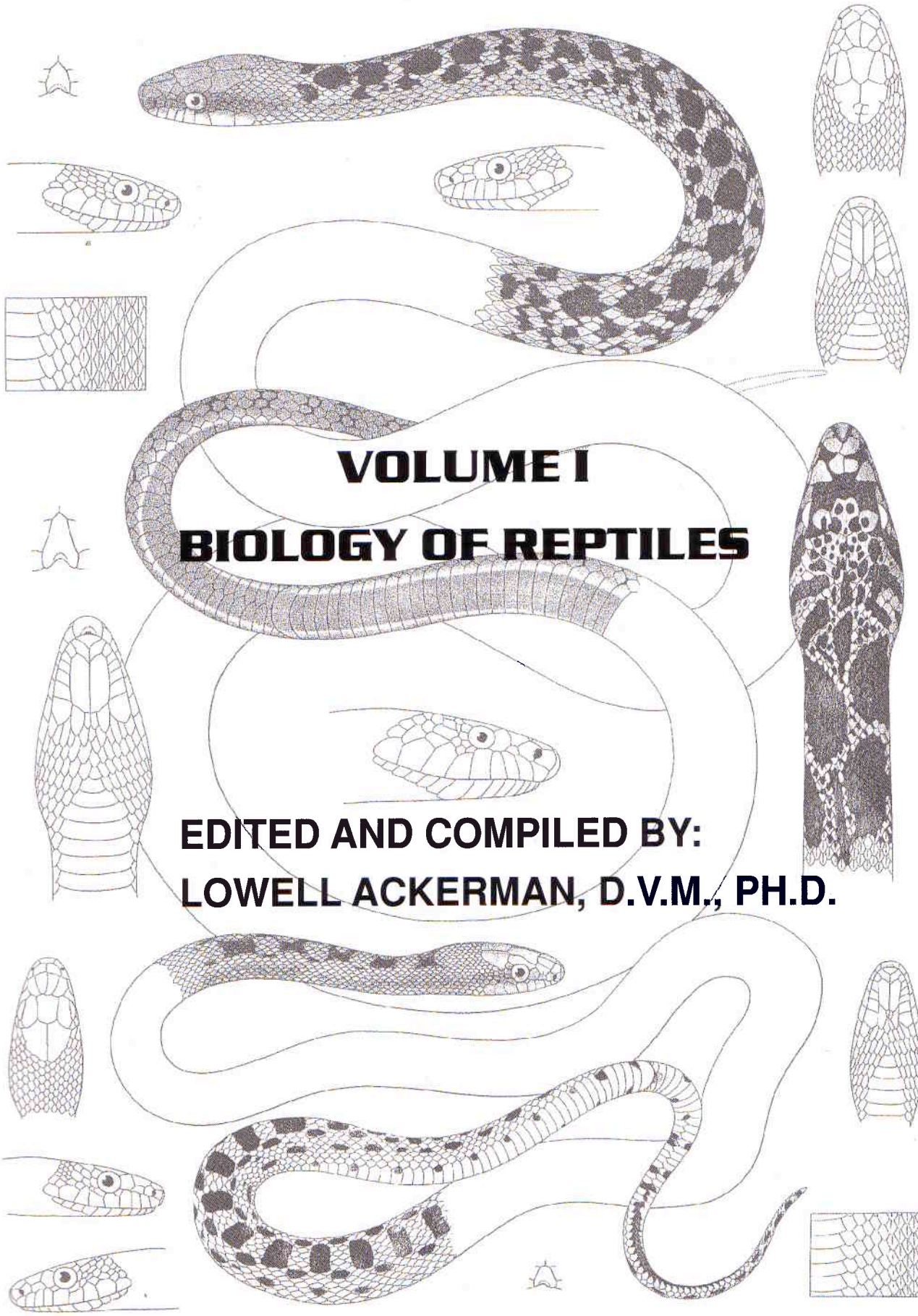
THE BIOLOGY, HUSBANDRY AND HEALTH CARE OF REPTILES



