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COST AND BENEFITS OF LIZARD THERMOREGULATION

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ABSTRACT

Lizards thermoregulate by behavioral and physiological adjustments. The resultant control over metabolic processes is generally assumed to be beneficial. However, these thermoregulatory adjustments have associated costs which, if extensive, make thermoregulation impractical. We extend this idea into an abstract mathematical, cost-benefit model of thermoregulation in lizards. Investigation of the model leads to a set of predictions which includes: (1) the physiologically optimal temperature is not always the ecologically optimal temperature; (2) thermoregulation is beneficial only when associated costs are low; (3) thermal specialists will normally thermoregulate more carefully than thermal generalists unless costs are high; and (4) lizards will thermoregulate more carefully if productivity of the habitat is increased or if exploitation competition is reduced. Data on lizards, where available, generally agree with these predictions.

INTRODUCTION

ALTHOUGH lizards are ectotherms, biologists have known for over thirty years that active diurnal lizards often maintain relatively high and constant body temperatures by making behavioral adjustments; for example, by basking in the sun when cool and moving to the shade when warm (Cowles and Bogert, 1944). A number of complementary physiological adjustments have recently been described (Templeton, 1970). Most workers generally as-

sume that these behavioral and physiological mechanisms of thermoregulation are adaptive, since thermoregulating lizards are likely to avoid dangerously extreme body temperatures and achieve some control over metabolic processes (Cowles and Bogert, 1944; Licht, 1965; Wilhoft, 1958). Yet, beyond these physiological considerations and despite the widespread interest in behavioral thermoregulation as a link in the evolution of endothermy (Bartholomew and Tucker, 1963), no synthetic theory of the ecology of thermoregulation in lizards exists.

Herpetologists have gathered voluminous

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data on behavioral thermoregulation of lizards in the field and laboratory (Brattstrom, 1965). Many of these data consist solely of body temperature records with restricted relevance to analyses of thermoregulation (Heath, 1964). Nonetheless, results from behavioral studies and from energy-balance models have generated certain qualitative and quantitative predictions of thermoregulatory behavior (Bartlett and Gates, 1967; Heath, 1965; Porter and Gates, 1969; Porter, Mitchell, Beckman, and DeWitt, 1973; Porter, Mitchell, Beckman, and Tracy, 1975).

Despite the abundance of data, few conceptual advances have been made because this subject has been dominated by static concepts, such as that most lizards thermoregulate carefully (Bogert, 1959; Templeton, 1970); that the evolution of optimal body temperatures is conservative within taxa (Bogert, 1949a,b; Brattstrom, 1965); and that thermoregulation is normally beneficial. These ideas, grounded on the concept of physiological homeostasis, have been widely accepted. Nonetheless, recent work on some tropical lizards and reanalyses of data on certain temperate species show clearly that a variety of lizards are frequently passive to ambient conditions (thermoconformers) (Alcala and Brown, 1966; Hertz, 1974; Huey, 1974b; Huey and Webster, 1975; Rand and Humphrey, 1968; Ruibal, 1961; Ruibal and Philibosian, 1970; Stebbins, Lowenstein, and Cohen, 1967), that "optimal" body temperatures are quite diverse and evolve rapidly in some genera (Ballinger, Hawker, and Sexton, 1969; Brattstrom, 1965; Clark and Kroll, 1974; Corn, 1971; Huey and Webster, 1976; Pianka, 1969; Soulé, 1963), and that careful thermoregulation may sometimes be maladaptive (DeWitt, 1967; Huey, 1974a,b; Huey and Webster, 1975, 1976; Pianka, 1965; Pianka and Parker, 1975; Regal, 1967; Soulé, 1963). The behavior of lizards obviously cannot be understood solely from physiological considerations, and thus lizard thermoregulation must be more complex than is generally believed.

A more useful conceptual framework for the problem might be obtained by considering both the benefits and costs of thermoregulation. We will argue that there are costs associated with each thermoregulatory act which effectively reduce any resultant physiological gains. Formulation of this basic argument as a mathemat-

ical model of costs and benefits allows us to gain specific insights into the ecology of thermoregulatory behavior of lizards. We shall use the model to predict the optimal amount of thermoregulation as a function of the cost of thermoregulation in various environments, the influences of environmental temperature gradients on body temperature, the influences of competition and predation on thermoregulation, and the relationship between degree of thermal specialization and habitat.

Physiological processes of lizards are strongly influenced by body temperature (Dawson, 1975). In an "ideal" environment, a lizard's gross physiological benefits (e.g., energy gained per unit time) are maximized if the lizard is always active at its optimal body temperature. Conversely, the less time active at that temperature, the lower are the benefits. These or similar premises form the core of a physiological explanation of behavioral thermoregulation within the limits of extreme temperatures.

Thermoregulatory behaviors utilized by lizards include shuttling between sun and shade or hot and cold microenvironments which alter heat flux (Hammel, Caldwell, and Abrams, 1967; Heath, 1965; Spellerberg, 1972c); modifying posture, which alters surface areas exposed to heat sources or sinks (Bartholomew, 1966; Bartlett and Gates, 1967; DeWitt, 1971; Heath, 1965); and regulating activity times (Heatwole, Lin, Villalón, Muñiz, and Matta, 1969; Huey, 1974a; Porter et al., 1973; Schmidt-Nielsen and Dawson, 1964). While lizards derive physiological benefits from such behavior, they must necessarily incur costs (Huey, 1974b; Huey and Webster, 1975; Parker and Pianka, 1973; Pianka, 1965; Pianka and Pianka, 1970; Soulé, 1963). For example, lizards shuttling between sun and shade expend energy in locomotion; moreover, such movements may well increase their conspicuousness to potential predators (Pianka and Pianka, 1970). Additionally, if microhabitats suitable for thermoregulation are unsuitable for food acquisition, net energy input may be reduced. Finally, thermoregulation may interfere with social, feeding, or predator avoidance (DeWitt, 1967) activities.

Costs associated with thermoregulation must be subtracted from gross physiological benefits, and thus reduce the net benefits of activity at particular body temperatures. Since the physiological benefits and the environmentally relat-

ed costs are independent, the physiological optimal temperature is not always the ecologically optimal temperature.

The model which follows is based on the assumption that the extent of thermoregulation is adjusted to maximize net energy gain during some specified period of time. Maximization of net energy gain will in general enable a lizard to deal more readily with environmental contingencies and thus maximize its fitness. Alternatively, recognizing that thermoregulatory strategies are influenced by more than energetic considerations (e.g., opportunities to mate, predator avoidance [DeWitt, 1967; Pianka and Pianka, 1970]), we could directly model gains or losses in fitness (indeed, this can be done simply by relabeling the axes of the following graphs) if all activities could be related directly to fitness. However, the basis for such a model would be more abstract than the present one.

Our model evaluates only the optimal extent of thermoregulation in a given context, not the use of specific thermoregulatory behaviors. However, the selection of optimal behaviors could be determined by a similar reasoning process.

GLOSSARY OF MAJOR SYMBOLS

x	Internal body temperature of lizard, assumed to be uniform throughout body
$b(x)$	Energetic gain per unit time to an active lizard, with body temperature x
x_0	Optimal body temperature (b is maximized)
y	Ambient temperature
$p(y)$	Frequency distribution of ambient temperatures during a specified time period in a specified habitat, given that a lizard uses a particular foraging and social movement strategy which is independent of thermoregulatory strategy
y_c	Lower ambient temperature threshold for activity
k	Thermoregulatory strategy ($0 \leq k \leq 1$) where 0 = perfect thermoregulation ($x = x_0$) and 1 = passivity ($x = y$)
$c(x - y)$	Energetic cost to a lizard per unit time for achieving a body temper-

$b_k(y)$ and $c_k(y)$	Energetic gains and costs to a lizard per unit time using strategy k at ambient temperature y . The transformations from $b(x)$ and $c(x - y)$ are possible because x is a function of y for given k [see equation (1)]
B_k	Total net energetic gain during a given time period while using strategy k

THE MODEL

We will first develop a cost-benefit model and then will use the model to derive predictions about the extent of thermoregulation under different conditions by assuming that an individual lizard acts in a way which maximizes its net energy gain. These predictions will then be compared with information available in the literature.

Consider a lizard in a given microhabitat during a given time period. The microhabitat is assumed to be homogeneous in terms of climate and food availability. The actual activity period within some potential time period is delimited by assuming that lizards are active only when net energy gains are positive. For any given lizard, activity periods vary among microhabitats because of different abundances of food (see Porter et al., 1973, 1975) or predator densities.

The thermoregulatory strategy of a lizard (i.e., whether it will thermoregulate or not) is here analyzed only in the context of a given microhabitat and a given potential activity period. The alternative options for a lizard to change microhabitats or periods of activity could, nonetheless, be analyzed within the conceptual framework of this model.

