ACTIVITY METABOLISM IN THE LIZARD SCELOPORUS OCCIDENTALIS[1]

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Standard levels of oxygen consumption and oxygen consumption and lactate production during and after burst activity were measured in the iguanid lizard *Sceloporus occidentalis*. The activity capacity of this animal is restricted; it sustains vigorous movement for only 1–2 min. The contribution of aerobic metabolism to that activity is strongly thermally dependent. Maximal levels of oxygen consumption are achieved during activity at 30–40 C. At lower temperatures, significant lags occur in oxygen uptake, which appear to result from restricted ventilation. The maximum aerobic increase above resting levels occurs at 35 C, preferred body temperature of this species. Repayment of the initial stages of oxygen debt is also most rapid at 35 C. Lactic acid concentration reaches high levels during activity, and its formation is greatest at 30 C. Anaerobic metabolism represents 62%–82% of the energy utilized during burst activity, accounting for nearly all of the carbohydrate catabolized. The combination of energy utilization in both aerobic and anaerobic modes gives *Sceloporus* its highest activity capacity at 30–35 C, the range of body temperatures normally experienced diurnally by this species throughout the year.

The capacity for rapid activity, the ability to mobilize energy for pursuit or escape, is a critical aspect of the adaptation of an organism. Failure in such an activity attempt may result in being eaten or not eating, and this performance consequently represents a focal point for the operation of natural selection. In poikilotherms, the problem of activity is compounded by the thermal dependence of the metabolic processes which support that activity. Not only must these animals function at preferred thermal levels if they are behavioral thermoregulators, but they must exhibit some escape capacity at lower body temperatures as well. Investigations of this capacity for activity, its magnitude, the contribution of various metabolic systems to its support, and its adaptations at various temperatures have only begun to be investigated.

The metabolism of reptiles during activity has recently received considerable study (see reviews by Dawson [1975] and Bennett and Dawson [1976]). Much of this information has been gathered on iguanid lizards, members of the most diverse and widespread saurian family in the New World. Studies on activity metabolism (Moberly 1968*a*, 1968*b*; Bennett 1972, 1973*b*; Bennett and Dawson 1972; Bennett and Licht 1972; Bennett, Dawson, and Bartholomew 1975; Bennett and Ruben 1975) have shown that the members of this group have rather limited powers of augmenting aerobic metabolism. Consequently, metabolic support of activity is derived primarily by anaerobic glycolysis. Concentrations of lactic acid rise rapidly to high levels, and most species are consequently capable of only 1 or 2 min of sustained exertion. Several hours may be required to eliminate the

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accumulated lactate, and the capacity for further activity is strongly curtailed during the recovery period. These generalizations also pertain to the activity metabolism of many other reptilian groups, but not to all (Bartholomew and Tucker 1964; Bennett 1973*b*).

Certain methodological difficulties have hampered the examination of total energy metabolism, both anaerobic and aerobic, during activity in the lower vertebrates. Anaerobic energy production can be estimated by the lactic acid concentration in whole-body homogenates, a procedure which avoids the ambiguities and lag periods associated with blood lactate sampling (Bennett and Licht 1972). To estimate the contribution of aerobic metabolism, measurements of oxygen consumption must be coincident with the bout of activity. Often the time course of oxygen consumption is not measured, and only maximal values or values integrated over longer time periods are reported. If such values occur during or include the postactive period, they represent a portion of the oxygen debt and may have little to do with energy mobilization during activity.

Simultaneous determination of aerobic and anaerobic factors during burst activity has previously been done on only one species of lizard, *Dipsosaurus dorsalis* (Bennett and Dawson 1972). Maximal rates for both the aerobic and anaerobic components of activity metabolism were found to occur at body temperatures (40 C) maintained during activity in the field by this species. The current experiments were designed to examine the thermal dependence of oxygen consumption and lactic acid production during activity in another iguanid lizard, *Sceloporus occidentalis*. Oxygen consumption was measured over 1-min intervals during and after stimulation to burst activity. These intervals are short enough to permit an accurate analysis of the contribution of aerobiosis to activity. In addition, they can yield information on the thermal dependence of the acceleration of oxygen consumption during activity and of maximal levels attained.

Sceloporus occidentalis, the western fence lizard, is one of the most common reptiles in southern California and occurs in a great variety of habitats. The animals are territorial and usually perch during the day on an exposed basking site of old lumber or rocks. Their diet consists mainly of insects and spiders, which are caught during short chases. When approached, these lizards will rapidly retreat into adjacent crevices. Thus, their normal activity pattern as sit-and-wait predators does not require capacities for sustained energetic output. This species behaviorally selects a body temperature of 35 C in both laboratory gradients and the field during most of the year (Brattstrom 1965; McGinnis 1966). Resting rates of oxygen consumption for this species have previously been reported by Dawson and Bartholomew (1956) and Francis and Brooks (1970), and rates of lactate formation during activity were examined by Bennett and Ruben (1975).