VOLUME I

BIOLOGY OF REPTILES

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THERMAL BIOLOGY, METABOLISM, AND HIBERNATION

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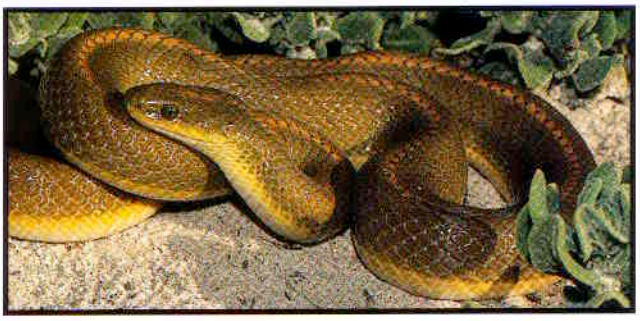
INTRODUCTION

Aspects of reptilian* thermal biology have been studied extensively for more than 60 years, and recent progress by investigators working at the interface between environmental physiology and ecology (i.e., physiological ecologists) has substantially increased our understanding of the interactions between reptiles and their environments. An understanding of these interactions is critical because they may influence the evolution of morphology, physiology, and behavior in reptiles. Additionally, these interactions, and adaptations to them, may influence the manner in which reptiles interact with other organisms.

The most widely studied area of reptilian physiological ecology has been thermal biology, perhaps because temperature has such a profound influence on the lives of reptiles, and also perhaps because it is generally easier to study the effects of temperature than other aspects of reptilian physiology. In many respects, metabolism and hibernation are also influenced by or are closely associated with aspects of reptilian thermal biology. Therefore, these subjects have been included in this review.

In this chapter, we provide an overview of the importance of body temperature. This chapter also addresses metabolism and hibernation as they relate to reptilian physiological ecology and to biology generally. Our goal is to focus on some key elements and noteworthy discoveries in these areas, rather than to attempt summarizing the vast literature in each field. The majority of the available knowledge in these areas is derived from research on lizards, particularly those from temperate and subtropical desert environments. For this reason, many of our examples are from this subset of reptiles. In some cases, what we have learned from studies on lizards is applicable to other reptiles. However, given the complexity and diversity among reptiles, generalizing beyond what is known for a handful of lizards to *all* reptiles, may lead to erroneous simplifications.



Aurora House Snake, *Lamprophis aurora*. Photo by Marius Burger.

THERMAL BIOLOGY

GENERAL REMARKS AND TERMINOLOGY

Until about 60 years ago, most biologists assumed that mammals and birds were the only organisms that could maintain high and constant body temperatures. Meanwhile, reptiles were generally assumed to have body temperatures closely resembling those of their ambient environment. An important paradigm shift occurred when Cowles and Bogert (1944) showed that reptiles were able to

* The term "reptile," as is currently used includes paraphyletic groups of vertebrates (see Chapter on taxonomy). Here we use this term to mean the extant Sphenodontia (tuatara), Testudomorpha (turtles and tortoises), Crocodylia (alligators, crocodiles, and their relatives), and the Squamata (lizards, snakes, and their relatives).

maintain fairly precise body temperatures by selecting specific thermal microsites within their environment. Additionally, body temperatures of reptiles are, in many cases, quite different from the ambient temperature. Some reptiles even maintain temperatures that are higher than those of so-called "warm-blooded" animals. Therefore, the use of the term "cold-blooded" in reference to reptiles is misleading and outdated.

The term **ectothermic** (Cowles, 1962) is used to characterize animals that regulate their body temperatures by utilizing thermal energy derived from external sources (e.g., solar radiation, sun-warmed objects). By contrast, birds and mammals are **endotherms**, which acquire most of their thermal energy as a byproduct of metabolism. Cowles (1962) further categorized ectothermic organisms by the two principal sources from which they acquire thermal energy:

—**heliotherms** (*helios* = sun) obtain heat from the radiant energy of the sun

—**thigmotherms** (*thigmo* = touch) exchange thermal energy by conduction with items in their environment such as warm rocks. The latter is essentially the type of thermal regimen provided in captive situations by "hot rocks," heating pads, and heat tape.