For the given microhabitat and potential activity period, we assume that the frequency distribution of ambient temperatures (y) encountered by a lizard can be specified, and we denote this frequency distribution $p(y)$. This distribution depends on a lizard's particular foraging and social movement patterns which are assumed to be independent of thermoregulatory activities. (This assumption may be invalid for lizards that appear to give first

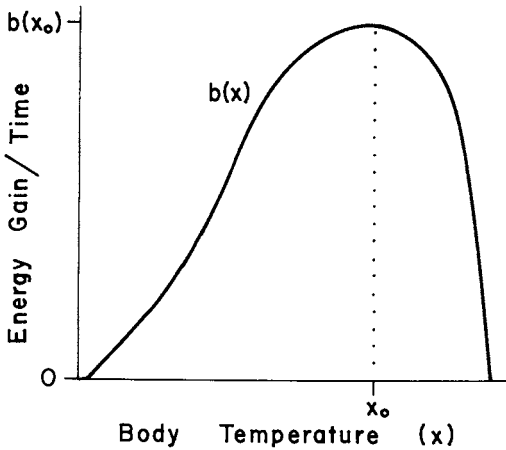


FIG. 1. PHYSIOLOGICAL BENEFIT CURVE

Assumed physiological benefit (energy gained per unit time) to a lizard as a function of body temperature x , where x_0 is the optimal body temperature.

priority to thermoregulatory activities, e.g., *Ameiva leptophrys*—Hillman, 1969).

We assume that the costs and benefits associated with normal activity at different body

temperatures can be specified. We define $b(x)$ as the energetic gain per unit time to a lizard which is active with internal temperature x . The ability of a lizard to gather and process energy is assumed to increase gradually with internal temperature to a single optimal temperature (x_0) and then to decrease steeply as body temperature approaches the upper lethal limit (see Fig. 1). This shape is based primarily on the observation that optimal temperatures of lizards are apparently close to the upper lethal limits (Cowles, 1945; Dawson, 1975; Licht, Dawson, and Shoemaker, 1966). The function $b(x)$ depends primarily on the physiological characteristics of a lizard, but is also influenced by certain environmental factors (e.g., pattern or extent of food availability can alter the function's height or position). [Note that this "benefit" function incorporates all maintenance metabolic costs except those directly due to thermoregulation. Note also that the possibility of two or more relative optima is ignored (Bustard, 1967; Pough, 1974; Regal, 1966).]

A lizard can behaviorally alter its internal temperature and thus change the benefit of activity at any particular time. For simplicity, we set two restrictions. First, we assume the lizard to be active only over the range of body temperatures $x \leq x_0$ (Fig. 1): since the slope of $b(x)$ is probably steeply negative for $x > x_0$ and since such high body temperatures can be hazardous (Dawson, 1975), a lizard should infrequently be active over this range. [Some desert lizards are an exception, at least at midday during summer months (DeWitt, 1967).] Second, we assume that a lizard will only raise its internal temperature above the environmental temperature (thus $x \geq y$): evaporative cooling by panting is probably an emergency measure for most lizards (Cowles and Bogert, 1944; Crawford, 1972; Mayhew, 1968).

We define a lizard's thermoregulatory strategy (k) to relate algebraically its internal temperature (x) and the environmental temperature (y). Although a large class of possible functional equations exists, we consider only the simplest,

$$x = x_0 + k(y - x_0) \quad (1)$$

The value of k specifies the intensity of thermoregulation ($0 \leq k \leq 1$). If $k = 0$ (perfect thermoregulation), the body temperature always equals the optimal temperature ($x = x_0$).

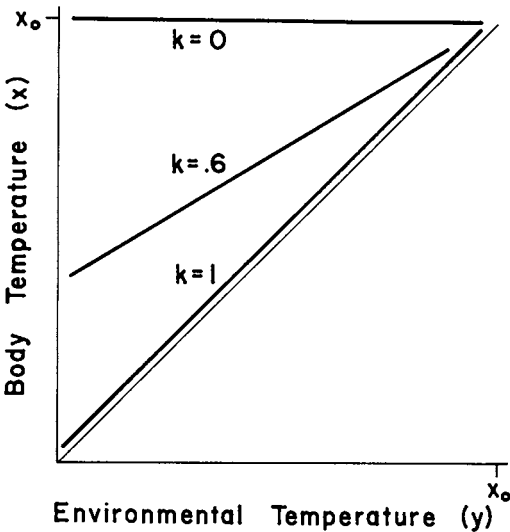


FIG. 2. BODY TEMPERATURE AND THERMOREGULATORY STRATEGY

Body temperature of a lizard at different environmental temperatures for three possible thermoregulatory strategies, k . See Equation (1) in text. The variance about the regression would partly reflect the level of spatial or temporal heterogeneity in a habitat (e.g., shifting patches of light in a forest or rapid fluctuations in air temperature).

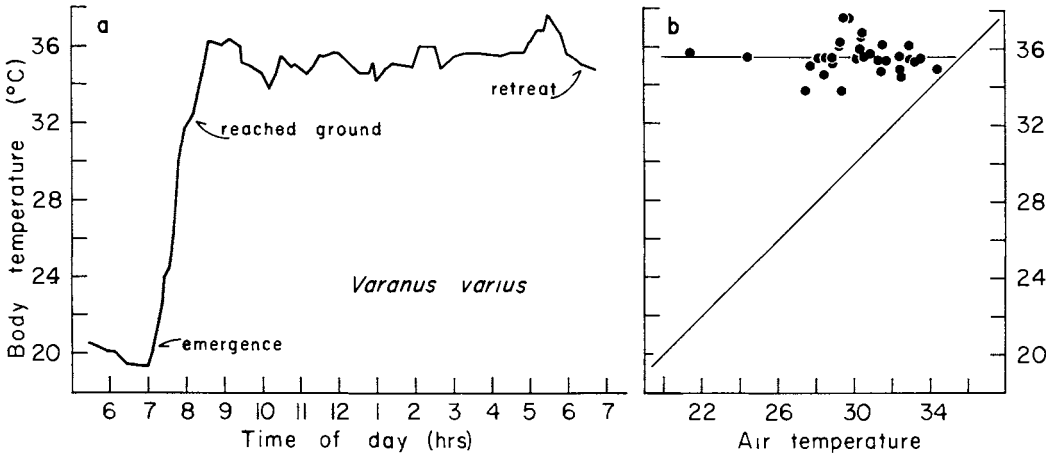


FIG. 3. BODY TEMPERATURE OF *Varanus varius*

Body temperature of *Varanus varius* of Australia during a single day (left) and vs. air temperature (using only temperatures once lizards had reached ground; several day's data pooled). Regression slope of body vs. air temperature (an estimate of thermoregulatory strategy, k) is not significantly different from 0. Data of Stebbins and Barwick (1968), courtesy of R. C. Stebbins; recorded by means of radio telemetry.

If $k = 1$ (passivity or thermoconformity), the internal temperature always equals the environmental temperature ($x = y$) (Fig. 2). [Apparently, some lizards can thermoregulate nearly perfectly when active. The slope of the body vs. air temperature regression (an estimate of k) for *Varanus varius* (Fig. 3) is, in fact, not significantly different from 0.]

Finally, we need an expression for the cost of thermoregulation and write $c(x - y)$ as the average energetic cost to a lizard per unit time for achieving a body temperature x while the environmental temperature is y (for simplicity, we assume that the cost depends only on the difference between x and y , not on their actual values). The cost incurred from thermoregulation should be a monotonically increasing function of the magnitude of the difference between x and y (see Fig. 4b); and the slope should depend primarily on the physical properties of the habitat (e.g., degree of shading) and secondarily on the physiological characteristics of a lizard (e.g., rates of heat gain and loss) and the magnitude of fluctuations in environmental temperature. As stated previously, normal maintenance "costs" are incorporated into $b(x)$, not $c(x - y)$, since maintenance costs occur whether the lizard thermoregulates or not.

Because x is a function of y as specified by (1), we can write $c(x - y)$ as a function of y

only for a given value of k . Thus $c_k(y)$ is the cost of thermoregulation per unit time while using strategy k at environmental temperature y . Similarly, for a given k , $b_k(y)$ is the energy gain per unit time at environmental temperature y . Substituting (1) for x in $c(x - y)$ and $b(x)$, we get

$$c_k(y) = c[(1 - k)(x_0 - y)] \tag{2}$$

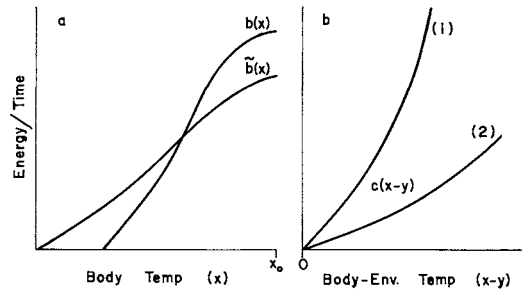


FIG. 4. BENEFIT AND COST CURVES

(a), benefit curves of a thermal specialist $b(x)$ and a thermal generalist $\tilde{b}(x)$ with the same x_0 . The integral of $b(x)$ is assumed constant by the Principle of Allocation. The crossing point of the two b curves is referred to in the text as x^* . (b), two possible cost curves for maintaining a difference between body and environmental temperatures ($x - y$). The cost curves are not necessarily concave. Costs are considerably greater for curve (1).

and

$$b_k(y) = b[x_0 - k(x_0 - y)]. \tag{3}$$

If the environmental temperature is y , then the net energy gain is simply

$$b_k(y) - c_k(y). \tag{4}$$

A lizard's total gain in energy, B_k , for the given time period while using strategy k is found by summing these net energy gains and weighting this sum by the frequency of occurrence of the possible environmental temperatures encountered for which the integrand is positive:

$$B_k = \int_{y_c}^{x_0} [b_k(y) - c_k(y)] p(y) dy \tag{5}$$

where y_c is the value of y for which $b_k(y_c) = c_k(y_c)$ (thus, the net benefit is 0). The optimal strategy of thermoregulation, that which maximizes B_k , can be determined simply by calculating B_k for all k .

