Temperature, Physiology, and the Ecology of Reptiles

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I. Introduction

There is a great mass of information available concerning temperature as an ecological factor, but its actual operation is sometimes difficult to evaluate.

Gunter, 1957

A. HISTORICAL VIEWS OF TEMPERATURE AND REPTILIAN ECOLOGY

The physiological differences of reptiles from other tetrapods have important ecological consequences. For example, their low metabolic rates (Bennett and Dawson, 1976) let reptiles drain environmental resources much less intensively than do birds and mammals. Their relatively impermeable integuments (Lillywhite and Maderson; Mautz, this volume) keep reptiles less closely constrained by hydric conditions than most amphibians (Kiester, 1971; Tracy, 1978; Nagy, this volume). These fundamental biological differences suggest that ecological and physiological studies of reptiles should complement rather than merely supplement parallel studies of other vertebrates (Pianka, 1977; Schoener, 1977; Regal, 1978; Schall and Pianka, 1978; Avery, 1979; Pough, 1980, in press).

The important discovery that desert reptiles behaviorally regulate body temperature was the first dramatic contribution of studies of reptiles to general ecological thought (Cowles and Bogert, 1944; Avery, this volume). By demonstrating that thermal homeostasis can be achieved by behavioral as well as by physiological adjustments and is a property of "lower" as well as of "higher" animals, this discovery revolutionized the philosophy and methodology of physiology and ecology. The demonstration that temperature is intimately involved with the daily lives of reptiles, provided a unique focus for early ecological studies of reptiles. Indeed, for many years, few

herpetologists departed for the field without several Schultheis thermometers!

The concept that temperature is a fundamental factor in the ecology of many reptiles is developed in many pioneering studies (Mosauer, 1936; Sergeyev, 1939; Mazek-Fialla, 1941; Cole, 1943; Cowles and Bogert, 1944; Strelnikov, 1944; Colbert et al., 1946; Bogert, 1949a, b, 1959; Carpenter, 1952; Norris, 1953, 1967; Pearson, 1954; Fitch, 1956; H. Saint Girons and M.C. Saint Girons, 1956; Reichling, 1957). This concept reflected the contemporary belief (Chapman, 1931) that physical concerns are the principal factors affecting animals. Additional support came later from the demonstration that the general activity patterns of reptiles can often be predicted from biophysical models of heat and mass exchange (Porter et al., 1973; Tracy, this volume).

Other ecologists stressed the importance to reptiles of biotic factors. These workers observed that temperature is not always the central concern of reptiles, especially of those species living in moderate thermal environments (Ruibal, 1961; Soulé, 1963; Regal, 1967; Rand and Humphrey, 1968). Thus the degree to which thermal concerns dominate reptilian ecology can differ among species and with circumstance (Gans and Dawson, 1976).

It is evident that no single approach adequately characterizes the ecology of all reptiles (Lang, 1979). An emerging, synthetic view suggests that reptilian thermal ecology must reflect a complex interaction among biophysical, biotic, economic, *and* phylogenetic concerns. Temperature regulation is not an end in itself, but rather a behavioral and physiological process that helps reptiles gather and process food, reproduce, and avoid becoming food for other animals. Temperature regulation is thus a proximate and practical activity that *indirectly* influences fitness by directly affecting physiological, reproductive, and ecological performance.

This chapter is conceived and developed within this conceptual framework. In many ways the chapter is a prospectus as well as a review: it attempts to emphasize what we need to learn about the thermal ecology of reptiles, not just what we already know. Reptiles are remarkably diverse, both ecologically and phylogenetically (Brattstrom, 1965; Gans and Dawson, 1976; Regal, 1978; Werner and Whitaker, 1978; Lang, 1979; Saint Girons, 1980; Avery, this volume). Because most studies of thermal biology have focused exclusively on diurnal lizards, generalizations about other reptiles are premature.

B. Variables in the Thermal Ecology of Reptiles

Figure 1 diagrams key variables in the thermal ecology of a reptile. The physical environment, which changes dynamically in time and space, sets
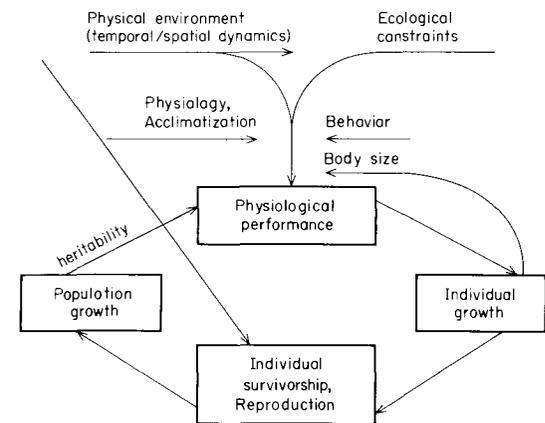
FIG. 1. Key variables in the thermal ecology of reptiles.

fundamental limits on reptilian activities. The actual activity pattern is further limited by complex interactions involving the behavioral repertoire of an individual, its physiological capacities (influenced by body size and by acclimatization), and certain ecological constraints (e.g. risk of predation), which in turn are influenced by the physical environment. The immediate result of these interactions is observable in the relative ability of an individual to perform certain activities that influence individual growth, survivorship, and reproduction. These features are basic to the growth and dynamics of the population. Each step leading to a population response is temperature dependent. Consequently, an understanding of the nature of these dependencies is fundamental to reptilian ecology.

Consider, for instance, a snake attempting to capture and digest a frog. The snake must first encounter the potential prey, stalk and strike successfully (avoiding defensive measures), and then extract needed nutrients and energy. Temperature actually or potentially affects each of these steps, but not always in parallel ways (Porter and Tracy, 1974; Greenwald, 1974; Skoczylas, 1978). Therefore, an analysis of the role of temperature in even simple ecological problems is necessarily complex. Such an analysis may well proceed by initial field and laboratory investigations of the thermal sensitivity of the component steps followed by their subsequent integration.

Estimation of encounter probabilities requires laboratory data on the biophysics of heat/mass flux between the animals and the environment as well as extensive field data on available microclimates (Porter et al., 1973; Tracy, this volume), on the acceptable activity temperatures of predators and prey, on behavioral properties of predators and prey (e.g. microhabitats

used, and whether predators can capture *inactive* prey), and on biotic and economic factors (Rand, 1964b; DeWitt, 1967; Huey and Slatkin, 1976). Capture probability is best estimated directly by measuring actual strike success at different body temperatures (Greenwald, 1974) or indirectly (and less desirably) by determining the effects of temperature on acceleration and maximum velocity not only of predator, but of prey (Elliott *et al.*, 1977; Huey and Hertz, 1981). Understanding a basic predator–prey interaction thus requires information from biophysics, behavior, ecology, physiology, and natural history (Waldschmidt, 1978).

Integration of these data also poses problems. One general formalization involves economic or cost–benefit models (Huey and Slatkin, 1976; Hainsworth and Wolf, 1978; Crowder and Magnuson, in press). [Limits of optimality approaches have been reviewed in Lewontin (1979) and Oster and Wilson (1978).] The general model is based on the assumption that reptiles incur costs (e.g. energy loss, risk of predation) as well as derive benefits (e.g. energy gain) from any activity, in this case thermoregulation. The model also assumes that reptilian behavior maximizes fitness by maximizing net energy gain in a particular environment. The use of these models requires information about the thermal environment, abundance of food, behavior, physiology, and ecology.

A second general optimality analysis has been proposed by McFarland (1976) and A. Houston (personal communication). Its mathematical framework (the Hamiltonian hypothesis) predicts the times of day that a lizard will be active as functions of thermal stress, desiccation, and risk of predation.

A third approach to thermal ecology has recently been advanced (Magnuson *et al.*, 1979; Mushinsky *et al.*, 1980; Roughgarden *et al.*, 1981). It views the environmental thermal regime as an ecological resource similar to food: thus, animals can compete for particular spots in the environment that have desirable thermal properties. This approach is largely complementary to the two optimality models.

II. Physiological Aspects of Ecology

A. PHYSIOLOGICAL PROCESSES RELEVANT TO ECOLOGY

A study of the effects of body temperature on physiological performance can proceed in two complementary directions. One approach is phenomenological and investigates, for example, "How does body temperature affect locomotor ability or predation success?" A second approach is mechanistic and investigates, "What is the mechanistic basis for the observed pattern of locomotor performance?" The former approach is

directed at integrated, whole-animal processes, whereas the latter approach is directed at lower level processes (tissue, cellular, biochemical).

Several considerations suggest that ecological analyses of physiological performance are in general more appropriately based on whole-animal (Table I) rather than lower level processes (Bartholomew, 1958; Huey and Stevenson, 1979). First, whole-animal processes should often correlate more directly with ecological performance for most lizards. For example, the effect of body temperature on success in predation might be more reliably predicted from data on sprint locomotion than from data on contractile velocity of isolated muscle fibers. Second, the functioning of a part may sometimes be a misleading predictor of the functioning of the whole. For example, the activity of alkaline phosphatase *in vitro* is greatest at temperatures that are lethal for some lizards (Licht, 1967). Third, and most importantly, lower level and *in vitro* studies necessarily eliminate behavior, which is an integral component of the performance of a reptile in nature (Fig. 1). For example, the defensive behavior of several lizards and snakes changes as a function of body temperature (Rand, 1964b; Gans and Mendelssohn, 1972; Hertz *et al.*, 1982). Such changes may play a crucial role in the ecology of these reptiles but would be overlooked in a lower level study.

The whole-animal processes listed in Table I can be grouped by the time-scale of the response. Some (e.g. locomotor ability) are short term or nearly instantaneous, whereas others (e.g. rate of egg production) are long term. Long-term processes, such as growth, are particularly interesting from an ecological perspective (Fig. 1). Nevertheless, such processes are difficult to study; acclimation at constant temperature, required to determine long-term measures of thermal sensitivity, is unnatural and may also be deleterious (Chapman, 1931; Wilhoft, 1958; Licht, 1965; Hutchison and Ferrance, 1970). Techniques that can estimate long-term performance from short-term indicators (e.g. RNA/DNA ratio to estimate growth; Bulow, 1970) may circumvent these problems.

Considerable information is now available about the effects of temperature on lower level processes of lizards (Dawson, 1975). However, studies of whole-animal responses (other than metabolism, Bennett and Dawson, 1976; Bennett, volume 13) are still relatively limited. Studies of intraspecific variation in whole-animal responses are rare (Hertz *et al.*, 1979; Hertz, 1981).

B. TYPES OF PHYSIOLOGICAL PARAMETERS

Figure 2 diagrams the effect of body temperature on a hypothetical physiological process. Performance initially improves with temperature, plateaus at some "optimal" range of temperature, and declines rapidly

TABLE I

Some ecologically relevant, whole-animal physiological systems (or physiological effects) with samples of reptilian examples

| Performance (effect)	Some examples for reptiles
I. Long-term=chronic	
Growth rate—Fig. 3A	Licht *et al.*, 1969
Healing from injury, disease—Fig. 3B,C	Evans and Cowles, 1959; Maderson and Licht, 1968; Kluger, 1979
Rate of egg production	No known references
(Hatching rate/success)—Fig. 3D	Licht and Moberly, 1965; Bustard, 1971a, b; Vinegar, 1973; Sexton and Marion, 1974; Muth, 1980;
(Sex-ratio at hatching)—Fig. 3E	Yntema, 1976, 1979; Bull, 1980
II. Intermediate-term	
Digestive rate/efficiency—Fig. 3G,H	MacKay, 1968; Skoczylas, 1970, 1978; Goodman, 1971; Avery, 1973; Diefenbach, 1975a, c; Harlow *et al.*, 1976; Harwood, 1979; Greenwald and Kanter, 1979
Learning/memory	Krekorian *et al.*, 1968; Burghardt, 1977; Brattstrom, 1978
III. Short-term=acute	
Predation success/rate/avoidance—Fig. 3F	Rand, 1964b; Greenwald, 1974; Christian and Tracy, 1981; Hertz *et al.*, 1982
Acceleration, velocity, agility—Fig. 3I	Heckrotte, 1967; Tracy, 1978; Waldschmidt, 1978; Bennett, 1980; Huey and Hertz, 1981
Endurance and aerobic capacity, recovery from exhaustion—Fig. 3J	Ruben, 1976a, b; Bennett, 1980, 1982
Behavioral dominance	Regal, 1971; Bury and Wolfheim, 1973; Auth, 1975
Behavioral displays	Stamps and Barlow, 1973; Parcher, 1974
Auditory sensitivity—Fig. 3K	Campbell, 1969; Werner, 1972, 1976; Gans and Wever, 1974
(Metabolism, resting/active/fasting)—Fig. 3L	Wilson and Lee, 1970; Greenwald, 1971; Bennett and Dawson, 1976; Bennett, volume 13.
(Evaporative water loss, water balance)	Shoemaker and Nagy, 1977; Mautz, this volume

Time course specified.
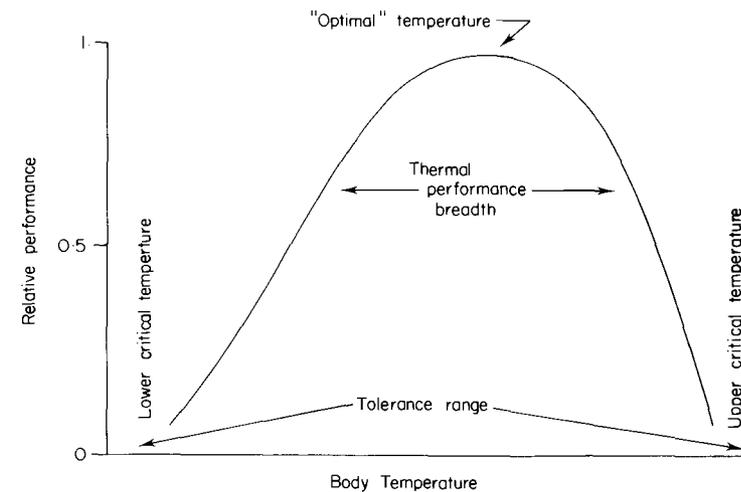
FIG. 2. Hypothetical performance of an ectotherm as a function of body temperature (Huey and Stevenson, 1979). (Copyright American Society of Zoologists.)

above this range. Similarly shaped curves depict the response of many processes of ectotherms (Dawson, 1975; Beitinger and Fitzpatrick, 1979; Fig. 3).

The thermal sensitivity of many physiological processes can be characterized by fitting a curve to the response data (Huey, 1975; Welch, 1978; Huey and Stevenson, 1979; Section IIC3). Three performance parameters (Fig. 2) can be calculated from the equation for this line, namely: (i) the maximal or "optimal"* temperature(s), (ii) the temperature range for mid-level performance ("thermal performance breadth"), and (iii) the temperature range between the upper and lower threshold or "critical" performance temperatures ("tolerance range"). In addition, the performance relative to that at the optimal body temperature can be calculated for any temperature.