MATERIAL AND METHODS

Sixty-five adult *Sceloporus occidentalis* (mean weight = 13.1 g, range = 9.5–18.0 g; mean snout-vent length = 74 mm, range = 68–80 mm) were collected in Orange and Riverside Counties, California, in April and May 1975. These animals were held in aquaria equipped with incandescent lights set on a natural photoperiod, permitting the lizards to regulate body temperature behaviorally. The animals were fed pupae of wax

moths (*Galleria* sp.) and had access to water ad libitum. The animals remained healthy and active and were generally held in captivity for less than 1 wk. Animals were fasted for at least 2 days before experimentation.

In the experiments which determined oxygen consumption and lactate production simultaneously during activity, a single animal was weighed and measured. Electrical leads were implanted in the base of its tail. The lizard was then placed in a rectangular Lucite metabolism chamber (volume = 534 cm^3) equipped with ports for air flow and sampling. The chamber also contained a thermistor connected to a YSI thermistor unit for measuring chamber temperature. This chamber was placed in a dark, thermostatically controlled box set at 20, 25, 30, 35, or 40 C ($\pm$0.5 C) at approximately 0900 hours PDT. Dry CO_2-free air was metered through the metabolism chamber at 30–90 cm^3/min. The relative humidity of the excurrent air line was measured with a Hygrodynamics sensor and indicating unit, and water and carbon dioxide were subsequently removed from the excurrent air by absorption with Drierite (anhydrous calcium sulfate) and Ascarite (sodium-hydrate asbestos), respectively.

Oxygen consumption of the undisturbed animal was measured in the afternoon and evening, at 1500 and 2000 hours PDT. The latter measurement was made just prior to stimulation to activity. The oxygen concentration of the excurrent air was determined by injection of 20-cm^3 samples into a Beckman E-2 oxygen analyzer (model 118523Y). Dry, CO_2-free room air was injected before and after each excurrent sample to provide reference values. Three samples of excurrent air were taken over a 15–min period, and the average oxygen decrement was used to determine oxygen consumption according to the method of Depocas and Hart (1957).

The environmental box was then opened and incurrent and excurrent air ports were closed, isolating the animal in the airtight chamber. The animal was stimulated to maximal activity with electrical shocks of low intensity, delivered with a Harvard stimulator via the implanted leads. In addition, the chamber was hit and shaken to frighten the animal, which responded with a burst of rapid running. Stimulation was continued for 5 min. Air samples of 20 cm^3 were removed from the chamber with a glass syringe through a small column of Ascarite and Drierite to remove water and CO_2. Samples were taken immediately prior to stimulation and at 1-min intervals during stimulation and for 5 min after the cessation of stimulation. After each sample was taken, a port was opened and the partial vacuum replaced the withdrawn sample with room air. The oxygen concentration in the chamber decreased less than 1% (i.e., it remained above 20.0%) during the measurement period. The air samples were stored in capped glass syringes approximately 5–10 min before being analyzed for oxygen content as outlined above. At the end of the 5-min postactive recovery period, the animal was removed from the chamber and immediately killed and homogenized in 0.6N perchloric acid. Samples of the supernatant fluid were centrifuged and stored for subsequent analysis of lactic acid content.

The oxygen concentration of the dry, CO_2-free samples from the chamber was corrected according to the formula $F_{O_2} = .7904\ F_{O_2}'/(1 - F_{O_2}')$, where F_{O_2} is the true fractional concentration of oxygen and F_{O_2}' is the apparent fractional concentration of oxygen measured by the

analyzer (see Depocas and Hart 1957). Oxygen consumption during each minute interval of activity and recovery was calculated according to the formula

$$\left[V - V\left(\frac{RH \cdot P_s}{100P_B}\right)\right] \times \left\{\left[\frac{F_{O_2}{}^i(V - V_s) + .2096V_s}{V}\right] - F_{O_2}{}^f\right\},$$

where

V = volume of chamber (cm^3) − volume of animal (cm^3)
V_s = volume of gas sample removed from chamber (cm^3)
RH = relative humidity in the chamber (%)
P_s = saturated vapor pressure of water (mm Hg)
P_B = barometric pressure (mm Hg)
$F_{O_2}{}^i$ = true fractional concentration of oxygen at the end of the prior interval
$F_{O_2}{}^f$ = true fractional concentration of oxygen at the end of the current interval.