Many reptiles use a combination of both strategies for thermoregulation. The terms Cowles (1962) proposed more precisely reflect the pathways through which energy is exchanged between an animal and its environment, and they also set the stage for studies addressing thermoregulation in reptiles.

Ectothermy and endothermy are occasionally confused, or incorrectly used interchangeably with two related terms: **poikilothermic** and **homeothermic**. Poikilotherms (*poikilo* = changeable) have variable body temperatures, while homeotherms (*homoios* = similar), maintain fairly constant body temperatures (± 2 °C; Bligh and Johnson, 1973). These terms can be confusing because reptiles do change their body temperatures, and they have different body temperatures during periods of activity and inactivity. However, many reptiles maintain remarkably constant body temperatures during periods of activity. Indeed, during the daytime, some lizards maintain body temperatures that are within narrower ranges than those regulated by endotherms. Thus, the terms poikilotherm and homeotherm are inadequate in describing the patterns of body-temperature change in a few reptiles. Of course, some reptiles live in situations in which body temperatures remain constant because environmental temperatures remain relatively constant (e.g., pelagic sea turtles and sea snakes, cave-dwellers, and animals restricted to deep burrows).

Numerous terms have been used to describe the processes of temperature regulation and associated behaviors in ectotherms (Bligh and Johnson, 1973; Gans and Pough, 1982; Hutchison and Dupré, 1992). Reptiles that actively regulate their body temperatures often **choose**, **prefer**, or **select** a limited range of body temperatures from those available in the environment. Although these terms refer to the same phenomenon, different investigators insist that their term is the least anthropomorphic and, therefore the most appropriate (Hutchison and Dupré, 1992). Occasionally, the average body temperature chosen, preferred, or selected by an active reptile also may be referred to as the **eccritic** temperature. Throughout this chapter we will most frequently use the term **selection**, which we define as: the process of temperature regulation by nonrandom use of the available thermal microsites found in a heterogeneous thermal environment.