These parameters of the thermal niche differ in ecological significance. Optimal temperature and thermal performance breadth are probably the most important ecological parameters; they reflect the range of body temperature within which a reptile performs best and well, respectively. These variables are closely related to the physiological concept of *capacity* adaptation (Precht *et al.*, 1973). In contrast, tolerance range defines the range of body temperature within which any activity (or survival) is possible; it is related to the concept of *resistance* adaptation (Precht *et al.*, 1973).

The three descriptive parameters have different physiological and ecological applications. Optimal temperatures provide a basis for evaluating

*As noted by many authors, "maximal" is not necessarily "optimal".

the mechanistic significance of selected body temperatures and for determining whether various physiological systems have similar patterns of thermal sensitivity (Dawson, 1975; Pough, 1974; Section IID). Such temperatures may be used in analyses of geographic distributions (Brattstrom, 1965; Licht et al., 1966a; Spellerberg, 1972a, 1973, 1976; Clark and Kroll, 1974; Greer, 1980), times and places of activity (Rand, 1964a; Corn, 1971; Porter et al., 1973; Huey et al., 1977; Hutchison, 1979), and competitive interactions (Inger, 1959; Rand and Humphrey, 1968; Pianka, 1969; Huey and Slatkin, 1976). These data are also useful for evaluating patterns of ecogeographic variation and for estimating rates at which physiological traits evolve (Bogert, 1949a; Corn, 1971; Section IVE).

Thermal performance breadth (Huey and Slatkin, 1976; Magnuson et al., 1979) is relevant to discussions of physiological adaptation to constant or fluctuating environments (Brattstrom, 1968; Levins, 1969; Brown and Feldmeth, 1971; Kour and Hutchison, 1970; Snyder and Weathers, 1975; Huey and Slatkin, 1976; Hertz, 1977), of tropical and temperate distributional patterns (Janzen, 1967; Feder, 1978; Huey, 1978), and of competitive interactions (Ruibal and Philibosian, 1970; Huey and Slatkin, 1976; Lister, 1976; Hertz, 1977). Interest in the theoretical and empirical aspects of thermal performance breadth is recent. Available data are limited, and discussions are often based on measurements of tolerance range.

Threshold or lethal temperatures set absolute limits or bounds on where or when animals can survive, and these are the descriptive statistics most commonly reported (Cowles and Bogert, 1944; Heatwole, 1970, 1976; Spellerberg, 1972a, 1973, 1976; Hutchison, 1976; Hutchison et al., 1966; Curry-Lindahl, 1979; Hertz, 1979a; Greer, 1980). Many workers who have studied desert lizards assume that most reptiles are active at body temperatures very close to their Critical Thermal Maximum (Cowles and Bogert, 1944; Cloudsley-Thompson, 1971; Hamilton, 1973; Curry-Lindahl, 1979). Nevertheless, field studies demonstrate that many reptiles are rarely *active* at near-threshold body temperatures, except in emergencies (DeWitt, 1967; but see Case, 1976; Swingland and Frazier, 1979). For example, in most groups of reptiles (Table II), the maximum body temperature ever recorded for active individuals is 6°C less than the Critical Thermal Maximum (= "Minimum Thermal Safety Margin" of Heatwole, 1970, 1976), and the lowest body temperature recorded for active lizards differs even more from the Critical Thermal Minimum. Similarly, mean activity temperatures differ substantially from critical temperatures (Table II).

The consistent magnitude of such differences suggests that a reptile ceases activity long before its body temperature approaches critical levels. This is probably more closely related to both the general decline in physiological performance at extreme body temperatures (Figs 2 and 3) and

TABLE II

Representative activity temperatures of reptiles in relation to critical temperatures

Group	$\bar{T}_b$ − CTMin X̄±SE	(N)	Min T_b − CTMin X̄±SE	(N)	CTMax − $\bar{T}_b$ X̄±SE	(N)	CTMax − Max T_b X̄±SE	(N)	References
Crocodilians									2,3,7
Turtles*			23	(1)	13.7±1.10	(15)	7.4±1.24	(12)	5
Sphenodon	7.4	(1)	2.7	(1)			1–2	(1)	1
Lizards									
diurnal species	26.7±1.53	(9)	20.3±3.17	(9)	10.4±0.56	(38)	6.4±1.03	(38)	2,4,6
nocturnal/fossorial species					13.0±1.36	(3)	6.5±1.17	(3)	2,4,6
Snakes					13.1±0.66	(19)	6.8±0.66	(18)	2,4,6

Symbols as follows: $\bar{T}_b$, = mean T_b of reptiles in field; Max T_b, maximum T_b recorded in field; Min T_b, minimum T_b recorded in field; CTMax, Critical Thermal Maximum; CTMin, Critical Thermal Minimum; N, number of species. CTMax−$\bar{T}_b$, "Ecological Thermal Safety Margin" and CTMax−Max T_b, "Minimum Thermal Safety Margin" of Heatwole (1970, 1976). References: 1. Bogert, 1953; Stebbins, 1958; 2. Brattstrom, 1965; 3. Colbert et al., 1946; 4. Heatwole, 1970 and 1976; 5. Hutchison, 1979; 6. Spellerberg, 1972a, b; 7. Smith, 1975. *$\bar{T}_b$ data include some laboratory values, see Hutchison (1979).
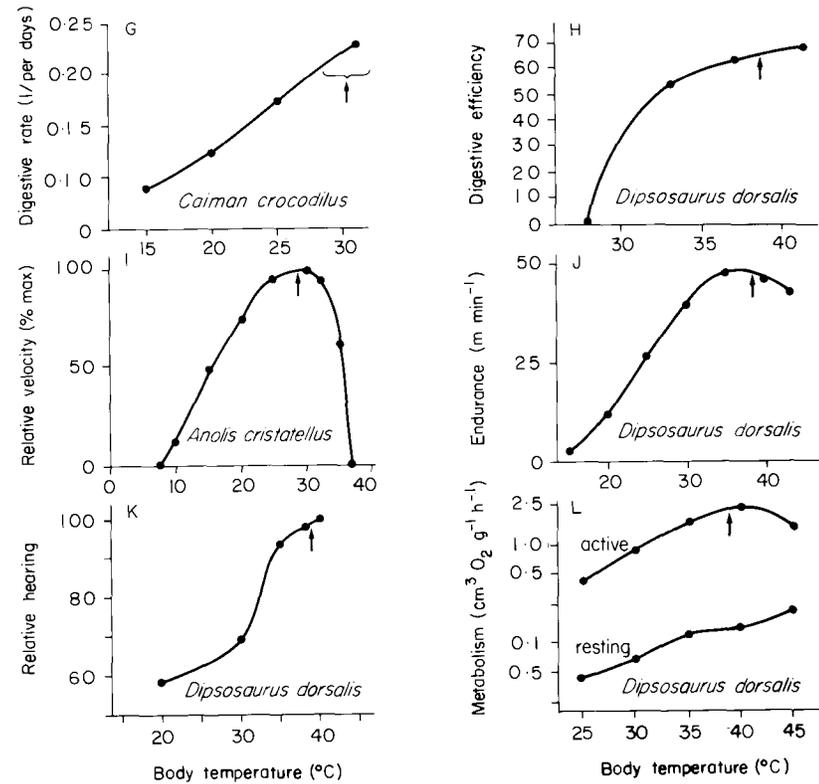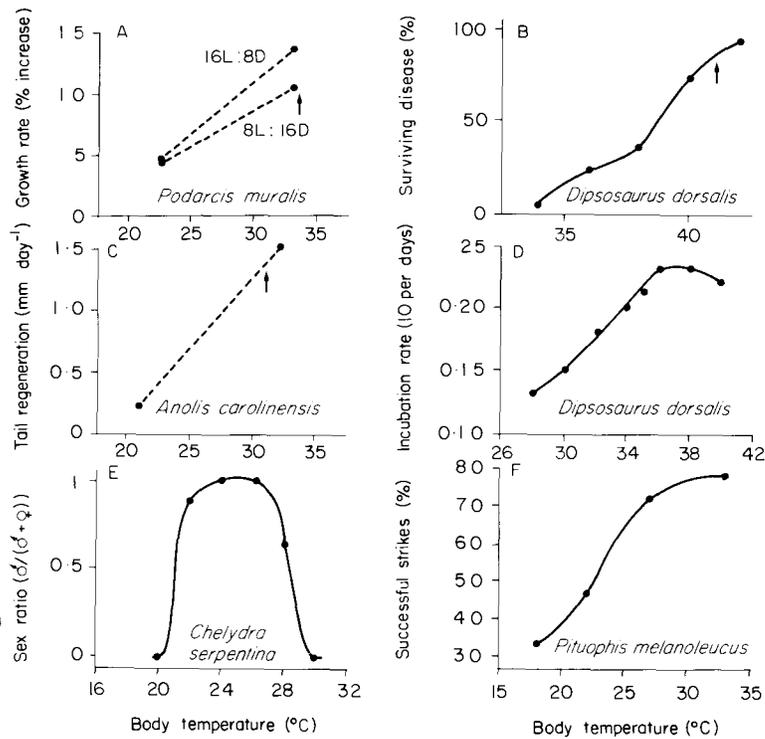
FIG. 3. Representative performance of whole-animal physiological systems of reptiles as functions of body temperature. Vertical arrow indicates selected body temperature. A (from data in Licht et al., 1969); B (survival after three days, from data in Kluger, 1979), C (from data in Maderson and Licht, 1968), D (from data in Muth, 1980), E (redrawn from Bull, 1980), F (from data in Greenwald, 1974), G (from data in Diefenbach, 1975a, b), H (from data in Harlow et al., 1976), I (Huey, 1982 and Huey and Webster, 1976), J (from data in Bennett, 1980), K (hearing at 1000 Hz, from data in Werner, 1972), L (redrawn from Bennett and Dawson, 1972).

the excessive metabolic costs at high body temperatures, than to an "avoidance" of threshold temperatures *per se*. Tolerance limits may generally have limited relevance (Feder, 1978; Gorman and Hillman, 1977) to the "fine-tuning of an animal's resource utilization" (Magnuson et al., 1979).

Nevertheless, the Critical Thermal Maximum may affect activity patterns of some reptiles in extreme environments. Adult *Uta stansburiana* will reach their Critical Thermal Maximum in less than 1 min if tethered on the surface of a desert at midday in summer (Tinkle, 1967). Hatchling *Uta* that are "placed between bushes seven or eight feet apart at midday often will die before reaching shelter" (Norris, 1967). Risk of overheating limits food intake and activity time of *Geochelone gigantea* (Swingland and Frazier, 1979).

Critical temperatures may affect some reptilian distributions (Heatwole, 1970, 1976; Prieto and Whitford, 1971; Spellerberg 1972a, b, 1973, 1976; Greer, 1980) because extreme temperatures may cause death or injury (Carr, 1952; Heatwole, 1970, 1976; Goodman, 1971). For example, reptiles

may be trapped above-ground by sudden cold fronts, leading to substantial winter mortality (Bailey, 1948, 1949).

Critical temperatures are traditionally measured during acute exposure of animals to extreme conditions (Lowe and Vance, 1955). Prolonged exposure to less extreme temperatures causes serious injury or death (Cowles and Burleson, 1945; Licht, 1965; Licht et al., 1966b). Chronic exposure to low temperatures may be the important factor that excludes reptiles from certain habitats. For example, the lowland tropical lizard *Anolis cristatellus* may be unable to colonize apparently suitable habitat in upland Puerto Rico. Although these lizards readily tolerate acute exposure to low body temperatures (Critical Thermal Minimum = 8.9°C, Huey 1982), they soon

die from chronic exposure to temperatures (16°C) that simulate winter conditions in rainforests (Gorman and Hillman, 1977).

Therefore, capacity and resistance traits appear complementary. Measures of capacity traits are probably more useful in analyses of daily activities of reptiles, whereas measures of resistance traits during acute and especially chronic exposure may be more useful in analyses of survival under extreme conditions. [Note that tolerance limits make convenient "first-approximations" of optimal temperatures (Section IIC1).]

C. METHODS OF ESTIMATING PERFORMANCE PARAMETERS

1. *Direct Estimates of Performance Parameters*

Direct estimates of thermal performance parameters (Fig. 2) may be obtained for a particular physiological process by fitting a curve to the performance data (Section IIC3). These procedures have recently been detailed (Huey and Stevenson, 1979) and are here summarized. The fitted curve used to estimate the descriptive statistics also specifies relative performance at any body temperature. Curve fitting can be extended to describe the joint effects of several variables (e.g. temperature and hydration state) on performance (Alderdice, 1972).

a. Thermal tolerance limits and range. The tolerance range is the difference between the upper and lower body temperatures at which physiological processes are deactivated. It may be determined without fitting a curve to the data.

b. Optimal temperatures, optimal temperature range. Optimal temperature may be estimated by selecting the best-performance temperature using analysis of variance or by taking the derivative of the fitted curve (Section IIC3). Because many (if not most) physiological processes do not have a narrow optimal temperature (Gans and Wever, 1974; Bennett, 1980), the range of optimal temperature may be a more meaningful measure (Heath, 1965; Huey and Stevenson, 1979). This range can be estimated by analysis of variance or by solving the fitted curve for the range of temperatures over which performance is approximately maximal.

c. Thermal performance breadth. The thermal performance breadth is calculated from the fitted performance curve by determining the range of body temperatures over which performance is at or above some level (e.g. 80% of maximum performance). [The level selected is, of course, arbitrary but should be chosen with reference to the ecology of the species being considered.]

2. *Indirect Estimates of Performance Parameters*

Direct estimates of performance of reptiles are rarely available. Nevertheless, several indirect techniques can substitute in ecological and physiological analyses.

a. Optimal temperatures. Optimal body temperatures of active reptiles are sometimes inferred from mean body temperatures of active reptiles (Clark and Kroll, 1974; Huey *et al.*, 1977) when more direct estimates are unavailable. Mean activity temperatures and mean selected temperatures measured in the laboratory (see below) are strongly correlated for diurnal lizards ($r = 0.899$, $N = 28$; Fig. 4; Dawson, 1967; Cloudsley-Thompson, 1971; Grenot and Loirat, 1973; Magnuson and Beitinger, 1978). [The correlation should be tested for other reptiles.]

