

ENERGY EXPENDITURE IN FREE-RANGING LIZARDS¹

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Abstract. Metabolic rates of the western fence lizard *Sceloporus occidentalis* (Sauria: Iguanidae) were measured in the laboratory by gas exchange, and in the field with doubly labeled H₂O. Field metabolic rates of adults during the spring reproductive season (0.22 ml CO₂ g⁻¹ h⁻¹ or 141.4J g⁻¹ day⁻¹) were not different from those during the fall nonreproductive season (0.20 ml CO₂ g⁻¹ h⁻¹ or 127.2J g⁻¹ day⁻¹). Field and laboratory metabolic rates of ♂♂ were not different from those of ♀♀ in spring or fall. Average daily field metabolic rates were 2.0 to 2.5 × resting laboratory rates measured on a simulated normal thermal cycle; estimated rates during the field activity period were 2.5 to 3.1 × resting levels measured at 35°C. Only 11 to 17% of total daily energy expenditure was used while lizards were inactive in their burrows. Daily field metabolism of this lizard is only 3 to 4% that of a bird or mammal of equal size.

Key Words: California; doubly-labeled water; energy expenditure; field metabolic rate; lizard; metabolic rate; reproduction; *Sceloporus*; thermoregulation.

INTRODUCTION

The measurement and analysis of metabolic rate in animals under laboratory conditions has been a favorite study of physiological ecologists. Minimal or maximal rates may be obtained and the influence of single factors upon metabolic performance can be evaluated. However, it has been difficult to apply these data to animals in their natural environments. The fundamental ecological questions concern how much it costs an animal to live in the field and the energetic impact of the organism on its environment. These questions can most profitably be approached with measurements on free-living organisms. A promising technique for field studies is the measurement of CO₂ production using doubly labeled H₂O (see Lifson and McClintock [1966], Mullen [1973], and Nagy [1975] for discussions of theory and practical application). Once labeled, an animal may be released in its own territory and left undisturbed until subsequent recapture. The average energetic expenditure during this interval is proportional to the turnover rates of the isotopes in the animal.

Most measurements of metabolic rate using doubly labeled H₂O have been made on small birds and rodents. The metabolic requirements of these animals, even for basal metabolism, are considerably in excess of those of small ectotherms. Reptiles at rest, even at mammalian or avian body temperatures, utilize only one sixth to one tenth as much energy as equal-sized resting endotherms (Bennett and Dawson 1976). Whether a proportionately smaller amount of energy is required for reptiles under natural living conditions is not known, nor do we know the influence of normally fluctuating body temperatures on energy economy in

these ectotherms. This study on a small lizard compared field metabolic rates with resting rates measured in the laboratory to evaluate the influence of field activity metabolism and cycling of body temperatures on energetic demand. By taking measurements on male and female adults during both reproductive and nonreproductive periods, we analyzed the effect of sex and reproductive activity on energy utilization.

MATERIALS AND METHODS

A population of *Sceloporus occidentalis* resident at the Ecology Research Area on the University of California, Los Angeles campus was used in this study. The area contains a coastal sage scrub community and an old orchard; it is fenced off from the surrounding campus and is infrequently visited. Measurements were made during the fall (September 1975) and the spring (May 1976). In May, all adult animals were reproductively active. Females had ovarian or oviducal eggs (mean number oviducal eggs = 8.2, range 7-9; mean dry mass = 1.23 g/clutch, range 1.08-1.51). Males had enlarged testes and epididymal sperm, and animals were observed copulating in the field. During the fall, gonads were completely regressed and most animals had enlarged abdominal fat bodies.

