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The metabolic cost of behavioral thermoregulation of body temperature in the northern alligator lizard *Gerrhonotus coeruleus*, and how it affects the classical concept of eurythermality

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AN ABSTRACT OF THE THESIS OF James Dudley Campbell for the Masters of Science in Biology presented January 15, 1981

Title: The Metabolic Cost of Behavioral Thermoregulation of Body Temperature in the Northern Alligator Lizard Gerrhonotus coeruleus, and How it Affects the Classical Concept of Eurythermality

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The effect of total metabolic cost expenditures on the precision of behavioral thermoregulation was investigated for the purportedly eurythermic Northern Alligator lizard (Gerrhonotus coeruleus). An operant apparatus was designed to test metabolic output at different heat reinforcement magnitudes. The mean T_B reflected in each trial was positively correlated to the length of reinforcement. The shuttle rate during each trial was inversely correlated to the length of reinforcement. The standard deviation and total metabolic costs did not vary significantly between trials undertaken at the same ambient temperature.

Eurythermality in G. coeruleus is caused by fluctuations in preferred body temperature and not by fluctuations around this temperature. The metabolic cost of behavioral thermoregulation did not change with corresponding changes in reinforcement magnitude. This indicates that eurythermality is the recorded effect of lizards behaviorally regulating to different T_B in a stenothermic manner, rather than of random T_B fluctuations in a wide range of normal activity (the classical view of eurythermality).

THE METABOLIC COST OF BEHAVIORAL THERMOREGULATION OF
BODY TEMPERATURE IN THE NORTHERN ALLIGATOR LIZARD
GERRHONOTUS COERULEUS, AND HOW IT AFFECTS THE CLASSICAL
CONCEPT OF EURYTHERMALITY

by

JAMES DUDLEY CAMPBELL

A thesis submitted in partial fulfillment of the
requirements for the degree of

MASTER OF SCIENCE
in
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Portland State University

1981

TO THE OFFICE OF GRADUATE STUDIES AND RESEARCH:

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CHAPTER I

INTRODUCTION

The behavioral regulation of body temperature (T_B) by lizards is a well known phenomenon. Lizards that normally maintain a very narrow range of T_B during activity are considered stenothermic, lizards with a wide range in T_B during activity are eurythermic. Many animals are considered to be heliothermic, since they utilize radiant heat energy as a predominant source in the maintenance of a constant T_B . Other lizards are considered to be thigmothermic, because they utilize conductive heat gain from contact with the substrate. However, most lizards utilize both radiant and conductive heat gain (Soule' 1963). The behaviors involved in behavioral thermoregulation are intricate, and include changing the amount of body surface that is exposed to the sun's rays by altering the angle between the body axis and the sun (Heath, 1965; Bartholomew, 1966; Bartlett and Gates, 1967; DeWitt, 1971; Muth, 1977), increasing or decreasing conductive heat losses by moving to warmer or colder substrates (Heath, 1965; Hammel et al, 1967; Weathers, 1970; Spellerburg, 1972), postural changes that minimize or maximize contact with conductive surfaces (Heath, 1964; Bartholomew, 1966; DeWitt, 1971; Muth, 1977), the utilization of panting (Ruibal, 1961; Case, 1972), and retreat to cooler subterranean or arboreal areas (Norris, 1948; Heath, 1964; Pianka and Parker, 1972; Muth, 1977). Control of heat flux is also possible through vasomotor responses

(Bartholomew and Tucker, 1963; Weathers, 1971; Morgareidge and White, 1969; White, 1973), and by temporal regulation of activity bouts (Schmidt-Nielsen and Dawson, 1964; Heatwole et al, 1969; Porter et al, 1973; Huey, 1974b).

The optimum T_B for many reptilian physiological processes occurs within the normal activity range of T_B , particularly for stenothermic species (Dawson, 1967). The ability to maintain T_B within this range and avoid body temperature extremes at either end of the preferred range is a major evolutionary adaptation in reptiles (e.g., Bogert, 1949). The lizard can optimize many physiological processes by maintaining T_B within the normal activity range and close to the preferred body temperature (PBT). However, this homeostatic advantage is counterbalanced by the metabolic cost of thermoregulation. Any deviation in T_B from the preferred range should require an energy expenditure to return T_B to the preferred level.

Huey (1974a) studied the effect of habitat type on precision of thermoregulation and T_B for Anolis cristatellus in two adjacent habitats. He introduced a "cost of thermoregulation" factor into his analysis by measuring the distance that a lizard had to shuttle from a perch to sun. The distance between basking sites of forest-habitat lizards was significantly greater than that of open park lizards. Huey (1974a) therefore inferred that the cost of thermoregulation would be greater in the forest habitat. In fact, the T_B of the forest lizards were found to correlate closely with ambient temperature (T_A) and there was a wider T_B range for normal activity. The open-park lizards were found to be heliothermic with a narrower normal activity range; i.e.,

they showed greater precision in regulating T_B . It was therefore apparent that Anolis cristatellus regulated T_B only in the open-park areas, presumably because the cost/benefit ratio was more favorable.

Huey and Slatkin (1976) suggested that an increase in available productivity in a given habitat would lead to more precise thermoregulation. Higher productivity in this case is defined as additional benefits in food acquisition with little or no added cost. If food is readily available a lizard will spend less time searching for food (low temporal cost) and will therefore have more time and energy available for thermoregulation. There might be a tradeoff for lizards between the time spent thermoregulating and foraging in an environment where the lizard has to spend the majority of its time searching for food. The tradeoff should result in a decrease in T_B or precision of regulation, and might be reflected by a poorer nutritional state e.g., a decrease in percentage of body fat, if food acquisition was significantly curtailed.

Lee (1980) used length-specific fat body weights as an index to a lizard's ability to gather and process available food. He assumed that fat, well-fed lizards react to their environment as though it were highly productive, whereas poorly-fed lizards react to their environment as though it were of low productivity. He reported that the relationship of environmental productivity to thermoregulatory precision or mean T_B of Anolis sagrei was positively correlated for open (sunny) versus closed (shady) habitats. This supports Huey and Slatkin's (1976) contention that lizards thermoregulate precisely only in those environments where food is readily available.

A study of Anolis oculatus on the island of Dominica (Ruibal and Philibosian, 1970) suggested that the eurythermal pattern of T_B for this species may have evolved in response to the absence of competition (ecological release). Huey and Webster (1975) suggest that eurythermy in Anolis is related to their evolutionary origins in moist tropical forests. The environmental constraints of such habitats to behavioral thermoregulation favor thermal passivity to T_A , and hence eurythermality.