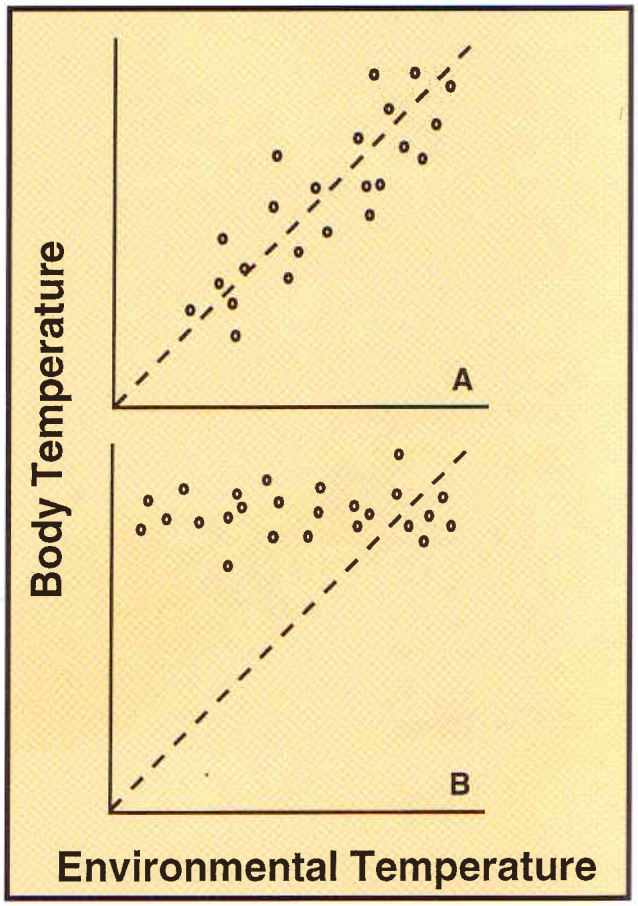
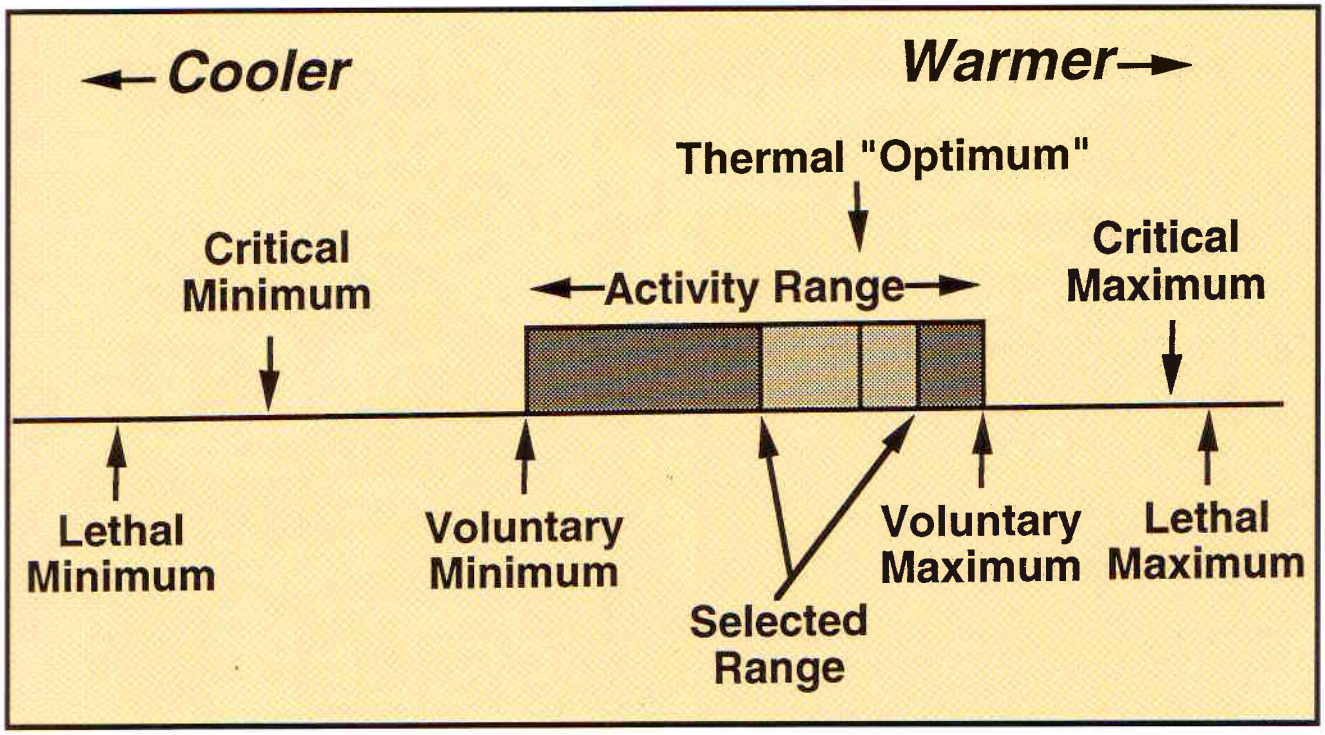


Figure 1.
Relationship for some environmental temperature variable (e.g., air or substratum temperature) and body temperature for a hypothetical reptile: A) thermoconformer; B) thermoregulator. Note body temperatures of the thermoconformer closely approximate those of the ambient environment, whereas body temperatures of the thermoregulator are independent of ambient temperature.