Field metabolic rates were determined by injecting doubly labeled water (³HH¹⁸O) and measuring the decline in specific activities of tritium and oxygen-18 in successive blood samples. Animals were noosed and transported to the laboratory where they were weighed and toe clipped and an identifying number was painted on their backs. They were injected intraperitoneally with 0.10 ml of H₂O containing 0.2 mCi³H and 90 atom-percent ¹⁸O and placed in a terrarium with a heat source. Three or more h later, a blood sample was taken from the infraorbital sinus. Labeled

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TABLE 1. Rates of CO₂ production and body mass in *Sceloporus occidentalis* during spring and fall

| | Adults | | | Juveniles |
|---|--------------------------------|--------------------|--------------------|-------------------|
| | ♂♂ | ♀♀ | Total | |
| SPRING | | | | |
| Metabolic rate (ml CO ₂ g ⁻¹ h ⁻¹) | | | | |
| Resting at 35°C | .192 ^a (.023, 5) | .178 (.022, 6) | .185 (.015, 11) | .300 (.052, 4) |
| Resting at 18.5°C | .037 (.003, 5) | .033 (.002, 6) | .035 (.002, 11) | .052 (.012, 4) |
| Field | .211 (.021, 5) | .227 (.031, 6) | .220 (.019, 11) | .290 (.015, 5) |
| Body mass (g) | 11.9 (1.1, 5) | 11.9 (0.8, 6) | 11.9 (0.6, 11) | 4.4 (0.5, 5) |
| FALL | | | | |
| Metabolic rate (ml CO ₂ g ⁻¹ h ⁻¹) | | | | |
| Resting at 35°C | .202 (0.24, 10) | .179 (.020, 9) | .192 (.017, 19) | |
| Resting at 20°C | .047 (.066, 10) | .051 (.011, 10) | .049 (.006, 20) | |
| Field | .233 (.071, 4) | .178 (.037, 7) | .198 (.034, 11) | |
| Body mass (g) | 12.1 (0.6, 10) | 10.8 (0.6, 10) | 11.5 (0.4, 20) | |

^a Mean (standard error, *N*).

H₂O equilibrated in <1 h in the side-blotched lizard, *Uta stansburiana*, another small iguanid (K. A. N., *personal observation*). The animal was then released at its point of capture. Animals were recaptured in ≈1 wk (\bar{x} = 7.4 days, range = 5–20 days), and blood samples were taken again. Tritium content of H₂O distilled from blood samples was measured by liquid scintillation; ¹⁸O content was determined by the proton-activation method of Wood et al. (1975). Carbon dioxide production was calculated using Eq. 8 in Nagy (1975). Although isotopes could have re-entered lizards when they were in burrows, no errors in CO₂ production estimates should occur from this as long as all the CO₂ in the burrow came from the lizard itself (Lifson and McClintock 1966). Eleven of 17 injected animals were recaptured in the fall; 16 of 21 injected animals were recaptured in the spring. During both field periods, lizards lost body mass at slow rates (1.54% body mass per day in spring and 1.52% in fall).

Rates of resting metabolism during a simulated natural thermal cycle were then determined for the recaptured animals by measurement of O₂ consumption and CO₂ production. During the fall, laboratory measurements were also made on nine uninjected lizards which were captured fresh from the study area. Measurements were made on resting animals at their preferred body temperature of 35°C (McGinnis 1966) during the day; nighttime temperatures were 20°C (fall) or 18.5°C (spring), the respective nocturnal burrow temperatures measured in the study area. Animals were

placed in ventilated metabolic chambers inside a dark controlled-temperature cabinet (regulated at ± 0.5°C) at 2300 h local time on the night before metabolic determinations. The thermal cycle of the cabinet was 35°C from 0800 to 1600 h and 18.5° or 20°C from 1600 to 0800 h. Metabolic rate was measured at 1000–1200 h and 2100–2300 h by sampling the gas composition of the air excurrent from the chamber. Water vapor and CO₂ were absorbed with Drierite® (anhydrous calcium carbonate) and Ascarite® (sodium asbestos anhydride), respectively. Oxygen partial pressure was measured with a Beckman™ O₂ analyzer, and O₂ consumption was calculated according to the method of Depocas and Hart (1957). Carbon dioxide production was measured on animals in the fall. Paired excurrent air samples were collected: H₂O vapor was absorbed from one, and both H₂O vapor and CO₂ were removed from the other. Carbon dioxide production was calculated from the difference in O₂ content of the two samples (method from G. MacLean, *personal communication*). All gas volumes were corrected to STPD conditions. All statistical comparisons were made by two-tailed Student's *t*-tests.

At the conclusion of the nocturnal measurements, the animals were dissected to determine reproductive condition. Total body water content was determined by drying the bodies at 65°C to constant mass.

