

Metabolic Expenditure and the Cost of Foraging in the Lizard *Cnemidophorus murinus*

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Metabolic expenditure of *Cnemidophorus murinus* (Sauria: Teiidae) was measured in animals walking on a motor-driven treadmill and compared to measurements of resting and maximal oxygen consumption. At normal field-foraging velocity (0.14 km/h), metabolic rate is approximately 4 times resting values: 0.89 vs. 0.23 cc O₂/(g·h). Maximal levels of oxygen consumption [1.6 cc O₂/(g·h)] are attained at 0.3 km/h, the greatest speed which can be sustained for over 30 min. Animals exhaust rapidly at 0.5 km/h. The ability of this lizard to sustain aerobic activity is limited, but foraging activity is restricted within these aerobically supportable limits. Foraging is energetically expensive and constitutes approximately 87% of the metabolic expenditure during diurnal activity and 71% of the total daily expenditure for this animal.

MACROTEIID lizards, members of the New World Teiidae, are active, cursorial animals. They are similar in body form, habits and activity level to the varanids and lacertids of the Eastern Hemisphere and, similar to these animals, are generally carnivorous or insectivorous. Teiids forage with an almost continual, low velocity patrol through their environment, unearthing insects and other food items (Milstead, 1957; Hardy, 1962; Bennett and Gorman, in press). With this continual foraging activity, they represent the antithesis of the sit-and-wait strategy of predation. Since locomotory activity is generally costly in the amount of energy required for its support, it is to be expected that food-gathering and habitat patrol should have a major impact on the energetic budgets of these animals. The measurement of respiratory gas exchange during this activity would permit the assessment of foraging costs and comparison to minimal and maximal rates of energy utilization. We have been successful in inducing a teiid lizard to walk on a motor-driven treadmill while metabolic gas exchange was measured.

The animals used in these experiments are *Cnemidophorus murinus ruthveni* Burt from the arid Caribbean island of Bonaire. Data on the natural history of this species are reported by Bennett and Gorman (in press), from which the following information is taken. They are very common animals (approximately 560 per hectare in thornscrub forest) of moderate body size (20-80 g adults). They spend 77% of the daily

active period in foraging activity and maintain an average velocity of 0.13 km/h during this time. Activity is restricted to the hottest times of the day (0900-1500), and body temperatures of field-active animals average 40.4 C during this period. They are very opportunistic feeders and will accept almost any food item. They are primarily, although not exclusively, herbivorous and are thus distinct in their dietary preferences from most teiids. We have made measurements of their metabolic rates during rest, during walking at normal foraging and maximum sustainable speeds, and during low-level electrical stimulation to elicit maximal exertion.

MATERIALS AND METHODS

Adult *C. murinus* were collected in live traps on Bonaire, transported to the United States, and housed in cages containing a photothermal gradient. They were kept in excellent health on a mixed diet of lettuce, dogfood, and mealworms. All experimental procedures were carried out at 40 C, the field-active body temperature.

Resting and maximal oxygen consumption were measured on 12 animals (mean mass = 55.2 g, range = 27.6-85.2 g). The experimental methodology was similar to that reported by Bennett and Gleeson (1976). Safety-pin electrical leads were implanted in the base of the tail and individual animals were placed in separate metabolic chambers, approximately 500 cc in volume. These were kept overnight in a dark-

ened environmental chamber set at 40 C. Air was metered through the chambers at approximately 60 cc/min. Carbon dioxide and water vapor were absorbed from the excurrent air line with Ascarite and Drierite, respectively. Oxygen concentration of the downstream air line was monitored before stimulation with a Beckman model E-2 oxygen analyzer. Resting values of oxygen consumption were calculated from these data according to the methodology of Depocas and Hart (1957). The chamber was then sealed and the animal stimulated for 2.0 min with sporadically administered electrical shocks of low intensity, to which the animal responded with rapid-running behavior. Air within the chambers was sampled before and after stimulation, and oxygen consumption during the active period was calculated according to the equation presented by Bennett and Gleeson (1976). All volumes reported are corrected to STPD conditions.