Oxygen volumes were converted to standard temperature and pressure (STPD) and expressed as cm^3 O_2/(g body weight × h).

Lactic acid concentrations of resting animals were determined by killing and homogenizing four unstimulated animals which were left undisturbed at each temperature for 14 h. The rate of lactate formation at 35 C was determined by stimulating four animals each for 1-, 2-, and 5-min periods and killing and homogenizing them immediately at the end of activity. Lactic acid concentrations in the homogenates were determined with a lactic acid analysis kit (Boehringer-Mannheim Corp.) on a Beckman Model 25 spectrophotometer at 366 nm.

RESULTS

The lowest rates of oxygen consumption observed for each animal are reported as standard metabolic rates in figure 1. The thermal dependence of this function is complex. Standard oxygen consumption is very strongly temperature dependent (Q_{10} = 5–6) between 25 and 35 C but is essentially temperature independent at 20–25 C and at 35–40 C. Such zones of thermal independence of oxygen consumption have been previously observed in other species (see Bennett and Dawson 1976). No pronounced decrement in resting oxygen consumption occurred during the evening: the average evening value was 15% below that in the afternoon, but this decrease is not significant ($.2 > P > .1$ by Student's t-test).

Activity was not sustained at high levels during the entire 5-min period of stimulation, but lasted only 1–2 min. Only a few sporadic movements occurred during the later 3 min of stimulation, and the animals generally stayed completely quiet during the 5-min recovery period. This observed pattern of activity followed that previously reported for this species (Bennett and Ruben 1975).

Oxygen consumption during the first 2 min of activity is also reported in figure 1. These values may not represent maximal values of oxygen consumption at each temperature (see below), but they provide a measure of the aerobic support for burst activity. Oxygen consumption during this period increases with increasing body temperature between 20 and 35 C (Q_{10} = 1.9–2.8) but does not increase above 35 C.

The mean increment in oxygen consumption during burst activity (i.e., the difference between paired values in fig. 1) is reported in table 1. This function is maximal at 35 C, the preferred body temperature of this species, but has a low thermal dependence over the range of 30–40 C (Q_{10} = 0.9–1.4).

Mean values for oxygen consumption measured each minute during and after

stimulation are reported in figure 2. The total amount of oxygen consumed during the period of stimulation increases with increasing temperature up to 35 C: Q_{10} 20–25 C = 2.9, Q_{10} 25–30 C = 1.4, Q_{10} 30–35 C = 2.2, Q_{10} 35–40 C = 1.0. In addition to the greater total oxygen consumption, the rate at which oxygen consumption increases above resting levels is also temperature dependent. At

