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Energy Requirements of *Uta stansburiana*

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Field data on the type and duration of above ground activity were obtained for a population of *Uta stansburiana*. These lizards were estimated to spend 2188 hr per year above ground, approximately ⅓ of this time in active movement, and 6652 hr per year in burrows. Air, substratum, and burrow temperatures were recorded weekly throughout the year. Resting and active oxygen consumption were measured in the laboratory by a modified manometric technique.

Resting oxygen consumption increased from a mean of 0.17 cc g/hr at 15° to 0.34 cc g/hr at 35° C. Active oxygen consumption increased from 0.64 cc g/hr at 15° to 1.1 cc g/hr at 35°C. Oxygen consumption was used with field estimates of activity and environmental temperatures to calculate the energy budget for an adult *U. stansburiana*, 58 KCal/yr. Approximately 0.1% of the net primary productivity of a creosote bush (*Larrea*) community was estimated to be dissipated by the *U. stansburiana*. Thus these lizards play a minor role in the energy transfers in a *Larrea* community.

INTRODUCTION

RATES of metabolism have been reported for many species of lizards, but little effort has been made to relate such measurements to population energy requirements. In order to evaluate the ecological significance of metabolic values for ectotherms like lizards, it is necessary to obtain estimates of daily activity, activity levels, and body temperatures of the animals in their natural environment. Pearson (1960) stated that variables such as temperature and activity can be handled with sufficient accuracy for making meaningful estimates of metabolic budgets for free-living populations of animals.

The side-blotched lizard, *Uta stansburiana*, is a common, conspicuous animal in the creosote bush desert community in southern New Mexico. The ecology and population structure of this species in a mesquite-yucca community near Kermit, Texas, have been studied in detail by Tinkle (1967a,b). Because of the abundance and possible importance of this lizard as a consumer in a *Larrea* community and the availability of pertinent ecological data, we undertook a study of the energy requirements of *U. stansburiana*.

Methods and Materials

Measurements of environmental temperatures and observations of activity and behavior of *U. stansburiana* were made throughout the year to obtain field data to be used in the interpretation of metabolic data from laboratory studies. The study area was in a desert scrub community with the scrub species producing a 19.63% cover of which 10.65% was due to creosote bush, *Larrea divaricata*, and 5.09% to whitethorn, *Acacia constricta* (Singh, 1964). The soil surface is a gravelly desert pavement. The sparse vegetation provides little shade or cover for diurnal lizards like *Uta*.

Monthly recordings of burrow, soil surface, and air temperatures were taken in the field every hour on seven or eight different days during each month. Air temperatures were recorded at a height of 2–2.5 inches above ground in shade, direct sunlight, and as close as possible to the position of a previously observed lizard. Most observations were made between 0600 and 1800 hr MST. Burrow temperatures were recorded with Yellow Springs Instrument Co. thermistors and telethermometer. A banjo tip thermistor was used to obtain soil surface temperatures. Burrow temperatures were obtained by attaching a bead thermistor to a fairly flexible length of wire which was pushed into a burrow as far as possible and the temperature recorded. Burrow temperatures were obtained at an average distance of 1 m from the surface of the burrow entrance.

Estimates of the daily activity of lizards were obtained by observing individual animals for extended periods of time. Observations were made on five to ten days per month for varying periods of time. The minimum total time spent in field studies was equivalent to three full days per month and encompassed all hours from sunrise to sunset. The behavior of the animal (emerging from cover, basking, feeding, moving from place to place, or remaining motionless in the shade) was timed by a stop watch and recorded. Observation of a lizard was terminated when the animal was obviously disturbed by the presence of the investigator.

Metabolic Studies

The animals used in the experiments were captured within a ten-mile radius of Las Cruces, New Mexico. Immediately after collection, the lizards were acclimated to the experimental temperatures and a 16 hr photoperiod in constant temperature chambers for a minimum of two weeks prior to metabolic studies. The animals were fed a diet of mealworms and fruit flies up to 48 hr prior to the experiments. Water was available at all times.

Measurements of active and resting oxygen consumption were made on ten individuals at each acclimation temperature. Resting oxygen consumption was measured in a respirometer consisting of a 250 ml Erlenmeyer flask closed by a rubber stopper with holes for the insertion of a 10 cc syringe and a manometer. A vial containing 20% NaOH and small strips of filter paper was attached to the side of the respirometer to absorb CO_2. A similar respirometer containing no animal was used as a thermobarometer. The respirometer is a modification of that described by Whitford and Hutchison (1963).

Active oxygen consumption was measured in a plexiglass respirometer of similar design with an electrical grid attached to the bottom. The grid was attached to the stimulator channel of an E and M Physiograph. The animals were stimulated into activity at 10 min intervals by a 15–25 volt, 50 cps, 30 sec duration, stimulus from the Physiograph. This regimen of stimulation resulted in periods of rapid running, walking, and slow movement comparable to normal activity patterns as judged by field observations.