To learn about the dependence of B_k on k , we consider representative forms for b and c . [We need not choose specific algebraic forms since a graphical analysis illustrates general features of the model.] For $x \leq x_0$, we assume that b has forms such as those of a thermal generalist and a thermal specialist (Fig. 4a). Two of the possible cost functions are shown in Fig. 4b. Curve (1) represents a high-cost habitat, presumably with few basking sites or with large fluctuations in temperature. Curve (2) represents a low-cost habitat, with more basking sites

or smaller fluctuations in temperature, or both.

To determine the value of k maximizing B_k for these situations, we first need to compute the endpoints, B_0 and B_1 . For $k = 0$, $b_0(y) = b(x_0)$ and $c_0(y) = c(x_0 - y)$. Therefore,

$$B_0 = \int_{y_c}^{x_0} [b(x_0) - c(x_0 - y)] p(y) dy \tag{6}$$

where y_c is the value for which $c(x_0 - y_c) = b(x_0)$. Graphically, B_0 is the area between the $b_0(y)$ and $c_0(y)$ curves (Fig. 5a), weighted by $p(y)$. For $k = 1$ (no regulation), $b_1(y) = b(y)$ and $c = 0$ (by assumption). Therefore,

$$B_1 = \int_{y_c}^{x_0} b(y) p(y) dy \tag{7}$$

where y_c is the value for which $b(y_c) = 0$. B_1 is simply the area under the $b_1(y)$ curve (Fig. 5b), weighted by $p(y)$.

In the two extreme cases, that of a specialist in a "low-cost" habitat and that of a generalist in a "high-cost" habitat, the model predicts the obvious result for almost any distribution of environmental temperatures. In the first case [curve (1), Fig. 6a], the lizard will regulate as carefully as possible ($k = 0$ maximizes B_k); in the second case [curve (2)], the lizard will remain passive ($k = 1$). The actual shapes of the curves in Fig. 6 depend on $p(y)$, but their general character does not.

The results are less obvious and more interesting when we consider the other two possibilities, that of a generalist in a low-cost habitat and a specialist in a high-cost habitat. In these cases, B_0 and B_1 could be approximately the same. When this is true, neither complete regulation nor complete passivity is clearly better. In fact, an intermediate strategy (partial thermoregulation) could be optimal under some conditions. Three possible cases are shown in Fig. 6b. For curves (1) and (2), the model predicts that a lizard would partly regulate its temperature, but not completely. However, for curve (3), an intermediate k is less beneficial than either complete regulation or passivity.

The shape of the B_k curve depends on the exact nature of the relationship between the $b(x)$ and $c(x - y)$ curves. To illustrate the different possibilities, we consider $b_k(y) - c_k(y)$ [the net gain in energy at temperature y with strategy k , see (2) and (3) above] for some typical, arbitrary value of y (say y^*). The graphs

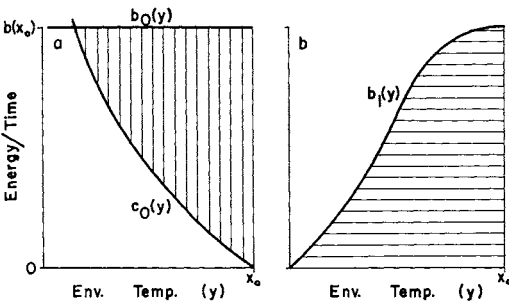


FIG. 5. NET BENEFITS OF THERMOREGULATION AND PASSIVITY

In (a), area shaded with vertical lines represents $b_0(y) - c_0(y)$. When weighted by $p(y)$, this equals the net benefit for perfect thermoregulation ($k = 0$). In (b), area shaded with horizontal lines represents $b_1(y) - c_1(y)$ where $c_1(y) = 0$. When weighted by $p(y)$, this equals net benefit for passivity ($k = 1$).

of $b_k(y^*)$ and $c_k(y^*)$ vs. k have the same shape as graphs of $b(x)$ and $c(x - y)$. [This can be seen with $b_k(y)$, for example, by noting that $b_k(y^*) = b(x_0 - k(x_0 - y^*))$.] The only difference is a linear change of the independent variable from x to $x_0 - k(x_0 - y^*)$. This change effectively expands that portion of the $b(x)$ curve between y^* and x_0 and that portion of the $c(x - y)$ curve between 0 and $x_0 - y^*$ to the range of $0 \leq k \leq 1$ (Fig. 7).

As examples we find B_k for a given b (Fig. 7a) and three different values of c (Fig. 7b) by considering $b_k(y^*) - c_k(y^*)$ at the arbitrary value of $y(y^*)$, indicated on the horizontal axes in Fig. 7a, b). The corresponding $b_k(y^*)$ and $c_k(y^*)$ curves are shown in Fig. 7c.

Because of the geometric properties of curve (3) of Fig. 7b, a k value of about 1/2 (Fig. 7c) provides the maximum net benefit at $y = y^*$. That is, partial thermoregulation yields greater net benefits than either complete thermoregulation or passivity. If environmental temperatures are frequently in this range, then B_k will be approximately like curve (1) in Fig. 6b.

With curve (2) of Fig. 7b, the cost curve is similar but not so convex. The benefits of partial thermoregulation are not as pronounced as in curve (1) of Fig. 7b, so the B_k curve will be more like curve (2) in Fig. 6b. Finally, for curve

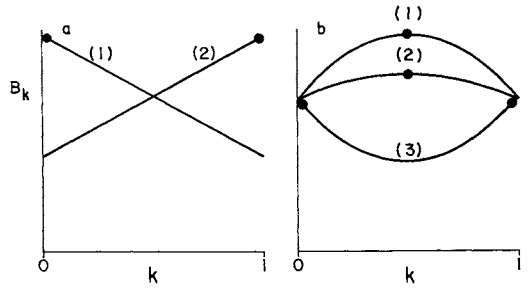


FIG. 6. TYPES OF NET BENEFIT CURVES
 (a), total net benefits (B_k) as functions of k . B_k for a thermal specialist in a low-cost environment, Curve (1), is maximized at $k = 0$; B_k for a thermal generalist in a high-cost environment, Curve (2), is maximized at $k = 1$. (b), some possible shapes of B_k curve. In both (a) and (b) the exact shapes of the curves would depend on $p(y)$. Only their general character is given here. Heavy dots indicate optimal strategy.

(1) (Fig. 7b, c), either $k = 0$ or $k = 1$ could be the optimal strategy, since an intermediate degree of thermoregulation will be disadvantageous [curve (3) of Fig. 6b].

We can see that for even the simplest kind of optimization model of thermoregulatory

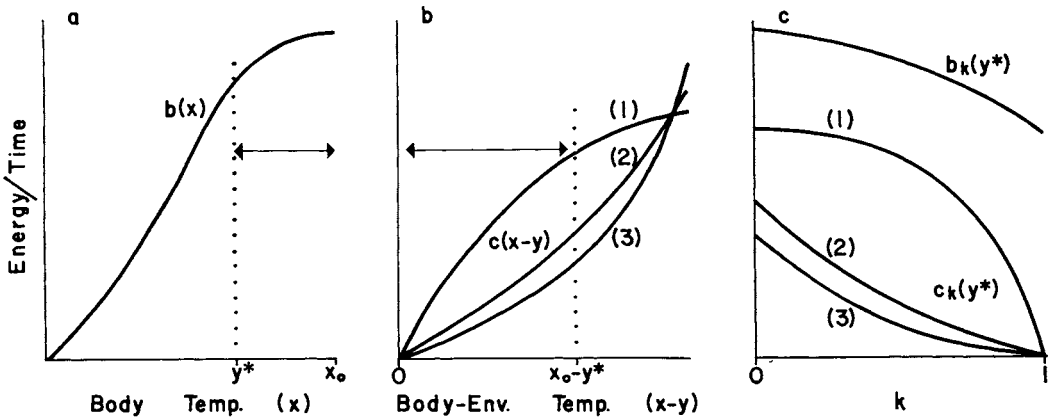


FIG. 7. BENEFIT, COST, AND NET BENEFIT CURVES

In (a), benefit curve for a lizard, the relevant portion of the curve discussed in the text is indicated with an arrow (y^* to x_0). In (b), three possible cost functions, relevant portions are indicated with an arrow (0 to $x_0 - y^*$). (c), gives graphs of $b_k(y^*)$ and the three possible $c_k(y^*)$ as functions of k for the benefit and cost curves in Fig. 6a,b. B_k is determined by the difference between $b_k(y^*)$ and $c_k(y^*)$. For curves (2) and (3), an intermediate level of thermoregulation is optimal; but for curve (1), only perfect thermoregulation or complete passivity could be optimal. See text.

behavior, a variety of results is possible. Present data are insufficient to explore all of the model's consequences. However, some predictions do not depend greatly on the exact functional forms of b and c . In Fig. 6b, for example, any changes in the system which cause B_0 to be larger or B_1 to be smaller will result in a lower value of k being optimal. We cannot say how much lower without more information: the optimal strategy could either be very sensitive [curve (2) of Fig. 6b], or insensitive [curve (1) of Fig. 6b] to changes in one of the functions. In the extreme, the optimal strategy could change abruptly from no regulation to complete regulation [curve (3) of Fig. 6b].