Nevertheless, the physical and biotic environment sometimes prevents reptiles from achieving selected temperatures (Licht *et al.*, 1966a; DeWitt, 1967; Porter *et al.*, 1973; Huey and Webster, 1976; Muth, 1977; Magnuson and Beitinger, 1978; Bury, 1979; Magnuson *et al.*, 1979). Furthermore,
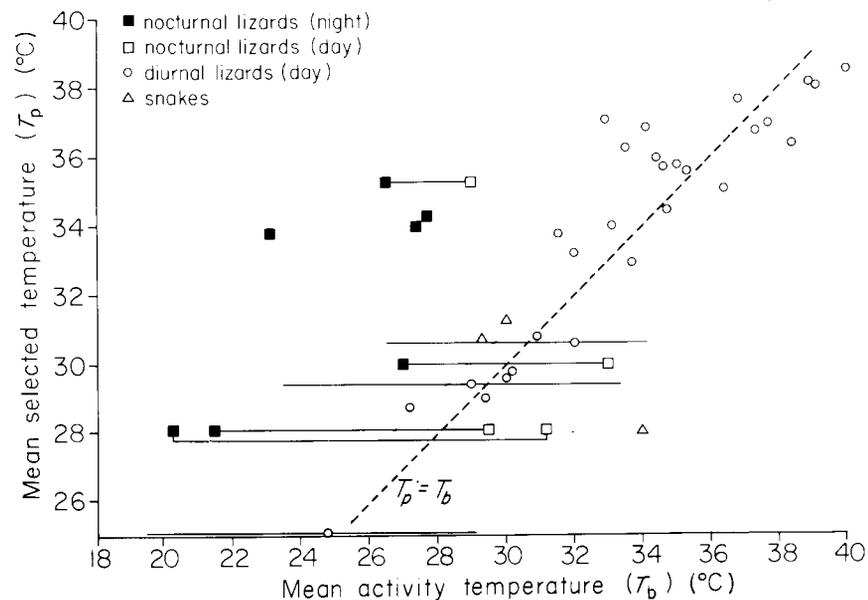

FIG. 4. Sample selected body temperature (T_p) versus mean activity temperature (T_b) for reptiles. Dashed line indicates $T_p = T_b$, and horizontal lines connect maximum and minimum mean activity T_b for three species of *Anolis* or the day and night activity T_b for two species of *Phyllodactylus*. (Data from Brattstrom, 1965; Heatwole, 1976; R. B. Huey, unpublished data; Huey and Webster, 1976; Licht *et al.*, 1966a; Spellerberg, 1972c; Pianka, unpubl. data; Pianka and Pianka, 1976.)

certain ecological and economic considerations (access to food, escape from predators, social interactions, costs of achieving a particular body temperature) may make temperature regulation costly (Section IIID). Consequently, caution is needed when using activity temperatures as estimates of optimal temperatures. Such use of activity temperatures from nocturnal reptiles (Licht *et al.*, 1966a; Werner and Whitaker, 1978) and from some populations of *Anolis* (Huey, 1974b; Lister, 1976; Lee, 1980) is especially unreliable (Fig. 4).

The mean body temperature selected in laboratory thermal gradients (Licht *et al.*, 1966a; Mathur and Silver, 1980) is often used as an estimate of presumed optimal temperature in ecological analyses (Corn, 1971; Licht *et al.*, 1966a; Huey and Slatkin, 1976; Hutchison, 1979). Indeed, the mean selected (or preferred*) temperature correlates with the optimal temperatures of many tissue and cellular functions (Dawson, 1975). Consequently, when direct measures of physiological performance are unavailable, mean selected temperature is probably the most meaningful measure in thermal ecology (Reynolds and Casterlin, 1979).

The selected temperature is not, however, a fixed physiological trait. It varies somewhat among individuals with time (day, season, age), and with hormonal or physiological state (McGinnis, 1966; Regal, 1966, 1967, 1980; Mayhew and Weintraub, 1971; Dill, 1972; Garrick, 1974; Hutchison and Kosh, 1974; Spellerberg, 1974; Diefenbach, 1975b; Schall, 1977; Magnuson and Beitinger, 1978; Patterson and Davies, 1978a; Lillywhite, 1980; Lang, 1981; but see Licht, 1968; Graham and Hutchison, 1979; Schuett and Gatten, 1980). Moreover, chronic exposure to their selected temperatures may injure reptiles (Cowles and Burleson, 1945; Bogert and Martín del Campo, 1956; Wilhoft, 1958; Licht, 1965). This observation may help to explain diurnal shifts in the selected temperature of some species (Regal, 1967; Hutchison and Kosh, 1974; Pough, 1974; but see Section IID).

The Critical Thermal Maximum (CTMax) is probably the most widely used indirect correlate of optimal body temperature during activity. Indeed, the positive correlation between values of sample CTMax and T_p for squamate reptiles supports this use ($r = 0.73$; standardization of methodology would certainly improve this correlation) when more direct measures are unavailable.

*Gunn and Cosway (1938) coined the term "eccritic temperature" to avoid anthropomorphic implications associated with "preferred". Unfortunately, they were actually referring to the preferred *ambient* temperature rather than the preferred *body* temperature, as subsequent workers have assumed. More importantly, Gunn and Cosway misderived "eccritic". The Greek roots of eccritic refer to "selection", but selection in the sense of *removing* or *excreting* rather than of choosing or preferring. Indeed, eccritic is defined as "having the power of secretion and excretion" (Oxford English Dictionary).

b. Thermal performance breadth. Several indirect estimates of the thermal performance breadth have been proposed, but none has been tested rigorously. The tolerance range (Fig. 2) is a logical index and correlates with distribution and ecology of some lizards (Kour and Hutchison, 1970; Section IVD). Nevertheless, this index is sometimes unreliable. For example, lizards often have broader tolerance ranges than do frogs, but their thermal performance breadths are strikingly narrower (Tracy, 1978; Huey, 1982).

Other indices include the variance of activity temperatures or the range among mean activity temperatures (Soulé, 1963; Ruibal and Philibosian, 1970; Huey and Webster, 1975, 1976; Lister, 1976; Hertz, 1977; Hertz *et al.*, 1979). Both measures are sensitive to local heterogeneity in the thermal environment (Soulé, 1963; Huey and Slatkin, 1976; Magnuson *et al.*, 1979) and may prove reliable only for animals in thermally equivalent habitats. Both measures assume that geographic variation in physiology is minor. The range among mean activity temperatures is only useful for abundant species (e.g. *Anolis*).

Philosophically similar measures are the variance or the range of selected temperatures (Huey and Slatkin, 1976; Neill and Magnuson, 1974) or the median $\pm 33\%$ of all records (Magnuson and Beitinger, 1978; Magnuson *et al.*, 1979). Nevertheless, correlations between these measures and the actual thermal performance breadths of various physiological processes should be established (see also Section IIIC). Such studies should consider both intra- and inter-individual components of variance (Mathur and Silver, 1980).

The extent of acclimation ability is another measure of thermal flexibility (Brattstrom, 1968; Levins, 1969; Feder, 1978). This is a long-term measure of performance breadth rather than a short-term measure, such as those considered here. Both long- and short-term estimates are necessary to obtain a complete picture of the physiological sensitivity of reptiles to temperature.

3. Fitting Curves to Physiological Performance Data

Many problems in physiological ecology require specification of relative or absolute performance as a function of body temperature. Ideally, this is achieved by fitting to performance data a theoretical curve that has previously been deduced from underlying physical principles. Unfortunately, the only deductive curves available are derived for chemical reactions and are far removed from whole-animal physiology. Various empirical or descriptive curves (Wollkind *et al.*, 1978) are available (Table III). Empirical curves are general mathematical functions and include polynomials, skewed normals, and poisson-density functions. Descriptive curves are special functions that specify biologically meaningful parameters (e.g. "optimal" temperature or a Q_{10} equivalent).

TABLE III

Examples of functions for describing the thermal sensitivity of physiological performance

Type of model	No. parameters	References
I. Empirical models		
1. Polynomial	n	Draper and Smith, 1966
2. Quartic	2	Taylor and Sexton, 1972
3. Skewed normal	4	Lehman et al., 1975
4. Generalized poisson-density	5	Abramowitz and Stegun, 1965
5. Modified poisson-density	3	Parker, 1973
II. Descriptive models		
1. Special poisson-density	4	O'Neill et al., 1972
2. Exponential/power (product function)*	4	Lassiter, 1975
3. Logistic/logistic (product)	7	Thornton and Lessem, 1978
4. Negative exponential/negative exponential (product)	5	Huey and Stevenson, 1979
5. Negative exponential/logistic (product)	6	Stevenson and Huey, in preparation
6. Exponential/negative exponential (additive)	5	Wollkind et al., 1978
III. Deductive Model		
1. Negative exponential/exponential (quotient)	4	Johnson et al., 1954

Abstracted from Stevenson and Huey (in preparation).
*In certain descriptive models (product, additive, quotient), two curves of the same or different shape are fitted together (Thornton and Lessem, 1978; Wollkind et al., 1978).

Choice among these curves involves several factors. To minimize the sum of squares of the residuals a curve must have an appropriate shape (Jennrich and Ralston, 1979). For instance, a logistic curve fits the success of *Pituophis* striking at prey (Fig. 3F), whereas a negative exponential is better for digestive efficiency of *Dipsosaurus* (Fig. 3H). Expense of calculation or requirements for confidence intervals (product and additive models) are additional factors influencing choice.

D. MULTIPLE PHYSIOLOGICAL OPTIMAL TEMPERATURES—DO THEY EXIST?

Knowing whether the various physiological processes of a reptile function best at the same temperatures is fundamental to analyses of the thermal niche. Implicit and sometimes explicit in some discussions of

reptilian thermoregulation is the belief that each species has a narrow zone of temperatures that optimizes all physiological functions.

Two sets of observations suggest that this view might be simplistic. First, some reptiles select higher body temperatures after feeding either in the laboratory (Chernomordikov, 1943; Cowles and Bogert, 1944; Regal, 1966; McGinnis and Moore, 1969; Gatten, 1974; H. Saint Girons, 1975, 1978; Witten and Heatwole, 1978; reviewed by Lang, 1979; Bradshaw et al., 1980) or in the field (Moll and Legler, 1971; Cogger, 1974; Schall, 1977), although certain other species apparently do not (Kitchell, 1969; Naulleau and Marquès, 1973; Diefenbach, 1975c; Case, 1976; Naulleau, 1976; Hammerson, 1979; Hennemann, 1979; Lysenko and Gillis, 1980). A particularly intriguing observation notes that a *Boa constrictor* places under a heat lamp only that portion of its body that actually contains a bolus of food (Regal, 1966). Second, selected temperatures of some nocturnal geckos are higher than their normal body temperatures (Licht et al., 1966a; Pianka and Pianka, 1976; Dial, 1978). These observations led to speculation that many reptiles have multiple physiological optimal temperatures (Bustard, 1967b; Pough, 1974, 1980; Lang, 1979), a lower zone for foraging and a higher zone for digestion. An hypothesis that different physiological processes have different optimal temperatures accounts for these two observations. However, this hypothesis is presently only inferred from behavioral data; direct comparisons of the thermal sensitivities of important physiological functions should be conducted.

Acceptance of the hypothesis of multiple physiological optimal temperatures will lead to two interesting questions: (1) why has selection favored multiple optimal temperatures? (2) why does one system have a higher and another system a lower thermal optimum? Multiple optima seem inefficient because no single body temperature simultaneously optimizes all systems (Huey and Stevenson, 1979). Perhaps the optimal temperatures are related to the thermal conditions at the time (Brett, 1971; Dawson, 1975) or place (Regal, 1980) where the particular system functions.

An alternative hypothesis can also account for the two observations (Brett, 1971; Warren, 1971; Magnuson and Beitinger, 1978; Kitchell, 1979; Greenwald and Kanter, 1979). In its most simple form, this hypothesis assumes that the rate at which food is processed increases with temperature but then becomes steady (plateaus) at some value (Hainsworth and Wolf, 1978; Fig. 5): the higher the digestive rate, the more the gross energy gained per unit time. Nevertheless, metabolic expenditures rise exponentially with increasing body temperature (Fig. 5A). Net energy per unit time should then be maximum at the temperature at which gross gain minus metabolic cost is maximal ("a" in Fig. 5B, assuming high food levels).

At a given body temperature the gross gain in energy, but not the resting
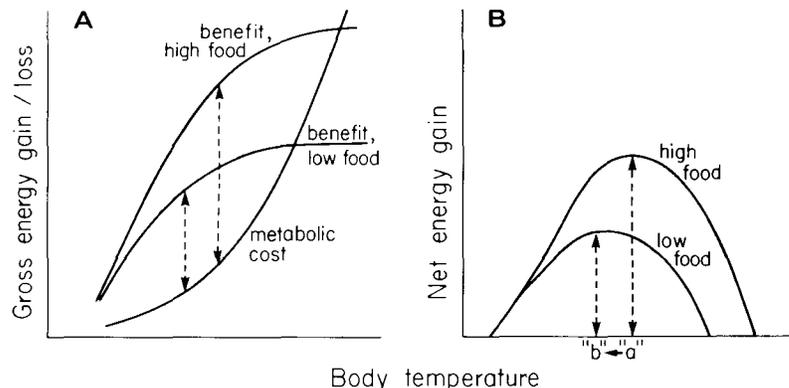
FIG. 5 (A) Gross energy gain (heavy line) at two food levels and metabolic cost (thin line) as a function of T_b (modified from Hainsworth and Wolf, 1978). (B) Net energy gain (metabolic cost subtracted from gross energy gain in Fig. 6A) as a function of T_b. The T_b that maximizes net energy gain is directly related to food intake.

metabolic expenditure, should increase with the level of food ration (Fig. 5A). Consequently, net energy gain is maximized at relatively low body temperature if a reptile has limited food ("b" in Fig. 5B). Thus, the selected temperature of reptiles could vary with the amount of ingested food even if different physiological functions had the same optimal temperatures (Brett, 1971; Warren, 1971; Huey and Slatkin, 1976; Hainsworth and Wolf, 1978; Magnuson and Beitinger, 1978; Greenwald and Kanter, 1979). This model can be tested by measuring net energy gain as functions of body temperature and of food level (Greenwald and Kanter, 1979).

Predictions from this simple model must be altered for reptiles that reach a steady metabolic rate near their normal activity temperatures (Fig. 6B; Bennett and Dawson, 1976). Depending on the position of the steady zone, a shift in food availability may or may not favor a change of body temperature. (Perhaps species that fail to change body temperature with food level have broad zones of steady metabolism.) This model oversimplifies digestive/metabolic considerations (Kitchell, 1979; Greenwald and Kanter, 1979). Also, even though a low body temperature conserves energy, it might also reduce the rate of prey capture or increase the risk of predation. Nevertheless, a reptile could circumvent these disadvantages by becoming hypothermic only when inactive (Regal, 1967).