RESULTS

Metabolic measurements under both laboratory and field conditions are given in Table 1. The average respiratory quotient measured in the laboratory was 0.67 ± 0.02 (\bar{x} ± SE), a value insignificantly different from 0.70, indicating fat catabolism. Consequently, all laboratory measurements are expressed as CO₂ production assuming a respiratory quotient (RQ) of 0.70. Because there was no difference (*p* = 0.89) between injected and uninjected lizards, laboratory metabolic data for these two fall groups are combined in Table 1.

There were no significant sexual or seasonal differences (*p* > .05) among groups of adults in either field or laboratory metabolism. The metabolic rates of the juveniles in both the field and laboratory during spring were greater than those of the adults (.04 ≥ *p* ≥ .01). Such a difference is expected on the basis of smaller body size of the immature animals as well as metabolic increments associated with rapidly growing tissue.

The elevation above resting levels which free existence entails was determined from the difference between laboratory and field metabolic rates. Lizards on the study site in both spring and fall emerged and were active at ≈0930 h and disappeared at ≈1730 h, although activity had begun to diminish around 1700 h. Thus, field animals apparently maintained their preferred body temperature (35°C) for ≈8 h every day and spent the remainder at burrow temperature. To estimate the daily cost of resting metabolism, we as-

TABLE 2. A comparison of resting and field metabolic expenditure for *Sceloporus occidentalis* on a daily basis. (To convert from joules to calories, divide by 4.184)

| | Metabolic cost (joules per gram per day) | | | | | | Total field ÷ Total maintenance | Field active ÷ Resting at 35°C |
|---------------|--|-----------------|----------------|---------------------------|--------------------|-------|---------------------------------------|--------------------------------------|
| | Maintenance in laboratory | | | Free-living in field | | | | |
| | 16 hr at 18.5 or 20°C | 8 hr at 35°C | Total daily | In burrow ^a | Active in field | Total | | |
| SPRING | | | | | | | | |
| Adult | 15.5 | 41.0 | 56.5 | 15.5 | 125.9 | 141.4 | 2.50 | 3.07 |
| Juvenile | 23.0 | 66.5 | 89.5 | 23.0 | 163.6 | 186.6 | 2.08 | 2.46 |
| FALL | | | | | | | | |
| Adult | 21.8 | 42.7 | 64.5 | 21.8 | 105.4 | 127.2 | 1.97 | 2.47 |

^a Estimated assuming metabolic rate in burrow is equal to laboratory metabolism at 18.5 or 20°C.

sume a biphasic temperature regime of 8 h at 35°C and 16 h at 18.5° or 20°C. Deviations from this biphasic model due to morning heating and evening cooling will be relatively minor. To examine daily metabolic rates in terms of energy expenditure, CO₂ volumes (Table 1) were converted to joules using the factors 0.0361 ml CO₂J⁻¹ for laboratory results (fat catabolism for fasting animals [Schmidt-Nielsen 1975]) and 0.0373 ml CO₂J⁻¹ for field results (mixed fat and protein catabolism, estimated for the lizard *Uta stansburiana* eating mealworms, K. A. N., *personal observation*). Results of these calculations are shown in Table 2. Thus, 40–50% of the energy utilized by a free-living *S. occidentalis* is allocated to resting or maintenance costs, and the cost of free existence entails approximately a doubling of these minimal levels.

Another aspect of energy expenditure may be analyzed if we assume that the additional cost involved in free existence is not spread evenly throughout a 24-h period, but is confined to the diurnally active hours. In this case, metabolic rate of field animals in their burrows would be close to that measured at night in the laboratory. This assumption is probably realistic since there must be only minimal activity for a lizard with low body temperature in the burrow. Field metabolism is partitioned into its active and inactive components in Table 2. The costs of field activity are apparently 2.5 to 3 × the resting metabolic rate of 35°C. This analysis of activity costs involves the assumption that field animals were active for 8 h during every day of the measurement period. We were not in the field each day to evaluate this assumption.

DISCUSSION

Two intriguing findings of this study are the absence of higher field metabolic rates during the reproductive season and the similarity of energy expenditures in male and female lizards. One might predict increased energy costs in spring as a result of heightened social behavior (territoriality, courtship, copulation) and the formation of eggs. These expenditures are either of little energetic significance, possibly due to their low

cost and/or time involvement, or they are balanced by comparable levels of activity or tissue synthesis in the fall. The latter suggestion is supported by declining egg production in summer and the subsequent augmentation of fat body size in this species (Goldberg 1973).