As previously stated, our model depends on the assumption of particular forms for the b , c , and p functions which are determined by the microhabitat and the potential activity period. The possibility of a shift to other activity periods or other microhabitats could be considered by calculating the B_k functions for the other habitats and periods using the appropriate b , c , and p functions. In this way, the relative merits of microhabitats and time periods could be compared.

PREDICTIONS AND DISCUSSION

In the following examples, predictions from the model are derived by fixing certain components of the model while varying others and then by determining the relative effects on B_0 and B_1 . For example, to determine the effect on B_k of lowered environmental temperatures, we lower $p(y)$ and hold b and c constant. The derived prediction can then be compared with field data when available.

Estimates of certain parameters are prerequisites for testing these predictions. The belief of early workers (e.g., Cowles and Bogert, 1944), that the mean body temperature (MBT) of lizards active in the field is the optimal body temperature (x_o), was superseded by a later realization that the MBT is merely the result of a compromise between physiology and ecological reality (DeWitt, 1967; Heatwole, 1970; Licht, Dawson, Shoemaker, and Main, 1966; Pianka and Pianka, 1970; Regal, 1967; Soulé, 1963). Later workers used the body temperature selected by lizards in laboratory thermal gradients, the "preferred" body temperature (PBT), to index optimal body temperatures.

With some exceptions, many physiological processes in fact proceed optimally near the thermal preferendum (reviewed by Dawson, 1975). However, because the PBT may (or may not; see Licht, 1968) be sensitive to the type of gradient used, acclimation, physiological state, simultaneous presence of conspecifics, hormonal state, and time of day (Ballinger, Hawker, and Sexton, 1969; DeWitt, 1967; Garrick, 1974; Hutchinson and Kosh, 1974; Mueller, 1970; Regal, 1966, 1967, 1971), PBT's, particularly when obtained by different workers, must be interpreted with caution. Additionally, because those laboratory and field conditions which can influence thermoregulatory behavior are never identical, PBT's can serve only as crude indexes of optimal body temperatures (x_o) in the field.

Some predictions require estimates of the width of the $b(x)$ curve (sometimes called "thermal niche breadth"). Relatively few workers (Brattstrom, 1968; Heatwole, 1970; Huey and Webster, 1975; Kour and Hutchinson, 1970; Licht, 1964b; Pianka, 1965; Ruibal and Philibosian, 1970; Snyder and Weathers, 1975; Soulé, 1963) have considered this aspect of thermal biology. Possible indexes of thermal niche breadth include the range of temperature over which a physiological or behavioral performance (e.g., strength of muscle contraction, ability to capture prey, growth rate) is above some arbitrary performance level (Licht, 1964b), acclimation ability (Brattstrom, 1968; Levins, 1969), variance of the PBT (Pianka, 1966), or the range of temperature between upper and lower critical (or lethal) temperatures (Snyder and Weathers, 1975) (see also Heath, 1965; Heatwole, 1970). Field estimates, such as variance in body temperature (Pianka, 1966; Ruibal and Philibosian, 1970; Soulé, 1963) or range of MBT's (Huey and Webster, 1975, 1976; Ruibal and Philibosian, 1970) are less reliable, since both measures are sensitive to the range of habitats and time periods sampled (Huey and Webster, 1975, 1976; Soulé, 1963). Unfortunately, the degree of concordance among these diverse indexes is at present unknown.

Estimates of the cost of raising body temperature are also required. This cost should be proportional to the distance necessary for shuttling between sun and shade or hot and cold microenvironments (Huey, 1974b), propor-

tional to body size (thus inversely proportional to heating rate), and proportional to the magnitude of fluctuations in environmental temperatures. It should often be possible to rank habitats in terms of costs of thermoregulation: for example, costs of raising body temperature should be greater in closed forests than in more open habitats. [In hot deserts at midday during summer, lizards incur a cost of seeking cooler microenvironments that will be *inversely* proportional to the degree of openness of the desert. However, we emphasize that this is a problem separate from that considered here, that is $x \leq x_0$.]

Finally, we need an estimate of k . The slope of the regression of body vs. shaded air temperature for sunny time periods is one index (e.g., see Fig. 3). [Temperatures of lizards tethered in the shade would be more appropriate estimates of y than shaded air temperatures, but to determine these is generally impractical.] Unfortunately, this statistic is rarely published. Variance in body temperature is strongly correlated with heterogeneity of local thermal environments (Fig. 8; Huey and Webster, 1975, 1976; Soulé, 1963). Thus, a low variance in body temperature need not imply that lizards thermoregulate behaviorally or physiologically (Heath, 1964; Rand and Humphrey, 1968); rather, it may merely reflect a stable thermal microenvironment. Variance in body temperature must be used with caution.

I. Effects of Differing Costs of Thermoregulation

First consider the effect of a change only in the cost function, with p and b constant. This corresponds to a situation of a single species or two closely related species living in two habitats which differ only in the cost of thermoregulation, either because of a reduced abundance of basking sites or because of increased magnitude of fluctuation in ambient temperatures (Fig. 9a). For all reasonable forms for c and b , we would predict that a lower value of k (increased thermoregulation) would be optimal in the habitat with the lower cost because B_1 would be unchanged while B_0 would necessarily increase (Fig. 9b). In addition, lizards can probably be active over broader ranges of ambient temperatures in habitats with lower costs because y_c would be lower.

Lizards living in shaded forests (excluding

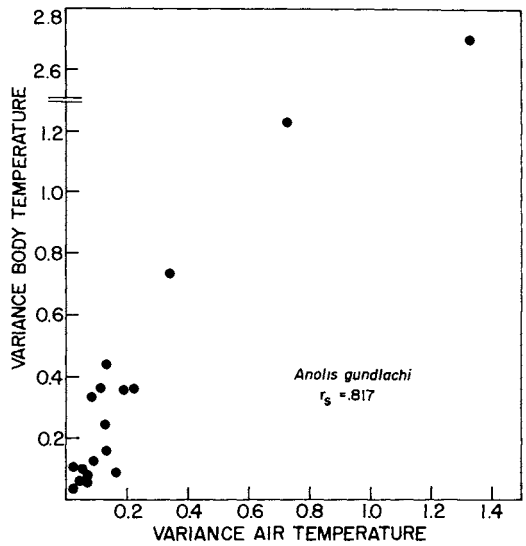


FIG. 8. BODY VS. AIR TEMPERATURE VARIANCE IN A LIZARD
Correlation of variance in body and air temperature ($r_s = 0.817$, $P < 0.01$) for samples of *Anolis gundlachi* in Puerto Rico. From Huey and Webster, 1976.

the canopy), where costs of raising body temperature should be much higher than in open habitats (patches of sun for basking are more widely spaced in forests), tend not to bask and seemingly are relatively passive to ambient conditions (Hertz, 1974; Huey and Webster, 1975, 1976; Rand, 1964a; Ruibal, 1961; Ruibal

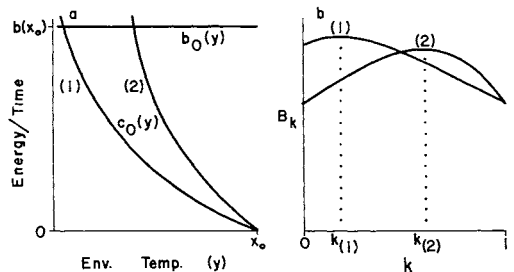


FIG. 9. NET BENEFITS IN A HIGH-COST AND IN A LOW-COST HABITAT

(a), $b_0(y)$ vs. $c_0(y)$ for a high-cost (Curve 2) and a low-cost (Curve 1) habitat. (b), B_k curves computed from Fig. 9a; note that B_0 is greater for the lizard in the low-cost habitat (Curve 1), but that B_1 is the same for both lizards (Curves 1 and 2) since $c_1(y) = 0$, by assumption.

