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THE INFLUENCE OF METABOLIC COST UPON THE LEVEL AND PRECISION OF BEHAVIORAL THERMOREGULATION IN AN EURYTHERMIC LIZARD

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Abstract—The mean T_B of *G. coeruleus* in each condition was positively correlated to the length of reinforcement, whereas the shuttle rate was inversely correlated to the length of reinforcement.

2. The precision of T_B regulation and the total metabolic expenditures of lizards did not vary significantly for different reinforcement regimes at the same ambient temperature.

3. Eurythermality in *G. coeruleus* is caused by variations in preferred body temperature and not by fluctuations in T_B around the particular regime body temperature.

1984

INTRODUCTION

A variety of behaviors associated with temperature regulation in lizards (Cowles and Bogert, 1944) have been well documented (see Crawshaw, 1980, for a recent review), but it has only recently been suggested that the metabolic costs associated with behavioral regulation of body temperature (T_B) in lizards may be of importance to the pattern of regulation (Huey, 1974; Huey and Slatkin, 1976; Gleeson, 1979; Lee, 1980).

Huey and Slatkin (1976) studied the concept of thermoregulatory cost, and presented a cost-benefit model for lizard thermoregulation. Their model predicted that stenothermic behavior in lizards was the consequence of being in a habitat with a low cost for behavioral thermoregulation. For example, the Desert Iguana (*Dipsosaurus dorsalis*) is a typical stenothermic lizard (Norris, 1953). The physical properties of its desert habitat (i.e. high T_A, high incidence of solar radiation, etc.) allow it to behaviorally maintain a precise mean T_B with little energy expenditure. The prediction of stenothermality in low cost environments has the corollary prediction of eurythermality in high cost environments.

The present study assesses the effects of variation in cost of thermoregulation to the level and precision of T_B control by a eurythermic lizard (*Gerrhonotus coeruleus*) in the laboratory. A major drawback to field studies of T_B regulation is the complex and varying environmental influences upon T_B regulation. Other important behaviors and activities such as food acquisition, reproduction, predator avoidance (Huey and Slatkin, 1976), and T_A were controlled in this experiment allowing the lizard to minimize costs not associated with temperature regulation. The experimental design used here allows the measurement of shuttling frequencies over a constant distance (1 m) in a system where the T_A and other factors influencing T_B regulation are held constant, and T_B can be accurately monitored on a continuous basis.

This experiment tests the hypothesis that the regulated mean T_B, and the precision of T_B about this mean are dependent on the cost of thermoregulation. The costs for thermoregulation can be altered by increasing or decreasing the period of radiant heat reinforcement. The lizard can respond to the altered cost by changes in shuttle rate, level of T_B, or precision of T_B regulation.

MATERIALS AND METHODS

Five Northern Alligator Lizards (*G. coeruleus*) were collected in June 1979, between Reedsport and Drain, in Douglas County, Oregon. Healthy adults were returned to the lab where they were provided with water, mealworms and crickets *ad lib*. The lizards were kept in an environmental chamber at 20°C. Light was provided by fluorescent and incandescent lamps, 12 hr daily starting at 9:00 a.m.

A shuttle apparatus with heat lamps at either end was used (Fig. 1). 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 (to prevent melting and ignition). The entire enclosure was balanced on a fulcrum. Tilting the chamber caused a proximity microswitch at each end of the balanced enclosure to turn on a 250 W infrared heat lamp suspended 33 cm above the end of the enclosure. The entire apparatus was in an environmental chamber and kept at a constant T_A.

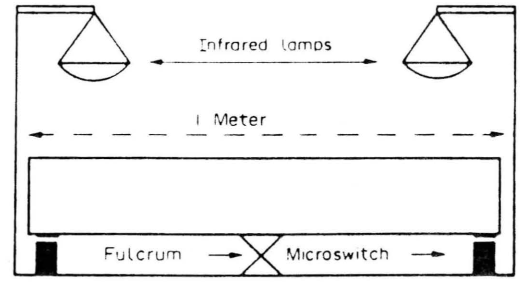

Fig. 1. Experimental apparatus. A shuttle apparatus with heat lamps at either end. An enclosure 1 m long, 23 cm high, and 23 cm wide was balanced on a fulcrum to tip the enclosure when a lizard walked to either end, thereby activating the magnetic proximity switch and turning on the heat lamps.