Metabolic rate while walking at several speeds on a treadmill was measured in five animals (mean mass = 70.7 g, range = 56.9–87.8 g). Each animal was placed in a cloth bag overnight in an environmental chamber at 40 C. The following day, the animals were rapidly fitted with light, clear plastic masks, approximately 5 cc in volume, closed except for an excurrent air line in the nasal region and open to room air about the neck. The mask was attached to the pectoral region of the animal with a string harness. The mask did not impede the animal's vision and was attached with only a minimum of struggling. Air was drawn through this mask at 400–600 cc/min by a downstream air pump connected to the mask with Tygon tubing. The animal was then placed on the treadmill under a cloth bag and left undisturbed for 20–30 minutes. The temperature at the surface of the treadmill was maintained at 40 C by radiant and convective heaters. The treadmill was constructed of a belt made of rubber-impregnated cloth and had an effective length of 70 cm and a width of 40 cm. It was powered by a D.C. motor and had a speed range of 0.1–3.2 km/h.

Oxygen consumption of the animals before activity was measured during the last 5 min of the equilibration period. The treadmill was then activated up to a single speed between 0.1 and 0.5 km/h. Animals were initially refractory to walking, but began to match tread speed with a regular gait after 3–8 min of gentle prodding on the tail. They sustained speeds up to 0.3 km/h and were tested for periods of 20–50 min at

these speeds. Oxygen concentration (and carbon dioxide concentration at speeds above 0.17 km/h) of air excurrent to the mask was measured continually. Metabolic rates were calculated during periods of activity in the latter portion of the run and represent the lowest continuous 5-min average measured. Animals were measured at only one speed per day and were returned to their cages to recover. Body temperature was measured cloacally before and after walking on the treadmill and averaged 39.7 C.

Gas concentrations in air excurrent from the mask were measured by splitting the air line for separate analysis of oxygen and carbon dioxide. In one line, water vapor and carbon dioxide were absorbed as above and air was metered through an Applied Electrochemistry model S-3A oxygen analyzer. In the other, water vapor was absorbed, and the gas concentration measured with a Beckman model LB2 infrared carbon dioxide analyzer, and then carbon dioxide was absorbed from the excurrent air. Downstream dry, CO₂-free flow rates were used to calculate oxygen consumption (STPD) according to the method of Depocas and Hart (1957). Oxygen concentrations in the mask air line never decreased below 20.5%.

RESULTS

Resting preactive metabolic rates measured in the metabolic chambers averaged 0.23 cc O₂/(g·h) (±0.022 S.E.). Active oxygen consumption during 2 minutes of stimulation averaged 1.63 cc O₂/(g·h) (±0.22). Individual factorial increments in oxygen consumption (active ÷ rest) averaged 7.2 (±1.1).

The oxygen consumption of animals on the treadmill is reported in Fig. 1. The animals had an average oxygen consumption of 0.34 cc/(g·h) (±0.051) prior to walking activity. This value is 1.5 times that measured in the metabolism chamber and is significantly greater (*P* = 0.03, *t*-test) than the latter values. Oxygen consumption increases with increasing speed up to 0.3 km/h. Considering all the data for walking animals (0.14–0.34 km/h), the following linear relationship best describes the relationship between speed and oxygen consumption:

$$\dot{V}_{O_2} = 0.53 + 3.68V \quad (r = 0.75; P < .01)$$

$$[\dot{V}_{O_2} = \text{cc O}_2/(\text{g}\cdot\text{h}); V = \text{velocity in km/h}].$$