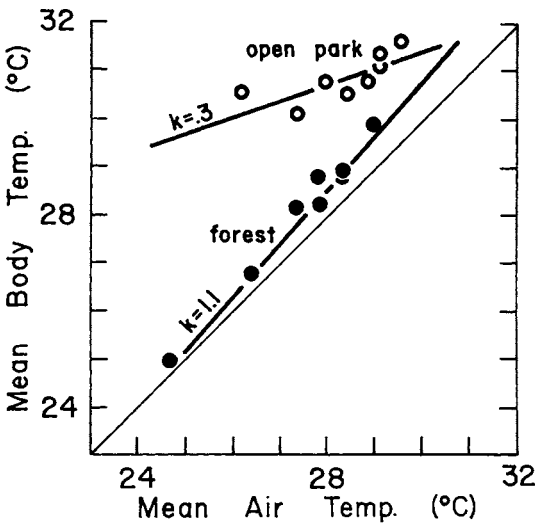


FIG. 10. THERMOREGULATORY STRATEGY OF A LIZARD IN TWO HABITATS

Mean body vs. mean air temperature of *Anolis cristatellus* in a low-cost habitat (open park) and a high-cost habitat (forest) (data of Huey, 1974b). These lizards thermoregulate more carefully in the low-cost habitat (lower k). Only post-sunrise, sunny census periods included. [Slope of regression (fitted by least-squares) indexes the thermoregulatory strategy, k .]

and Philibosian, 1970). For example, in Bêlêm, Brazil, all seven edge and open habitat lizards are baskers, whereas at least five of seven forest species are non-baskers and are probably relatively passive (Rand and Humphrey, 1968). Similarly, three Cuban *Anolis* living in open or edge habitats are heliothermal whereas two forest-dwelling species are not (Ruibal, 1961). *Anolis cristatellus*, occupying both an open park and an adjacent well-shaded forest in lowland Puerto Rico (Huey, 1974b), thermoregulates carefully only in the open park ($k = .3$, Fig. 10), where certain costs are demonstrably lower than in the forest (where $k = 1.1$). *Anolis sagrei* on Great Abaco Island behaves similarly (Lister, 1974).

Pianka (1965) and Parker and Pianka (1973) have suggested that careful thermoregulation would be relatively economical for arboreal desert lizards because of the close proximity of perch sites differing radically in microclimates. Indeed, the two arboreal species (*Sceloporus magister* and *Urosaurus ornatus*) had

a lower variance in body temperature than other flatland U.S. desert lizards.

Nocturnal geckos, skinks, and pygopodids are perhaps the extreme cases. At night, opportunities for raising body temperature are few at best (thus c is large): not surprisingly, gecko temperatures closely approximate environmental temperatures (Parker and Pianka, 1974; Pianka and Pianka, 1976) and are often 5° to 10° below "preferred" body temperatures in laboratory thermal gradients (Licht, Dawson, Shoemaker, and Main, 1966; Vance, 1973; but see Parker and Pianka, 1974). During the day some geckos, however, can and may thermoregulate under bark or rock flakes (Bustard, 1967) and achieve temperatures near preferred levels (Licht, Dawson, Shoemaker, and Main, 1966). [Two distinct optimal temperatures might be involved, a lower one for foraging at night and a higher one for digestion during the day (Bustard, 1967). However, because the temperature for maximal skeletal-muscle twitch tension closely approximates the PBT of geckos (Licht, Dawson, and Shoemaker, 1969), this hypothesis is unsupported.]

Not all lizards living in "high-cost" habitats are entirely passive to ambient conditions while active. Some mobile terrestrial forest lizards, such as *Kentropyx calcaratus*, follow sun flecks on the forest floor (Rand and Humphrey, 1968). For such species, $p(y)$ is clearly not independent of the thermoregulatory strategy (see section, The Model). Note also that the relative advantage of thermoregulation in "low-cost" habitats is reduced as environmental temperatures approach x_0 . In fact, when $y = x_0$, $B_0 = B_1$ because $c_k(y) = 0$ [see Equations (6) and (7)]. As possible examples, only montane populations of *Anolis oculatus* on Dominica (Ruibal and Philibosian, 1970) and *A. marmoratus* on Guadeloupe (Huey and Webster, 1975) are known to bask, even though both species occur in open habitats in the lowlands. [Alternatively, if overheating is a problem for these lowland anoles, non-basking behavior could reflect avoidance of sunny, hot perches.]

As a corollary, lizards will generally be active at body temperatures closer to optimal in habitats with lower costs. With reservations previously discussed on equating "preferred" with optimal field temperatures, data on *Anolis cristatellus* seemingly support this prediction (Huey, 1974b; Huey and Webster, 1976). Body

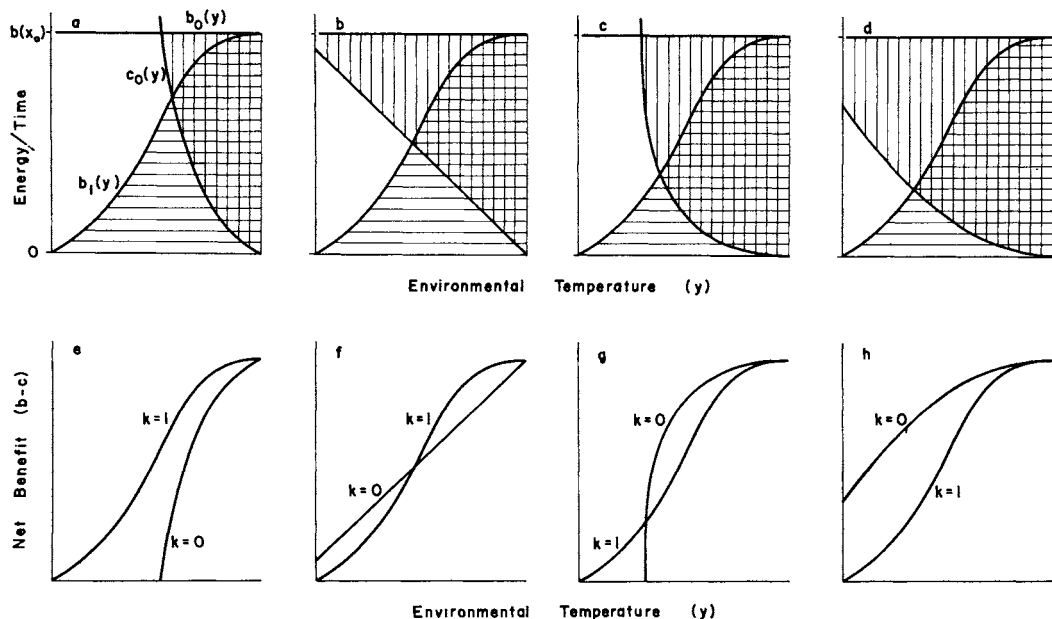


FIG. 11. BENEFIT, COST, AND NET BENEFIT CURVES

(a - d), benefit and cost curves of a lizard in four habitats with differing cost functions. Net benefit, weighted by $p(y)$, if $k = 0$ is indicated by the area hatched with vertical lines; net benefit if $k = 1$ is indicated by the area hatched with horizontal lines. In (e-h), net benefit curves of $k = 0$ and $k = 1$ are shown for the four respective cases above. Curve $k = 1$ in each case represents $b_1(y) - c_1(y) = b_1y$. Curve $k = 0$ represents $b_0(y) - c_0(y)$.

temperatures of lizards in the open park are much closer to the PBT than are those of lizards in the forest, which may be as much as 4° to 5°C below the PBT at certain times of day. (Note, however, that air temperatures are also lower in the forest; thus, $p(y)$ is not the same.)

II. Ambient Temperatures and Thermoregulation

We next consider a situation in which a species lives in habitats with different mean environmental temperatures: for example, habitats differing latitudinally or altitudinally (spatial differences), or the same habitat at different times of day or seasons (temporal differences). In terms of the model, we fix b (thus we assume that acclimatization and geographic variation are unimportant) and c and consider different mean p 's.

The effect of a change in the mean of $p(y)$ is variable and depends on the relationship of the b and c curves. Graphically, we can determine the relative net benefit of the two extreme

strategies ($k = 0, k = 1$) by comparing the area (horizontal hatching) under the $b_1(y)$ curve with the area (vertical hatching) under $b_0(y) - c_0(y)$ (Fig. 11, a-d). For example, if the area under $b_1(y)$ is greater, $k = 1$ is better than $k = 0$. Such comparisons result in four reasonable pairs of curves of net benefits (Fig. 11, e-h; others are possible). When multiplied by $p(y)$, these lower curves determine values of B_0 and B_1 [see Equations (6) and (7)].

In Fig. 11a, costs of perfect thermoregulation rise steeply (this might represent the situation for a lizard in a closed-canopy forest) and B_1 will be greater than B_0 (Fig. 11e) for any y except $y = x_0$. Lowering the mean of $p(y)$ would increase the difference between B_1 and B_0 . Thus, if $k = 1$ were not already the optimal strategy, then k would increase somewhat. The reverse is true in Fig. 11d: here costs of thermoregulation are low (perhaps an open habitat), and $B_0 > B_1$ for any y except $y = x_0$. If $k = 0$ were not already the optimal strategy, then the optimal value of k would decrease with a lowering of ambient temperature (Fig. 11h).

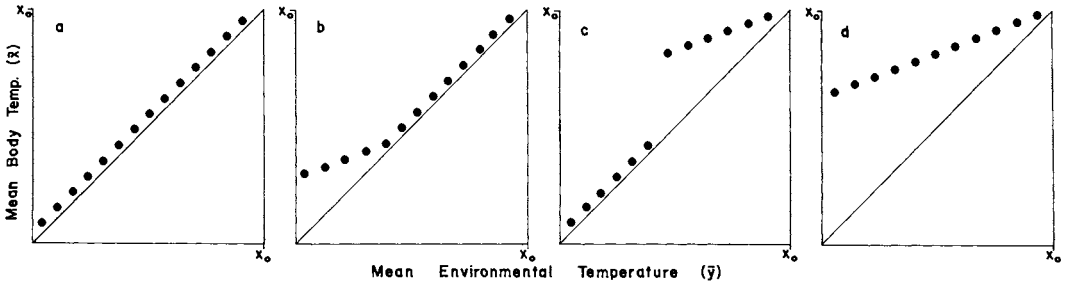


FIG. 12. EXPECTED MEAN BODY TEMPERATURES AT VARIOUS MEAN ENVIRONMENTAL TEMPERATURES

Curves of average measured body temperatures vs. average environmental temperature of lizards corresponding to the four cases illustrated in Fig. 11. Note that body temperatures are directly influenced by environmental temperatures, and that the influence can be smooth or abrupt.