Results

Field Studies

Estimates of the number of hours per month that the individual *U. stansburiana*

TABLE 1. ESTIMATED TOTAL HR/MONTH SPENT BY *Uta stansburiana* RESTING ABOVE GROUND, IN ACTIVITY ABOVE GROUND, AND IN BURROWS.

Month	Above Ground		In Burrow
	Resting	Active	
Jan.	12	6	732
Feb.	37	12	635
Mar.	70	28	674
Apr.	193	78	527
May	285	100	459
June	290	130	430
July	327	146	417
Aug.	325	167	419
Sept.	291	126	429
Oct.	239	91	505
Nov.	95	29	625
Dec.	24	9	720
Total/Yr	2188	922	6652

spend in active movement, resting above ground, and in burrows were made by multiplying the hours per day spent in these activities by the number of days in the month (Table 1). These estimates were based on the average time in these activities for one day of observations and climatological data for the area (U. S. Weather Bureau, 1960). The activity patterns of *U. stansburiana* changed with the season. In early spring and late fall, a majority of the lizards were observed above ground in the morning and a reduced number in the afternoon. During the summer the situation was reversed, with fewer lizards above ground in the morning than in the late afternoon. From late May until mid-September few and at times no *Uta* were active above ground at mid-day on bright clear days, while under cloudy conditions periodic activity was observed throughout the day. Little above ground activity was observed during the winter months of December, January, and February. Emergence from burrows during these months was limited by weather conditions. Above ground activity during the winter was observed on clear days when substratum temperatures exceeded 20° C. Activity in the late fall and early spring was directly correlated with soil surface temperatures. From the data on activity periods and environmental temperatures (Table 2), it was possible to obtain fairly accurate estimates of levels of activity and body temperatures throughout the year to be used in the calculation of energy budgets.

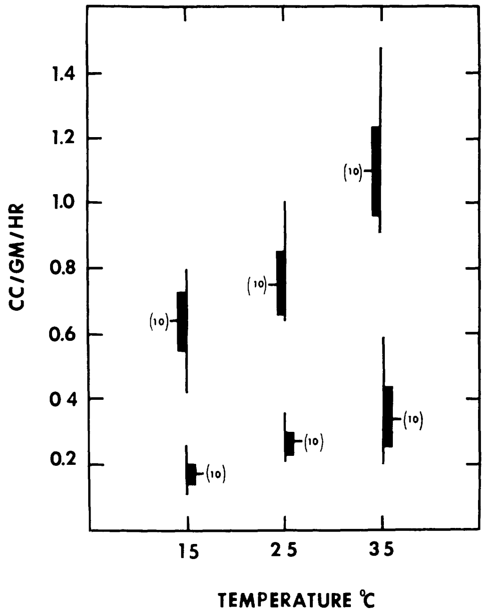

FIG. 1. Resting and active oxygen consumption in *Uta stansburiana* at different temperatures. Upper bars represent active oxygen consumption; lower bars, resting oxygen consumption. Horizontal lines represent mean; vertical lines, range; black rectangle on either side of mean, the 95% confidence intervals. Number in parentheses represents number of individuals in sample.

Calculation of Energy Requirements

The data on resting and active oxygen consumption in *U. stansburiana* are summarized in Fig. 1. The mean oxygen consumption for resting individuals increased from 0.17 cc g/hr at 15° to 0.34 cc g/hr at 35° C. In active lizards the mean oxygen consumption increased from 0.64 cc g/hr at 15° to 1.1 cc g/hr at 35° C. Active metabolism for animals acclimated at 15°, 25°, and 35° C was 27%, 36%, and 31% higher, respectively, than resting metabolism at those temperatures. Q_{10} values ranged from 1.17 for active animals between 15° and 25° to 1.55 for resting individuals between 15° and 25° C. These values are slightly lower than those reported by Dawson and Bartholomew (1956) for *U. stansburiana* over a temperature range of 10°–41.5° C.

Data on resting and active oxygen consumption were used to calculate the oxygen consumption per animal per month as summarized in Table 3. During the winter months of December, January, and February the average body temperature above ground, used in the calculation of monthly oxygen consumption, was taken as 25° C,

TABLE 2. MONTHLY ENVIRONMENTAL TEMPERATURE AND TEMPERATURE RANGES FOR A CREOSOTE DESERT AREA THREE MILES EAST OF UNIVERSITY PARK, NEW MEXICO.