The net cost of transport (Schmidt-Nielsen,

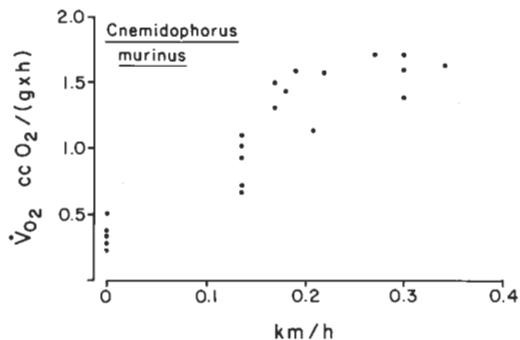


Fig. 1. Steady-state oxygen consumption (\dot{V}_{O_2}) of *Cnemidophorus murinus* walking on a motor-driven treadmill for 20+ min.

1972) is $3.68 \text{ cc O}_2/(\text{g}\cdot\text{km})$. If data at only 0.17–0.34 km/h are considered, the net cost of transport is $1.34 \text{ cc O}_2/(\text{g}\cdot\text{km})$. Oxygen consumption at 0.14 km/h, equivalent to foraging speeds in the field, averaged $0.89 \text{ cc O}_2/(\text{g}\cdot\text{h}) (\pm 0.084)$. The mean value for animals walking at 0.25–0.34 km/h was $1.61 \text{ cc O}_2/(\text{g}\cdot\text{h}) (\pm 0.059)$. This value is not significantly different from the value measured for active animals in the metabolic chamber experiments ($P = 0.94$, t -test).

Animals could not sustain speeds of 0.5 km/h and became exhausted in less than 5 minutes at these levels. The animal measured at 0.34 km/h could not sustain this speed and became exhausted after 20 minutes of activity.

The values for the respiratory exchange ratios ($R = \dot{V}_{CO_2}/\dot{V}_{O_2}$) averaged $0.97 (\pm 0.032)$ for nine determinations of animals walking at 0.17–0.30 km/h. These values are indicative of aerobic carbohydrate catabolism ($R = 1.0$). The final respiratory exchange ratio of the animal which could not sustain activity at 0.34 km/h was 1.28. Values in excess of 1.0 during activity may be obtained from high levels of carbon dioxide release caused by the buffering (via the bicarbonate-carbonic acid system) of anaerobically-formed lactic acid (see Bullard, 1966, for a discussion). At sustainable speeds, our animals often had a transient rise in R above 1.0 during the initiation of activity, but this soon declined to values consistent with completely aerobic metabolism (Fig. 2).

DISCUSSION

Locomotor activity associated with foraging in this lizard increases metabolic rate to 3.9 times resting levels. Since these animals spend

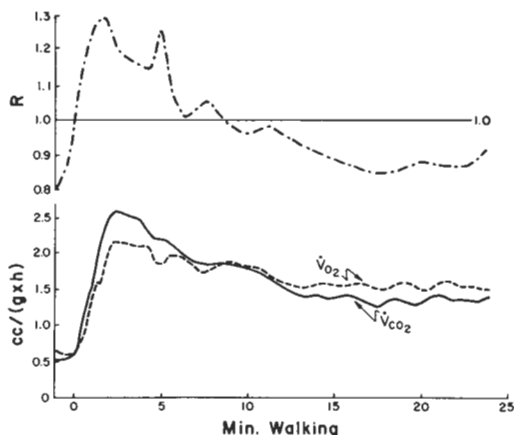


Fig. 2. Respiratory gas exchange in a 57-g *Cnemidophorus murinus* walking at 0.18 km/h. Oxygen consumption (\dot{V}_{O_2}) is indicated by a dashed line; carbon dioxide production (\dot{V}_{CO_2}), by a solid line. The respiratory exchange ratio ($R = \dot{V}_{CO_2}/\dot{V}_{O_2}$) is given by the dotted-and-dashed line.

three-fourths of their active day foraging, this activity is a major component of their daily energy expenditure. The remainder of the daily active period is taken up with postural adjustments, scratching behavior, and the like. If we assume this activity requires a doubling of resting metabolic rate (n.b., covered animals on the treadmill had a metabolic increment of 50% over rest), approximately 87% of the energy utilized during the active period of the day is devoted to foraging behavior. Assuming the metabolic values calculated for the inactive period of the day (principally resting under rocks at 27°C) by Bennett and Gorman (in press), 71% of the metabolic expenditure of the entire day is expended in foraging, over twice that allocated for resting, maintenance and sleep. The active foraging behavior of this species clearly involves a major energetic commitment.

