers were placed in a constant temperature cabinet at 25°C with a L:D 15:9 photoperiod. Animals were allowed 24 hr to adjust to the chambers before air samples were collected. The downstream air was sampled outside the temperature cabinet, so that the lizards were not disturbed during the 24 hr measurement period. Oxygen consumption (corrected to STP) was calculated according to Bennett and Gleeson (1976) using equation (8) of Depocas & Hart (1957).

After SMR had been measured for 24 hr, maximal rates of oxygen consumption were assessed by flipping for 3 min in closed chambers to force them to struggle (Seymour, 1973). A 50-ml air sample was taken before and just after activity and the decrement in P O₂ measured with a Beckman E2 Paramagnetic Oxygen Analyzer. Metabolic rate during activity was measured between 1200-1400 hr.

Rates of water loss were measured by placing lizards individually in small desiccators containing Silica Gel. The change in body weight was measured at 3-10 hr intervals for two days and rate of water loss calculated assuming water loss accounted for the entire weight loss. Water loss rates during the first measuring period and all periods where the animal had urinated or defecated were discarded, and the remaining hourly rates were averaged for each animal.

All values are reported as the X ± 1SE of the mean.

RESULTS

The metabolic rates over 24 hr are shown for A. switaki (Fig. 1) and C. variegatus (Fig. 2). The SMR
Fig. 1. Metabolic rate ($V_{O_2}$) of *A. switaki* vs time of day. Each symbol represents the values for one individual.

Fig. 2. Metabolic rate ($V_{O_2}$) of *C. variegatus* vs time of day. Each symbol represents the values for one individual.

Fig. 3. Variation in metabolic rate over a 24 hr period. The metabolic rate for each animal has been normalized to lowest rate measured for that animal (defined as 100%). The horizontal lines represent the average of all individuals for a given time period.
for each animal was calculated by averaging the three lowest measured metabolic rates. SMR was 0.074 ± 0.016 ml O2/hr for A. switaki and 0.146 ± 0.018 ml O2/hr for C. variegatus. Figure 3 shows the variation in metabolic rate (normalized to the lowest value for each animal) over 24 hr. Metabolic rate varied 2- to 4-fold in both species during the day exhibiting clear daily rhythms. In A. switaki, metabolic rate was minimal during late night and early morning (0200-1000) and reached a maximum during the evening (1800-2400). C. variegatus exhibited minimum metabolic rates in the afternoon (1200-1600) and attained highest rates in the evening (2200-0200). These rhythms correspond to the primarily nocturnal habits of these two lizards.

Metabolic rates increased 5- to 6-fold during maximal activity, attaining values of 0.378 ± 0.091 ml O2/hr during the evening (1800-2400). C. variegatus exhibited minimum metabolic rates in the afternoon (1200-1600) and attained highest rates in the evening (2200-0200). These rhythms correspond to the primarily nocturnal habits of these two lizards.

Rates of water loss averaged 0.29 ± 0.04 mg H2O/g/hr (range 0.23-0.37 mg H2O/g/hr) in A. switaki and 0.34 ± 0.06 mg H2O/g/hr (range 0.25-0.46 mg H2O/g/hr) in C. variegatus. These rates are equal to a water loss of 1% body weight per day. Following the desiccation experiments, A. switaki were returned to their cage with available free water, but no food. During the next 2 hr, no animal was observed to drink and no weight gain was measured. However, by the next morning, all animals had returned to 105% of their original weight. One A. switaki was found in the process of shedding, and its rate of water loss measured over a 7.5 hr period was 1.8 mg H2O/g/hr.

**DISCUSSION**

The SMR of A. switaki is 0.074 ml O2/hr, but this conceals different values among the animals. One lizard was a gravid female with an SMR of 0.106 ml O2/hr while the other two values were 0.055 and 0.060 ml O2/hr, so SMR in this species may be less than 0.074 ml O2/hr. The SMR predicted for a 9.5 g lizard at 25°C from a regression equation for lizards ranging from 1-4400 g body mass (estimated from Bennett & Dawson, 1976—see below) is 0.100 ml O2/hr. Using the equation reported by Mautz (1979) for SMR at 25°C for lizards from 1 to 70 g body mass for a 9.5 g lizard, an SMR of 0.113 ml O2/hr would be anticipated for A. switaki. Therefore, the SMR of A. switaki measured in this study is considerably less than predicted values. In contrast, the SMR of 0.146 ml O2/hr measured for C. variegatus is similar to the predicted value of 0.120 ml O2/hr for a 3.6 g lizard. Metabolic rate was high in both species during stimulation to maximal activity. The factorial scorpions (maximum oxygen consumption/SMR) are 5 for A. switaki and 6 for C. variegatus, similar to factorial scorpions in other groups of vertebrates (Bennett & Ruben, 1979). The maximum oxygen consumption is lower in A. switaki than that measured for other small lizards (Bennett & Dawson, 1976). It would be of interest to study maximum oxygen consumption in other lizard species with reduced SMR to see if there is a parallel reduction in maximum aerobic capacity as is found in this species.