The T_A of the inside of the environmental chamber and the T_B of the lizards were monitored using 30 gauge thermocouple wire and Omega thermal reference junctions. The ther-

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mocouple was inserted through the cloaca and into the large intestine, and taped to the lizard's tail.

The T_A, T_B and shuttle responses (activation of heat lamps by shuttling from end to end) were monitored using a Rockwell Aim 65 microprocessor, or a Leeds and Northrup 12 channel multiplex recorder. T_B was measured every 6 sec. At 5 min intervals, the mean of the previous 50 T_B values were 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, and standard error of the 12 hourly means, were computed. The same information was obtained manually from the multiplex recorder.

The 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 one 12-hr period (9:00 a.m. to 9:00 p.m.) to orient to the experimental apparatus, and conditioning was started the day following enclosure orientation. The lizards were behaviorally shaped, using standard operant conditioning techniques, to walk back and forth in the balanced enclosure. The lizard, by moving to one end of the box, tipped the apparatus and triggered a switch at that end to turn on the heat lamp. The lamp had a preset time interval to remain on (from 0 to 240 sec), and then the lamp turned off. In order to reactivate the same heat lamp, the lizard had to first move to the opposite end of the apparatus and turn on that lamp for the same preset time interval. Therefore, the lizard had to move a known distance (at a constant metabolic cost) in order to procure the radiant heat energy needed to elevate and regulate T_B. By varying the length of time the lights remained on, it was possible to alter the cost for thermoregulation and force the lizard to shuttle more or less frequently, thereby, expending more or less energy for thermoregulation.

Using this operant apparatus the following regimes were used. The lizards were investigated at T_A 10°C with a 45 sec heat reinforcement; at T_A 10°C with a 90 sec heat reinforcement; at T_A 10°C with a 180 sec heat reinforcement; and at T_A 20°C with a 180 sec heat reinforcement.

The mean T_B ($\bar{x}$ T_B) 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. from the time of first response to time of last response). All lizards actively thermoregulated for at least 2 hr during all trials.

The mean shuttle rate (responses/hr) was also calculated for those hours that the lizard actively thermoregulated during that trial.

Mean standard deviations ($\bar{x}$ SD) of T_B and shuttle rate were calculated for periods when the lizard was actively thermoregulating.

The metabolic expenditure during thermoregulation ($\dot{V}O_2$; ml O_2 g^{-1} hr^{-1}) was calculated by adding the standard metabolic expenditure at the experimental T_A to the additional metabolic cost due to having an elevated T_B during behavioral thermoregulation, and the energetic cost of shuttling from one end of the balanced enclosure to the other.

The metabolic cost of shuttling was calculated using the summary data of Schmidt-Nielsen (1972) for locomotor costs in mammals. Lizards and mammals of the same weight have similar energy expenditures for locomotion (Bakker, 1972). At speeds less than 1.1 km/hr, the energy cost of running for lizards is independent of T_B (Dmi'el and Rappeport, 1976). The decrease in total cost of locomotion due to an increase in speed (John-Alder and Bennett, 1981) can be ignored in these experiments due to the low speeds involved (0.0001–0.0040 km/hr).

An analysis of variance with Bartlett's test for homogeneity of variance (Snedecor, 1956) was used to determine whether various parameters (e.g. response rate, $\bar{x}$ T_B, etc.) were significantly different for any trial. A probability level of 0.05 was considered significant if the corresponding χ^2 value for Bartlett's test was not significant.

RESULTS

The accumulated data for trials 10°C 45 sec, 10°C 90 sec, 10°C 180 sec, and 20°C 180 sec were analyzed in three ways. Those trials at 10°C (45, 90 and 180 sec) were compared to each other. The trials run at 10°C were compared to trials run at 20°C. Finally a comparison was made between the trials at 10°C and 20°C where the reinforcement periods were both 180 sec.

The mean T_B ($\bar{x}$ T_B) for trials 10°C 45 sec, 10°C 90 sec, and 10°C 180 sec were significantly different ($P < 0.01$), as were $\bar{x}$ T_B for trials 10°C 45 sec, 10°C 90 sec, 10°C 180 sec, and 20°C 180 sec ($P < 0.001$), and $\bar{x}$ T_B for trials 10°C 180 sec and 20°C 180 sec ($P < 0.05$) (Table 1). These data indicate that $\bar{x}$ T_B varies if reinforcement time or T_A is changed.