Various researchers have examined the field T_B of lizards as they relate to habitat (see Brattstrom, 1965, for a detailed list). The PBT over which lizards are active are known for many species. However, such studies often do not necessarily address the question of whether there are genetic differences in thermoregulation between various species. For example, because of greater surface area to volume ratios smaller species equilibrate thermally with their environment at a faster rate than larger species, so it is more difficult for small species to maintain an elevated T_B . Furthermore, field T_B data may also reflect differences in habitat temperature profiles and not necessarily genetic differences of lizard species. That is, the environment may be eurythermal so the lizard is also eurythermal, even though the lizard is really not different in thermoregulatory capabilities from so called stenothermic species from stenothermic environments.

Many authors (see Berk and Heath, 1975, for a recent review) have tested lizards in a temperature gradient in the laboratory and found that the temperatures selected are often significantly higher than PBT for the same species in the field. There are also data which

suggests that photoperiodicity (Ballinger et al. 1969) and feeding schedules (Regal, 1966; Hoffman, 1973) may alter PBT in lizards. Huey and Slatkin (1976) suggest that competition for resources and risk of predation may alter PBT. Lizards may also regulate differently between separated high and low set points (Barber and Crawford, 1976, 1978). None of the above authors assessed quantitatively the metabolic cost of thermoregulation. Thermal gradients demand virtually no thermoregulatory effort by the lizard, and therefore are no-cost environments, obviously not comparable to a real environmental situation.

One way to assess the cost of thermoregulation in the laboratory is to use an operant conditioning paradigm where the cost of shuttling can be calculated. Burghardt (1977) reviewed the literature on operant conditioning of reptiles in a laboratory environment. The reinforcements used in conditioning mammals are usually related to hunger, thirst or reproductive drives. The low caloric intake of food by reptiles precludes using the hunger drive as a reinforcement in the operant conditioning. However, exogenous heat provides a useful reinforcement for conditioning reptiles.

Rozin and Mayer (1961) conditioned goldfish in an aquarium of hot water to press a disc and thereby regulate the temperature of water in the aquarium by rewarding the disc press with a reinforcement of cold water. The fish effectively regulated their T_B by increasing or decreasing the disc press response rate. This experiment demonstrated that ectotherms would respond operantly to regulate their T_B . Heat avoidance by disc pressing was also used by Kemp (1969) as an operant

technique to study the thermoregulatory behavior of the Desert Iguana, Dipsosaurus dorsalis. This was the first recorded experiment using heat reinforcement to study the behavioral thermoregulation of a lizard.

Kellogg and Pomeroy (1936) trained water snakes (Tropidonotus fasciatus) to negotiate a maze, using heat (warm water) as a reinforcement.

Regal (1971) also used an operant technique to study the thermoregulatory behavior of the Island Spectacled Lizard (Klauberina riversiana), but he used the onset of heat as the reinforcer instead of the heat avoidance method utilized by Kemp (1969).

Richardson and Brown (1975, 1976) also used the onset of heat as a reinforcement in the operant conditioning of Dipsosaurus dorsalis and the Collared Lizard (Crotaphytus collaris). They found that other paradigms of operant techniques, such as fixed ratio schedules of reinforcement (i.e., the animal is reinforced only every second, third, fourth,.....etc., response instead of every response) did not work for studies of behavioral thermoregulation. The same conclusion was reached earlier by Crawford et al, (1968) in their study on the effect of fixed ratio reinforcements to response rates in turtles. Both studies showed that a continuous reinforcement schedule was the best way to study selective thermoregulatory behaviors in reptiles.

In experiments with Sprague-Dawley rats and Squirrel Monkeys, Carlisle (1969) found that endotherms in a cold environment would respond to heat reinforcements at a level sufficient to ensure homeostasis only if the reinforcements were continuous. The animals

failed to thermoregulate behaviorally at a level sufficient to ensure homeostatis during trials using ratio schedules.

Although reinforcement schedules of the variable or fixed (F2 or greater) ratio do not increase the frequency of response, the magnitude or reinforcement does. Weiss and Laties (1960) found that variations in heat source intensity or longevity inversely affect the response rate of lever pressing by rats for thermal reinforcement.

Reptiles are easy to shape for operant experiments (Burghardt, 1977) and may require little or no shaping when the operants are simple (Linton, 1976). Experiments in operant conditioning using heat reinforcements have shown that reptiles quickly learn simple operants, exhibit the desired operant regularly with continuous reinforcements, and will change the response rate if the magnitude (length or strength) of the reinforcement is changed.

The experimental apparatus used here is a thermoregulatory system in which the energetic cost of thermoregulation and ambient temperature can be modified experimentally. This system is essentially a shuttle apparatus with heat lamps at either end. The lizard, by shuttling to one end of the box, triggers a switch at that end (by gravity) which turns on the heat lamp. There is a preset time interval for the lamp to remain on (from 0 - 240 seconds), and at the termination of this interval the lamp turns off. In order to reactivate a heat lamp, the lizard must move to the other lamp at the opposite end of the box so as to turn that lamp on for the same preset time interval. Therefore, the lizard must move a known distance (at a predictable metabolic cost) in order to procure the radiant heat energy needed to elevate and regulate

T_B . By varying the length of time that the lights remain on, it is possible to force the lizard to shuttle more or less frequently, thereby forcing the lizard to expend more or less energy in order to thermoregulate. The shuttle box apparatus is maintained in a constant temperature cabinet, so that T_A , the thermal gradient that the lizard works against, is varied; this also alters the cost required for behavioral thermoregulation. When the cost of thermoregulation becomes too great (light on for short interval and/or low ambient temperature), or the T_A becomes too high, the lizard would be expected to cease behavioral thermoregulation.

The physical habitat diversity (Stebbins, 1966; Vitt, 1974) of Gerrhonotus coeruleus and its reported passivity to a wide range of environmental temperatures (Brattstrom, 1965; Vitt, 1974) make this lizard a good subject for the study of eurythermality.

CHAPTER II

MATERIALS AND METHODS

Experimental Animals

Northern Alligator Lizards (Gerrhonotus coeruleus) were collected in June 1979, between Reedsport and Drain, in Douglas County, Oregon. All healthy adults found at this location were collected and returned to the lab.