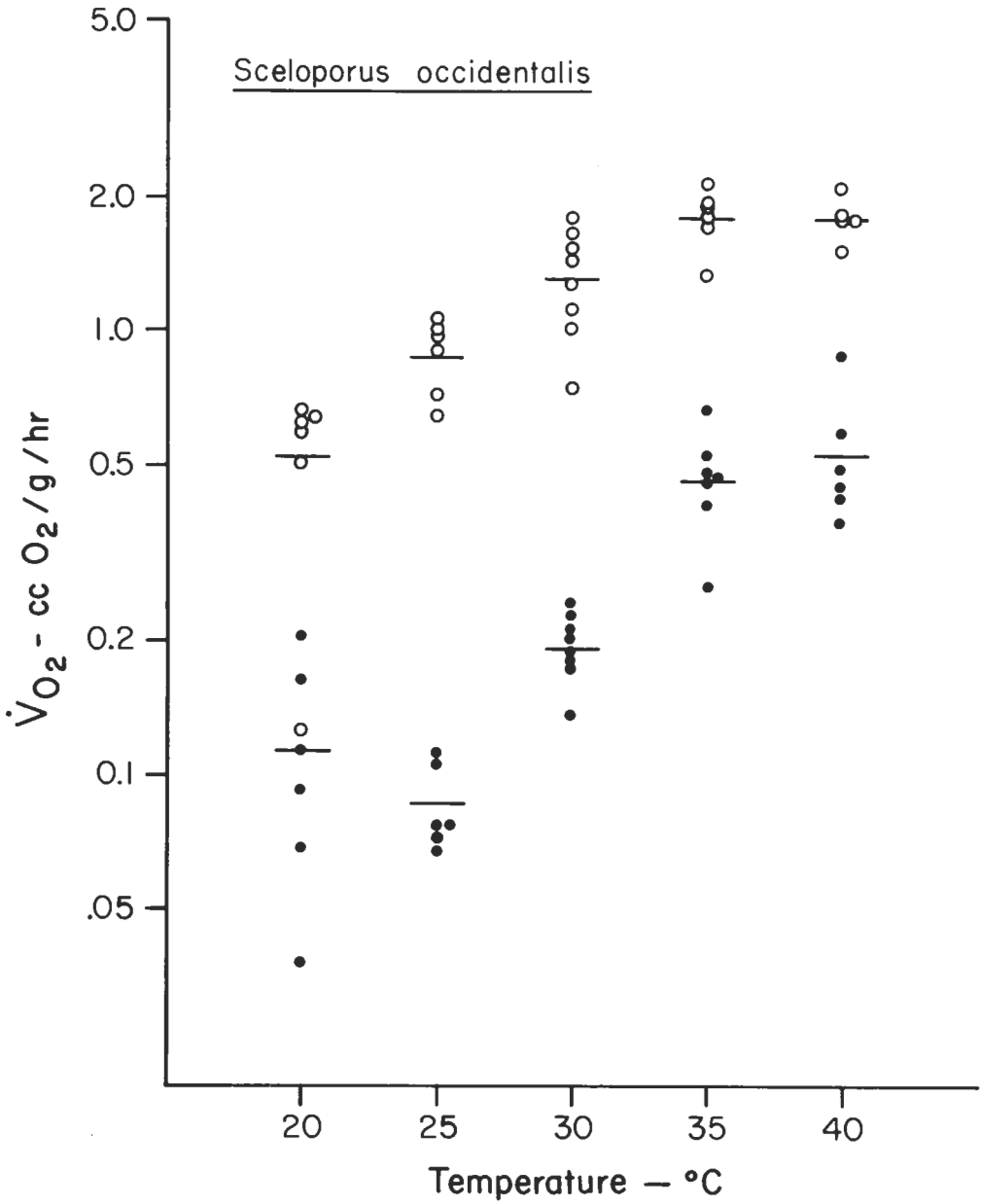

FIG. 1.—Standard oxygen consumption (closed circles) and oxygen consumption during 2 min of burst activity (open circles) in *Sceloporus occidentalis*. Mean values are indicated by horizontal bars. Thirty-three animals were used for the resting measurements; 31 were then stimulated to activity.

20 C, maximal levels are not attained until after the cessation of activity and stimulation. As body temperature increases, the rate at which maximal rates of oxygen consumption are achieved also increases until maximal levels of oxygen consumption are coincident with the activity burst at 30–40 C (table 1). The acceleration of oxygen consumption during the first minute of activity is very great between 20 and 25 C (Q_{10} = 7.3). Ventilation during burst activity is re-

TABLE 1

THE AEROBIC INCREMENT DURING 2 MIN OF BURST ACTIVITY AND AEROBIC SCOPE (MAXIMAL MINUTE AEROBIC INCREMENT) IN "SCELOPORUS OCCIDENTALIS" STIMULATED FOR 5 MIN

			Aerobic Scope	
Temp. (°C)	N	Aerobic Increment during Activity (cm³ O_2/[g h])	(cm³ O_2/[g h])	Time after Initiation of Activity (min)
20	6	0.422±0.090	0.924±0.072	6.2±0.5
25	6	0.783±0.068	1.051±0.063	4.3±1.2
30	8	1.120±0.121	1.390±0.143	2 0±0.5
35	6	1.315±0.157	1.722±0.120	2.0±0.5
40	5	1.253±0.056	1.591±0.093	1.2±0.2

NOTE.—Values shown are means±SE.