Regulation is advantageous at lower environmental temperatures in Fig. 11b,f, but at higher environmental temperatures in Fig. 11c,g. In these cases, there could be an abrupt transition from little or no regulation to nearly complete regulation. For example, in Fig. 11f we would expect to find regulation at lower temperatures, but passivity at high temperatures.

While the effect of a change in $p(y)$ on k is thus complex, the effect on the mean body temperature is relatively straightforward. In all cases in Fig. 11, the mean body temperature (MBT) should be lowered in response to lower ambient temperatures; however, the magnitude of change in MBT per degree change in y depends on whether more or less regulation was optimal. (This is shown graphically in Fig. 12 where expected MBT's for cases in Fig. 11 are plotted against particular average ambient temperatures.) A change in $p(y)$ also affects the lower temperature threshold of activities (y_c). When more regulation is favored at low ambient temperatures, y_c would be lower, and thus the activity range would increase. Conversely, when less regulation is favored, y_c should be higher; and the activity range would decrease.

Early field work, which suggested that body temperatures were relatively unaffected by changes in ambient temperatures, was interpreted as evidence of the efficacy of behavioral thermoregulation (Bogert, 1949a, b, 1959). Reanalysis of some old data (Brattstrom, 1965; Clark and Kroll, 1974), however, plus the addition of recent information requires a more flexible view of body temperatures in the field.

Changes in ambient temperature, correlated with the following, are known to influence body temperature directly: elevation (Brattstrom, 1965; Clark and Kroll, 1974; Huey and Webster, 1975, 1976; Ruibal and Philibosian, 1970; Fig. 13a), habitat (Clark and Kroll, 1974; Huey, 1974b; Huey and Webster, 1975, 1976; Lister, 1974; Ruibal and Philibosian, 1970; Fig. 13b), time of day (Deavers, 1972; Heatwole, 1970; Hertz, 1974; Huey, 1974b; Huey and Webster, 1975, 1976; Jenssen, 1970; Kiester, 1975; Ruibal, 1961; Stebbins and Barwick, 1968; Fig. 13b), latitude (Parker and Pianka, 1975; Pianka, 1965, 1970; Vitt, 1974; but see Clark and Kroll, 1974; Fig. 13c), season (Burns, 1970; Deavers, 1972; Gates, 1963; Pianka and Pianka, 1976; Mayhew, 1963; Mayhew and Weintraub, 1970; McGinnis, 1966; Pianka, 1971; Pianka and Pianka, 1976; Fig. 13d), and weather (Clark and Kroll, 1974; Heatwole, 1970; Licht, Dawson, Shoemaker, and Main, 1966; Huey and Webster, 1976; Packard and Packard, 1970; Ruibal and Philibosian, 1970; Stebbins, Lowenstein, and Cohen, 1967).

The foregoing assumes, of course, that lizards do *not* shift habitats or activity times along gradients of ambient temperatures. Such shifts can alter p and c functions in ways which reduce the above postulated influence of y on body temperature. For example, occupation of more exposed habitats and slopes at higher elevation by *Sceloporus jarrovi* (thereby altering c and p) may explain why body temperatures of this species are unrelated to elevation over a 1200 m altitudinal gradient (Burns, 1970). Similar habitat and microhabitat shifts occur in other

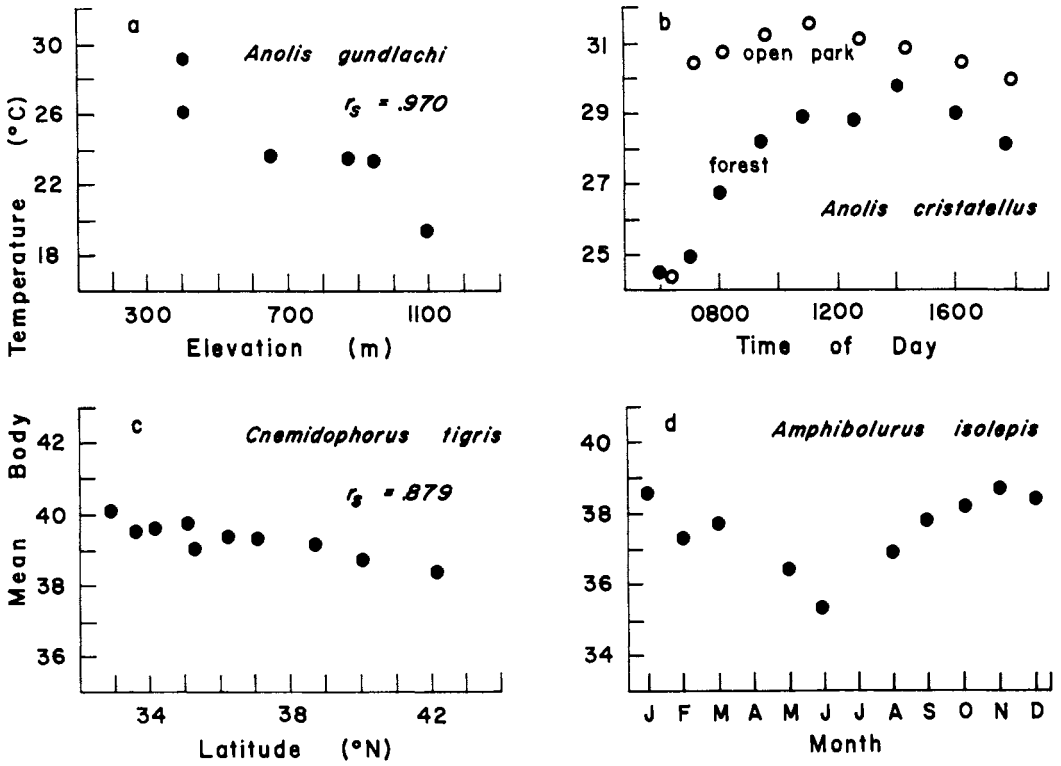


FIG. 13. ENVIRONMENTAL INFLUENCES ON MEAN BODY TEMPERATURE

(a), mean body temperature (MBT) vs. elevation for *Anolis gundlachi* on Puerto Rico (from Huey and Webster, 1976). (b), MBT vs. time of day for *Anolis cristatellus* in two habitats in Puerto Rico (from Huey, 1974b). (c), MBT vs. latitude for *Cnemidophorus tigris* in deserts of North America (from Pianka, 1970). (d), MBT vs. month of collection for *Amphibolurus isolepis* in Australia (from Pianka, 1971).

species along latitudinal, altitudinal, and seasonal ambient temperature gradients (Campbell, 1971; Clark, 1973; Fitch, 1954; Huey and Webster, 1976; Morafka and Banta, 1973; Mueller, 1969; Rand, 1964a), and probably reduce the influence of environmental differences (Bogert, 1949a, b).

Shifts in time of activity can have the same effect. Many lizards are active only at midday during cool and cold seasons but become active early and late in the day in summer (Mayhew, 1964; Pianka, 1969; Porter et al., 1973). [Moreover, lizards active in winter tend to be juveniles or subadults, for which surface-area to volume ratios are favorable and reduce costs of raising body temperature when environmental temperatures are low (Cowles, 1941, 1945).] For some desert lizards (*Cnemidophorus tigris* and *Uta stansburiana*, Pianka, 1965, 1970;

Parker and Pianka, 1975), mean time of activity is directly related to latitude; and time of activity seems directly related to altitude in the few species examined (Alcala, 1966; Duellman, 1965).

Two lizards superficially show a relation between body and ambient temperatures which is opposite to that proposed here. *Anolis limifrons* (Ballinger, Marion, and Sexton, 1970) and *Sceloporus occidentalis* (McGinnis, 1970) have lower body temperatures during warm seasons (dry season in Panama) and on hot days, respectively (see also Soulé, 1968). Ballinger, Marion, and Sexton (1970) noted that a lower body temperature might be adaptive during the dry season by reducing evaporative water loss (Templeton, 1970; Warburg, 1965); thus using our terminology, x_0 would be shifted to a lower temperature during dry periods.

The magnitude of a change in body temperature in response to a given change in y may be related to the width of the $b(x)$ function. Thermal specialists [narrow $b(x)$] should show a smaller change in body temperature because the generalist gains benefits over a much broader range of environmental temperatures and because specialists have more to gain from being active at particular body temperatures (see below). We expect, therefore, thermal specialists to be more restricted in their distribution along environmental gradients or to show more pronounced habitat or temporal shifts (assuming, of course, that local adaptation among populations is minimal).