The lizards were kept in an Environator Model I-3236 environmental chamber at 20°C, with lights on from 9:00 a.m. until 9:00 p.m. The lizards were fed mealworms and crickets and given water ad lib.

Five female lizards (mean mass 10.2 ± 2.6 g, range 6.6 to 14.4 g) were placed in individual cages within the environmental chamber.

Operant Apparatus

An enclosure 1 m long, 23 cm high and 23 cm wide was constructed with a bottom of styrofoam and sides of plastic covered with duct tape. a 5 cm lip encircled the otherwise open top to prevent lizards from climbing out. White styrofoam was used on the bottom because it reflected light and therefore did not store much heat from the lamps. The plastic sides and lip were covered with duct tape to prevent melting or ignition from the heat lamps.

The entire enclosure was balanced on a fulcrum such that a weight of 1 g at either end would tip the enclosure in that direction. Two 8PK-8246-8FY (Microswitch) sealed, metal clad proximity microswitches

were incorporated at each end of the balanced enclosure in such a manner that a tilt of 2 cm would close the switch circuit and register an electronic response.

Two sylvania 250 watt infrared heat lamps were suspended 33 cm above the ends of the balanced enclosure in such a manner as to provide radiant heat energy when turned on to the last 10 cm of the enclosure. A lizard seeking heat influx would have to walk to the very far ends of the balance enclosure.

A General Electric 25 watt bulb was wired in series with each heat lamp and inserted in a plastic tube with a photocell. An operant response from the lizard that turned on a heat lamp also turned on the 25 watt bulb in series, which in turn illuminated the photocell and produced a small voltage. This small voltage was detected by the microprocessor or millivolt recorder as an operant response on that end of the shuttle apparatus.

The entire operant apparatus was placed into an environmental chamber (Environator model 3486AL) and kept at a constant T_A . The environmental chamber containing the balanced enclosure was illuminated by 4 Sylvania 72 inch Coal White F72112-CW-VHO flourescent bulbs suspended 85 centimeters above the shuttle box.

The T_A of the inside of the environmental chamber and the T_B of the lizard were monitored using 30 gauge thermocouple wire and Omega thermal reference junctions. The T_A thermocouple was placed in the enviromental chamber so that it was out of any drafts and away from possible radiant influence of the heat lamps. The temperature of the environmental chamber (T_A) was not changed appreciably by the operant

apparatus. The T_A always remained a constant $10^{\circ}\text{C} \pm 1^{\circ}\text{C}$ (trials A, B, and C) or $20^{\circ}\text{C} \pm 1^{\circ}\text{C}$ (trial D). The thermocouple used to monitor T_B was inserted through the cloaca and into the small intestine and taped to the lizards' tail.

The electronic circuit for turning the heat lamp on and off at the proper moment and for the proper time sequence was designed using transistor-transistor-logic.

The T_B , T_A , and responses (activation of heat lamps from shuttling) were monitored using an Aim model 65 microprocessor or a Leeds and Northrup 12 channel multiplex recorder. Every six seconds the microprocessor measured T_B from the thermocouple inserted in the lizard's small intestine. At 5-min intervals, the mean of the previous 50 T_B values (6 sec X 50 = 5 min) were accumulated and averaged. At the end of each hour, the mean, variance, standard deviation and standard error of the 12 5-min T_B average readings were calculated. The microprocessor simultaneously monitored the activity of the lizard (i.e., when and how many times it shuttled from end to end. The mean, standard deviation, variance, and standard error of the twelve hourly means were computed. The same information was obtained manually from the multiplex recorder.

The 5 lizards used in this experiment were introduced individually to the balanced enclosure while it was in the environmental chamber at 10°C . The lizards were given 1 12-hr period (9:00 a.m. to 9:00 p.m.) to orient to the experimental apparatus. Gleeson (1979) found that Western Fence Lizards (Sceloporus occidentalis) became familiar with an experimental apparatus after a single exposure and

required no further training period. The behavior of the G. coeruleus used in the baseline studies supported this conclusion. The day following enclosure orientation, operant conditioning was started.

The lizards were shaped, using standard operant conditioning techniques, to walk back and forth in the balanced enclosure. Shaping reinforcements were provided when the lizard moved towards the far end of the balanced enclosure. Using the principle of successive approximations to desired response, the lizards had to move progressively closer to the other end of the balanced enclosure in order to be heat reinforced. Eventually the animals were walking along the balanced enclosure far enough to tip it in the opposite direction and activate the proximity switch, at which time the heat lamp immediately above that switch (and the animal) would turn on for the prescribed length of time and reinforce that animal with heat. Shaping time varied from 5 minutes to 45 minutes. The animals were considered to have reached the shaping criterion when they had a relatively constant temperature ($\pm 3^{\circ}\text{C}$) while regulating for at least 6 hours continuously. The cessation of thermoregulation was considered to be the point at which T_B was equal to T_A and no further activity took place.

Using this operant apparatus the following trials were run. Lizards number 1, 2, 3 were run at 10°C with 90 second heat reinforcements for 5 trials each (preliminary trials); Lizards number 1, 2, 3, 4, and 5 were run at 10°C with 45 second heat reinforcements for 5 trials each (trial A); 10°C , with 90 second heat reinforcements for 3 trials each (trial B); 10°C , with 180 second heat reinforcements for 3 trials each (trial C); and 20°C , with 180 second heat reinforcements

for 3 trials each (trial D). There was no statistical difference between the data from the preliminary trial and the data from trial B (both run at 10°C with 90 second heat reinforcements). Therefore, there was no apparent ordering effect observed. The data from trial B was used for comparison purposes in the results because all five lizards were represented in trial B as compared to only three lizards in the preliminary trial.

STATISTICAL COMPUTATIONS

Mean Body Temperature ($\bar{x}T_B$)

The mean body temperature for any given trial was computed by taking the mean of all the hourly temperatures, during the entire trial sequence, when the lizard was actively thermoregulating (i.e., shuttling).

Shuttle Rates (resp/hr)

The shuttle rate in responses per hour was calculated by adding all the responses for a given trial period, divided by the number of hours the lizard actively thermoregulated during that trial.

Mean Standard Deviation ($\bar{x}SD$)

Mean standard deviations for any given trial period were computed by taking the mean of the standard deviations for those hours, during the entire trial period when the lizard was actively thermoregulating.