A test of these hypotheses superimposes available data on the thermal dependence of performance of various physiological systems for adult *Dipsosaurus dorsalis* and for *Sceloporus occidentalis*; these are the only reptiles for which sufficient data are available (Fig. 6). Within the range of normal body temperatures of each species, possible differences in ranges of
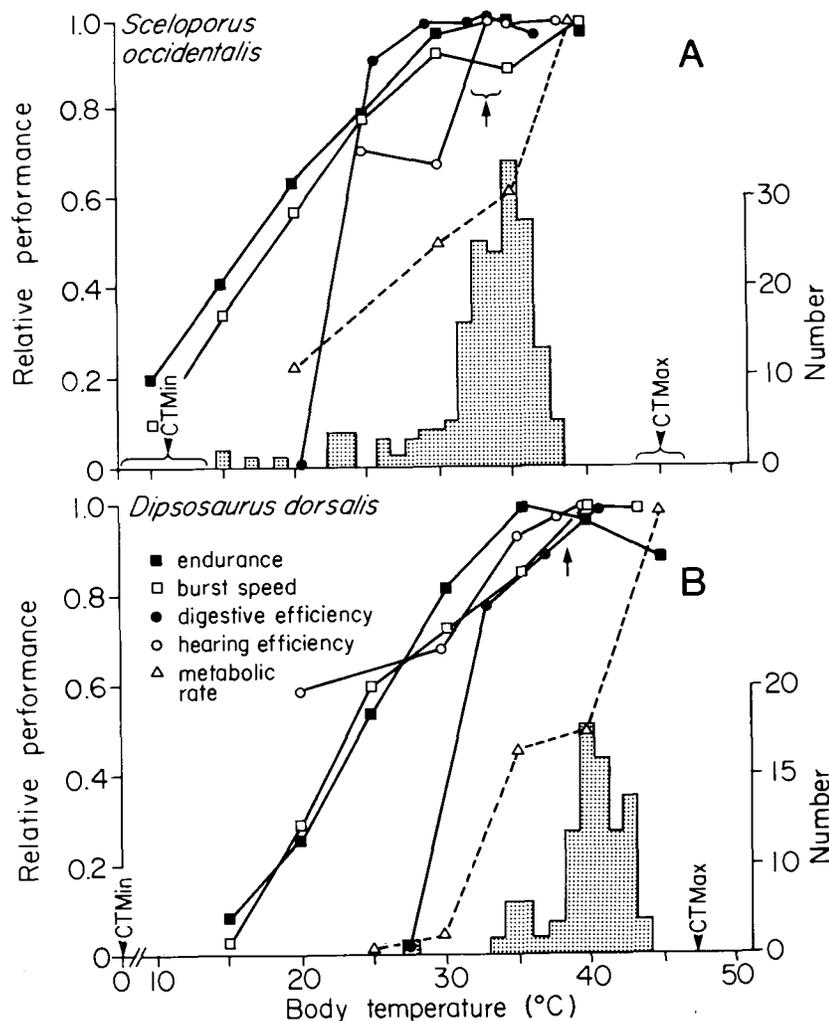

FIG. 6. Relative performance of several physiological systems and the relative metabolic rate for the lizards *Sceloporus occidentalis* (A) and *Dipsosaurus dorsalis* (B). Arrow indicates selected body temperature(s). References for A: Brattstrom, 1965; McGinnis, 1966; Werner, 1972; Harwood, 1979; A. F. Bennett, 1980, personal communication. References for B: Brattstrom, 1965; DeWitt, 1967; Bennett and Dawson, 1972; Werner, 1972; Harlow et al., 1976; Bennett, 1980).

optimal temperatures of physiological performance functions (metabolic rate is, of course, not a performance function) are obscure.

Physiological processes can, of course, have different sensitivities (i.e. have different Q_{10}s) even when optimal temperatures are similar. For example, low temperatures inhibit sprint velocity less than digestion (Fig. 6). This difference might reflect selection for enhanced ability to escape predators or inclement conditions at a variety of body temperatures (Bennett, 1980). The significant factor is not that digestion has a higher optimal temperature than does locomotion, but only that the performance profiles of these functions differ.

We cannot yet discriminate conclusively between these two hypotheses. We need much more information of the type in Figs 3 and 6 (especially from reptiles other than lizards), information on performance and metabolism at narrower temperature intervals (the 5°C intervals traditionally used may give insufficient resolution), and much larger sample sizes so that possible differences in optimal physiological temperatures can be tested statistically. In any case, these views may oversimplify reptilian thermal biology because no single temperature characterizes all parts of a reptile's body and because some diurnal variation in T_b may be essential to reptiles (Regal, 1967).

E. Analytical Problems

A laboratory estimate of the thermal sensitivity of physiological performance may scale only directly with the thermal sensitivity of ecological performance. Thus a 50% reduction in physiological performance may not represent a 50% reduction in fitness. For example, the Q_{10}s of several indices of locomotor performance (average velocity, maximum velocity, mean acceleration) of gopher snakes (*Pituophis melanoleucus*) striking at mice vary from 1.1 to 2.4 (between 18° and 27°C), whereas the Q_{10} for actual strike success is 2.5 calculated from data in Greenwald, (1974); Fig. 3F). A related problem concerns comparisons among physiological processes; a 50% reduction in acceleration will almost certainly have a different effect on fitness than a 50% reduction in digestion. Such scaling problems complicate attempts to integrate physiology and ecology.

Some ecologically important processes are long term (Table I) and thus require long-term laboratory studies. Nevertheless, few reptiles experience constant temperatures for extended periods, and temperatures that are optimal for short periods may become detrimental for longer ones (Cowles and Burleson, 1945; Bogert and Martín del Campo, 1956; Wilhoft, 1958; Licht, 1965; Pough, 1974, 1980; Regal, 1980). Moreover, the thermal sensitivity of physiological performance following cycling acclimation regimes may not always be predicted from knowledge of performance

following constant acclimation regimes (Hutchison and Ferrance, 1970; Feldmeth *et al.*, 1974; Humphreys, 1975; Regal, 1980; White and Somero, 1982).

If optimal temperature ranges differ among physiological processes or with age, sex, time, or metabolic state (Section IID), then no single zone of body temperature simultaneously optimizes all processes. If the shapes of the performance curves differ among physiological processes (Fig. 6), then a given zone of body temperatures may have relatively different effects on the various processes. The significance of particular body temperatures may be best interpreted by ordering processes in terms of their importance to an animal. If optimal body temperature is higher for prey capture than for growth, then a high body temperature might be selected only when the ability to capture food is of more importance than is the ability to grow quickly.

The productivity of the environment will itself influence ecological performance (Lillywhite *et al.*, 1973; Huey and Slatkin, 1976; Parmenter, 1980; Crowder and Magnuson, in press). For example, the optimal temperature for growth of salmon (Brett, 1971) is directly related to food availability. When food is abundant, these animals grow fastest at high body temperatures; when food is scarce, they grow fastest at a low body temperature.

III. Ecological Context of Temperature Regulation

A. Introduction

Early field studies (Cowles and Bogert, 1944) strongly emphasized the precision of temperature regulation by reptiles. Early workers had to overthrow a long established tradition in biology that reptiles were incapable of controlling body temperature and to convince others that attention to thermal considerations was a *sine qua non* for meaningful physiological/ecological/behavioral studies on reptiles (reviews in Greenberg, 1976; Gans and Pough, this volume).

The universality of precise temperature regulation was challenged in the 1960s by the discovery that several reptiles, especially tropical and nocturnal ones, sometimes do not thermoregulate carefully while active. Such thermoconformity was first documented in classic studies of Caribbean *Anolis* (Ruibal, 1961; Rand, 1964a). Imprecise thermoregulation has now been confirmed in many other reptiles (Fig. 7; Brattstrom, 1965; Alcala, 1967; Heatwole, 1970; Ruibal and Philibosian, 1970; Barbault, 1974; Hertz, 1974, 1977; Huey, 1974a, b; Lee, 1975; Huey and Webster, 1975, 1976; Clark and Kroll, 1974; Greenberg, 1976; Lister, 1976; Nicholas, 1978; Lee,

1980). Field and laboratory analyses demonstrate that thermoregulatory precision (Regal, 1980) is influenced by competitors or predators (DeWitt, 1963, 1967; Regal, 1968; Regal and Connolly, 1980), food level (Regal, 1968; Swingland and Frazier, 1979), time of day (Regal, 1967), weather (Licht *et al.*, 1966a), and environmental heterogeneity (Soulé, 1963). Inter-specific differences in thermoregulatory precision integrate with general aspects of reptilian ecology, namely microhabitat associations and foraging behavior (Pianka, 1967; Pianka and Pianka, 1970; Lee, 1980). Imprecise thermoregulation and broad thermal tolerances (eurythermy) may increase potential activity times, thereby outweighing the presumed physiological advantages (Somero, 1978; Heinrich, 1981) associated with precise thermoregulation and narrow thermal tolerances (stenothermy).

These studies emphasize that nature bears little resemblance to the biotic sterility of a laboratory thermal gradient. Predators or competitors may limit access to heat sources or sinks, suitable thermoregulatory sites may be inaccessible or distant from food and conspecifics, and ambient conditions may be periodically unsuitable for activity. Moreover, thermoregulatory
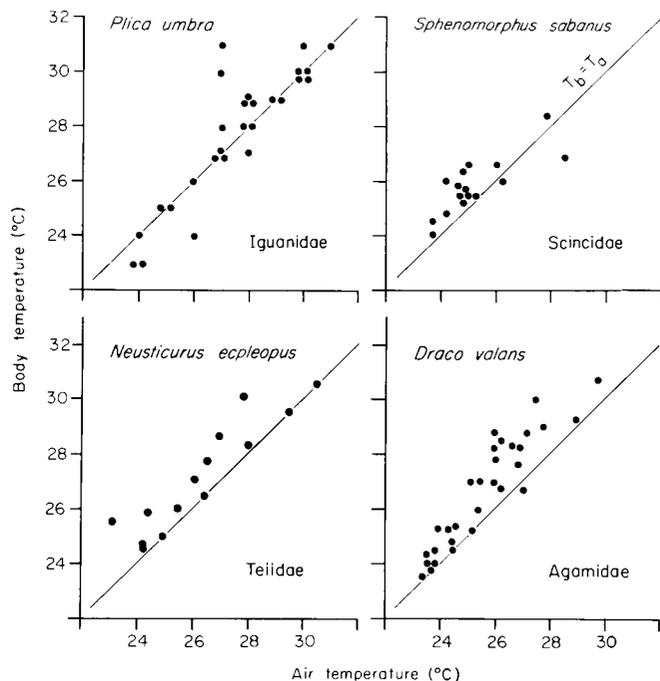

FIG. 7. Activity temperature versus air temperature for diurnal lizards from several families, which appear to be thermoconformers. Data sources: *Plica umbra* (redrawn from Rand and Humphrey, 1968), *Sphenomorphus sabanus* (Inger, 1959), *Neusticurus ecpleopus* (H. S. Fitch personal communication), *Draco volans* (redrawn from Alcala, 1967, excluding questionable records).

adjustments take time and energy and may expose a reptile to significant hazards. This is the ecological context of temperature regulation.

Theoretical studies propose that the evolution of behavior and physiology may be sensitive to these factors as well as to the obvious physiological benefits of temperature regulation (Soulé, 1963; Regal, 1968, 1980; Ruibal and Philibosian, 1970; Huey, 1974b; Avery, 1976, 1979, this volume; Greenberg, 1976; Huey and Slatkin, 1976; McFarland, 1976; Humphreys, 1978; Magnuson and Beitinger, 1978; Pianka, 1978; Magnuson *et al.*, 1979). Viewed from this perspective, fitness might be a function of the *net* rather than of the gross benefit of temperature regulation.

Empirical study of the effects of ecological factors on reptilian thermal biology is recent, and available data largely have indirect and weak bearing on the issues. However, direct experimental paradigms have been developed in studies of fishes (reviewed in Reynolds, 1977; Magnuson and Beitinger, 1978) and could readily be adapted to reptiles.

B. TOWARD AN ECOLOGICAL DEFINITION OF TEMPERATURE REGULATION

An ecologically based definition of temperature regulation is fundamental to analyses in thermal ecology. Temperature regulation may be diagramed as a negative feedback system (Fig. 8) involving both the animal and its environment. The animal monitors or anticipates (Heath, 1962; Hammel *et al.*, 1967; Lang, 1976; Pearson and Bradford, 1976; Pooley and Gans, 1976; Swingland and Frazier, 1979) an environmentally induced change in body temperature, compares this with some internal reference (set-points; Heath, 1965; Berk and Heath, 1975; Barber and Crawford, 1977; Firth and Turner, this volume), and activates appropriate behavioral and physiological
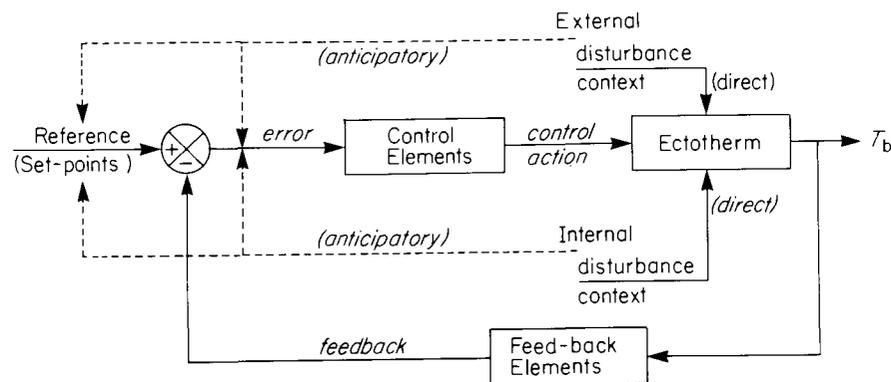

FIG. 8. A negative feedback control system for reptilian thermoregulation that incorporates the impact of the environment on both heat flux and set-points. Modified (see text) from Mitchell *et al.* (1970).

adjustments to achieve body temperatures within the reference zone (White, 1973; Avery, this volume; Bartholomew, this volume). Changes in the environment can affect temperature regulation in two ways. First, environmental (external or internal) heat loads directly alter body temperature and prompt a thermoregulatory response. Second, environmental conditions (e.g. productivity, presence of predators or competitors, availability of sunlight) may alter the set-points themselves or may cause a reptile to abandon thermoregulation (Regal, 1967, 1971; Heatwole, 1970; Brett, 1971; Lillywhite et al., 1973; Huey, 1974b; Greenberg, 1976; Huey and Slatkin, 1976; Done and Heatwole, 1977; Reynolds, 1977; Magnuson and Beitinger, 1978; Hainsworth and Wolf, 1978; Cabanac, 1979). Changes in the physiological state of an animal may also alter set-point temperatures (Garrick, 1974; Regal, 1980; Avery, this volume).

Definitions of temperature regulation are well established in the physiological literature (Heath, 1970; Bligh and Johnson, 1973). A modified definition for ecological analyses might read:

> Temperature regulation is a dynamic process involving behavioral and physiological adjustments that attempt to achieve body temperatures within a zone in response to actual or anticipated changes in external and internal heat loads. The zone may depend on the ecological and physiological context.

Temperature regulation is thus a process that involves an adjustment (the behavioral/physiological activities), a reference (zone or set-points), and a result (control of body temperature). Thermoconformity may be viewed as one extreme of a continuum of thermoregulatory options (Huey and Slatkin, 1976). The physical and biotic environment interact intimately (Fig. 8).

C. ESTIMATING THE EXTENT OF TEMPERATURE REGULATION

Temperature regulation is a multifaceted process. Consequently, no single method estimates all its aspects. Several indices measure the extent to which thermoregulatory adjustments are utilized. For example, the frequency of movement between sun and shade (or any hot and cold microenvironments) is a direct measure of shuttling behavior (Heath, 1965; Grenot, 1967; Spellerberg, 1972d). Similarly, the percentage of time in sun (Spellerberg, 1972d) and the proportion of the population in sun (Rand, 1967; Huey, 1974b; Obbard and Brooks, 1979; Hertz, 1981) index basking intensity.