	Burrow Temp.		Soil Surface Temp.				Air Temp.			
			Shade		Sunlight		Shade		Sunlight	
Month	$\bar{x}$	Range	$\bar{x}$	Range	$\bar{x}$	Range	$\bar{x}$	Range	$\bar{x}$	Range
Jan.	12.8	6.5–18.2	18.4	13.2–24.6	20.7	18.0–26.0	17.1	13.0–22.0	19.8	17.8–23.0
Feb.	11.8	6.8–18.1	26.0	15.8–33.0	31.6	23.0–43.0	17.9	14.0–23.0	23.1	14.0–38.0
Mar.	15.0	10.5–18.7	31.2	23.0–40.0	42.4	32.0–49.2	25.5	19.0–30.0	30.8	23.0–34.0
Apr.	22.7	21.5–24.8	26.1	13.2–39.2	37.8	15.2–52.0	24.4	12.0–31.5	29.9	14.0–41.5
May	21.7	19.1–24.6	29.3	23.0–39.0	41.5	29.0–51.6	25.0	16.1–32.0	33.8	23.0–41.8
June	28.4	25.9–30.0	33.4	25.6–43.6	37.8	30.6–57.0	30.7	26.0–41.5	36.0	28.0–43.0
July	28.6	24.0–31.0	29.0	20.0–40.0	39.2	22.0–59.0	30.3	23.0–37.0	34.9	24.0–43.0
Aug.	29.2	27.0–32.5	37.1	26.7–46.0	44.3	27.0–59.8	32.1	27.0–38.2	36.3	25.0–44.0
Sept.	22.7	20.5–32.0	26.3	17.8–32.4	37.2	18.5–50.8	24.3	17.5–32.5	28.6	18.0–40.5
Oct.	21.0	17.3–28.0	28.1	17.0–37.0	32.2	23.0–42.0	24.5	17.5–34.0	27.1	21.0–34.5
Nov.	17.7	17.0–20.2	20.1	16.0–29.0	25.7	18.0–36.0	21.2	17.0–27.2	27.0	21.5–34.1
Dec.	18.1	16.0–20.0	18.5	14.8–26.0	22.0	18.1–33.0	18.0	13.0–23.0	21.8	17.6–31.2

which is close to the body temperature of 27.4°C for *U. stansburiana* in winter reported by Roberts (1966). Oxygen consumption during the summer months was calculated on the basis of the mean preferred temperatures for this lizard based on 36 records of cloacal temperatures taken from May to July 1965 in an adjacent area. The mean preferred temperature for *U. stansburiana* was 36.03°C (Medica, pers. comm.). Oxygen consumption in the burrow was estimated on the basis of the mean burrow temperature for that month, since the body temperature of the lizard would probably be the same as ambient in the burrow environment.

Estimates for heat production by an average sized adult *U. stansburiana* (4.0 g, Tinkle, 1967a) for a year are given in Table 3. Since the diet of *Uta* is chiefly insect material, a caloric equivalent of 4825 cal/l of oxygen consumed was used to calculate energy dissipation. This is the equivalent suggested by Brody (1945) for food material containing a mixture of fat, carbohydrate, and protein.

Although *U. stansburiana* spend 75% of their time in a burrow (Table 2), and only 14% of their time in activity, the yearly oxygen consumption for activity is nearly equal to the total oxygen consumption while in the burrow environment (Table 3). The types of activity observed in the field in relative order of importance were: movement between shade and sun in behavioral thermoregulation, walking to feeding stations and feeding, and head bobbing or strutting in territorial or mating behavior. These activities required 33% of the total yearly energy budget as compared to 41% for energy expended while in the burrow environment.

DISCUSSION

Differences in composition and cover of vegetation between our study area and that of Tinkle *et al.* (1962) are apparently important in the activity patterns of these lizards. The vegetation in the area studied by Tinkle *et al.* (1962) provides considerably more cover and shade than the sparsely leaved shrub *L. divaricata* in our study area. Consequently most of the lizards in our area moved to underground retreats during midday in the summer months rather than remaining active during the daylight hours as reported by Irwin (1965) in west Texas populations.

Tinkle (1967a) estimated the biomass of *Uta* as approximately 100 g/acre for his west Texas population. Tinkle and Woodward (1967) estimated the population density of *U. stansburiana* in a *Larrea* community in Nevada to be 12.6/acre, which is 75% of the density of the west Texas population. Using the density figures for *Uta* in a *Larrea* community (Tinkle and Woodward, 1967), combined with a corrected estimate of biomass from the data of Tinkle (1967a) this species would dissipate approximately 1,003 KCal/yr/acre. Chew and Chew (1965) presented data for the net annual productivity of a *Larrea* community similar to our study area. Based on their data, the net primary productivity of the area inhabited by *Uta* would be 2,468,670 KCal/acre/yr.