A large proportion of reptiles actively regulate their body temperature. However, among reptiles, the spectrum of thermal interactions with the environment ranges from little or no regulation, to precise regulation, to near endothermy. Within this continuum, reptiles with body temperatures closely resembling those of their environment are known as **thermoconformers**, while those maintaining body temperatures different from ambient temperatures, are termed **thermoregulators** (Fig. 1). Thermoconformity is largely limited to those reptiles living in aquatic or deeply-shaded environments (e.g., forest understories, leaf litter, underground burrows, caves), or those which are active at night. In these environments, few opportunities may exist for maintaining body temperatures above or below ambient temperatures. Additionally, most thermoconformers have small body sizes, which tends to limit opportunities for physiological regulation of body temperature (Claussen and Art, 1981; Bartholomew, 1982; Fraser and Grigg, 1984; also refer to the *Morphological and Physiological Aspects of Thermoregulation* section). However, thermoconformity is an appropriate strategy in environments that provide a suitable thermal regime. For example, some reptiles from tropical forests spend little time each day actively selecting particular thermal microsites within their environment (Hertz, 1974; Huey and Slatkin, 1976; Shine and Madsen, 1996). Ambient temperatures may provide these reptiles with the necessary thermal energy they require, thereby freeing them from the potential costs of finding thermal microsites throughout the day. Thermoregulators, by contrast, actively maintain their body temperatures using a suite of behavioral and/or physiological mechanisms. Considering either thermoconformity or thermoregulation as a "better" strategy is not a worthy endeavor, because members of both groups are well represented in nature. However, to appreciate fully the adaptive value of either strategy, a thorough examination of the costs and benefits associated with both thermoregulation and thermoconformity must be considered (Huey, 1974; Huey and Slatkin, 1976; Pough, 1980, 1983).

Some investigators have hypothesized that reptiles have a single optimal temperature for *all* forms of performance (e.g., hearing, locomotion, digestion, prey capture, etc.; Licht, 1967*c*; Dawson, 1975; DeWitt and Friedman, 1979; Huey, 1982; Huey and Bennett, 1987). The **thermal optimum** is expected to be coincident with the average body temperature maintained by a reptile in nature or in the laboratory (Fig. 2). Although this hypothesis has not been tested exhaustively, recent studies have not detected a single body temperature over which performance of more than a few traits

Figure 2.
Body temperature continuum showing the terms commonly used in reptilian thermal biology. The horizontal line within the selected range is the mean (occasionally also reported as the modal) activity or selected body temperature. The thermal optimum is suggested to be coincident with the mean value, but see text regarding evidence to support this hypothesis. Note that the position of each term on the continuum may be species and individual specific. Refer to text for specific definitions.



are optimized. However, performance of some single traits have been shown to be optimal within the thermal range maintained by active reptiles (Werner, 1972, 1976; Huey and Bennett, 1987; Mautz *et al.*, 1992). The existence of a single optimum temperature is not supported by evidence from one of several proposed thermoregulatory mechanisms. This hypothesis suggests that reptiles regulate their body temperature not at a single temperature, or "set point," but instead respond to the extremes of a range of temperatures (Cabanac *et al.*, 1967; Barber and Crawford, 1977, 1979; Fig. 2). In these cases, body temperatures appear to be regulated by "turning on" the appropriate cooling or warming behaviors that once body temperature has drifted out of a particular range. However, we generally know little about the abilities of reptiles to distinguish among, and respond to, small differences in body temperature. For example, reptiles may truly regulate their body temperature about a single "set point." But, if reptiles "measure" body temperature less precisely than do humans, then their patterns of thermoregulation may be misleading. For example, we might erroneously conclude from patterns of thermoregulation that 1) reptiles are selecting a range of temperatures, or 2) they are responding to upper and lower "set point" temperatures surrounding a range of body temperatures when they are actually, albeit imprecisely, thermoregulating around a single body temperature.

The range of body temperatures over which reptiles engage in their normal activities is termed the **activity temperature range** (Fig. 2). This range differs among species, and within a species for animals under different conditions (e.g., digesting, pregnant; see below). Activity ranges can start at body temperatures as low as 10 °C for the tuatara, *Sphenodon punctatus* (Stebbins, 1958), to highs approaching 46 °C for the desert iguana, *Dipsosaurus dorsalis*

Desert Iguana, *Dipsosaurus dorsalis*. Photo by Michael Cardwell.