Cost ($\dot{V}O_2$)

The cost in $\dot{V}O_2$ was calculated in all cases by adding the metabolic cost of having an elevated T_B during behavioral thermo-

regulation to the energetic cost of moving from one end of the balanced enclosure to the other.

The mean metabolic cost per hour of maintaining T_B at any particular temperature was calculated using the data of Hoffman (1973) for the Southern Alligator Lizard (Gerrhonotus multicarinatus webbi).

The metabolic cost of shuttling was calculated using the data of Schmidt-Nielsen (1972) for mammals. Lizards and mammals of the same weight have similar energy expenditures (Bakker, 1972). At speeds less than 1.1 km/hr, the energy cost of running for lizards is independent of body temperature (Dmi'el and Rapoport, 1976). All speeds in these experiments were far below this level.

$\dot{V}O_2$ While Regulating ($\dot{V}O_2$, reg)

The mean cost in $\dot{V}O_2$ for those portions of the 12-hr trials when active behavioral regulation was taking place was calculated by adding the cost of maintaining the mean body temperature during hours of regulation to the metabolic cost of the total number of responses, divided by the hours spent regulating. The mean cost of thermoregulating in $\dot{V}O_2$ per g for those parts of the 12-hr periods when the lizards were actively behaviorly thermoregulating was calculated by dividing $\dot{V}O_2$ regulating by the mass of the lizard (mass specific $\dot{V}O_2$, reg).

$\dot{V}O_2$ Average ($\dot{V}O_2$, avg)

The mean cost in $\dot{V}O_2$ was computed for each entire 12-hr trial by taking the metabolic cost of shuttling and the metabolic cost of maintaining T_B during periods of active regulating, and adding this to

the metabolic expenditures during those hours when T_B equalled T_A , divided by 12 to give $\dot{V}O_2$ based on each entire 12-hr period. The mean cost of thermoregulating in $\dot{V}O_2$ per gram for each entire 12-hr period was calculated by dividing $\dot{V}O_2$ average by the mass of the lizard (Mass Specific $\dot{V}O_2$, avg).

Scaling

A least-squares regression was computed for the mass specific $\dot{V}O_2$ regulating for trails A through D. A probability of less than .05 (P .05) was considered significant. A t-test for slope and intercept was used to see if they were significantly different from 0 and to test if the slope was significantly different from the expected value for mass versus mass specific metabolic rate (slope of -.25).

Statistics

An analysis of variance with Bartlett's test for homogeneity of variance was used to determine if various parameters (e.g., response rate, $\bar{x}T_B$, etc.) were significantly different for any trial (Snedecor, 1956). A probability level of less than .05 (P .05) was considered significant if the corresponding χ^2 (Chi-square) value for Bartlett's test was not significant.

CHAPTER III

RESULTS

The accumulated data for trials A, B, C, and D were analyzed in three ways. Those trials at 10°C (trials A, B, and C) were compared to each other. The trials run at 10°C were compared to trials run at 20°C (trial D). Finally a comparison was made between the trials at 10°C and 20°C where the reinforcement periods were both 180 seconds (trial C versus D).

Mean Body Temperature ($\bar{x}T_B$)

The values for mean body temperature for each trial are shown in Table I ($\bar{x}T_B$). The $\bar{x}T_B$ for trials A, B, and C were significantly different ($P = .01$) as were $\bar{x}T_B$ for trials A, B, C, and D ($P = .001$), and $\bar{x}T_B$ for trials C and D ($P = .05$). These data indicate that $\bar{x}T_B$ varies if reinforcement time or T_A is changed.

Shuttle Rate (\bar{x} resp/hr)

The values for the mean shuttle rate for each trial are shown in Table I (\bar{x} resp/hr). The \bar{x} resp/hr for trials A, B, and C were significantly different ($P = .01$), as were the \bar{x} resp/hr for trials A, B, C, and D ($P = .001$). The \bar{x} resp/hr for trials C and D are not significantly different. These data indicate that the shuttle rate varies if the reinforcement time varies, but is not affected by changes in T_A .

TABLE I

SUMMARY OF MEAN BODY TEMPERATURE (\bar{x}_T^B), MEAN STANDARD DEVIATIONS (\bar{x}_{SD}), MEAN SHUTTLE RATE (\bar{x} RESP/HR), METABOLIC RATE PER HOUR FOR REGULATING TIME ONLY ($\dot{V}O_2$, REG), METABOLIC RATE PER HOUR FOR ENTIRE 1.2 HOUR TRIALS ($\dot{V}O_2$, AVG), METABOLIC RATE PER GRAM FOR ENTIRE 1.2 HOUR TRIALS (MASS SPECIFIC $\dot{V}O_2$, AVG), AND METABOLIC RATES PER GRAM FOR REGULATING TIME ONLY (MASS SPECIFIC $\dot{V}O_2$, REG), FOR FOUR EXPERIMENTAL TRIALS: TRIAL A ($10^\circ\text{C } T_A$ WITH A 45 SECOND HEAT REINFORCEMENT), TRIAL B ($10^\circ\text{C } T_A$ WITH A 90 SECOND HEAT REINFORCEMENT), TRIAL C ($10^\circ\text{C } T_A$ WITH AN 180 SECOND HEAT REINFORCEMENT), AND TRIAL D ($20^\circ\text{C } T_A$ WITH AN 180 SECOND HEAT REINFORCEMENT). ALL VALUES ARE MEAN \pm STANDARD DEVIATIONS WITH THE NUMBER

OF OBSERVATIONS INDICATED FOR EACH TRIAL

TRIAL	\bar{x}_T^B	\bar{x}_{SD}	\bar{x} RESP/HR	$\dot{V}O_2$, REG	$\dot{V}O_2$, AVG	MASS SPECIFIC	
						$\dot{V}O_2$, REG	$\dot{V}O_2$, AVG
A (N=25)	20.1 \pm 2.5	3.1 \pm 0.8	15.4 \pm 3.7	1.0 \pm 0.4	0.77 \pm 0.6	0.068 \pm 0.03	0.10 \pm 0.02
B (N=15)	23.7 \pm 0.8	2.8 \pm 0.7	12.1 \pm 2.3	1.1 \pm 0.1	0.76 \pm 0.2	0.076 \pm 0.02	0.11 \pm 0.02
C (N=15)	24.8 \pm 2.4	3.5 \pm 1.0	6.7 \pm 2.3	1.1 \pm 0.5	0.72 \pm 0.4	0.068 \pm 0.03	0.10 \pm 0.03
D (N=15)	27.8 \pm 1.0	2.0 \pm 0.2	7.2 \pm 3.0	1.5 \pm 0.5	1.30 \pm 0.7	0.120 \pm 0.04	0.14 \pm 0.02

Mean Standard Deviation (\bar{xSD})

The values for the mean standard deviation for each trial are shown in Table I (\bar{xSD}). The \bar{xSD} for trials A, B, and C were not different; similarly the \bar{xSD} for trials A, B, C, and D were not significantly different. The \bar{xSD} for trials C and D were significantly different ($P < .025$). These data indicate that the \bar{xSD} is not affected by changes in reinforcement time but is affected by changes in T_A .