The most unique feature of the physiology of A. switaki is its reduced SMR. There are four possible reasons why SMR is lower than predicted in this small lizard: (1) the scaling of metabolic rate to body mass may differ in small lizards compared to lizards of larger mass; (2) various phylogenetically related groups of lizards may have reduced SMR when compared to other groups of lizards; (3) reduced SMR could serve as a water-conserving mechanism in xeric-adapted lizards; and (4) reduced SMR could limit the daily energy demands of lizards in habitats with restricted food resources.

If the SMR of small lizards scale differently than the values for all lizards, most of the literature values for SMR in small lizards should fall significantly below a regression line of lizards of all size. The effect of body mass on SMR in lizards has recently been reviewed (Bennett & Dawson, 1976). Values of Q10 for SMR between 20° and 30°C were obtained for 1-20 g lizards from the regression equations of Bennett and Dawson (1976). SMR was then calculated for 25°C and a regression equation calculated (Fig. 4). This regression equation is \( \log_{10}(Q_{10}) = 0.153 - 0.19 \log(g) \). This is similar to the equation for SMR vs body mass at 25°C in small lizards calculated by Mautz (1979). Confidence limits (95%) for estimated values were calculated according to Sokal & Rohlf (1969, p. 424) for regression equations of Bennett & Dawson (1976) at 20° and 30°C and averaged to obtain an estimate of the confidence limits for the regression equation at 25°C. In Fig. 4, values of SMR at 25°C in 19 species of small lizards are plotted with the regression line (only points 16 and 18 were used by Bennett & Dawson in calculating their regression equations). Only species in which SMR was measured at 25°C or over a temperature range including 25°C were included. Only a few points fall below the 95% confidence limits. The only small iguanid lizard with low SMR is Uma notata (Vance, 1959). Values for other species of iguanid lizards agree with predicted values (Kramer, 1934; Vance, 1959; Mayhew, 1965; Roberts, 1968; McManus & Nellis, 1973). Similarly, A. switaki, Gona-
oxygen. This could serve to reduce respiratory evaporative water loss (REWL) by reducing tidal volume. Snyder (1971) has proposed water conservation as the adaptive significance of reduced SMR in *Sphaerodactylus vigilis*, a xeric-adapted lizard. *A. switaki* are found in the lower deserts of extreme southwestern California and Baja, Mexico. They appear to be nocturnally active during dry months. Thus, any water-conserving mechanism would appear to be of importance to this species. EWL is lower in *A. switaki* than in the mesic-adapted gekkonids, *Hemidactylus frenatus* and *Sphaerodactylus macrolepis* (Snyder, 1975; Snyder & Weathers, 1976) but is comparable to other xeric-adapted lizards including *C. variegatus*. However, reduced SMR is poorly correlated with reduced EWL for lizards in general, for there are many xeric-adapted lizards which do not have reduced SMR but have EWL rates comparable to *A. switaki*. In addition, Mautz (1979) has recently shown that SMR is reduced in certain mesic-adapted xantusiids. Therefore, reduction of SMR is probably unrelated to adaptations for reduced EWL in xeric-adapted lizards.

A major consequence of reduced SMR would be a reduced requirement for energy. Bustard (1967) reported that *Coleonyx variegatus* could ingest and convert enough food in four days to increase their weight by about 50%. Fat was deposited not only in the tail, but throughout the body. If given only water, it was predicted that these geckos could sustain themselves on the stored lipid reserves for periods of 6–9 months. Though we have no evidence, it is highly likely that *A. switaki* could sustain itself in a similar fashion, especially considering the relative size of its fat, stubby tail. Indeed, at its SMR at 25°C *A. switaki* would require only 19 kcal/yr. This amount of energy could be derived if the animal ate about twice its body weight in insect matter in a year, or stored 2 g of fat. Since the SMR of *A. switaki* is 70% of the predicted value, approximately 8 kcal/yr could be saved by *A. switaki* due to its reduced SMR alone.