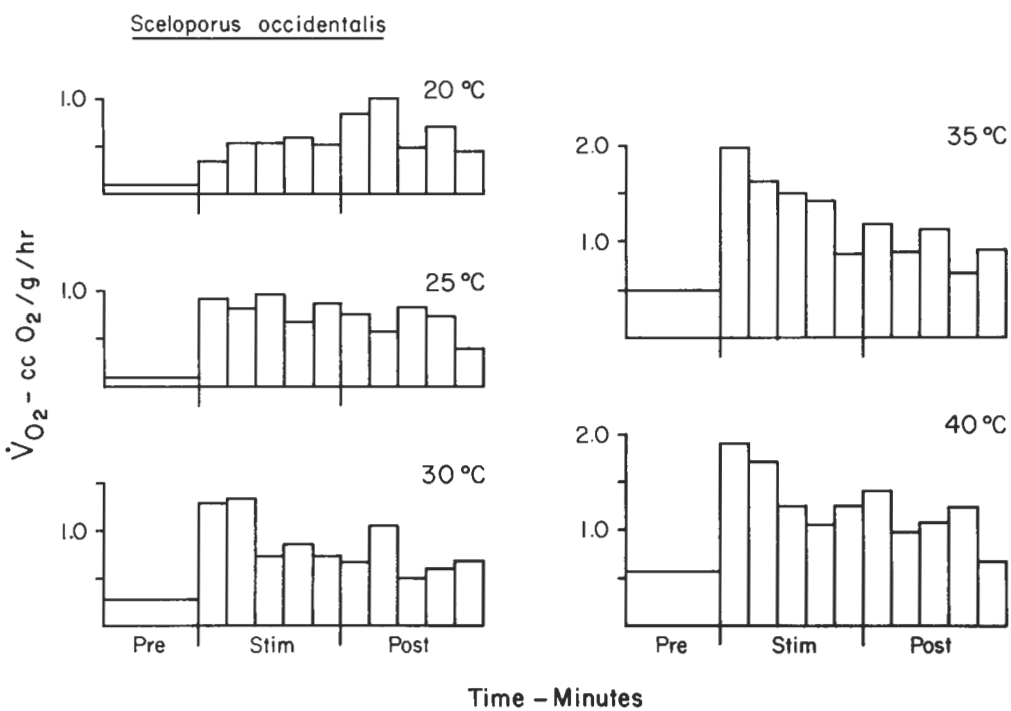

FIG. 2.—Oxygen consumption in 31 *Sceloporus* prior to stimulation and at minute intervals during 5 min of stimulation and 5 min of recovery. Mean values are reported; each group contains 5–8 animals. Burst activity lasted only during the first 2 min of stimulation.

TABLE 2

INCREMENTS ABOVE PRESTIMULATION LEVELS DURING 5 MIN OF STIMULATION AND 5 MIN OF RECOVERY IN "SCELOPORUS OCCIDENTALIS"

Temp. (°C)	Increment during Stimulation (cm^3 O_2/[g h])	Increment during Recovery (cm^3 O_2/[g h])	Change in Increment (cm^3 O_2/[g h])	Recovery ÷ Activity (%)
20.....	.480	.537	+.057	112
25.....	.756	.557	−.199	74
30.....	.709	.410	−.299	58
35.....	.974	.448	−.526	47
40.....	.885	.504	−.381	57

NOTE.—Values shown are means of 5–8 animals.

stricted at low body temperature: no costal movements are evident during the initial stages of activity. At higher temperatures, the animals breathe continuously during burst activity.

Oxygen consumption during the 5-min recovery period is lower than during the stimulation period at all temperatures except 20 C. A complete analysis of oxygen debt is beyond the range of these experiments. However, a comparison of the aerobic increment during and after stimulation (table 2) indicates that return toward prestimulation levels of oxygen consumption occurs most rapidly at 35 C, the preferred body temperature.

Whole-body lactate contents are reported in figure 3 for unstimulated control animals and for animals at the end of 5 min of stimulation and 5 min of recovery. There is no thermal dependence in lactate contents of unstimulated animals ($.25 > P > .10$ by Kruskal-Wallis test); the mean value is 0.31 ± 0.016 SE mg lactate/g body weight. The thermal dependence of lactate content after stimulation is complex. No change occurs between 20 and 25 C, but the capacity for lactate formation increases greatly between 25 and 30 C (Q_{10} for formation = 2.8). The capacity for lactate formation decreases over the range between 30 and 40 C (Q_{10} for formation = 0.6–0.8).

Lactate formation is coincident with the bout of burst activity (table 3). Lactate content increases through the initial 2-min activity period but does not increase during the subsequent 3-min period of stimulation. No detectable net amounts of lactate are catabolized during the 5-min recovery period. A similar pattern of lactate formation for this species during activity was reported by Bennett and Ruben (1975).

DISCUSSION

Aerobic factors associated with activity, the aerobic increment during burst activity and aerobic scope, are maximal in *Sceloporus occidentalis* at the preferred body temperature, 35 C. The coincidence of maximal aerobic scope and behaviorally selected thermal level has now been demonstrated for many species of lizards (Wilson 1974). This factor appears to be one of the few physiological variables which are clearly maximized in most species at preferred temperature (Dawson 1975). Return to prestimulation levels of oxygen consumption (repayment of oxygen debt) also appears to proceed most rapidly at 35 C in *Sceloporus*. A similar relationship occurs in the only other lizard examined, *Sauromalus hispidus* (Bennett 1972). Moberly (1968*a*) found that after activity in *Iguana iguana*, lactate is eliminated from the

blood most rapidly at 35 C. All of these iguanids have preferred thermal levels of 35–38 C. The interrelationships of oxygen debt, lactate elimination, and recovery in reptiles have not been examined, however, and it would be premature to speculate about their interdependence or physiological significance.