\dot{VO}_2 While Regulating (\dot{VO}_2, reg)

The values for \dot{VO}_2 while regulating are shown in Table I (\dot{VO}_2, reg). No significant difference was found in any comparison. Therefore, changes in reinforcement time or changes in T_A have no effect on \dot{VO}_2, reg .

\dot{VO}_2 Average (\dot{VO}_2, avg)

The values for \dot{VO}_2 for each entire 12-hr trial are shown in Table I (\dot{VO}_2, avg). No significant difference was found in any comparison. Therefore, changes in reinforcement time or changes in T_A have no effect on \dot{VO}_2, avg .

Mass Specific \dot{VO}_2 Average

The values for mean mass specific \dot{VO}_2 for each trial are shown in Table I (Mass Specific \dot{VO}_2, avg). The mass specific \dot{VO}_2, avg for trials A, B, and C were not significantly different; neither were trials A, B, C, and D. The mass specific \dot{VO}_2, avg for trials C and D were significantly different ($P < .05$). Therefore, mass specific \dot{VO}_2, avg was not affected by changes in reinforcement time but was affected by changes in T_A .

Mass Specific $\dot{V}O_2$ While Regulating

The values for mass specific $\dot{V}O_2$ while regulating are shown in Table I (Mass Specific $\dot{V}O_2$, reg). The mass specific $\dot{V}O_2$, reg for trials A, B, and C were not significantly different. The mass specific $\dot{V}O_2$, reg for trials A, B, C, and D were significantly different ($P < .05$), as were mass specific $\dot{V}O_2$, reg for trials C and D ($P < .05$). Therefore, mass specific $\dot{V}O_2$, reg were not affected by changes in reinforcement time but was affected by changes in T_A .

Scaling

The R, intercept and slope values for regression of mass versus mass specific $\dot{V}O_2$, reg are shown in Table II. The slopes in trial C and D were not significantly different from zero. The R values for trials C and D did not differ significantly. All other values were significant ($P < .05$). The slope in trial C is not significantly different from the expected value of -0.25 , the expected norm for mass versus metabolic rate. All other slopes were significantly different from -0.25 . Therefore, it is not possible to predict the metabolic expenditures for thermoregulating lizards of different mass because the scaling relationship varies greatly with environmental factors such as magnitude of reinforcement and T_A .

TABLE II

SUMMARY OF STATISTICS FOR LEAST SQUARES REGRESSION ANALYSIS OF MASS SPECIFIC OXYGEN CONSUMPTION RATE FOR LIZARDS WHILE REGULATING, AS A FUNCTION OF BODY MASS. N=5 FOR ALL REGRESSIONS. SEE TABLE I FOR TRIAL LEGEND

TRIAL	R VALUE	INTERCEPT	SLOPE
A	0.82 (P .025)	$-1.5^{\pm} 0.20$ (P .055)	$0.54^{\pm} 0.22$ (P .05)
B	0.98 (P .05)	$-0.3^{\pm} 0.06$ (P .01)	$-0.66^{\pm} 0.06$ (P .005)
C	0.61 NS	$-1.6^{\pm} 0.42$ (P .025)	$0.56^{\pm} 0.42$ NS
D	0.37 NS	$-1.1^{\pm} 0.32$ (P .025)	$0.22^{\pm} 0.32$ NS

NS = NOT SIGNIFICANT

CHAPTER IV

DISCUSSION

All lizards can be considered as obligatory ectotherms (Soule', 1963). Lizards maintain T_B well above T_A by behavioral means. The level of PBT obtained above T_A and the precision about that PBT has been used as an index to determine eurythermality and stenothermality in lizards. Variations in T_B have been attributed to sex and size differences (Bogert, 1949; Fitch, 1956), environmental factors (Ruibal, 1961; Huey 1974a; Lister, 1976), and cost (Ruibal, 1961; DeWitt, 1967; Regal, 1967; Hertz, 1974; Huey, 1974a; Lister, 1976). Eurythermal lizards were considered to have a wide tolerance to T_B fluctuations that had evolved in response to the absence of competition (Ruibal and Philibosian, 1970).

The thermoregulatory behaviors normally associated with purported eurythermic species (i.e., wide T_B fluctuations) were absent in this experiment. G. coeruleus was found to be an active and precise regulator of T_B .

Feeding schedules were found to be of importance during early baseline studies. G. coeruleus would thermoregulate only for 24 hours after feeding. Therefore, it was necessary to feed the experimental animals the day before each trial.

Under the constraints imposed on the lizards by the physical limitations of the experimental design, three behavioral thermoregu-

latory strategies were possible:

- I. The lizard could adjust the response rate.
- II. The lizard could adjust its mean body temperature.
- III. The lizard could adjust the amount of time it spends regulating.

These are not mutually exclusive responses. The lizard could adjust one or all of the above in any combination to affect cost of behavioral thermoregulation. The lizard could regulate for varying lengths of time and still achieve the same daily energy expenditures by varying its response rate. For example, a response rate of 10 responses per hour for 12 hours that provides a T_B of 20°C may have the same energy expenditure as a response rate of 20 responses per hour for 6 hours to maintain a T_B of 28°C .

If G. coeruleus maintained its T_B at a constant level, regardless of the metabolic cost (mass specific $\dot{V}O_2$, reg) then the data should show a similar mean T_B between trials for a given individual or for the individuals as a group. An examination of T_B between the different trials shows a progressive increase in T_B between trials A through D with a significant difference in T_B between trials. Thus G. coeruleus, under different conditions, appears to regulate to different T_B . The T_B selected would appear to depend upon the costs required (mass specific $\dot{V}O_2$, reg) to maintain that temperature in a given situation.