The mean shuttle rate ($\bar{x}$ resp/hr) for trials 10°C 45 sec, 10°C 90 sec and 10°C 180 sec were significantly different ($P < 0.01$), as were the $\bar{x}$ resp/hr for trials 10°C 45 sec, 10°C 90 sec, 10°C 180 sec, and 20°C 180 sec ($P < 0.001$). The $\bar{x}$ resp/hr for trials 10°C 180 sec and 20°C 180 sec are not significantly different (Table 1). These data indicate that the shuttle rate varies if the reinforcement time varies, but is not affected by changes in T_A.

The mean standard deviation ($\bar{x}$ SD) for trials 10°C 180 sec and 20°C 180 sec were the only trials found to be significantly different [($P < 0.025$) Table 1]. These data indicate that the $\bar{x}$ SD is not affected by changes in reinforcement time but is affected by changes in T_A.

No significant difference was found in any comparisons of $\dot{V}O_2$ while regulating [($\dot{V}O_2$, reg) Table 1]. Therefore changes in reinforcement time or changes in T_A have no effect on $\dot{V}O_2$, reg.

DISCUSSION

Lizards are ectothermic, but most can maintain T_B well above T_A by behavioral means (Soulé, 1963).

Table 1. Summary of mean body temperature ($\bar{x}$ T_B), mean standard deviations of T_B ($\bar{x}$ SD), mean shuttle rate ($\bar{x}$ resp/hr), metabolic rate per hour for regulating time only ($\dot{V}O_2$ reg), for four experimental conditions; 10°C T_A with a 45 sec heat reinforcement, 10°C T_A with a 90 sec heat reinforcement, 10°C T_A with a 180 sec heat reinforcement, and 20°C T_A with a 180 sec heat reinforcement. All values are mean ± SD with the number of observations indicated for each condition. Five animals were used in each condition.

Condition	N	$\bar{x}$ T_B	$\bar{x}$ SD	$\bar{x}$ resp/hr	$\dot{V}O_2$ reg
10°C 45 sec	25	20.1 ± 2.5	3.1 ± 0.8	15.4 ± 3.7	1.0 ± 0.4
10°C 90 sec	15	23.7 ± 0.8	2.8 ± 0.7	12.1 ± 2.3	1.1 ± 0.1
10°C 180 sec	15	24.8 ± 2.4	3.5 ± 1.0	6.7 ± 2.3	1.1 ± 0.5
20°C 180 sec	15	27.8 ± 1.0	2.0 ± 0.2	7.2 ± 3.0	1.5 ± 0.5

Preferred T_B (PBT) above T_A and the precision of T_B regulation have been used as an index to characterize the divergent thermoregulatory patterns in lizards. Some eurythermal lizards (*Anolis oculatus*) are considered to have secondarily evolved tolerance to a wide variation in T_B that has evolved in response to the absence of competition and ecological release (Ruibal and Philibosian, 1970). Other eurythermal lizards (*G. coeruleus*) have presumably never evolved precise thermoregulatory patterns.

The lack of thermoregulatory patterns normally associated with eurythermality (i.e. imprecise or no T_B regulation, and thermal passivity or wide T_B fluctuations) were not observed here for *G. coeruleus* in any particular thermal regime. *G. coeruleus* is an active and precise regulator of T_B, in a controlled laboratory environment. Feeding schedules were found to be important during preliminary studies. *G. coeruleus* would only thermoregulate for 24 hr immediately after feeding. Therefore, it was necessary to feed the experimental lizards on the day before each trial.

Three behavioral thermoregulatory strategies are possible under the constraints and variations in cost for thermoregulation imposed on the lizards by the experimental design; the lizard could adjust the shuttling rate to maintain a constant T_B; the lizard could alter its mean T_B or precision; or the lizard could adjust the amount of time spent thermoregulating. These are not mutually exclusive possibilities, since the lizards could adjust one or all of the above factors in any combination to alter the metabolic expenditure during behavioral thermoregulation. The lizard could regulate T_B 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/hr for 12 hr that provides a T_B of 20°C may have the same total energy cost as a response rate of 20 responses/hr for 6 hr to maintain a T_B of 28°C.