The delay at low body temperature in achieving maximal levels of oxygen consumption is not completely unexpected, considering the number of physiological systems involved in oxygen transport. A similar lag has previously been reported for the marine iguana, *Amblyrhynchus cristatus* (Bennett et al. 1975). The low oxygen consumption at low

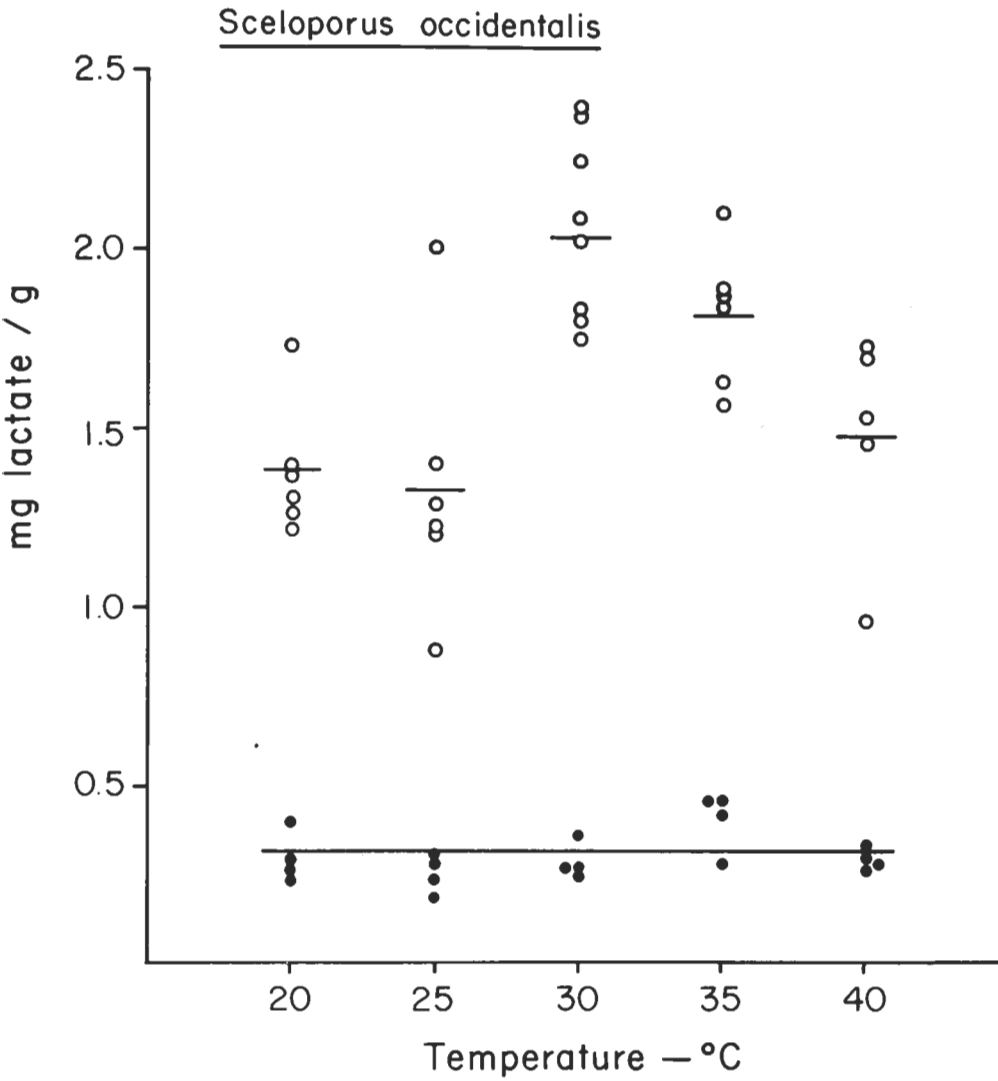

FIG. 3.—Whole-body lactate concentration of unstimulated *Sceloporus* (closed circles) and animals after 5 min of stimulation and 5 min of recovery (open circles). The mean lactate concentration of unstimulated animals is 0.31 mg/g body weight; mean values for active animals are indicated by horizontal lines. Each point pertains to a separate animal.