III. Optimal Temperatures in Differing Thermal Environments

Lizards with benefit curves [$b_1(y)$] which overlap considerably with the distribution of environmental temperatures $p(y)$ will receive greater net benefits than lizards with $b(x)$ curves for which there is less overlap. Thus, in high-temperature environments we would expect primarily lizards adapted to high temperatures. [Acclimatization, by shifting $b(x)$ curves, is similarly adaptive as long as the incurred physiological costs are less than the derived benefits.] This prediction refers primarily to habitat selection. For those genera in which optimal body temperatures are sensitive to selective pressures, however, this prediction also holds for evolutionary change. We assume that high optimal body temperatures are not inherently more beneficial than low optimal temperatures; thus the integral of $b(x)$ is assumed to be independent of a particular x_0 . However, many workers have argued that high optimal temperatures are more advantageous (e.g., Hamilton, 1972; Heath, 1962; but see Cowles, 1941; Cunningham, 1966), an assumption seemingly justified because of the thermal dependence of molecular energy. Nonetheless, since the nature of the physiological advantage remains unknown, we ignore it.

This thermal-matching argument has been discounted because sympatric lizards often have quite different body temperatures, whereas conspecifics in thermally distinct habitats may have relatively similar body temperatures (Bogert, 1949a, b). However, this view is untenable for several reasons: species differ considerably

in physiological and physical properties which determine the direction and magnitude of heat flux (Norris, 1967; Porter, 1967); sympatric species are often active at different times and places which are correlated with body temperature (Huey and Pianka, in prep.); and individuals of a single species may vary time and place of activity in response to thermally distinct areas. Thus, evidence of matching of optimal and environmental temperatures can be difficult to interpret.

Licht, Dawson, Shoemaker, and Main (1966) made the first attempt to correlate PBT and climate for entire lizard faunas: they noted that agamids (lizards with high PBT's) were better represented in hot areas of Western Australia, whereas skinks (low PBT's) were more conspicuous in cooler regions. [Skinks of the genus *Ctenotus* are, however, probably adapted to high temperatures and are in fact quite numerous in some hot Australian deserts (Pianka, 1969).] Other faunal data are now available for more detailed analysis. For flatland, terrestrial desert lizards in the southwest U.S. (data of Pianka, 1966 and unpub.), the average PBT of lizard species at a given locality is strongly correlated with the long-term mean July temperature (Fig. 14b, $p < 0.01$). Similarly, there is a negative correlation (Fig. 14a, $p < 0.05$) between average PBT and elevation on Mt. San Jacinto in Southern California (distributional data of Atsatt, 1913; PBT data compiled from several authors). Thus, average PBT's of lizards in entire faunas correlate well with environmental temperatures as predicted.

Trends at the generic level are less clear-cut, undoubtedly reflecting the limited thermal divergence within many genera (Bogert, 1949a, b). Some lizards, such as *Phrynosoma* (Heath, 1965) and particularly *Anolis*, fit the predicted pattern: for example, open habitat or lowland anoles prefer higher temperatures and are more heat-resistant than forest or highland species (Ballinger, Marion, and Sexton, 1970; Corn, 1971; Heatwole et al., 1969; Huey and Webster, 1976; Ruibal, 1961). Data available for other genera, however, show relatively little or no obvious evidence of thermal matching (Bradshaw and Main, 1968; Licht et al., 1966; Licht, Dawson, and Shoemaker, 1969; Spellerberg, 1972a). Spellerberg's studies (1972a, b, c) on four species of skinks (*Sphenomorphus*), which differ in thermal environment, are in-

structive. These species have similar critical thermal maxima and PBT's (the species from colder areas are, however, somewhat more tolerant of exposure to low temperatures); this similarity suggests that the evolution of optimal temperatures has been relatively conservative. However, Spellerberg found interspecific differences in body size (inversely related to environmental temperatures), integumentary reflectance [directly related to $p(y)$], and especially behavior [extent of basking is inversely related to $p(y)$], all of which effectively compensate for the limited matching of optimal and environmental temperatures.

Data now available support in general Bogert's (1949a, b) proposals that evolution of optimal temperatures is conservative within genera and that flexibility of thermoregulatory behaviors minimizes any resulting ecological disadvantages. Only *Anolis* is at present known to display marked lability in thermal optima (this may be partially related to the remarkable diversity and success of this genus). Unfortunately, PBT's of some other ecologically diverse genera (e.g., *Ctenotus*, Pianka, 1969; *Chamaeleo*) are unavailable.

IV. Thermal Specialists and Generalists

Next we assume that p and c are constant and consider the differences between two lizards which have different widths of $b(x)$. This represents a situation in which two lizards of similar size live in the same habitat and have the same optimal temperature, x_0 . Differences between a wide and narrow $b(x)$ correspond to concepts of thermal generalist and specialist, respectively. There is probably a trade-off between the ability to withstand a large range of temperatures and the ability to be very efficient at some small range: thus a $b(x)$ with a large value at x_0 should also be narrow (Fig. 4a). While we do not know the exact nature of the trade-off between height and width of $b(x)$, we assume here that the integral of $b(x)$ has some constant value.

Since $b(x_0) > \tilde{b}(x_0)$ in Fig. 4a, it follows that $B_0 > \tilde{B}_0$ for any distribution of environmental temperatures (Fig. 15a, b). In other words, the specialist gains more from perfect thermoregulation than does the generalist. However, whether the specialist also gains more from passivity ($k = 1$) depends on ambient tempera-

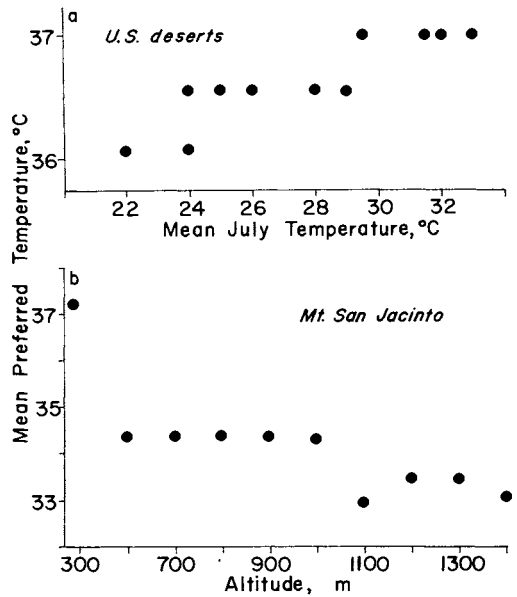


FIG. 14. RELATION BETWEEN OPTIMAL TEMPERATURES OF LIZARDS AND ENVIRONMENT

(a), mean preferred body temperature of lizards (when available) at localities differing in mean July temperature ($P < 0.01$) (data from Pianka, 1965 and pers. commun.). (b), mean preferred body temperature of lizards at different elevations on Mt. San Jacinto, California ($P < 0.05$) (data of Atsatt, 1913, and other authors).

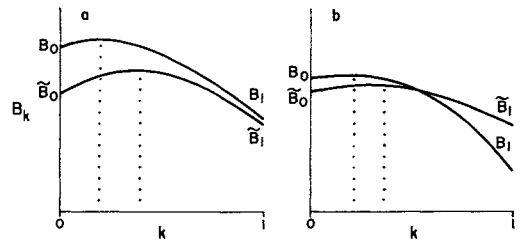


FIG. 15. BENEFITS OF THERMOREGULATION AND PASSIVITY FOR A THERMAL SPECIALIST AND A GENERALIST

(a), net energy (B_k) vs. k for a thermal specialist (B) and for a thermal generalist (\tilde{B}) when the distribution of environmental temperatures is greater than x^* (see Fig. 4a). Note that the optimal k (indicated by dots) for the specialist is lower than that for the generalist. (b), net energy vs. k for thermal specialist and generalist when $p(y)$ is less than x^* (see Fig. 4a). As in Fig. 12a, the specialist will thermoregulate more carefully than the generalist.

TABLE 1

Number of species of lizards living in forest or in open (including edge) habitats at some tropical and temperate zone localities

LOCALITIES	FOREST	OPEN
Tropical		
Bélèm, Brazil (Crump, 1971)	15	10
Barro Colorado Island, Canal Zone (Rand, pers. commun.)	8	7
La Palma, Dominican Republic (Rand and Williams, 1969)	5	6
Temperate		
Osage Co., Kansas (Clarke, 1958)	2	5
Kansas Nat. Hist. Res. (Fitch, 1956)	2	6
Louisiana Pinelands (Anderson, Limer, and Etheridge, 1952)	0	3

tures. If y is mostly warmer than x^* (the crossing point of the two b curves, Fig. 4a), then $B_1 > \tilde{B}_1$ (Fig. 15a). If y is mostly cooler than x^* , then $B_1 < \tilde{B}_1$ (Fig. 15b). In either case, however, the specialist will tend to thermoregulate more carefully (lower k) than the generalist (Fig. 15a, b). [This is not true in a high-cost, low-temperature habitat. However, high-temperature specialists probably cannot gain sufficient energy to survive in such habitats.]

Thermal specialists will have a large B (relative to thermal generalists) in those habitats where either costs of raising body temperature are low (thus favoring regulation of x near x_o), or where these costs are high but $p(y)$ has a low variance and a mean near x_o . For example, even in a closed-canopy tropical forest, thermal specialists could have a large B if x_o were nearly the ambient temperature. Thermal generalists would have a relatively large B where ambient temperatures are frequently low or variable and where costs of raising body temperature are high.