One way for a lizard to have a lower mean T_B would be if it regulated less precisely. For example, allowing T_B to periodically approach T_A in high cost situations (shorter reinforcement times) would

be reflected by a greater variation in standard deviation of mean T_B between trials A through C. Since standard deviations between trials A through C were not significantly different, differences in precision of thermoregulation does not appear to be a mechanism of lowering mean T_B .

If the mean T_B is an important variable during thermoregulation, then the shuttle rate should increase with a decrease in reinforcement. Shuttle rate was inversely related to reinforcement time during trials A through C. However, the increase in shuttle rate at lower reinforcement times was not sufficient to keep the mean T_B constant.

The cost of behavioral thermoregulation (mass specific $\dot{V}O_2, \text{reg}$) appears to be an important variable for determining the T_B attained since shuttling frequencies between trials A through C were such that the various metabolic costs did not change between these trials.

The metabolic cost (mass specific $\dot{V}O_2, \text{reg}$) did differ significantly between trials C and D when the ambient temperature was increased from 10°C to 20°C . There was also a significant difference in standard deviation between these two trials, but there is no significant difference in the shuttle rate. G. coeruleus regulated more precisely in trial D than trial C (lower SD) but did not change its shuttle rate; therefore the increase in cost can be attributed to the higher levels of mean temperature ($\bar{x}T_B$) and the more precise (lower SD) regulation. Both of these changes are the result of a smaller thermal difference between the lizard and its environment at 20°C than at 10°C (i.e., lizards will gain radiant heat faster and lose heat slower at 20°C).

Another way G. coeruleus could vary metabolic cost (mass specific $\dot{V}O_2$, reg) is to regulate at the same T_B but for shorter periods of time at lower reinforcement times and lower T_A . There was no significant difference between lizards for trials A through D, even though in some cases the largest lizard regulated more than 7 times longer than the smallest.

As the reinforcement periods increase the amount of energy the lizard spends for resting metabolism as compared to the amount of energy expended for shuttling increases. A comparison of resting metabolic cost ($\dot{V}O_2$ at T_A), temperature maintenance cost ($\dot{V}O_2$ at $\bar{x}T_B$), and shuttling cost ($\dot{V}O_2$ per meter times shuttle rate) shows that the cost of shuttling is the major cost component during trial A, the cost of shuttling and maintaining $\bar{x}T_B$ are about equal during trial B, and the cost of maintaining temperature ($\bar{x}T_B$) during trials C and D were the major costs. The total metabolic costs during trials A, B, and C ($\dot{V}O_2$, reg) were not significantly different. The larger metabolic expenditure during trial D is due to the larger resting metabolic cost ($\dot{V}O_2$ at T_A). These changing metabolic cost components are reflected in Figure 1.

G. coeruleus has been described in the literature as a diurnal nonbasking, eurythermic species with a wide range of mean T_B (Brattstrom, 1965). Their reported eurythermality is assumed to be the consequence of living in an environment where the cost of behavioral thermoregulation to within narrow limits in a stenothermic manner would greatly outweigh the benefits in a physiological sense (Huey, 1974a).

Eurythermality can be examined in two different contexts. If a

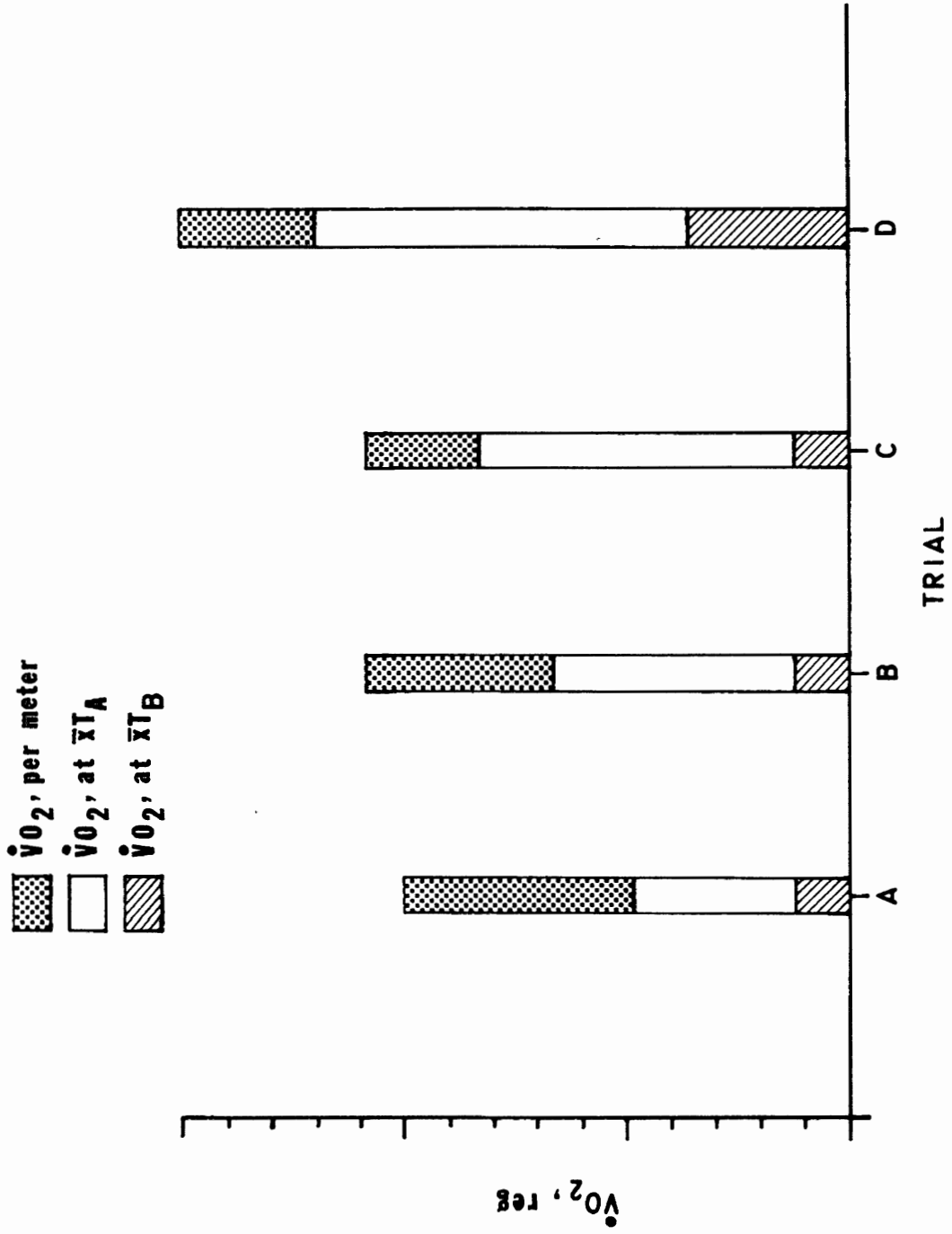


Figure 1. Histogram of the mass specific $\dot{V}O_2, \text{reg}$ and its statistical metabolic components.