If *G. coeruleus* maintained its T_B at a constant level, regardless of the metabolic cost ($\dot{V}O_2$, 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 at 10°C (45, 90 and 180 sec) and 20°C 180 sec, with a significant difference in T_B between trials. Thus *G. coeruleus* under different conditions, appears to regulate precisely about different $\bar{x}$ T_B. The T_B selected would appear to depend upon the energy expenditures required to maintain T_B in a given environmental situation.

A lizard would appear to have a lower T_B if it regulated less precisely. For example, if the lizard stops regulating in high cost situations (shorter reinforcement times, lower T_A) and allows T_B to drop to T_A for a time before resuming temperature regulation at the previous level, then the data would show a lower $\bar{x}$ T_B (because of the lower temperature readings) and also a greater variation in standard deviation of $\bar{x}$ T_B between trials undertaken at the same T_A, 10°C. Standard deviations in T_B between trials at 10°C were not significantly different (i.e. there was no tendency for the lizard to allow T_B to approach T_A in high cost situations). Therefore, differences in precision of thermoregulation does not appear to be responsible for the altering of $\bar{x}$ T_B.

If the $\bar{x}$ T_B is an important physiological variable which is maintained at a high value during regulation, then the shuttle rate should increase with a decrease in reinforcement time. Shuttle rate was inversely related to reinforcement time during trials at 10°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 appears to be an important variable for determining the pattern of regulation since shuttling frequencies and $\bar{x}$ T_B between trials at 10°C were adjusted such that the total metabolic costs did not change between these trials.

The metabolic cost did differ significantly between 10°C 180 sec and 20°C 180 sec when the ambient temperature was increased from 10 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 20°C 180 sec than trial 10°C 180 sec (lower SD) but did not change its shuttle rate, therefore the increase in energy expenditures can be attributed to the higher levels of mean T_B and the more precise (lower SD) regulation. Both of these changes are the result of there being a smaller thermal difference between the lizard and its environment at 20°C than at 10°C (i.e. lizards with any particular T_B will gain radiant heat faster and lose heat slower at 20°C.

Another mechanism whereby *G. coeruleus* could adjust the metabolic cost of thermoregulation 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 in time spent thermoregulating for trials at 10 and 20°C.

As the reinforcement period increased, the amount of energy which the lizards expended for resting metabolism increased relative to the amount of energy expended for shuttling (Fig. 2). A comparison of resting metabolic cost ($\dot{V}O_2$ at $T_B = T_A$), temperature maintenance ($\dot{V}O_2$ increment at $\bar{x}$ T_B), and shuttling cost ($\dot{V}O_2$ per meter times shuttling rate) shows

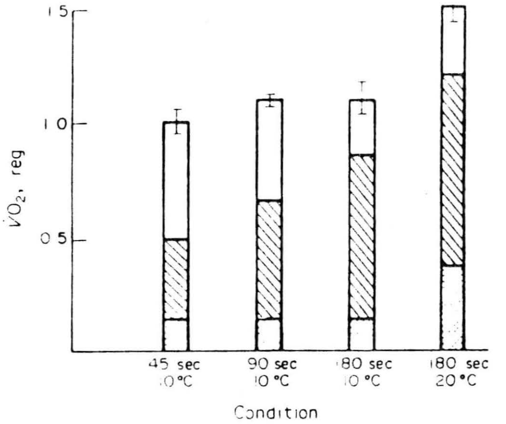

Fig. 2. Histogram of the mass specific $\dot{V}O_2$ reg and its components. The stippled region is the resting metabolic expenditures ($\dot{V}O_2$ at T_A). The hatched region is the metabolic expenditures at PBT ($\dot{V}O_2$ at $\bar{x}$ T_B). The open region is the metabolic expenditures for shuttling ($\dot{V}O_2$/m times the shuttling rate).

that the cost of shuttling is the major cost component during trial 10°C 45 sec, the cost of shuttling and maintaining $\bar{x}\,T_B$ are about equal during trial 10°C 90 sec, and the cost of maintaining $\bar{x}\,T_B$ during trial 10°C 180 sec and trial 20°C 180 sec were the major costs (Fig. 2). The total metabolic costs during trials at 10°C ($\dot{V}O_2$, reg) were not significantly different. The larger metabolic expenditures during trial 20°C 180 sec are due to the larger standard metabolic cost ($\dot{V}O_2$ at $T_B = T_A$).