(Norris, 1953). Furthermore, reptiles regulate their body temperatures with varying degrees of precision (e.g., Bowker, 1984), such that activity ranges may be as narrow as 4 °C, to as broad as 10 °C. Within the normal activity range, many reptiles have a more narrowly-defined range of temperatures known as the **selected** (= preferred) body temperature range (Fig. 2). Generally, the selected body temperature range is measured by recording the temperatures of animals in the field or laboratory during their activity cycle under conditions that permit unihibited thermoregulation. The selected range is typically reported as the mean (or occasionally modal) body temperature recorded for a number of individuals. The activity range and selected range are sometimes used imprecisely and interchangeably in the literature, which has led to some confusion. We suggest that the term "selected" body temperature be reserved for body temperatures that have been measured in the laboratory, and that researchers reserve the term "activity range" for (animal) body temperatures that have been measured in the field.

Bounding the normal activity range are the **voluntary minimum** and **maximum** temperatures which are also known as the thermal "set points" (Fig. 2). As body temperatures approach or reach these points, the animal will generally seek an appropriate thermal refuge such as moving into the sun or shade. Beyond these tolerances are the **critical thermal minimum** and **maximum** (Fig. 2). These are the temperatures at which an animal ceases to function normally (defined more precisely as the temperature at which the "righting reflex" is lost; Cowles and Bogert, 1944; Spellerberg, 1973). In many desert reptiles, voluntary maxima are near the critical thermal maxima (Cowles and Bogert, 1944). Similarly, reptiles living in cool environments may have voluntary minima that approach their critical thermal minimum (see e.g., Autumn *et al.*, 1994). Beyond the critical temperatures are the **lethal minimum** and **maximum** (Fig. 2). As the terms imply, sustaining body temperatures at or beyond these extremes will lead to death.

Another pair of terms groups animals by their range of tolerable body temperatures. Animals that tolerate, or are active over, a narrow range of body temperatures are called **stenothermal** (*steno* = narrow). In contrast, **eurythermal** (*eury* = wide) animals tolerate, or are active over, broader ranges of body temperatures. As with several of the terms defined above, steno- and eurythermal are relative concepts because they do not specify particular ranges of temperatures. Examples of stenothermal reptiles include: the desert iguana (*Dipsosaurus dorsalis*), and coachwhip snakes (*Masticophis flagellum*) which maintain high activity temperatures

with notable precision (DeWitt, 1967; Secor, 1995, respectively). The tuatara (*Sphenodon punctatus*), box turtles (*Terrapene* spp.), and alligator lizards (*Elgaria* [= *Gerrhonotus*] spp.) are examples of eurythermal reptiles because they are often active over a relatively broad range of body temperatures (Saint-Girons *et al.*, 1980; Avery, 1982; Kingsbury, 1993, respectively).

MORPHOLOGICAL AND PHYSIOLOGICAL ASPECTS OF THERMOREGULATION

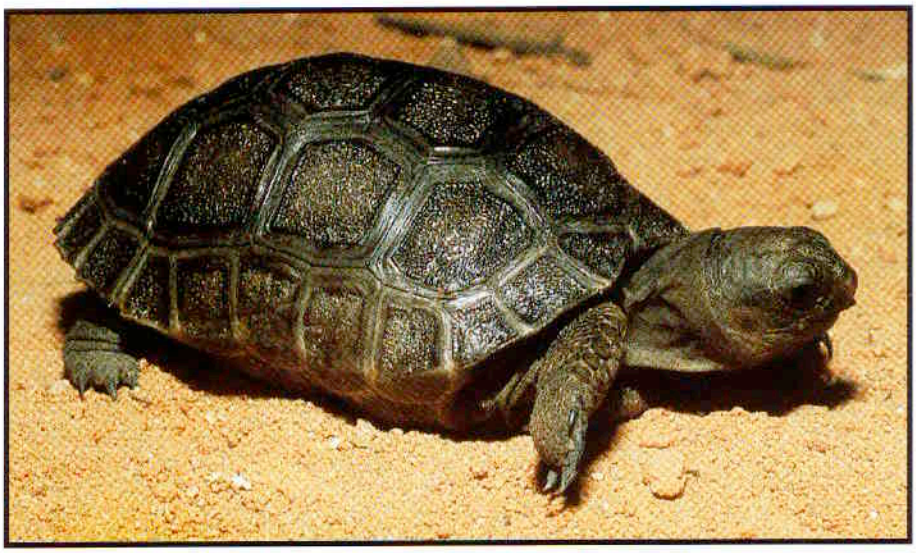
Many reptiles possess anatomical and physiological mechanisms which enable them to alter the rate at which they heat or cool. These mechanisms include altering heart rate, cardiac and vascular shunts, vasomotor dilation and constriction, and counter-current vascular exchanges (see reviews in White, 1976; Bartholomew, 1982). Reptiles can increase their heart rates during periods of heating (Bartholomew, 1982; Turner and Tracy, 1983, 1985; Turner, 1987). Pumping blood through the body increases the rate of temperature change. By the same principle, reptiles can also reduce rates of temperature change by decreasing heart rates. All reptiles, with the exception of the crocodilians, possess a three-chambered heart (see Chapter 3 this volume). The three-chambered heart is particularly well suited for altering rates of bodily heating and cooling. With a four-chambered heart, deoxygenated blood travels from the systemic circuit to the heart and is then sent to the lungs to be oxygenated. The oxygenated blood then returns to the heart and is pumped back through the systemic vessels. Generally, it is not possible for animals with four-chambered hearts to bypass either the systemic or pulmonary circuits during the circulatory cycle because the atria and ventricles are physi-