lizard is to be considered eurythermal in the classical sense, then the levels of mean T_B realized should be of no consequence to the animals as long as these T_B fall within the lizards normal activity range (i.e., above critical thermal minimum and below critical thermal maximum). There should also be a wide variation in realized metabolic cost in various environmental situations. The only metabolic costs associated with thermoregulation in such a lizard, in this situation, would be shuttling costs required to avoid critical minima and maxima. Brattstrom's (1965) field data for T_B of G. coeruleus seem to indicate that this lizard is eurythermal, because it has a range of T_B from 11.0°C to 19.4°C with a mean T_B of 15.8°C . G. coeruleus in a no-cost thermal gradient in the laboratory will select a T_B of around 29 to 31°C (Campbell, personal observation). The implication has always been that this difference in PBT between field and lab indicates the species can exist equally well at both temperature extremes.

A second way to view eurythermality is to assume that the lizard would have a temperature preference range as narrow as a traditional stenothermic lizard (Dipsosaurus dorsalis) if the metabolic costs of maintaining this narrow range were low. This has already been shown to some degree by the higher preferred body temperatures of eurythermic lizards in laboratory thermogradients where the metabolic cost of thermoregulation has only a resting metabolic component with no shuttling costs involved.

These data indicate that eurythermality of G. coeruleus is caused by fluctuations in preferred T_B and not precision around this temperature. Eurythermality is also associated with changes in the

metabolic cost of shuttling and the metabolic cost of maintaining higher T_B .

When G. coeruleus is presented with shorter reinforcement times it responds by shuttling more frequently, but at a lower mean T_B . The importance of this observation is that the metabolic cost of behavioral thermoregulation does not change with a corresponding change in reinforcement time at any given T_A , but the mean T_B and shuttle rate do change.

In these experiments G. coeruleus regulated precisely around a selected T_B in all experiments, or did not regulate at all. In over 1000 hours of detailed observation the mean deviation from selected T_B was only $\pm 2.8^\circ\text{C}$ with a range of 1.7°C to 4.8°C . Statistically the deviation from the mean T_B did not change during the 10°C trials (trials A through C). At any given trial any individual lizard should be considered to be stenothermic in that it had a narrow range of T_B around a selected mean T_B . It is only in the examination of the mean selected T_B of all lizards examined together for all the trials that eurythermality was exhibited. This supports the findings of Huey and Stevenson (1979) that examination of data for populations as a whole may indicate a broad optimal temperature range when instead individual members of that population are regulating precisely.

At longer reinforcement times or higher T_A trials the metabolic costs of thermoregulation remained the same when compared to all trials. Any drop in the metabolic cost of shuttling was counterbalanced by the increase in the resting metabolism of the higher mean T_B realized at higher reinforcements.

These experiments indicate that G. coeruleus must derive some benefit from short term stenothermic behavior. This lizard still precisely regulated to a mean T_B of $27.8^{\circ}\text{C} \pm 1^{\circ}\text{C}$ during trial D, when the T_A (20°C) was higher than the mean T_B recorded for this species in the field (15.8°C) and higher than the recorded upper limit of its normal activity range (19.8°C). If the lizards had shuttled during trial C with the frequency that they shuttled during trial B (16.2 resp/hr at trial B as compared to 11.5 resp/hr at trial C) then they could have easily regulated to 27.8°C during trial C as well as trial D. That this did not occur may indicate that the metabolic cost of shuttling was the limiting factor and that the lizards gained some advantage at a T_B of 24.4°C (trial C) as well as at a T_B of 27.8°C (trial D).

These results imply that the wide range of T_B recorded for G. coeruleus in the field may be measurements of different lizards regulating stenothermically to their own individual mean T_B rather than just random T_B associated with a normal activity range, or they are not regulating at all ($T_B = T_A$). A calculation of the mean T_B for all lizards during all hours of the 12-hr trials (regulating temperatures and resting temperatures ($T_B + T_A$)) in these experiments shows that using the typical field methods employed in Brattstrom (1965) the mean T_B of these lizards during these experiments would be 17.8°C . In fact, during periods of active behavioral thermoregulation, T_B consistently this low were only recorded twice during the entire experiment and those two recordings took place in trial A when the reinforcement period and T_A were at their lowest.

G. coeruleus either regulates T_B for short stenothermic periods (7-8 hours average) or does not regulate at all. In a complex field environment where many microenvironments exist and the cost associated with behavioral thermoregulation varies widely from location to location, or day to day, the T_B of G. coeruleus will show wide variations. However, these variations are not the recorded effect of lizards operating a wide normal activity range but the recorded effect of lizards regulating close to a mean T_B that is dictated by the metabolic cost associated with the environment at that time.

Patterns of eurythermy and stenothermy may be determined as much by the environment in which the animal lives as by evolutionary, physiological, or behavioral considerations. It is possible that purported eurythermal species would thermoregulate with the same precision and for equal lengths of time as stenothermic species if they are presented with the same uniform low cost environments within the limits of their critical thermal temperatures. This idea is supported by these experiments where G. coeruleus thermoregulates around high T_B ($27.8^{\circ}\text{C} \pm 1.0^{\circ}\text{C}$) as precisely as Dipsosaurus dorsalis does ($42.4^{\circ}\text{C} \pm 1.8^{\circ}\text{C}$ (Norris, 1953)), but at lower temperature values. Similarly, purported stenothermic lizards in high cost environments would decrease their PBT. Therefore, evolutionary interpretations (Huey, 1974a) of purported eurythermal species by be premature.