Nevertheless, these measures may result in misleading conclusions about the extent of thermoregulation in the absence of information about the environment (Heath, 1964). For example, a lizard on a tree trunk typically basks only early and late in the day. The graph of the percentage of time spent in the sun with respect to time of day is generally U-shaped. The conclusion, that such a lizard thermoregulates by shuttling between sun and

shade is superficially reasonable but may be unwarranted. The proportion of a tree trunk that is in the sun also changes with time of day; consequently, the percentage of time in the sun for a lizard that was moving *randomly* (hence, not thermoregulating) with respect to sun and shade also plots as a U-shaped curve (Huey et al., 1977).

The variance in body temperature has been used as a measurement of the precision of the thermoregulatory process (Pianka, 1966; Ruibal and Philibosian, 1970; Parker and Pianka, 1973; Huey and Slatkin, 1976; Magnuson et al., 1979), but there are major objections to its use. The variance (i.e. descriptor of central tendency) is a statistically inappropriate measure, because reptiles do not regulate their body temperature about a mean value, but change between upper and lower set points (Berk and Heath, 1975; Barber and Crawford, 1977). Moreover, variance underestimates thermoregulatory precision when set-points vary. Variance also provides ambiguous information about the extent of thermoregulatory adjustments. The variance of body temperature of an active thermoregulator can be high in a thermally heterogeneous environment (Soulé, 1963; Ruibal and Philibosian, 1970; Huey and Webster, 1975), whereas this variance would be low for an inanimate object in a homogeneous environment (Heath, 1964). Finally, variance in body temperature is partially dependent on body mass (Mackay, 1964; Spotila et al., 1973; McNab and Auffenberg, 1976; Smith, 1979; Bartholomew, this volume).

Both the adjustments and the results of temperature regulation may be integrated indirectly by calculating the slope of the linear regression of body temperature on ambient temperature; a slope near 0 suggests perfect temperature regulation (body temperature independent of ambient temperature), whereas a slope near 1 suggests thermoconformity (body temperature dependent on ambient temperature). This method is sensitive also to changes in set-points, but it is partially independent of variance in ambient conditions.

The method has some limitations (Hertz and Huey, 1981). First, a reptile that thermoconforms while active (slope = 1) may still achieve a low variance in body temperature by restricting its activity to times and habitats with suitable microenvironments. Second, the slope for a lizard on a tree trunk is biased toward 0 because of diurnal changes in the availability of sun. Third, ambient temperature is only a convenient estimate of ambient heat loads on reptiles (Tracy, this volume). Fourth, additional problems arise when high ambient temperatures force body temperatures above optimal levels (Huey and Slatkin, 1976).

Methods of measuring the precision of thermoregulation are crude. For the present, choice among methods depends on the hypothesis being addressed. Both direct (e.g. frequency of behaviors) or indirect (slope)

measures are relevant to hypotheses that address the extent of thermoregulatory adjustments (Hertz and Huey, 1981), whereas variance in body temperatures is more relevant to hypotheses that focus on body temperature itself. Nevertheless, comprehensive statements about the extent of temperature regulation require information about behavior, temperature, and the environment (Cowles and Bogert, 1944; Heath, 1964, 1965).

D. Costs and Risks of Temperature Regulation

1. Costs in Energy

Energetic costs associated with temperature regulation are of two distinct types. First, metabolic rate is a function of body temperature (Bennett and Dawson, 1976; Fig. 3L); consequently, any change in body temperature during temperature regulation necessarily alters basic metabolic costs. Second, positional adjustments associated with temperature regulation (e.g. shuttling, Avery, this volume) require the expenditure of energy. These two costs must be deducted from any resultant physiological benefits (Section II) to estimate net benefits of temperature regulation (Huey and Slatkin, 1976; Greenwald and Kanter, 1979; Crowder and Magnuson, in press).

The actual energetic cost of locomotion is not great for reptiles (Bennett, vol. 13); but the cumulative energy expended might be considerable. For example, a four- to sixfold increase in the time a reptile is moving may increase its daily energy expenditures by 30% to 50% (Huey and Pianka, 1981).

Theoretical cost–benefit models predict that precise temperature regulation is practical (i.e. maximizes net benefit per unit time) only when the associated costs are low relative to the resulting benefits: in other words, body temperatures that are physiologically optimal may be ecologically optimal only if the costs necessary to achieve them are low (Huey and Slatkin, 1976; Hainsworth and Wolf, 1978; Magnuson et al., 1979).

This prediction may be tested indirectly by comparing the behavior of reptiles living in habitats that differ in potential costs of shuttling. For example, potential costs should be greater in a shaded forest than in an open one, because distances to patches of sun for basking are more widely spaced (Hertz, 1974; Huey, 1974b; Lee, 1980). Indeed, Anolis living in shaded forests tend to be passive to ambient conditions, whereas lizards living in open habitats tend to bask and thermoregulate more carefully (Ruibal, 1961; Rand, 1964a; Rand and Humphrey, 1968; Fitch, 1973; Hertz, 1974; Huey and Slatkin, 1976; Lister, 1976; Lee, 1980). This general relationship is not limited to Anolis but has been described or can be inferred for a variety of other lizards (Fig. 7; Table IV). This radical difference in behavior with habitat may hold even on a microgeographic scale within species. Anolis

TABLE IV

Percentage of species that bask in open and edge versus forest habitats at two tropical localities

Locality	Forest		Open-edge		References
	Bask	(N)	Bask	(N)	
Belém, Brazil	28.6	(7)	100	(7)	Rand and Humphrey, 1968
Santa Cecilia, Ecuador	27.3	(22)	100	(4)	Duellman, 1978

cristatellus and A. sagrei bask and achieve high body temperatures in open habitats, but in adjacent forests they are passive and only maintain low body temperatures (Huey, 1974b; Lister, 1976; Lee, 1980; Fig. 9).

Tree trunks in open habitats can represent an extremely low-cost microhabitat to a lizard because diurnal changes in the extent of shading on tree trunks favor precise temperature regulation (Huey et al., 1977; Hertz and Huey, 1980) and ensure that distances to sun and shade are small (Parker and Pianka, 1973). Variance in body temperatures is lower in two
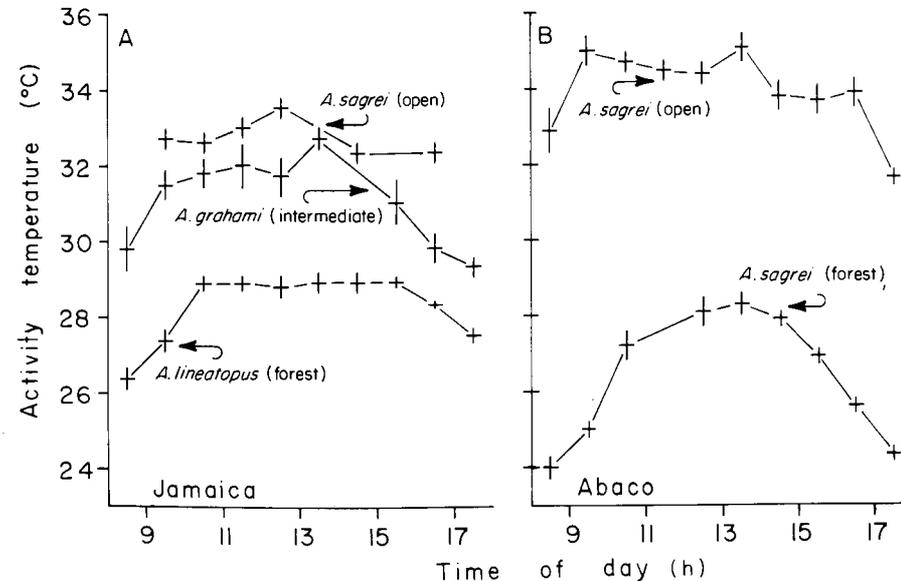

FIG. 9. (A) Body temperature of Anolis from several Caribbean islands and habitats. Populations of A. sagrei in Jamaica are sympatric with several congeners, are restricted to open habitats, and have a narrow range of T_b. (B) Populations of A. sagrei on Abaco are allopatric, occur in forest and open habitats, and have a broad range of T_b. (Redrawn from B. C. Lister, personal communication.)

semi-arboreal lizards (*Sceloporus magister* and *Urosaurus ornatus*) than in sympatric, terrestrial lizards in North American deserts (Parker and Pianka, 1973).

The thermoregulatory cost of a habitat is, of course, partially a function of the biology of the reptile under consideration. A shaded forest is a high-cost habitat to a territorial reptile (e.g. *Anolis*). The same forest may be a low-cost habitat to a reptile that follows sun flecks across the forest floor (e.g. *Kentropyx calcarata*, Rand and Humphrey, 1968) or shuttles to the forest edge (e.g. *Ameiva leptophrys*, Hillman, 1969).

In very open and structurally simple habitats the potential costs of raising body temperature by basking are minor, but the potential costs of seeking shade (Asplund, 1974) or of panting (Cowles and Bogert, 1944) may be excessive (McFarland, 1976). Thermoconformity might also be adaptive in these habitats. For instance, the lacertid *Aporosaura anchietae*, which lives on open dunes without vegetation in the Namib Desert, is a thermocon-former (M. D. Robinson, personal communication), has simple thermore-gulatory behavior (Louw and Holm, 1972) and is active over a broad range of body temperatures (23.2–40.9°C).

These arguments are consistent with the prediction that the precision with which reptiles thermoregulate should reflect the potential costs that their habitats impose upon that behavior. Nevertheless, other non-exclusive considerations lead to similar predictions; thus, these arguments do not represent a rigorous test of the energetic hypothesis.

Potential costs of thermoregulation may not explain thermoconformity in all forest reptiles. In equitable habitats some species may always be active at near-optimal body temperatures without using overt thermoregulatory behaviors (Huey and Slatkin, 1976); this appears to be the case for tropical, forest species that have relatively low selected temperatures. For example, *Anolis gundlachi* neither basks nor regulates its time of activity in the forests of Puerto Rico (Heatwole *et al.*, 1969). Nevertheless, the central 50% of all body temperatures selected in a laboratory thermal gradient bracket most values of body temperature determined in the field during the summer (Fig. 10). However, thermoconformity at high elevations would probably result in activity at body temperatures well below the selected temperatures. Many widespread *Anolis* are thermoconformers in lowland forest habitats; they shift to open habitats and thermoregulate only at higher elevations (Rand, 1964; Ruibal and Philibosian, 1970; Clark, 1973; Clark and Kroll, 1974; Huey and Webster, 1975, 1976; Huey and Slatkin, 1976; Hertz, 1977; Hertz and Huey, 1981; but see Hertz *et al.*, 1979).

2. Costs in Time

A reptile can lengthen its potential activity period by careful thermoregu-
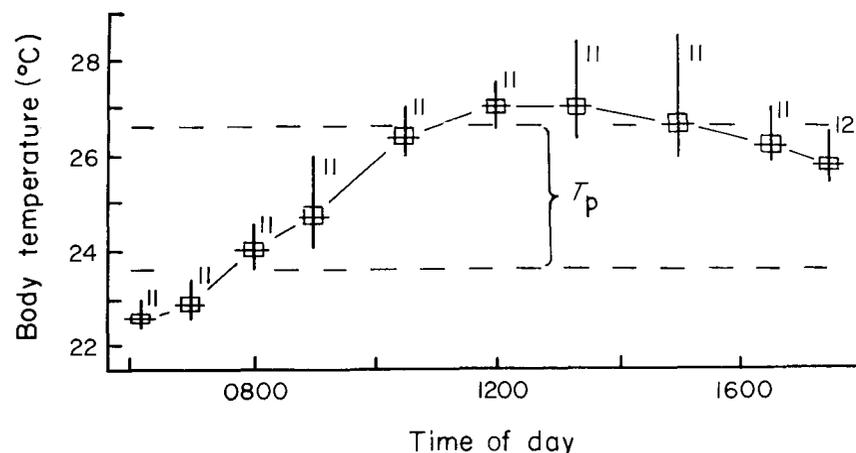
FIG. 10. *Anolis gundlachi* is a thermoconformer in the forests of Puerto Rico. Nevertheless, this species is normally active at T_b within selected limits (T_p), at least during summer months. Vertical lines represent ranges, horizontal lines represent means, boxes represent ± 1 SE, and associated numbers represent sample sizes. Selected limits (dashed lines) set by central 50% of records of T_p from lizards in laboratory thermal gradients. (Modified from Huey and Webster, 1976.)

lation (Porter *et al.*, 1973). Nevertheless, the time devoted to thermoregula-tion can sometimes reduce the time available for other important activities. For instance, thermoregulatory requirements to bask periodically force tropical *Ameiva* to cease foraging in the interior of a forest (Hillman, 1969).

The time required to regulate body temperature should be high where distances to sunlight or to shade are long (e.g. in shady forests or in open deserts), where environmental conditions fluctuate greatly, and where ambient temperatures differ strikingly from the thermal preferences of a reptile. As examples, time spent basking is relatively high in northern populations of lacertids (Avery, 1976, 1979), in montane populations of iguanids (Ruibal and Philibosian, 1970; Burns, 1970; Huey and Webster, 1975, 1976; Hertz and Huey, 1980), and during cool seasons (Berry, 1974; Huey *et al.*, 1977).

The consequences of devoting time to thermoregulation may have broad behavioral and ecological significance. For example, the behavioral com-plexity among European lacertid lizards is inversely related to latitude, possibly because thermoregulation occupies a greater fraction of the time budgets of lizards in the north (Avery, 1976, 1979). These considerations may not always be important (R. Ruibal, personal communication). Time may not be limiting to some tropical reptiles, for instance to snakes that have just captured large prey, or to reptiles that can thermoregulate and forage simultaneously.

3. Risk of Predation

The relationships between thermoregulation and risk of predation are complex and have received little attention (Magnuson and Beitinger, 1978; Shine, 1980b). Thermoregulation should enhance the ability of a reptile to detect (Fig. 3K; Werner, 1972) or evade potential predators (Fig. 3I and J; Webb, 1978; Bennett, 1980). Failure to thermoregulate carefully may have serious consequences. For example, hatchling *Conolophus pallidus* that are probably cold are susceptible to predation by hawks in the Galapagos (Christian and Tracy, 1981). Survivorship of juvenile *Uta stansburiana* is correlated with temperature (Fox, 1978). Several species of lizards seemingly compensate for reduced motor effectiveness when cold by fleeing from potential predators at greater distances (Rand, 1964b; Tinkle, 1967; Huey, 1974a; Greenberg, 1976; but see Avery, 1979). Some other reptiles become more aggressive toward predators at low body temperatures (Gans and Mendelssohn, 1972; Hertz *et al.*, 1982).

On the other hand, many thermoregulatory behaviors involve movements that may increase both the conspicuousness of reptiles and their rates of encounter with predators. The associated risk of predation might be especially high in shaded habitats. Here patches of sunlight are few, and mobile predators could learn to search a trap-line for basking reptiles. These postulated factors suggest that thermoregulation can sometimes increase risk of predation (Pianka and Pianka, 1970; Huey, 1974b; Huey and Slatkin, 1976; H. Saint Girons, 1978).