The above calculations are not meant to represent the actual energy budget for an *A. switaki* for a year, but to underscore the low level of energy required for a lizard to maintain itself. In order to estimate the true energy requirement of an animal demands a complete knowledge of its life history. Temperature regimes and activity are particularly important parameters which affect an animal’s energy budget. Little is known of the life history of *A. switaki*, but its nocturnal habits mean it is probably eurythermal. Air temperatures at night when *A. switaki* were collected ranged between 25°–30°C, so 25°C may represent a fairly average temperature during the summer. The impact of activity on the energy budget of *A. switaki* is impossible to assess without field time/energy budgets. Bennett & Nagy (1977) showed that daily field metabolic rates of *Sceloporus occidentalis* averaged 2–2.5 times higher than SMR measured in the laboratory. The lower maximum oxygen consumption of *A. switaki* may reduce the effect of activity on its true energy budget for a year. However, activity in *A. switaki* could have a major impact on its energy requirements and minimize any potential energy savings due to a reduced SMR.

Mautz (1979) argues that a reduced SMR lowers energy requirements in xantusiids that live in restricted foraging ranges (caves, rock crevices, yucca debris) where resources may be in short supply. Feder (1976) presents similar arguments for metabolic energy savings in salamanders. The fact that *A. switaki* has only recently been described and has resisted intensive collecting efforts suggests it is also highly secretive and may be abroad only rarely. However, this lizard may not be confined to as restricted a habitat as xantusiids since it has been collected from a variety of habitats including arroyos, on boulders, on sparsely vegetated

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**Fig. 4.** Curve predicting metabolic rate ($\dot{V}_{O_2}$) from body mass at 25°C with 95% confidence limits (dotted lines). Symbols represent values from the literature for individual species of various families. □—Gekkonidae: 1—*Sphaerodactylus beattyi* (Snyder, 1979); 2—*Sphaerodactylus macrolepis* (Snyder, 1975); 3,4,5—*Hemidactylus frenatus*, *Lepidodactylus huebneri*, *Cosymbotus platyurus* (Feder & Feder, 1981); 6—*Gonatodes antillensis* (Bennett & Gorman, 1979); 7—*Hemidactylus frenatus* (Snyder & Weathers, 1976); 8—*Coleonyx variegatus* (Vance, 1959); 9,10—*Coleonyx variegatus*, *Anarbylus switaki* (this study); 0—Anniellidae: 11,12,13,14,15—*Scleropus gracius*, *Scleropus occidentalis*, *Callisaurus draconoides*, *Petrosaurus mearnsi*, *Uma notata* (Vance, 1959); 16—*Uta stansburiana* (Roberts, 1968); 17—*Anolis acutus* (McManus & Nellis, 1973); 18—*Phrynosoma m'calli* (Mayhew, 1965); ▲—Xantusiidae: 19—*Xantusia vigilis* (Vance, 1959; Snyder, 1971); 20—*Xantusia henshawi* (Vance, 1959); ⋆—Anniellidae: 21—*Anniella pulchra* (Vance, 1959).
flats and both gravel and asphalt roads (Ottley, personal communication; Murphy, unpublished data). If A. switaki actively forage abroad, then their reduced metabolic rate cannot be related to restricted foraging range. While it can be argued that any reduction in metabolic rate can be of adaptive value, it seems more conservative to view all ectotherms as low-energy adapted (Pough, 1980) and to view small fluctuations in SMR to be of minor physiological significance.

None of the four proposed theories of reduced SMR appear to be reasonable when applied to all species of small lizards. Only the proposal of Mautz (1979) relating reduced SMR to restricted foraging range in small lizards is consistent with the available data on metabolism in small lizards. Detailed ecological data on the habitat, food resources and foraging strategy of A. switaki are required to see if this species is consistent with the proposed theory and does in fact have a restricted foraging range. Whatever the explanation, caution should be exercised before concluding that low standard metabolic rates are of adaptive significance, at least until more substantial data base can be obtained.

Acknowledgements—John R. Ottley kindly made the geckos available to us. The specimens were imported from Mexico on Scientific Collecting permit No. 1/78/832 issued to Ottley from the Dirección General de la Fauna Silvestre by Dr Antonio Landazuri O. Without their cooperation this research would not have been possible. We would also like to thank Drs G. A. Bartholomew and A. F. Bennett for allowing us to use various equipment from their laboratories. Thanks to Drs A. F. Bennett, W. Mautz and M. Feder for comments on this manuscript. Field work for this research was supported in part by the Theodore Roosevelt Foundation and the University of California Regents Travel Grant No. 780000-07427-5 to RWM. John Cram assisted in the field.

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