C. murinus regulates its natural foraging activity at rather slow rates, which are sustainable for long periods of time. Work loads associated with these speeds appear well within the capacity of the animals to sustain aerobically; only half the aerobic scope for activity is utilized. There is no evidence that anaerobic energy input is required at speeds double normal foraging rates, according to the respiratory exchange ratios. However, the capacity of these animals for aerobic activity is clearly limited. These lizards could not sustain speeds much in

excess of 0.3 km/h, a rather slow walk, and exhausted rapidly at 0.5 km/h. They are capable of travelling at much faster speeds and will flee rapidly if approached in the field. In our laboratory, *Cnemidophorus murinus* will run at an average speed of 3.2 km/h for 1 min (fastest animal: 4.7 km/h) and has a burst speed over short distances of 8.2 km/h (fastest animal: 11.1 km/h) ($T_B = 40$ C). Consequently, these lizards are capable of exceeding sustainable speeds by 10- to 30-fold for brief periods of time, undoubtedly using anaerobic metabolism to support these levels of performance.

The net cost of transport is substantially greater than anticipated for a lizard of this size [predicted values: 1.3 cc $O_2/(g \cdot km)$, calculated from allometric analysis of data for lizards including teiids from Bakker, quoted in Taylor, 1973; 0.74 cc $O_2/(g \cdot km)$, data for lacertids from Cragg, quoted in Hughes, 1977)]. When data from only higher velocities (0.17–0.34 km/h) are considered, anticipated values are obtained. These results may indicate that foraging at normal speeds in the field is less expensive than would otherwise be anticipated by allometric analysis of data for all lizards. We are investigating further the cost of locomotion in teiids.

Relatively few observations have been made on the metabolic rates of teiid lizards. Values of resting metabolic rate measured for *C. murinus* measured here are very similar to a value of 0.23 cc $O_2/(g \cdot h)$ for *C. tigris*, obtained by averaging the data of three authors (Cook, 1949; Vance, 1959; Asplund, 1970) and adjusting their data for differences in body mass and temperature ($b = 0.80$; $Q_{10} = 2.0$). These values are also consistent with those predicted by Bennett and Dawson (1976) for lizards of this body size, after appropriate temperature adjustment. The value of maximal oxygen consumption reported by Asplund (1970) for *C. tigris* is almost identical to that reported here after adjustment for differences in mean mass of the animals ($b = 0.80$). Asplund interpreted these values as indicating an exceptionally high degree of aerobic capacity, even greater than that reported for varanid lizards. This analysis, however, failed to take mass-dependent effects into consideration. Subsequent studies on iguanid lizards of small body size (*Dipsosaurus dorsalis*, Bennett and Dawson, 1972; *Sceloporus occidentalis*, Bennett and Gleeson, 1976) have produced equivalent levels of oxygen consumption during activity. On the basis of data presently available, it appears that *Cnemidophorus*

does not possess aerobic capabilities unusual for a lizard of its size.

In conclusion, *C. murinus* appears to be an animal of limited ability to sustain aerobic activity. However, it normally regulates its foraging behavior to levels within its aerobic scope, and resorts to maximal levels of oxygen consumption and anaerobic metabolism only during escape or rapid pursuit. Its foraging activity is expensive in comparison to its resting behavior and constitutes a major share of its total energy turnover.

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