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 outweighs physiological benefits (Huey, 1974).

It is clear from this study that the term eurythermality can be interpreted in two different ways. If a lizard is to be considered eurythermal in the normal sense, then the levels of $\bar{x}\,T_B$ realized should be of no consequence to the lizards as long as these T_B fall within the lizard's normal activity range (i.e. above critical thermal minimum and below critical thermal maximum). The only metabolic costs associated with thermoregulation in such a eurythermic lizard would be any shuttling cost required to avoid critical minima and maxima. Brattstrom's (1965) field data for T_B of *G. coeruleus* 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. In contrast *G. coeruleus* in a no-cost laboratory thermal gradient will select a T_B of around 29–31°C (personal observation).

However, a second and very different interpretation of eurythermality is indicated by this study. A "eurythermal" lizard such as *G. coeruleus* has a T_B range as narrow as that of a traditional stenothermic lizard (*Dipsosaurus dorsalis*) if the environmentaliy determined metabolic costs of regulating T_B are constant, but the regulated T_B will vary markedly if the environmental costs vary. This effect of cost on T_B regulation is demonstrated by the higher PBT of eurythermic lizards in laboratory thermal gradients than in the field, where there is no metabolic cost for thermoregulation (i.e. no shuttling costs involved).

The observed "eurythermal" patterns of *G. coeruleus* in the field (Brattstrom, 1965; Vitt, 1974) are presumable caused by fluctuations in the environmentally determined costs for regulation, hence variation in PBT, and not precision of T_B regulation.

When *G. coeruleus* is presented with shorter reinforcement times it responds by shuttling more frequently, but at a lower T_B. The important effect of this is that the total metabolic expenditure of lizards during the 12-hr daytime period did not change with a corresponding change in reinforcement time at any given T_A, even though the $\bar{x}\,T_B$ and shuttle rate did alter.

G. coeruleus regulated precisely around a variable preferred T_B in all experiments. In over 1000 hr of detailed observation, the mean deviation from preferred T_B was only 2.8°C with a range of 1.7–4.8°C. The mean deviation from the mean value did not change during the 10°C trials. 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 $\bar{x}\,T_B$. 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 is similar to the findings of Huey and Stevenson (1979) that data used for whole populations may be obscuring precise T_B regulation by individual lizards. The data for *G. coeruleus* also indicated consistent intra-individual variability correlated with body mass.

Patterns of eurythermality and stenothermality 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 environments as stenothermic species within the limits of their critical thermal temperatures. This hypothesis is supported by these experiments where *G. coeruleus* thermoregulated as precisely [± 1.8°C at a high T_B (27.8°C)] as *Dipsosaurus dorsalis* [42.4 ± 1.8°C (Norris, 1953)]. Similarly, purported stenothermic lizards, when placed in high cost environments might decrease their PBT (further experiments are in progress to test this hypothesis). Therefore, evolutionary interpretations (Huey, 1974) of purported eurythermal and stenothermal patterns of T_B regulation in various lizard species may be premature.

SUMMARY

The effect of the metabolic cost of behavioral thermoregulation on the level and precision of body temperature maintenance was investigated for the supposedly eurythermal Northern Alligator Lizard (*Gerrhonotus coeruleus*). An operant shuttle apparatus was used to examine metabolic expenditures at different radiant heat reinforcement regimes. The mean T_B of *G. coeruleus* in each regime was positively correlated to the length of reinforcement, whereas the shuttle rate was inversely correlated to the length of reinforcement. The precision of T_B regulation and the total metabolic expenditures of lizards did not vary significantly for different reinforcement regimes at the same ambient temperature. Apparently eurythermality in *G. coeruleus* is caused by variations in preferred body temperature and not by fluctuations in T_B around the particular regime body temperature. These data indicate that the apparent eurythermality of *G. coeruleus* is the effect of lizards behaviorally regulating to different T_B depending upon the environmentally determined cost of T_B regulation rather than T_B passively following T_A, or random fluctuations in a wide range of normal activity (the classical view of eurythermality). *G. coeruleus* is a precise T_B regulator (i.e. stenothermic) at any constant environmental cost.

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