Western Coachwhip, *Masticophis flagellum testaceus*. Photo by Paul Freed.

Eastern Box Turtle, *Terrapene carolina*. Photo by Aaron Norman.

cally separated. By contrast, animals with three-chambered hearts can redirect or "shunt" blood from their single ventricle to either the pulmonary or systemic circuit. This phenomenon is generally known as **cardiac shunting**. As blood passes through the lungs and contacts the moist respiratory surfaces, it can lose heat due to evaporative cooling. By bypassing the pulmonary circuit, reptiles avoid cooling their blood, and by shunting warmed blood back to their core, they further enhance their rate of heating. Blood shunting is controlled by changing the pressure at which blood flows into the heart (Bartholomew, 1982). During heating, peripheral blood vessels are generally dilated to enhance the flow of warmed blood from the appendages, which can heat more rapidly than the core due to their smaller size and shape. When body temperatures drop due to abiotic or biotic disturbances that interfere with "normal" thermoregulatory behaviors ...and shunt blood to their core to reduce the rate of heat exchange.

Body size and shape importantly affect physiological control of thermoregulation (Spotila *et al.*, 1973; Bartholomew, 1982; Stevenson, 1985). On the basis of physical properties alone, larger animals should heat and cool more slowly than should smaller individuals. That is, larger animals have a greater **thermal inertia**, or resistance to temperature change. Thermal inertia can be an important component of thermoregulation in large reptiles. Once a large reptile has warmed itself, the physiological mechanisms discussed above can be used effectively to reduce heat loss. Moreover, these mechanisms are more effective for larger animals. For example, the giant Aldabra tortoises (*Geochelone gigantea*) can maintain particularly stable body temperatures throughout the day, despite experiencing different thermal environments (Swingland and Frazier, 1980). Some large snakes,



Aldabra Tortoise, *Geochelone gigantea*. Juvenile photo by R. D.

tortoises, and crocodilians use a combination of physiological and behavioral mechanisms to maintain relatively high body temperatures through the night, despite significant declines in ambient temperatures. For instance, a large snake can lower its heart rate to physiologically reduce the rate of cooling, and coil up to further reduce its rate of heat exchange by behaviorally reducing its surface area (Heatwole and Taylor, 1987). However, the thermal tradeoff in body size is apparent once that large snake has cooled. Larger-bodied reptiles will take longer to heat up than will smaller reptiles. Smaller reptiles are said to be more coupled to their thermal environment because of their lower thermal inertia. Actually, because of their size, smaller reptiles use a greater range of thermal microsites than can larger individuals (Bowker, 1984). This may partially explain why smaller heliothermic reptiles are able to thermoregulate with noteworthy precision (i.e., exhibit narrow activity temperature ranges), despite their low thermal inertia (see e.g., DeWitt, 1967; Avery, 1982; Bowker, 1984; Pianka, 1986; Heatwole and Taylor, 1987). The minimum body mass at which physiological control is suggested to be effective in enhancing thermoregulatory capabilities is roughly 15-20 g (Claussen and Art, 1981; Fraser and Grigg, 1984). However, reptiles as small as 3-7 g may exhibit some physiological capacity to control rates of heating and cooling (Bartholomew, 1982).