No data are available on the effects of predators on times of activity. Reptiles might restrict activity to times when their defensive abilities are most acute (McFarland, 1976). Alternatively reptiles could shift activity periods and thus reduce exposure to predators; such shifts could result in reduced thermoregulatory precision (Magnuson and Beitinger, 1978). Gravid *Cnemidophorus* are very secretive but nevertheless thermoregulate carefully in the safety of their burrows (Schall, 1977; Shine, 1980).

Interactions with predators may also force reptiles to abandon thermoregulation temporarily (DeWitt, 1967). Conversely, low pressure from terrestrial predators may permit adult marine iguanas (*Amblyrhynchus*) to thermoregulate on exposed sites (White, 1973).

4. Social Interactions

Some reptiles compete physically for limited thermoregulatory sites (Magnuson *et al.*, 1979). The turtle *Clemmys marmorata* defends basking sites along edges of streams (Bury and Wolfheim, 1973). Dominant *Klauberina riversiana* (Regal, 1971) and *Sphenomorphus kosciuskoi* (Done and Heatwole, 1977) prevent subordinates from gaining access to heat sources in the laboratory. Large male *Anolis* seemingly exclude smaller males from habitats that may be thermally optimal (A. S. Rand, personal

communication; Huey and Webster, 1975; Schoener and Schoener, 1980). Dominance in female *Lacerta viridis* is related to basking frequency (M. C. Saint Girons, 1977). Competition for shade can lead to death of small *geochelone gigantea* (Swingland and Frazier, 1979).

Social interactions may interfere with thermoregulation. *Dipsosaurus* abandon thermoregulation while fighting and allow body temperature to rise to near lethal levels (DeWitt, 1967). Dominant *Tupinambis teguixin* may prevent subdominant individuals from being active at certain times (Regal and Connolly, 1980). Such territorial encounters may influence the evolution of high thermal tolerances in some reptiles (Curry-Lindahl, 1957, 1979).

5. Influence of Interspecific Competitors

The theoretical and empirical effects of competition on the precision of temperature regulation deserve attention (Huey and Slatkin, 1976; Magnuson and Beitinger, 1978; Magnuson *et al.*, 1979; Lee, 1980). The impact of thermal biology on competition is suggested by observations that differential patterns of habitat associations or times of activity of species often appear to be physiologically based (Carpenter, 1952; Inger, 1959; Ruibal, 1961; Rand, 1964a; Schoener and Gorman, 1968; Heatwole *et al.*, 1969; Pianka, 1969; Corn, 1971; Spellerberg, 1972a; Huey and Webster, 1976; Gorman and Hillman, 1977; Schoener, 1977; Gregory and McIntosh, 1980; Mushinsky *et al.*, 1980; also see Schoener, 1977; Wiens, 1977). Species of *Anolis* that occur without congeners on an island are active over a broad range of body temperatures (Ruibal and Philibosian, 1970; Huey and Webster, 1975). This range is much larger than that of anoles in the complex Cuban fauna (Ruibal, 1961), suggesting that interspecific competition may restrict thermoregulatory activities. Nevertheless, many anoles in complex faunas are now known to be active over a broad range of body temperatures (Hertz, 1982).

The most direct demonstration that interspecific competition affects thermoregulation comes from studies of species of *Anolis* (Fig. 9; Lister, 1976). On Caribbean islands (Exuma, Abaco) where shade-tolerant congeners are absent, *A. sagrei* has invaded shaded forests and is active over broad ranges of body temperatures. Congeneric species occupy such habitats in Jamaica; as a result, *A. sagrei* is restricted to open habitats and is active over a narrower range of body temperature (Fig. 9; Lister, 1976). Similarly, the solitary *Anolis monensis* shows a greater variance in body temperature on Mona Island than does the closely related *A. cooki*, which occurs sympatrically with other anoles on mainland Puerto Rico (Lister, 1976). It would be very interesting to learn whether these shifts reflect present or past competition (see Schoener, 1974a).

6. Abundance of Food

The relationship between food level and thermoregulatory precision is probably significant, but virtually all empirical studies have been conducted on fishes (Magnuson and Beitinger, 1978). An increase in the abundance of food in a habitat may increase the rate of food intake of a reptile or increase the time it has available for non-foraging behaviors (e.g. thermoregulation). Cost–benefit considerations suggest that reptiles should respond by thermoregulating more carefully (Pianka and Pianka, 1970; Huey and Slatkin, 1976; Magnuson et al., 1979). Thus, well-nourished Anolis sagrei thermoregulate more precisely than do poorly-nourished individuals in closed habitats where the potential costs of thermoregulation are high (Lee, 1980).

If sites with abundant food are suboptimal for thermoregulation, behavior is more difficult to predict (Brett, 1971; Reichert and Tracy, 1975; Magnuson and Beitinger, 1978; Swingland and Frazier, 1979; Crowder and Magnuson, in press). Marine iguanas (Amblyrhynchus, Bartholomew, 1966) and Gonatodes (Heatwole, 1966) temporarily abandon sites suitable for thermoregulation in search or in pursuit of food. The amount of time animals spend foraging in such sites may depend on the degree of thermal stress (Magnuson and Beitinger, 1978; Swingland and Frazier, 1979).

7. Do Most Reptiles Thermoregulate Precisely?

Early studies generalized that most lizards (and presumably other reptiles) thermoregulate; however, the discovery of thermoconforming species in several lizard families (Fig. 7) demonstrates that the generalization requires revision. Many tropical reptiles do not bask, but nevertheless achieve body temperatures near optimal levels (Fig. 10). Thus, if maintenance of body temperature near the mean temperature selected in a thermal gradient is the criterion for precise thermoregulation, then these reptiles may thermoregulate precisely (Fig. 4).

On the other hand, if overt thermoregulatory behavior is the criterion for thermoregulation, then many reptiles do not thermoregulate. For example, species living in tropical forests are far more likely to be non-baskers than are species living in adjacent open habitats (Table IV) or species living in deserts. Even though temperate-zone deserts support many species of reptiles (Bogert, 1949a; Schall and Pianka, 1978), the tropics support as many or more (Dobzhansky, 1950; Table V), many of which live in forests and may rarely bask (Table IV). Moreover, overt thermoregulatory behaviors may be inconspicuous in nocturnal reptiles (Pianka and Pianka, 1976; Pianka and Huey, 1978; Werner and Whitaker, 1978; Avery, this volume). Nocturnality is more prevalent among snakes than among lizards (Table VI).

TABLE V

Percentage of species of lizards living in shaded forest or in open (including edge) habitats at some tropical and temperate-zone localities. Species occurring in both counted as 1/2 in each habitat.

Locality	Taxon (N species)	Percentage of species		References
		Forest	Open	
Tropics				
Barro Colorado Island, Panama	lizards (22)	60.0	40.0	C. W. Myers and A. S. Rand, 1969, personal communication
Belém, Brazil	lizards (23)	63.0*	37.0	Crump, 1971
Iquitos, Peru	lizards (34)	67.6	32.4	Dixon and Soini, 1975, 1977
	snakes (72)**	56.9	43.1	
La Palma, Dominican Republic†	Anolis lizards (9)	44.4	55.6	Rand and Williams, 1969
Sakaerat, Thailand††	lizards (26)**	63.5	39.3	Inger and Colwell, 1977
	snakes (14)**	60.7	39.3	
Santa Cecilia, Ecuador	lizards (29)	86.2	13.8	Duellman, 1978
Temperate Zones				
Osage Co., Kansas	lizards (7)	28.6	71.4	Clarke, 1958
Kansas Nat. Hist. Reserv.	lizards (8)	25.0	75.0	Fitch, 1956
Louisiana Pinelands	lizards (3)	–0–	100.0	Anderson et al., 1952

*Dominant occurrence of species in closed (terre firme, varsea) or open (Igapó, capoeira, open, edge).
**Includes some nocturnal species.
†Elevation=800 m.
††Occurrence of species in forest (evergreen+½ deciduous) and open (agricultural+½ deciduous).

TABLE VI

Frequency of diurnality and nocturnality in some squamate communities.

	Lizards			Snakes			
	Diurnal (%)	Nocturnal (%)	N	Diurnal (%)	Nocturnal (%)	N	References
Northeastern Thailand	63.3	36.7	30	41.1	59.0	39	Inger and Colwell, 1977
Santa Cecilia, Ecuador	96.3	3.3	30	51.9	48.1	53	Ducllman, 1978
Iquitos, Peru	95.0	5.0	40	41.7	54.5	48	Dixon and Soini, 1975; Henderson et al., 1979
Kade, Ghana	66.7	33.3	15	47.5	52.5	40	T. J. Papenfuss, pcrsonal communication

Species active at both times are considered $\frac{1}{2}$ diurnal, $\frac{1}{2}$ nocturnal. Species with uncertain activity periods are excluded. N, number of species.

At the present time data are inadequate to determine whether most reptiles thermoregulate precisely. Studies of secretive and fossorial species are especially needed (Miller, 1944; Lee, 1975; Bury and Balgooyen, 1976) Papenfuss, 1979; Bradshaw et al., 1980; Gregory, 1980; Avery this volume). In any case, available data suggest that the old generalization requires reevaluation. At this moment it appears that some reptiles thermoregulate precisely, some do not, and some regulate only part of the time (Fig. 4).

IV. General Aspects of Thermal Ecology

A. TIME OF ACTIVITY

1. *Overview*

The daily and seasonal activity patterns of reptiles are strongly influenced by thermal biology (Klauber, 1939; Sergeyev, 1939; Cowles and Bogert, 1944; Porter et al., 1973). Reptiles with the highest selected temperatures are typically active at the hottest times of the day and year (Fitch, 1956; Pianka, 1969; Hirth, 1963; Huey et al., 1977; Mushinsky et al., 1980). Nevertheless, this relationship is complex and invites further elaboration.

Limits to potential activity times (Bartlett and Gates, 1967; Porter and Gates, 1969; Porter et al., 1973; Tracy, this volume) are set by biophysical (thermal/hydric) characteristics of the habitat and by biological characteristics of a species (range of body temperature that is acceptable for activity, thermoregulatory repertoire, species-specific patterns of heat and mass flux). Actual times of activity may be further limited by the influences of

predators (McFarland, 1976) and competitors (Schoener, 1970, 1974b, 1977; Regal, 1971; Magnuson et al., 1979) as well as by the availability of food or water (Porter et al., 1973; Nagy, 1973; Huey and Slatkin, 1976; Magnuson and Beitinger, 1978).

A simple graphical technique (Porter et al., 1973) demonstrates how differences in temperature selection by two hypothetical species affect potential activity periods though all other characteristics of these species (e.g. size, shape, color, thermoregulatory repertoire) are assumed to be identical (Fig. 11). Diurnal changes in maximum and minimum potential body temperatures are predicted using standard biophysical procedures (Bakken, 1976; Porter and James, 1979; Tracy, this volume). The range of acceptable body temperatures for each species is then determined empirically; in Fig. 11, the range for two hypothetical reptiles has arbitrarily been set as 30–35°C and 35–40°C, respectively. The graph shows the times when acceptable body temperatures will be available in the habitat, thus predicting the biophysical limits on activity periods. In this example the "high-temperature" reptile should be active nearer midday. When seasonal variations in maximum/minimum potential body temperatures and in acceptable activity temperatures are graphed, one may similarly predict seasonal patterns of times of activity (Porter et al., 1973; Porter and James, 1979; Tracy, this volume).

The evolution of important thermal properties (e.g. range of acceptable body temperatures, thermoregulatory repertoire, size, color) may partially reflect the effects of these properties on activity periods (Porter, 1967; Muth, 1977; Pearson, 1977). Biophysical models (Tracy, this volume) should prove
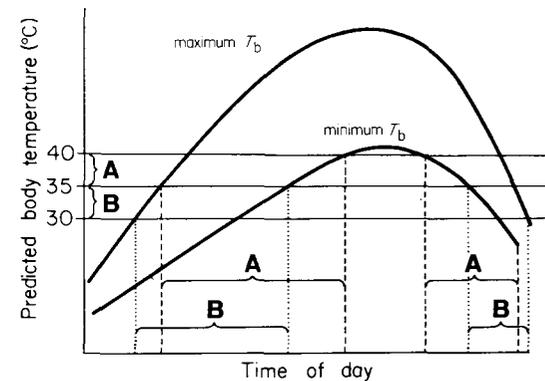

FIG. 11. Prediction of potential activity periods of two reptiles with nonoverlapping ranges of activity T_b. Maximum and minimum potential T_b are determined (assumed equal for both reptiles) by biophysical techniques (see text), and the potential times when each species can achieve its activity T_b are specified by projection.

useful in elucidating whether selection for these species-specific properties is sensitive to an increase in the total time of activity, an increase in the net energy gain, or to other considerations.

2. Relationship to Competition

The evolution of activity times may be influenced by interspecific competition. The degree of interspecific asynchrony in activity can be related to the intensity of competition in two basic ways (Schoener, 1974a, 1977; Jaksić et al., 1981; Huey and Pianka, 1983). (1) If differences in times of activity lower frequencies of direct encounters between competitors, interference competition may be reduced (Case and Gilpin, 1974; Magnuson et al., 1979). (2) If such temporal differences lower overlap in diet, exploitation competition for food can also be reduced (Levins, 1968; Mushinsky and Hebrard, 1977a).

Reptiles are well suited for analysis of nonsynchronous spatial overlap (Schoener, 1977; Frankenberg, 1978); only a few studies rigorously examine this relationship (Jaksić et al., 1981). Interspecific differences in activity times are more common among reptiles than among endotherms (Schoener, 1977), which probably reflects the relatively small climate spaces of reptiles (Porter and Gates, 1969). Low-temperature skinks in Borneo and Australia (Inger, 1959; Pianka, 1969), anoles in the Caribbean (Schoener, 1970; Schoener and Schoener, 1971), lacertids in France (M.C. Saint Girons, 1976), and lizards in the Kalahari (Huey et al., 1977) occupy given habitats at cooler times than do related species with higher thermal preferences.

Diets of water snakes (Nerodia) partly reflect time of activity (Mushinsky and Hebrard, 1977b); for example, only the nocturnal N. sipedon eat frogs and crawfish (Mushinsky and Hebrard, 1977a). Nevertheless, the overall overlap in diet of nocturnal versus diurnal water snakes (Mushinsky and Hebrard, 1977a) is surprisingly high, despite differences in activity times. Diets of some other diurnal and nocturnal predators are similar (Jaksić et al., 1981; Huey and Pianka, 1983). Consequently, differences in times of activity (day versus night) may not invariably reduce dietary overlap. The explanation for this is unclear; reptiles may capture inactive as well as active prey, inactive reptiles may capture prey that approach them, or the prey species themselves may be active by day and night.

Figure 11 suggests another reason for doubting that the evolution of times of activity is strongly related to exploitation competition. Even though the activity temperature of the two hypothetical reptiles do not overlap, their activity times still overlap considerably; such overlap is inevitable in thermally heterogenous environments. A major divergence in thermal properties may be necessary to reduce overlap in activity times. Nevertheless, adaptive changes in some aspects of reptilian thermal biology are slow

(Section IVE), and the competitive environment might shift before selection could force a change.