Evaluation of these predictions requires independent determination of thermal niche breadth and carefulness of thermoregulation (i.e., variance in body temperature cannot simultaneously be used for both indexes). Unfortunately, even direct evidence that lizards differ in thermal niche breadth is very limited (above). There is indirect evidence on some Puerto Rican

Anolis, however, which may support certain of these predictions. *Anolis cooki*, living in a low-cost, high-temperature environment, appears to be thermally specialized, whereas *A. cristatellus*, which lives in habitats differing in costs of raising body temperature and in mean temperature, seems thermally generalized (Huey, 1974b; Huey and Webster, 1976).

Finally, in high-cost habitats with quite variable environmental temperatures, the net energy gains even to a thermal generalist would be very low and perhaps insufficient for survival (Huey, 1974b). A temperate zone forest is such an environment: this may help to explain the relative absence of lizard species from these forests (Table 1).

V. Abundance of Food and Thermoregulation

An increase in the abundance of food in a habitat will correspond to raising the benefit curve without influencing either $p(y)$ or $c(y)$. We expect that $b(x)$ will be increased more near x_o than at lower temperatures, since the efficiency at low temperature is probably not dependent on food supply but on the decreased ability of lizards to gather and process energy. Since lizards at higher abundances of food will generally have greater efficiencies, any degree of thermoregulation becomes more advantageous; and thus lizards should thermoregulate more carefully. Moreover, as noted by Pianka and Pianka (1970), lizards in high-productivity environments will have more time available for thermoregulation.

A direct test is not possible at present. However, ants (Formicidae) are seemingly more abundant in the Australian than in the North American deserts (Pianka and Pianka, 1970). Interestingly, *Moloch horridus*, the Australian ant-specialist, has a lower variance in body temperature than its ecological counterpart in North America (*Phrynosoma platyrhinos*) despite *Moloch's* activity over a longer period seasonally (see Pianka and Pianka, 1970; Pianka and Parker, 1975). In contrast, however, variance in body temperature of *Cnemidophorus tigris* at different localities is directly correlated ($r_s = 0.790$, $P < 0.05$) with predicted net above-ground plant productivity [body temperature data from Pianka, 1970; productivity predicted from estimated long-term actual evapotranspiration (Thorntwaite Associates, 1964), see

Rosenzweig, 1968]. This correlation, however, based on long-term predicted plant productivity, may be irrelevant to insectivorous lizards, as between-year comparisons at particular localities suggest: for at Pianka's (1970) two study areas with relatively stable populations, variance in body temperature tended to decrease with increased rainfall. Since rainfall in deserts probably correlates strongly with productivity (Rosenzweig, 1968), these data seem to support the prediction (Pianka and Pianka, 1970; see p. 378) that lizards should thermoregulate more carefully when productivity is increased.

VI. Competition and Thermoregulation

Exploitation competition (Park, 1962) for resources may influence thermoregulatory behavior by reducing $b(x)$ at some temperatures. There are two conditions. First, if competitors have the same or similar optimal temperatures, their efficiencies would be more strongly reduced near x_0 than at lower temperatures. Thus, exploitation competition would have a result identical to a decrease in productivity of the habitat (above). Second, when competition occurs between species with significantly different optimal body temperatures, reductions in $b(x)$ occur only within the range of overlap. The effects are to increase k for both species during times of overlap and to reduce their activity periods. This may lead to partial separation of activity periods or habitats, as is observed in some *Anolis* lizards (Schoener, 1970).

However, the situation is different when competing species are interspecifically territorial or aggressive (interference competition, Park, 1962). If the ability of a lizard to hold a territory is partly a function of body temperature (see Regal, 1971), then a lizard may increase its net energy gain by continuing to thermoregulate carefully (contrary to the above prediction) so that it excludes potential competitors from its territory.

Factoring out the relative influence of competition from that of the physical environment is always difficult in descriptive field studies, particularly so in analyses of the role of competition on thermoregulatory behavior, because the type of interspecific interaction (exploitation or interference, Park, 1962) must be known. The few available discussions for

lizards are of limited relevance and generally emphasize the impact of thermoregulation on competition and not the reverse (Inger, 1959; Pianka, 1969; Ruibal, 1961; Schoener and Gorman, 1968). For intraspecific competition, however, Regal's (1971) laboratory studies document that male *Klauberina riversiana* thermoregulate more carefully in the presence of another male and are able to prevent the latter from gaining access to a heat lamp.

VII. Predation and Thermoregulation

Predation may also influence thermoregulatory behavior, because the ability to escape predators is undoubtedly a function of body temperature. Some *Anolis* lizards flee from approaching predators at greater distances when cold than when they are warm and more agile (Rand, 1964b): this presumably decreases risk of capture but simultaneously reduces $b(x)$ at such times. This result may reduce the range of temperatures for activity, of times of activity, and of overall energy intake (B_k).

Risk of predation per se, because it is a hazard rather than a cost in energy, cannot be included directly in our model. Nonetheless, certain qualitative predictions are possible. If predation is high and if patches of sunlight for basking are few, lizards may reduce the risk of predation by avoiding sunny patches (predators otherwise could easily learn to associate lizard prey with sunny patches). Moreover, long thermoregulatory movements might attract predators (Pianka and Pianka, 1970). High predation rates in such habitats may reinforce the advantage of limited thermoregulation. Conversely, in open habitats where sun is readily available, lizards may reduce the risk of predation by thermoregulating more carefully (the generally shorter shuttling movements are less likely to attract predators). Finally, if predation is restricted to certain times, lizards might simply avoid activity at those times.

VIII. Thermoregulation at High Ambient Temperatures

We have thus far considered only the range of body temperatures $x \leq x_0$. In hot areas at midday in summer, however, environmental temperatures may frequently be too hot for lizards to be active over this range for long periods of time, and lizards may thus be forced

to be active over the range $x > x_0$ (DeWitt, 1967).

Our model is probably inapplicable to this range, since k values of less than 1 can be achieved only if lizards routinely use evaporative cooling, which is a wasteful strategy in a desert environment except in emergencies (Cowles and Bogert, 1944; Crawford, 1972; Mayhew, 1968; but see Schmidt-Nielsen and Dawson, 1964). Instead, lizards should restrict their activity to microhabitats with relatively low environmental temperatures. [Thus, the thermoregulatory strategy would no longer be independent of a lizard's foraging and social movement strategy (above), and this is a second reason for excluding the range $x > x_0$.] If ambient temperatures continue to increase, body temperatures of a "perfect" thermoregulator would necessarily increase (see Fig. 11 in DeWitt, 1967) unless the lizard had easy access to even cooler microhabitats (Porter et al., 1973). [Unlike the cost of raising body temperature (above), the cost of avoiding heat stress may be inversely related to the degree of shade in a habitat.] Ultimately, lizards would cease their activity when body temperatures approached detrimental levels (Cowles and Bogert, 1944).

CONCLUSIONS

We have presented one possible model of thermoregulation, one which assumes that considerations of both costs and benefits are involved in the determination of optimal behavior. Our analysis stresses that lizard thermoregulatory behavior is complex. For example, passivity may at times yield greater benefits than careful thermoregulation; or thermoregulation to particular, physiologically defined optimal temperatures may be ecologically maladaptive.

The widely held opinion that most lizards thermoregulate carefully (Templeton, 1970) may partially be an artifact of the preponderance of thermoregulatory studies on desert or open-habitat lizards. The careful thermoregulation seemingly characteristic of these species is related both to the low cost of raising body temperature (basking sites are readily available) and to the necessity of avoiding heat stress at midday during summer (Huey, 1974b). Because so many species of lizards live within tropical forests (Crump, 1971; Lloyd, Inger,

and King, 1968; see Table 1), the generalization that most lizards thermoregulate carefully will surely need qualification as more and more tropical species are studied.

We summarize our predictions as follows:

Ia. Lizards should thermoregulate carefully only in environments where associated costs are low.

Ib. Lizards will be active at body temperatures near optimal levels in low-cost habitats.

IIa. Body temperatures of lizards will vary directly with ambient temperatures, and thermal generalists (defined as species which can gain energy over broad ranges of body temperatures) will show a greater change in body temperature than will thermal specialists.

IIb. Depending on the shape and the position of the composite functions, the optimal amount of thermoregulation can increase, decrease, or switch abruptly along a gradient of ambient temperatures.

III. Optimal temperatures of lizards should be high in hot environments and low in cool environments.

IV. Specialists will normally thermoregulate more carefully than thermal generalists and will tend to live either in low-cost habitats or where environmental temperatures approach optimal levels.

V. Lizards will thermoregulate more carefully if the productivity of the habitat is raised.

VIa. Exploitation competition for resources between species with similar optimal temperatures will lead to less careful thermoregulation by both species.

VIb. Exploitation competition between species with different optimal temperatures will lead to less careful thermoregulation only when both are active and may also lead to a partial separation of activity periods or habitats.

VIc. Interference competition may be reduced by more careful thermoregulation.

VII. High risk of predation may result in (a) more careful thermoregulation in low-cost habitats, but in (b) less careful thermoregulation in high-cost environments.

In the absence of more detailed data on the costs and benefits associated with thermoregulation, an exact test of the hypothesis that lizards adjust their internal temperatures to maximize their net energy intake is impossible. However, we hope that our model will serve as a conceptual framework for organizing dis-

ussions on the ecology of lizard thermoregulation.

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