TABLE 3

WHOLE-BODY LACTATE CONCENTRATIONS OF "SCELOPORUS OCCIDENTALIS" BEFORE, DURING, AND AFTER SPECIFIED PERIODS OF ACTIVITY AT 35 C

Condition	*N*	Lactate Concentration (mg/g wt)
Unstimulated.....	4	0.40±0.04
1 min active.....	4	1.34±0.16
2 min active.....	4	1.73±0.10
5 min active.....	4	1.70±0.25
5 min active+ 5 min recovery...	6	1.82±0.08

NOTE.—Values shown are means±SE.

temperatures in active *Sceloporus* is not, however, solely a function of a temporal displacement of aerobic scope; the rates never reach those attained at higher body temperatures. The curtailment of ventilation at low temperature during burst activity is certainly involved in the low acceleration of oxygen consumption. Even after a bout of activity, minute volume has a strong thermal dependence in *S. hispidus* and *Varanus gouldii* (Bennett 1973*a*). It is undetermined whether this restriction of ventilation is the limiting factor in the acceleration of oxygen consumption and the thermal dependence of aerobic scope or whether other factors, such as heart rate increment, are involved.

Metabolic scope for activity, the differential between maximal and standard rates of oxygen consumption at any single temperature, was proposed by Fry (1947) as an index of the work capacity of an organism. This relationship may have little relevance, however, if the aerobic scope is not fully utilized until after the termination of activity. Such a situation occurs at lower body temperatures in *Amblyrhynchus* (Bennett et al. 1975) and in the amphibians *Batrachoseps attenuatus* and *Hyla regilla* (Bennett and Licht 1973) as well as in *Sceloporus*. A more relevant criterion for examining aerobic work capacity is the aerobic increment during activity.

The thermal dependence of anaerobic activity metabolism in lizards may be more complex than was previously supposed. A low temperature dependence over a wide range of body temperatures was postulated on the basis of observations on whole-body lactate formation (Bennett and Licht 1972) and on blood lactate concentrations (Moberly 1968*a*; Bennett et al. 1975). The measurement of whole-body lactate content over narrow thermal increments in *Sceloporus* and *Dipsosaurus* (Bennett and Dawson 1972) has revealed definite peaks in lactate production. In *Sceloporus*, maximal lactate production occurs at 30 C, which is below preferred body temperature. Lactate production is greatest at 40 C in *Dipsosaurus*, the normal field active temperature for this species. Overall, however, anaerobic function is relatively temperature insensitive when compared to aerobic metabolism. This thermal independence is particularly evident at lower body temperatures, at which anaerobiosis must furnish nearly all of the energetic support for activity.

The relative contributions to ATP production during burst activity of both aerobic and anaerobic metabolism can be calculated according to the equations stipulated in Bennett et al. (1975). For these calculations, a 2-min interval of activity is assumed and lactate contents at the end of the recovery period are used to estimate lactate production during the first 2 min of stimulation (see table 3). Calculated values are reported in figure 4 and table 4. The anaerobic component exceeds that of the aerobic at all body temperatures, ranging from a minimum of 62% of the total ATP production at 40 C to 82% at 20 C. A minimum of 95%–99% of the carbo-