B. ACTIVITY VERSUS INACTIVITY

1. Introduction

Observations on the thermal biology of inactive reptiles which are sequestered under rocks or in burrows were difficult or impossible until the development of radiotelemetry. A few pioneering papers (Sergeyev, 1939; Cowles, 1941; Cowles and Bogert, 1944) were able to examine the behavior of reptiles during activity and inactivity. These examples were rarely followed; four decades later the thermal biology of reptiles while inactive (but not hibernating) remains virtually unknown (Hirth, 1963; Bustard, 1967b; Regal, 1967; Stebbins and Barwick, 1968; Heatwole, 1970; White, 1973; Case, 1976; Turner et al., 1976; Jacob and Painter, 1980; King, 1980; Parker and Brown, 1980; Boersma, 1981).

This deficiency could have serious consequences; a view of reptilian thermal biology that is based exclusively on their periods of activity is necessarily limited and possibly misrepresentative. The behavior of reptiles differs from that of mammals and inactivity may be a fundamental, dynamic, and integral aspect of reptilian thermal ecology (Gans and Dawson, 1976; Pough, 1974, 1980, in press; Regal, 1978, 1980).

2. Extent of Activity in Reptiles

Lowland tropical lizards of the genus Anolis may be active during most daylight hours (Heatwole et al., 1969) and thus are active nearly 50% of the total time during a year. This probably represents the maximum period of activity among reptiles; actual times of activity are short in most other reptiles (Table VII), especially in herbivorous species (Wilson and Lee, 1974) and those of temperate zones (Avery, 1976, 1979). The annual activity of lizards is negatively correlated with latitude ($r_s = -0.79$, $N = 7$, $p < 0.05$: using full-year samples in Table VII).

Population values (Table VII) actually overestimate activity periods of individual reptiles for two reasons. First, not all individuals of some temperate-zone species are active daily, even when weather conditions permit (Nagy, 1973; Simon and Middendorf, 1976; Bradshaw et al., 1980). For example, an individual Gopherus agassizii is active a maximum of seven out of ten days (Marlow, 1979; Table VII), and Sceloporus virgatus may or may not be active daily, depending on sex and reproductive season (Rose, 1981; Table VII). Klauberina riversiana have seven- to ten-day activity rhythms in the laboratory (Regal, 1974). Second, the activity period of an individual reptile on any given day will be shorter than that for its

TABLE VII

Surface activity of some reptiles, compiled largely from Marlow, 1979

Species (locality, latitude)	Year active (%)	Days active (%)	References
Turtles			
Gopherus agassizii (California, 35°N)	3	0–70*	Marlow, 1979
Gopherus polyphemus (Florida, 30°N)	9	25–93*	Auffenberg and Iverson, 1979
Lizards			
Agama agama (Ghana 5°N)	41**		Porter and James, 1979
Agama agama (Nigeria, 11°N)	32**		Avery, 1976
Dipsosaurus dorsalis (California, 33°N)	6*		Porter *et al.*, 1973
Egernia cunninghami (Brisbane, 27°S)	8†		Wilson and Lee, 1974
Lacerta agilis (Italy, 48°N)	14**		Avery, 1976
Lacerta vivipara (United Kingdom, 52°N)	13**		Avery, 1976
Podarcis muralis (Italy, 44°N)	19**		Avery, 1976
Sceloporus jarrovi (Arizona, 32°N)		36	Simon and Middendorf, 1976
Sceloporus virgatus (Arizona, 32°N)			Rose, 1981
males, breeding season		97	
males, nonbreeding season		29	
females, breeding season		76	
females, nonbreeding season		71	
Uta stansburiana (New Mexico, 32°N)	25†		Alexander and Whitford, 1968

"Active" implies outside retreats, but not necessarily moving. With the exception of *Gopherus* spp. and *Sceloporus* spp., the estimates are for populations: an individual reptile would have more limited activity periods.
*Varies seasonally.
**Estimated roughly from graph.
†Percentage of waking hours.
††This estimate (Alexander and Whitford, 1968, p. 681) differs from a value in Table I of that paper.

population (Kay *et al.*, 1973; Nagy, 1973); for example, during the summer an individual *Dipsosaurus dorsalis* is active only 50–60% as long as is the whole population (Minnich and Shoemaker, 1970).

It is interesting that 70% of the annual energy budget of *Gopherus agassizii* is used while the animals are inactive (Marlow, 1979). Even during the primary activity season, this value will be 34% (Marlow, 1979). This pattern may not apply to all reptiles. For example, *Sceloporus occidentalis* are inactive about 67% of the time during seasons of high activity, but are believed then to expend only 11–17% of their energy budget (Bennett and Nagy, 1977).

Most of the species studied to date are relatively active by reptilian standards. Yet, even for these species, inactivity seems to be an important behavioral state in terms of time and often of energy. Most snakes and most reptiles belonging to secretive taxa remain to be studied, even though

appropriate techniques now exist (Gans and Bonin, 1963; Bennett and Nagy, 1977; Fitch and von Achen, 1977).

3. Thermoregulation during Inactivity

It is easy to assume that an inactive reptile has relinquished control over its thermal fate and is thermally passive. However, reptiles have two ways of thermoregulating during inactivity. (1) Selection of the retreat controls microclimates experienced during inactivity. For example, some reptiles select retreats in burrows, leaf litter, or boulders to gain access to warm and stable thermal microenvironments (Sergeyev, 1939; DeWitt, 1963; Heatwole, 1970; Porter *et al.*, 1973; Ruben, 1976c; Nicholas, 1978; see also Humphreys, 1978). (2) Reptiles can regulate body temperature by changes of position within such retreats (Cowles and Bogert, 1944; Cogger and Holmes, 1960; Case, 1976; Schall, 1977; Henderson *et al.*, 1980). For example, nocturnally active geckos regulate body temperature at high levels during the day by subtle movements under bark (Bustard, 1967b) or rocks (Dial, 1978). Thus, it may be a misconception that reptiles are always cold or thermally passive while in a retreat.

Some reptiles may be able to control body temperature more precisely while in retreats than when above ground (Cowles and Bogert, 1944; DeWitt, 1963). This can be demonstrated with a graphical technique derived from Porter *et al.* (1973). The maximum (in sun) and minimum (in shade) potential body temperatures of hypothetical reptiles on the surface and also in burrows are determined (Section IVA), and a range of acceptable body temperatures is also specified. The potential times when such reptiles can achieve desired body temperatures, both above and below ground, are easily predicted from these data (Fig. 12). Above ground these reptiles can achieve these body temperatures for only a few hours per day, but they can achieve them for about 19 h per day below ground by moving in a burrow between the surface and a depth of 20 cm. Even reptiles that remain stationary at a depth of 20 cm can achieve suitable body temperatures for about 14 h per day. Indeed, *Dipsosaurus dorsalis* during the summer may be able to maintain their selected temperature for 24 h per day without leaving their burrows (DeWitt, 1963). Of course, such precision is impossible in some retreats and in cooler seasons.

4. Benefits of Activity versus Inactivity

Activity has important benefits for reptiles (Schoener, 1974b; Schoener, 1977; Congdon *et al.*, 1979): it increases access to food, opportunities for temperature regulation (during cool seasons when temperatures are low), access to potential mates, and opportunities to monitor and to defend territories. Activity also has important disadvantages: it increases the risk of
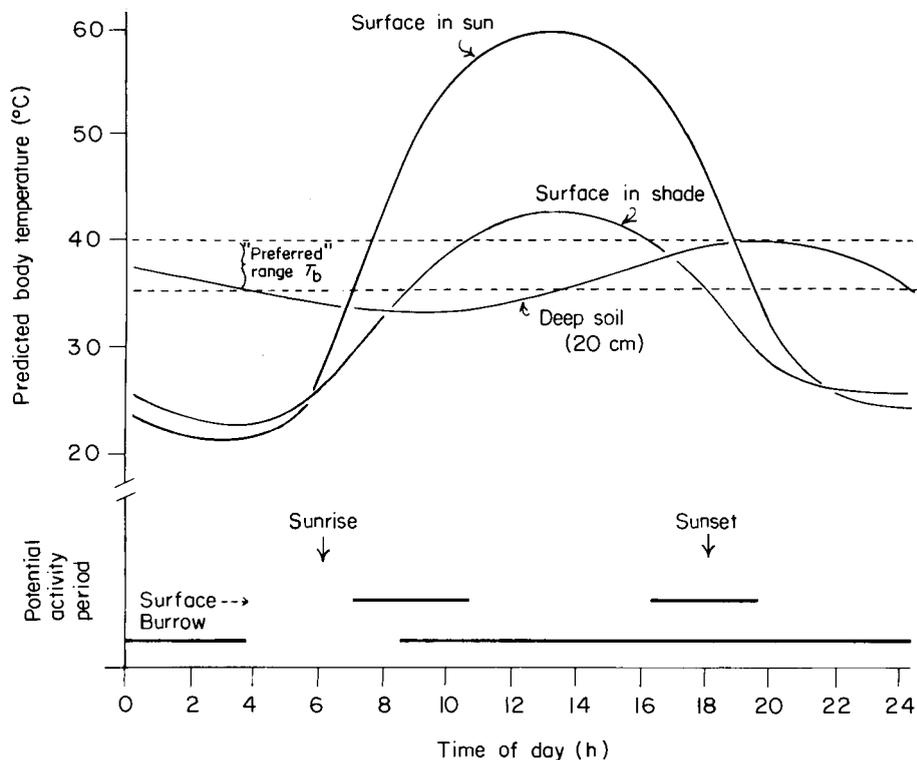
FIG. 12. Prediction of times when a hypothetical reptile can achieve acceptable T_b both above and below ground. By moving between the surface and a depth of 20 cm within its burrow, a reptile can achieve T_b within the acceptable range for much longer than it can achieve these T_b by shuttling between hot and cold microenvironments above ground. Note also that the coolest microenvironment at night is above ground. Thermal profiles adapted from Porter et al. (1973) and Hadley (1970).

predation, risk of injury in territorial encounters, and the expenditure of energy and water. A *Sceloporus occidentalis* might expend to two to three times more energy by being active for 8 h per day than by remaining in its burrow (Bennett and Nagy, 1977).

At certain times the food a reptile may capture provides less benefit than the costs of activity, and inactivity may then be favored (Schoener, 1977; Pough, 1980; Gans and Pough, this volume). For example, when the water content of their food (vegetation) is low, *Sauromalus obesus* reduce their rate of water loss by fasting and by retreating to rock crevices for long periods (Nagy, 1972, 1973). Many reptiles survive for extended periods with limited food because of their low metabolic rates (Benedict, 1932; McNab, 1963; Belkin, 1965; Bennett and Dawson, 1976) and fat storage (Bustard, 1967a; Vitt et al., 1977).

Undoubtedly, the relative advantages of activity versus inactivity are complex and will vary as a consequence of sex, reproductive condition, and ecological context. As examples, male *Sceloporus virgatus* increase activity dramatically during the breeding season (Table VII; Rose, 1981), but female *Cnemidophorus* are secretive while gravid (Schall, 1977).

5. *Voluntary Hypothermia*

Some reptiles voluntarily and actively select relatively low body temperatures at night (Regal, 1967; Grenot and Loirat, 1973; Hutchison and Kosh, 1974; Spellerberg, 1974; Grenot, 1976; Cowgell and Underwood, 1979; Naulleau, 1979; van Berkum, 1980; but see Wilhoft, 1958; Regal, 1967; Bradshaw and Main, 1968; Vernet, 1977; Hutchison and Maness, 1979). Voluntary hypothermia at night may reduce the risk of predation on *Klauberina*; after sunset lizards searching for warm microenvironments may be further away from shelter and may be more vulnerable to predators (Regal, 1967).

Some diurnal desert reptiles occasionally bypass their burrows and spend the night in shallow forms (e.g. *Gopherus agassizii*; McGinnis and Voigt, 1971; Marlow, 1979) or in vegetation (e.g. *Gambelia wislizenii*; Nicholas, 1978) the ambient temperatures of which are much lower than those of burrows (Fig. 12). Consequently these reptiles cool quickly and have low body temperatures. In these cases nocturnal hypothermia would seem to increase rather than decrease exposure to predators; thus a distinction between hypothermia and retreat to cover may be important.

Voluntary nocturnal hypothermia may also prolong potential foraging time the following day. For example, on a hot morning a *Gopherus* that initiates activity at a low body temperature might presumably forage longer before overheating than can one that initiates activity at a high initial body temperature (McGinnis and Voigt, 1971). Nevertheless, tortoises that spend the night in forms often have shorter foraging times; apparently they spend a long period basking before being able to commence foraging (Marlow, 1979). In contrast, *Gambelia*, which are much smaller than tortoises and warm rapidly, do increase foraging time by spending the night in vegetation (Nicholas, 1978).

Voluntary hypothermia may also conserve energy and may be adaptive for reptiles that have failed to obtain food recently. High nocturnal body temperatures might be adaptive for fed reptiles to prevent food spoilage and promote digestion (Harlow et al., 1976). This reasoning suggests a direct and testable prediction; reptiles that have not eaten recently should spend the night in cooler microenvironments than those which have just fed. Even some fed lizards become hypothermic in the laboratory at night (Regal,

1967; Grenot and Loirat, 1973), but their degree of hypothermia relative to that of unfed lizards remains unspecified.

Finally, voluntary hypothermia and periodic inactivity may be essential for health, at least of captive reptiles. Long exposure to constant, high temperatures can be stressful and periodic relief may be necessary. However, the physiological and evolutionary bases of this phenomenon are unclear (Regal, 1981).

6. *Implications for Physiology*

Some reptiles are inactive much of the time, and their body temperatures may differ between activity and inactivity. Consequently, attempts to interpret the thermal sensitivity of some physiological systems only in terms of activity temperatures may be misleading (1) if certain systems are used primarily by inactive reptiles or (2) if the observed thermal sensitivities represent an evolutionary compromise between body temperatures experienced during active and during inactive periods (Dawson, 1975; Hutchison and Maness, 1979). Finally, acclimation regimes in laboratory studies can be made ecologically realistic and physiologically healthful by incorporating normal diel cycles of body temperature (Chapman, 1931; Dawson, 1975; Patterson and Davies, 1978b; Carey, 1979; Hutchison and Maness, 1979; Regal, 1980; White and Somero, 1982).

C. TEMPERATURE AND SEX DETERMINATION

A recent development that may have profound significance for population ecology is the discovery that sex of some reptiles is affected by the temperature during embryogenesis (Charnier, 1966; Pieau, 1974; Yntema, 1976, 1979; Bull and Vogt, 1979). Temperature-sensitive sex determination is particularly surprising because some reptiles have sex chromosomes (King, 1977), which implies genetic rather than environmental sex determination. Nevertheless, temperature-sensitive sex determination has been demonstrated in some but not in all families of turtles and lizards (Bull, 1980). This topic has recently been analyzed by Bull (1980); the following summarizes his review.