Englemann (1966) indicated that the assimilation efficiency of poikilotherms is at

TABLE 3. ESTIMATED MONTHLY OXYGEN CONSUMPTION AND ENERGY DISSIPATION BY INDIVIDUAL *Uta stansburiana*.

Month	Above Ground cc O_2 Consumed At Rest	Above Ground cc O_2 Consumed In Activity	cc O_2 Consumed In Burrow	Tot. Liters O_2 Consumed	Tot. Cal.
Jan.	14.4	20.5	409.4	.4439	2137.9
Feb.	44.8	45.6	323.0	.4134	1993.2
Mar.	84.0	106.4	387.6	.5780	2832.3
Apr.	270.2	344.0	374.4	.9886	4767.6
May	399.0	440.0	375.0	1.2140	5857.5
June	406.0	572.0	431.5	1.4095	7194.5
July	453.6	640.6	424.0	1.5232	7349.0
Aug.	455.0	737.0	409.2	1.6012	773.5
Sept.	407.7	554.4	391.7	1.3538	6528.7
Oct.	334.8	400.4	422.0	1.1572	5583.0
Nov.	114.5	110.2	449.0	.6737	3247.7
Dec.	28.8	34.2	520.5	.5838	2813.4
Total/Yr	3012.8	4005.3	4917.3	11.9403	58,078.3

most 30%. Consequently a population of *Uta* would require at least 3,000 KCal/yr of food material for maintenance, growth, and reproduction. This is a minimal estimate based on the biomass data of Tinkle (1967a). This is approximately 0.1% of the net primary productivity of a *Larrea* community. Using data from Hemmingsen (1960) on the energy metabolism of insects, an insect biomass sufficient to supply the energy requirements of *U. stansburiana* would account for the turnover of 12,374 KCal. Including this estimate with that for a *Uta* population, this food chain would account for 0.6% of the net primary productivity of a *Larrea* community.

There are, of course, many sources of error in estimates of this kind. Even if we assume a ten-fold error in our estimates, *U. stansburiana* would still account for a small percentage of the net primary productivity. This supports the suggestion that *U. stansburiana* is of minor importance in energy flow (Tinkle, 1967a). It is apparent from this study that measurements of assimilation efficiency and energy requirements for growth and reproduction are necessary before meaningful estimates of the role of lizards in desert communities can be adequately evaluated.

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Electrophoretic Patterns of Proteins of Salamanders of the Genus *Desmognathus* (Family Plethodontidae)

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Four species of salamanders in the genus *Desmognathus—quadramaculatus, monticola, fuscus,* and *ochrophaeus*—were examined to determine the feasibility of distinguishing between them by starch-gel electrophoresis. *D. quadramaculatus* can be separated from the other three species on the basis of characteristic hemoglobin and lactate dehydrogenase (LDH) patterns. No distinction can be made between the hemoglobin patterns of *monticola, fuscus,* and *ochrophaeus*. *D. monticola* may usually be distinguished from *fuscus* and *ochrophaeus* by the much higher amounts of LDH-1 and LDH-2 that appear in tissue extracts of *monticola*. *D. monticola* is also separable from many *fuscus* individuals by the cathodal migration of LDH-5 in *monticola*. No distinction can be made between *fuscus* and *ochrophaeus* on the basis of LDH patterns. Aquatic species of *Desmognathus* examined appeared to contain larger quantities of predominantly HLDH isozymes than did the more terrestrial species. Staining gels for esterases indicated that these proteins are very polymorphic and too variable to be useful in taxonomic work. The degree of intraspecific biochemical variation is correlated with the degree of variation in external morphology within each species and with the range of each species.

Introduction

Electrophoresis, combined with specific histochemical stains, is being used with increasing frequency by vertebrate taxonomists. This process takes advantage of the different migration rates of protein molecules in an electric field, the rates depending in turn on the net charge of the molecules. Electrophoretic patterns obtained from mixtures of whole proteins are often species specific, although the technique appears to vary in usefulness, especially when closely related animals are being studied. In the following study, electrophoresis and protein specific stains were used in an attempt to distinguish biochemically between four species of plethodontid salamanders in the genus *Desmognathus*. A comparison of the four species was made on the basis of the patterns generated by electrophoresis of hemoglobins, liver esterases, and liver lactate dehydrogenases.

Materials and Methods

Animals

The species involved in the study were *Desmognathus fuscus fuscus* (Rafinesque), *Desmognathus monticola* Dunn, *Desmognathus ochrophaeus carolinensis* Dunn, and *Desmognathus quadramaculatus* (Holbrook). Adults of both sexes, including gravid and non-gravid females, were used so that the possible effects of age and sex on the protein patterns could be examined. Most animals of the mountain species were collected in or near streams within a 30-mile radius of Highlands, North Carolina, including Macon and Transylvania counties, North Carolina, Oconee, Pickens, and Spartanburg counties,