SCALING

The mass specific $\dot{V}O_2$, reg expressed in these experiments is the sum of metabolic rates of shuttling ($\dot{V}O_2$ per gram meter) and the

constant T_B energy requirements ($\dot{V}O_2$ at $\bar{x}T_B$) combined in various combinations to reflect the total energy dynamics of a fluctuating thermoregulatory system. Shuttling rates and the metabolic cost of being at constant T_B do not change in direct proportion to one another. The effect of reinforcement length (45 seconds, 90 seconds, or 180 seconds) and T_A changes (10°C and 20°C) on the relationship between mass specific $\dot{V}O_2$, reg and mass is illustrated in Figure 2.

The reinforcement period of 45 seconds at a T_A of 10°C , during trial A, was not sufficient to allow the smallest lizard (6.6 g) to maintain a T_B as high as the largest lizard. The largest lizard (14.4 g), however, maintained a constant T_B ($23.3 \pm 2.3^\circ\text{C}$) by shuttling at a greater rate (19.5 resp/hr). The three intermediate-sized lizards had slightly lower shuttle rates (16 resp/hr). Therefore, their total metabolic expenditure (mass specific $\dot{V}O_2$, reg) per gram was midway between the largest and smallest lizard.

The reinforcement period of 90 seconds at T_A 10°C , during trial B, was sufficient to allow the smallest lizard to maintain a T_B slightly higher than the T_B reached by the larger lizard during trial A, but only at a much higher response rate (14.2 resp/hr for the small lizard versus 9.1 resp/hr for the large lizard). This resulted in greater energetic expenditures per gram (mass specific $\dot{V}O_2$, reg) for the smaller lizard. The intermediate-sized lizards shuttled less frequently to a slightly higher temperature than trial A and therefore had the same total metabolic expenditures per gram (mass specific $\dot{V}O_2$, reg) during trial B as they did in trial A.

The reinforcement period was extended to 180 seconds at 10°C ,

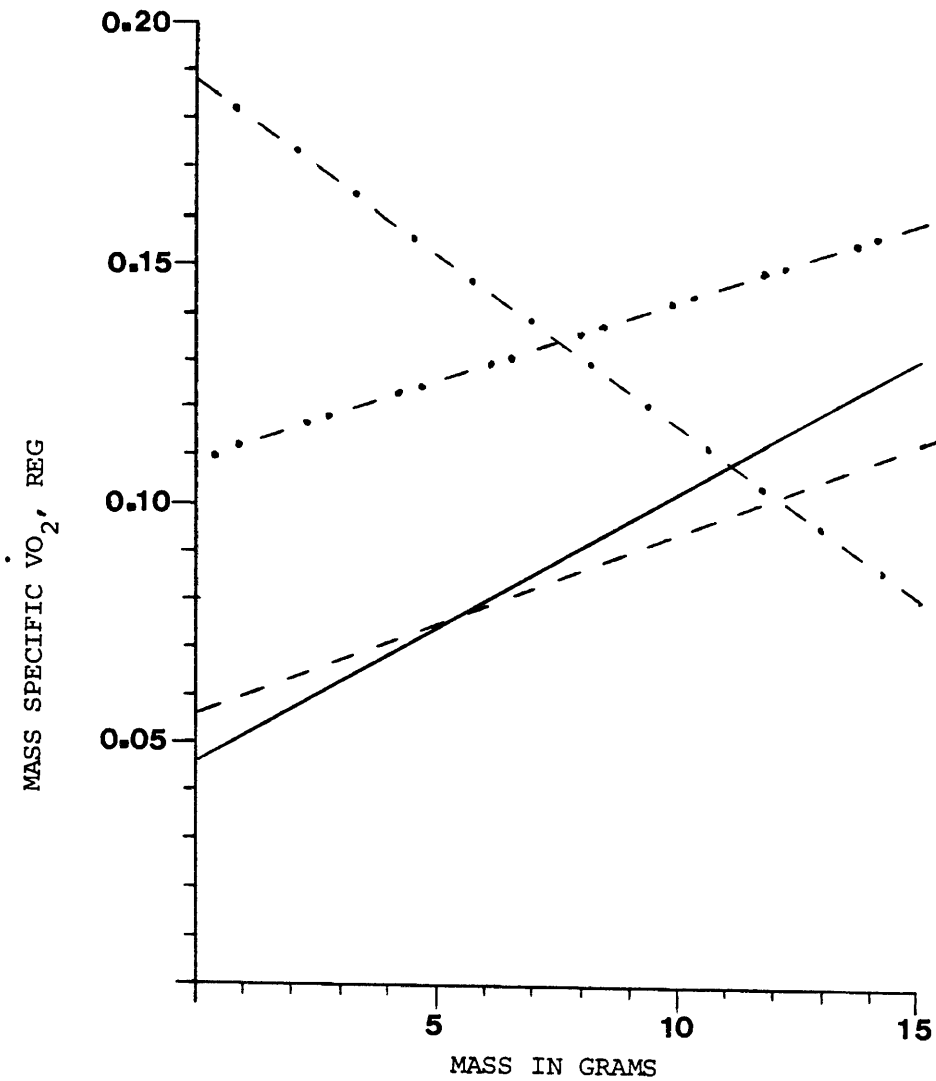


Figure 2. Graph of mass specific $\dot{V}O_2$, reg versus mass for all trials

- - - = 45 seconds (trial A)
- . - . - = 90 seconds (trial B)
- = 180 seconds (trial C) 10°C
- . . - = 180 seconds (trial D) 20°C

during trial C. The smaller lizard regulated in this situation to a lower T_B than the other lizards with a correspondingly lower shuttle rate. The largest lizard regulated T_B to a temperature higher than the other lizards with a correspondingly higher shuttle rate.

All the lizards thermoregulated to a slightly higher temperature during trial D, than trial C, but maintained the same shuttle rate.

The main fluctuations in metabolic cost per gram (mass specific $\dot{V}O_2$, reg) between trials was due to the differences between the largest and smallest lizard (Figure 2).

The largest metabolic expenditure during trial A was the cost of shuttling ($\dot{V}O_2$ per gram meter). The costs of shuttling and maintenance of temperature ($\dot{V}O_2$ at $\bar{x}T_B$) were about equal during trial B. The cost of having a high T_B was the largest metabolic expenditure during trials C and D. The total metabolic expenditures (mass specific $\dot{V}O_2$, reg) during trial D were larger than during trial C because of the greater metabolic cost ($\dot{V}O_2$ at $\bar{x}T_B$) at 20°C as compared to 10°C , and a slightly higher body temperature (see Table I). These variations are illustrated in Figure I.

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