When eggs of certain species are incubated in the laboratory, the sex of the hatchlings depends on the temperature of incubation. Typically, eggs incubated at constant, low temperatures produce only one sex, whereas those maintained at constant, higher temperatures produce only the other. Curiously, low incubation temperatures result in females in turtles but induce males in lizards (Bull, 1980). In *Chelydra serpentina* females are produced at both extreme high and low temperatures, whereas males are produced at intermediate temperatures (Fig. 3E; Yntema, 1976). Biased sex

ratios are neither a function of differential mortality of sexes (Yntema, 1979; Bull and Vogt, 1979) nor an artifact of incubation at constant temperatures (Bull and Vogt, 1979). Whether sex induced by temperature remains fixed throughout the life of an individual and whether all individuals are actually fertile has not yet been established.

Genetical considerations suggest that temperature-sensitive sex determination and the occurrence of sex chromosomes are incompatible (Bull, 1980). Environmental sex determination has been demonstrated only in those groups of reptiles for which few species have sex chromosomes. The apparently recent evolution of reptilian sex chromosomes implies that temperature-sensitive sex determination may be primitive in reptiles (Bull, 1980).

The occurrence in reptiles of both genetic and environmental sex determination suggests either that selection for mode of sex determination varies among reptilian groups or that both modes are acceptable alternatives (Bull, 1980; Mrosovsky, 1980). Environmental sex determination would seemingly be disadvantageous in fluctuating environments because climatic variations could cause fluctuations in the sex ratio of the population (Charnov and Bull, 1977). Nevertheless, the life histories of some reptiles are well suited to minimize these problems, and environmental sex determination might persist despite the selective disadvantage associated with it (Bull, 1980; Mrosovsky, 1980).

On the other hand, the disadvantage of environmental sex determination might be countered by several advantages. If, for example, incubation at low temperature results in very fit males (but unfit females) but incubation at high temperatures results in very fit females (but unfit males), then environmental sex determination would permit each offspring to develop into the sex that is optimal for particular nest conditions (Charnov and Bull, 1977; Bull, 1980). Alternatively, if hatching early in the season is especially important to one sex (e.g. to increase size at maturity, see Trivers and Willard, 1973), then selection might favor induction of that sex by low incubation temperatures (C. H. Stinson, personal communication).

A female might select warm or cold nest sites in response to the current sex ratio of adults in the population; a sex ratio that is strongly biased toward males would favor selecting nest sites that induce all female offspring (Werren and Charnov, 1978). This explanation would seem improbable for turtles or other animals that have greatly delayed maturity; current sex ratios might be unreliable cues of future sex ratios.

The adaptive significance, ecological setting, and populational consequences of environmental sex determination remain unresolved. One important practical sidelight is evident: breeding programs for endangered species will have little benefit if incubation temperatures are inducing only a single sex (Mrosovsky and Yntema, 1980).

D. Thermal Specialists and Generalists

Reptiles differ in the degree of specialization of physiological performance. Animals with narrow performance ranges are often called physiological specialists or stenotherms, whereas animals with broader performance ranges are called physiological generalists or eurytherms. Presumably there is a trade-off between the ability of an animal to perform very efficiently at some small range of body temperatures (stenothermy) and its ability to perform at some lesser level over a broad range of body temperatures (eurythermy). In other words, a jack-of-all-trades may be a master of none (Levins, 1968; Huey and Slatkin, 1976). However, this proposition is based largely on extrapolation from biochemical considerations (Somero, 1978; Heinrich, 1981) rather than on direct evidence.

The assumptions that most reptiles are stenothermal (because they thermoregulate carefully) and that stenothermy is generally adaptive were implicit in early discussions of reptilian thermoregulation. Both assumptions reflected a widespread belief in the adaptive significance of homeostasis (Greenberg, 1976). Counter-advantages of eurythermy were also noted; namely that eurythermy increases the ranges of times, habitats, and body temperatures in which activity can be maintained (Soulé, 1963; Lee and Badham, 1963; Norris, 1967; Jacobson and Whitford, 1971; Kay, 1970; Bennett, 1980). In particular, eurythermy might be adaptive in situations of reduced inter-specific competition or for certain predatory lizards that rely on cryptic behavior and morphology to avoid detection by predators (e.g. *Phrynosoma*; Pianka, 1966, 1978; Pianka and Pianka, 1970; Pianka and Parker, 1975; but see also Whitford and Bryant, 1979).

Cost–benefit models (Huey and Slatkin, 1976; Crowder and Magnuson, in press) predict that thermal specialists achieve greater net benefits per unit time than do thermal generalists when costs of thermoregulation are low or when environmental temperatures allow activity at near-optimal body temperatures even if potential costs are high. Conversely, these models predict that thermal generalists achieve greater net benefits than do specialists in environments in which the temperatures are frequently low or are variable and in which the costs of thermoregulation are high (Huey and Slatkin, 1976; Nicholas, 1978).

Direct laboratory evidence that reptiles differ in degree of physiological specialization for temperature is limited. Table VIII ranks some lizards by relative degree of thermal specialization for several physiological traits. *Gerrhonotus* is relatively eurythermal for some but not all traits. Lack of concordance is evident.

Average tolerance range for several lizards (*Anolis carolinensis* = 29.0°C, *Sceloporus occidentalis* = 31.5°C, *Xantusia vigilis* = 34.8°C, and *Phrynosoma*

cornutum = 39.2°C) correlates with variability of microhabitats and daily behavior patterns for those lizards (Kour and Hutchison, 1970). Similarly, the average tolerance range for species of Australian *Sphenomorphus* increases with altitude (Spellerberg, 1972b).

TABLE VIII

Evidence for inter-specific variation among lizards in degree of thermal generality

Species	Rank order			
	ATP*	Muscle**	CTMax–T_p†	SD T_b††
Dipsosaurus dorsalis	1	4	4	1
Eumeces obsoletus	—	2	1.5	—
Elgaria multicarinata	4	1	5	3
Sceloporus undulatus	3	5	1.5	—
Uma notata	2	3	3?	2

Rank score of 1 indicates most specialized species (criteria specified in footnotes), larger ranks indicate increasingly generalized species. Lack of concordance among these indices is evident.
*Relative range of high activity (80% maximum ATPase activity), from data of Licht, 1967.
**Range of activity (80% maximum twitch tension) for skeletal muscle, from Licht, 1967.
†Difference between CTMax and T_p (selected temperature), from data of Licht, 1967. Rank for *Uma* is a minimum.
††Standard deviation in activity T_b for *Dipsosaurus* and *Uma* (W. W. Mayhew, personal communication) and for *Elgaria* (Cunningham, 1966).

A specific case that warrants investigation is the relative degree of physiological specialization of reptiles of the tropical and temperate zones. Tropical animals are often presumed to be relatively specialized because the yearly variance in ambient conditions in the tropics is low (Janzen, 1967; Taylor, 1981). Evidence supporting this hypothesis is available for frogs (Snyder and Weathers, 1975) and salamanders (Feder, 1978). Also, the mean tolerance range of four lizards is positively, but not significantly ($r_s = 0.40$, $p < 0.10$) correlated with northern range limit of the species (Kour and Hutchinson, 1970). Northern populations of *Gambelia wislizenii* are active over relatively broad ranges of body temperature (Nicholas, 1978), suggesting that a study of geographic variation in physiological specialization of this species would be of interest. The altitudinal range of lizards and snakes, which is partly a function of thermal specialization, is positively correlated with latitude (Huey, 1978).

E. RATE OF EVOLUTION OF THERMAL SENSITIVITY

How fast does the thermal sensitivity of physiological processes evolve? This question is basic to analyses of adaptations to changing environments (Levins, 1969; Brown and Feldmeth, 1971; Slobodkin and Rapoport, 1974). Not surprisingly, this or related questions have been asked early (Cowles and Bogert, 1944; Bogert, 1949a, b) and often in studies of reptilian thermal biology (Curry-Lindahl, 1957, 1979; Brattstrom, 1965; Heath, 1965; Hutchison et al., 1966; Licht et al., 1966a, b; Ushakov, 1967; Cloudsley-Thompson, 1971; Müller, 1971; Corn, 1971; Spellerberg, 1972a, b, c, 1973; Clark and Kroll, 1974; Heatwole, 1976; Huey and Slatkin, 1976; Huey and Webster, 1976; Schall, 1977; Hertz, 1979a; Saint Girons, 1980).

The rarity of physiological (e.g. Bakker, 1980) and geological (Hirshfield et al., 1980) "indicators" in the fossil record forces the use of indirect methods to estimate rates of physiological evolution. Bogert (1949a, b) developed one approach: if differentiation in a trait is extensive within a genus, then that trait is assumed to have evolved rapidly, whereas if the differentiation is minor, that trait has probably evolved slowly.

Early applications of this approach suggested that thermal physiology evolves slowly in reptiles. Closely related species from differing climates are active at similar body temperatures, whereas distantly related species in sympatry may be active at dissimilar body temperatures (Bogert, 1949a, b, 1959). For example, the mean body temperatures of *Phrynosoma* from coastal and desert habitats in California differ by only 2°C (Cowles and Bogert, 1944), and those of *Sceloporus* show minor differences among species distributed from sea level to 1800 m (Bogert, 1949a, b; 1959; but see Brattstrom, 1965, Table IX).

Many subsequent, large-scale studies and reviews have supported this pattern. Analyses of body temperatures, selected temperatures, or measures of heat or cold stress demonstrate limited variation within most genera or species (Soulé, 1963; Schmidt-Nielsen and Dawson, 1964; Brattstrom, 1965; Heath, 1965; Hutchison et al., 1966; Licht et al., 1966a, b; Bradshaw and Main, 1968; Hillman, 1969; Heatwole, 1970, 1976; Templeton, 1970; Cloudsley-Thompson, 1971; Spellerberg, 1972a, b, c, 1973; Huey and Slatkin, 1976; Huey et al., 1977; Schall, 1977; H. Saint Girons, 1978; Fuentes and Jaksić, 1979). Moreover, even the limited differentiation observed in some genera (Licht et al., 1966a) may be a function of uncontrolled acclimation regimes rather than being genetically determined (Bradshaw and Main, 1968).

Australian skinks of the genus *Sphenomorphus* have been extensively studied from this perspective. Distributed in an altitudinal series, four species show remarkably little variation in body temperature, selected

TABLE IX

Variation in thermal statistics within genera (or species groups) distributed along altitudinal gradients

Genus (species group)	Elevational range	T_b	T_p	CTMin	CTMax	References
Sphenomorphus	1668	+1.0	+1.2	−3.2	0	Spellerberg, 1972b, c
Sceloporus	1800	−2.0	—	—	—	Bogert, 1949b; Brattstrom, 1965
Anolis (*cybotes*)	2195	−1.3	—	—	+0.2	Hertz, 1980; Hertz and Huey, 1981
Anolis (*cristatellus*)	1080	−9.0	−7.9	—	−6.2	Huey and Webster, 1976

Variation expressed as units of change in °C per 1000 m change in elevation (Hertz and Huey, 1981). Because average values were used for each species, these estimates are crude. T_b = activity temperature, T_p = selected temperature, CTMin = Critical Thermal Minimum, CTMax = Critical Thermal Maximum.

temperature, and Critical Thermal Maximum (Table IX; Spellerberg, 1972b, c). Only the differentiation in Critical Thermal Minimum is significant, but even this is small (3.2°C per 1000 m change in elevation, Table IX). Similarly, three species of the *cybotes* group of *Anolis* on Hispaniola (Table IX; Hertz, 1979b; Hertz and Huey, 1981) show extremely limited variation in body temperatures and Critical Thermal Maxima.

Nevertheless, this pattern is not absolute. Differences within some closely related groups and sometimes within species are increasingly being documented. Geckos, for example, are remarkably diverse (Licht *et al.*, 1966a, b; Werner and Whitaker, 1978); and similarly, skinks, which were once thought to be low-temperature lizards (Brattstrom, 1965; Licht *et al.*, 1966a, b; Curry-Lindahl, 1979), include many high-temperature desert species (Stebbins, 1961; Pianka, 1969; Huey *et al.*, 1977; Greer, 1980). Some agamids (Grenot and Loirat, 1973; Licht *et al.*, 1966a, b; Alcala, 1967; Bradshaw and Main, 1968; Hertz and Nevo, 1982; but see Curry-Lindahl, 1979), lacertids (Sergeyev, 1939; Ushakov and Darevsky, 1960; Stebbins, 1961; Duvdevani and Borut, 1974; Avery, 1976, 1979; Huey *et al.*, 1977), and turtles (at the family level, Hutchison *et al.*, 1966; Hutchison, 1979) show significant differences in thermal relations that may correlate with altitude, habitat, or latitude.

Thermal differentiation seems to be the rule rather than the exception in the iguanid genus *Anolis*. Workers on this genus have documented variation that crosses phylogenetic lines but that closely reflects ecological distributions (Ruibal, 1961; Rand, 1964a; Heatwole *et al.*, 1969; Ballinger *et al.*, 1970; Corn, 1971; Fitch, 1972, 1973; Clark and Kroll, 1974; Huey and Webster, 1976; Lister, 1976; Gorman and Hillman, 1977; Hertz, 1977, 1979a; Hertz *et al.*, 1979). For example, anoles of the *cristatellus* group show striking differentiation in body temperatures, selected temperatures, and Critical Thermal Maxima along an altitudinal transect in Puerto Rico (Table IX); they thus represent a remarkable contrast to the Australian *Sphenomorphus*.

Obviously, thermal physiology is occasionally more labile than was originally apparent. Nevertheless, the overall generalization that the evolution of thermal physiology is conservative still appears valid for most lizards, with the possible exception of *Anolis* and a few other genera. Other reptiles remain to be examined in detail from this perspective.

Actually these studies do not measure the rapidity of thermal evolution as the comparisons are based on rates of speciation rather than on time *per se*. However, divergence times for populations can be estimated by use of the assumption (Sarich, 1977) that most biochemically detectable mutations are selectively neutral, so that the magnitude of biochemical divergence from

the ancestral condition changes constantly through time (Langley and Fitch, 1974), and that the degree of divergence can be calibrated using populations for which divergence times are known (Wilson *et al.*, 1977). Information about divergence times and the magnitude of physiological differences allows estimation of an average rate of evolution of the physiological trait. This speculative approach requires caution, the average rates of evolution may be slow, but the maximum rates could have been rapid (Gould, 1980).

One reptilian example recently re-examined with this approach involves the trunk-ground lizards of the *cristatellus* species group of *Anolis* on Puerto Rico. Traditional criteria (Bogert, 1949a, b) suggest that their physiological differences (Table IX) evolved rapidly (Huey and Webster, 1976). However, recent biochemical evidence derived from electrophoretic and from immunological data suggests that the *cristatellus* radiation occurred seven million years ago (Gorman *et al.*, 1980a, b). Consequently, the average rate of physiological evolution might have in fact been slow.

V. Concluding Remarks

This review of the thermal physiology and ecology of reptiles has been based almost exclusively on studies of diurnal lizards—studies of other reptilian groups are few. Nevertheless, a persistent theme throughout this volume is that reptiles are ecologically and phylogenetically diverse. Thus, any present generalizations derived from studies of diurnal lizards may be expected to have limited applicability to other reptiles. Basic studies of these groups are required before a comprehensive review of reptilian thermal biology will be possible.

Acknowledgements

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