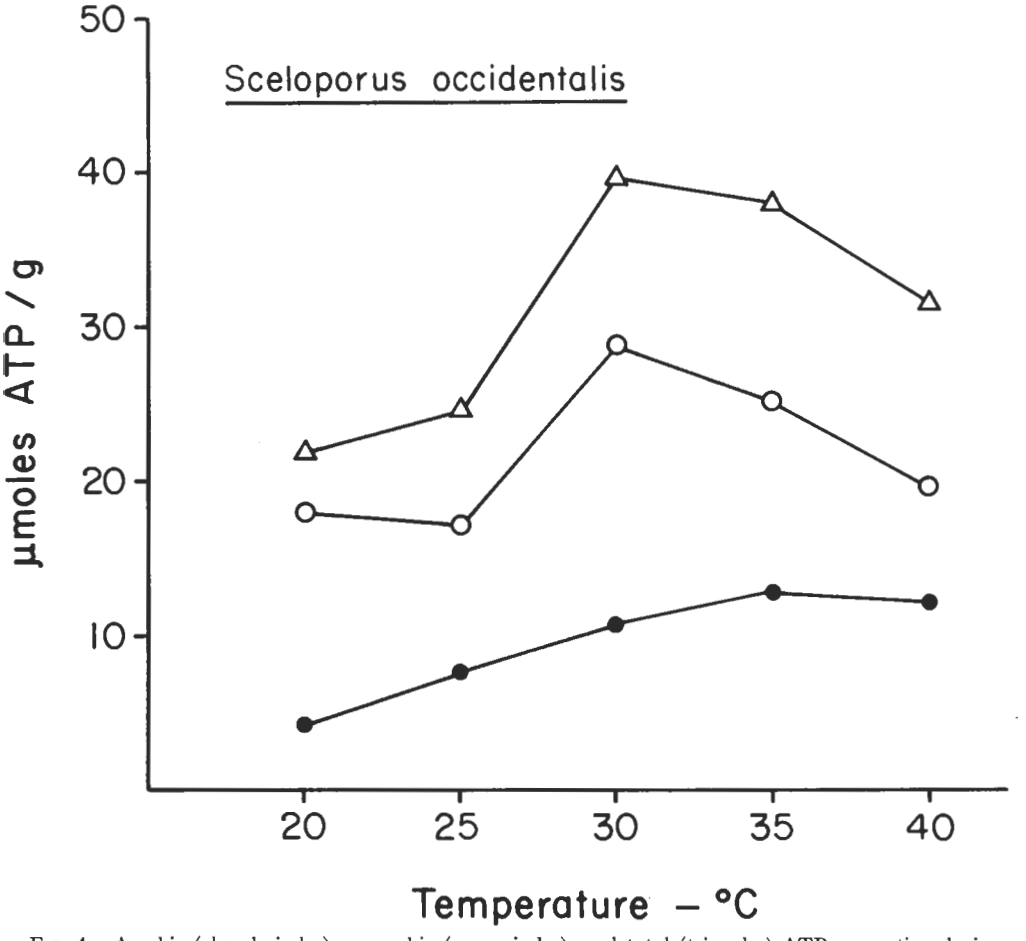

FIG. 4.—Aerobic (closed circles), anaerobic (open circles), and total (triangles) ATP generation during 2 min of burst activity in *Sceloporus*. See text for method of calculation.

TABLE 4

AEROBIC AND ANAEROBIC ATP PRODUCTION IN "SCELOPORUS OCCIDENTALIS" AND "DIPSOSAURUS DORSALIS" DURING 2 MIN OF BURST ACTIVITY

TEMP. (°C)	*Sceloporus*			*Dipsosaurus*		
	Aerobic	Anaerobic	Total	Aerobic	Anaerobic	Total
20.....	4.1	17.9	21.9	...	...	...
25.....	7.6	17.1	24.7	3.8	18.5	22.3
30.....	10.8	28.8	39.6	7.9	21.5	29.4
35.....	12.7	25.3	38.0	14.6	22.0	36.6
40.....	12.1	19.6	31.7	21.9	30.3	52.2
45.....	...	...	...	13.0	22.2	35.2

SOURCE.—Data for *Dipsosaurus* are from Bennett and Dawson (1972).
NOTE.—Column entries are µmol ATP/g body weight.

hydrate catabolized enters anaerobic pathways (see Bennett et al. 1975).

Energetic output during burst activity is maximal over the range of 30–35 C in *S. occidentalis*. Body temperature of animals in the field appears to have some seasonal lability over this range (McGinnis 1966). Groups of animals caught in the field during spring through fall have mean body temperatures of 34.3–35.9 C. A similar group of winter-active animals, however, had a mean body temperature of 30.4 C. All groups tested in the laboratory had preferred body temperatures between 34.1 and 35.0 C. These data indicate that this species may accept and be active under less than preferred thermal conditions during the cooler season. This range of body temperatures coincides with the plateau in maximal energetic output during burst activity measured in this study.

An interesting comparison can be drawn between activity metabolism in *Sceloporus* and *Dipsosaurus*, since both were measured under similar conditions (see table 4). In the latter species, maximal weight-specific aerobic scope (cm^3 O_2/g) is nearly twice as high as in *Sceloporus*, in spite of the fact that *Dipsosaurus* is 2–3 times as large. Maximal anaerobic energy production is almost identical in the two species, peak production occurring at 30 C in *Sceloporus* and 40 C in *Dipsosaurus*. Total output is maximized in both energetic modes at preferred body temperature, 40 C, in *Dipsosaurus*, and maximal output is consequently higher in this species (52 vs. 40 μmol ATP/g). If all of this increment is assumed to be in support of muscular activity, and if the locomotory efficiency of these species is similar, we would expect a differential performance capacity by these two species depending on body temperature. At 30 C, *Sceloporus* should be able to outperform *Dipsosuarus* (40 vs. 30 μmol ATP/g). Activity capacity should be nearly equal at 35 C (38 vs. 37 μmol ATP/g), and *Dipsosaurus* should do much better at 40 C (32 vs. 52 μmol ATP/g for *Sceloporus* and *Dipsosaurus*, respectively). These types of measurements and comparisons may ultimately assist in our understanding of the thermal dimensions of niche adaptation of different saurian species.

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