Although the energy investment in a clutch of eggs (≈31.8kJ, based on an average value of 25.9kJ/g dry wt for *Sceloporus* spp. [Ballinger and Clark 1973]), is rather high in comparison to daily energetic expenditure, the metabolic cost of forming a clutch (as measured by CO₂ production) may be low. This increment includes only the cost of increased feeding and conversion of food to egg material; the energy content of the egg mass does not appear as a metabolic cost. The cost of the synthesis involved in egg formation may be rather low since at least a portion of the egg material is derived from lipids remaining in the abdominal fat bodies from the previous year (Hahn and Tinkle, 1965; W. W. Mayhew, *personal communication*). However, we are not certain that our field measurements include yolk deposition, although egg formation in *S. occidentalis* normally occurs during the time of our study (W. W. Mayhew, *personal communication*) and five of the six females in our study had oviducal eggs at autopsy. Obviously, more extensive studies must be undertaken to clarify the energetic cost of reproduction in small lizards.

Given the observation that ectothermic vertebrates at a body temperature of 37°C have resting metabolic rates that are 10 to 17% of those in endotherms (Hemmingsen 1960, Bennett and Dawson 1976), it is of considerable ecological relevance to know whether energy expenditures of free-living animals show a similar ratio between the two groups. King (1974) has calculated allometric regression equations that predict the daily energy cost of free-living birds and rodents, based on doubly labeled H₂O studies as well as other methods involving less direct measures. These equations predict daily energy expenditures of 58.6 and 38.87 kJ for an 11.9 g bird and rodent, respectively. The daily expenditure of an adult *S. occidentalis* in spring is 1.67kJ, or only 3–4% of the predicted endotherm level. A similar ratio (4–7%) can be calculated for the iguanid

lizard *Sauromalus obesus* during spring; these ratios decrease to 1–2% when calculated on a yearly basis (Nagy and Shoemaker 1975). However, the ratio of cost of free living to maintenance cost is remarkably similar in these vertebrate groups: the ratios for lizards are 2.0 to 2.5 in *S. occidentalis* (Table 2) and 1.7 in *Sauromalus obesus* (Nagy and Shoemaker 1975); for birds, 2.8 in *Progne subis* (Utter and LeFebvre 1970) and 2.3 in *Mimus polyglottos* (Utter 1971); and for rodents (mean monthly averages), 2.8 in *Perognathus formosus* (Mullen 1970), 2.4 in *Dipodomys merriami* and 2.5 in *Dipodomys microps* (Mullen 1971a), and 3.5 in *Peromyscus crinitus* (Mullen 1971b). The primary reason for this discrepancy is that the free-living increment ratio is calculated from daily resting metabolism at both warm (diurnal) and cool (nocturnal) body temperatures for the lizards, so the denominator of this ratio is < 10–17% of endotherm levels stated above. Thus, an iguanid lizard can live on much less energy than can a similar-sized bird or mammal. This economy of the saurian mode of life is illustrated by the observation that the amount of food required by a small insectivorous bird for 1 day is sufficient for a *S. occidentalis* for ≈35 days.

It is apparent that the cyclic thermal regime of these lizards results in a large energetic savings in comparison to a homeothermic endotherm. Despite the fact that ≈67% of the day is spent underground, only 11–17% of the daily energy expenditure is used there (Table 2). If a lizard remained underground all day, instead of emerging and being active, it would reduce its daily energy requirement by ≈80%. While active in the field, *S. occidentalis* uses ≈15.90 and 12.97 J g⁻¹ h⁻¹ in spring and fall, respectively. The maximal rate of aerobic metabolism is 42.68 J g⁻¹ h⁻¹ at 35°C for adults of this species, assuming an RQ of 0.7 (Bennett and Gleeson 1976). Thus, the average metabolic rate during field activity is about one fourth the potential scope. However, utilization of the full aerobic scope entails considerable anaerobic metabolism, which would restrict activity rapidly (Bennett and Dawson 1976).

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