Body shape varies widely among reptiles and is known to influence several aspects of their thermal biology. For example, many terrestrial turtles have domed shells, and thus their morphology roughly approximates that of a sphere. Spherically-shaped animals are generally more resistant to changes in body temperature because a small proportion of their surface area is exposed to the environment relative to their total body volume. By contrast, snakes and many lizards are more elongate, and have a relatively large surface-area-to-volume ratio. Therefore, more of a snake's total body area interacts with the external environment. The elongate shape of snakes also has important implications for thermoregulation. That is, snakes can exhibit remarkably different temperatures in different regions of their bodies. This phenomenon is generally known as **regional heterothermy**, and is well documented in larger reptiles which live in thermally heterogeneous environments. Because of the vasomotor abilities discussed above, a large snake can maintain some parts of its body at one temperature, while other portions of its body experience different temperatures due to their proximity to various thermal resources or sinks. Regional heterothermy is also common in smaller reptiles. For instance, smaller lizards and turtles commonly exhibit differences between head and body temperatures during periods of heating and cooling (Bartholomew, 1982). Many heliothermic lizards will first expose their heads during their initial heating in the morning, and once the head reaches a specific temperature, they will expose the rest of their body (e.g., Heath, 1965). This thermoregulatory strategy avoids exposing the entire animal when it is cool, and therefore most vulnerable to predators.

Although metabolic heat is generated by reptiles, the amount produced is thermodynamically insignificant. Even if reptiles could produce substantial amounts of thermal energy, that heat would be quickly dissipated because reptiles lack insulation, such as fur, feathers, or fat. A lack of an insulating layer is also why thigmothermy, or conductive heat exchange, can provide an effective means of changing body temperatures. There is, however,

Leatherback Turtle, *Dermochelys coriacea*. Photo by Peter Pritchard.

at least one important exception to this generality. The leatherback turtle (*Dermochelys coriacea*) is among the world's largest living reptiles with adult body masses commonly surpassing 600 kg. *Dermochelys* also has one of the highest and broadest latitudinal ranges of all reptiles. Adults have been seen as far north as the frigid waters off Nova Scotia, yet females nest in the tropics (Mrosovsky and Pritchard, 1971). Unlike most reptiles, *Dermochelys* has a thick, oil-saturated subdermal layer which functions to insulate the animal from the cold of the northern oceans, much in the same way blubber keeps marine mammals insulated. Additionally, adult leatherbacks can generate an appreciable amount of metabolic heat which is produced primarily from their working muscles as they swim (Frair *et al.*, 1972). Leatherbacks may elevate their body temperatures by as much as 18 °C above sea water temperatures (Frair *et al.*, 1972). Rates of heat loss are low due to their large body size and insulation, and are probably further reduced by minimizing blood flow to the extremities (i.e., head, flippers, and tail), and through specialized vascular systems (see reviews in White, 1976; Bartholomew, 1982). These systems are generally known as **counter-current exchangers**. Counter-current vascular networks are relatively common among vertebrates, and are usually associated with conserving a specific physiological resource (e.g., oxygen, water, various ions, body temperature). In many cases, the blood vessels associated with these systems surround each other in dense bundles or form complex networks. In the case of reptiles such as *Dermochelys*, they function by passing vessels containing heated blood from the body core traveling in one direction, past vessels containing cooled blood from the extremities traveling in the opposite direction. In this manner, body heat can be conserved by effectively recycling the thermal energy (Greer *et al.*, 1973).

The underlying neurological control mechanisms of reptilian thermoregulation are not fully understood, and have been examined in only a few species. As with other vertebrates, the hypothalamus appears to play an important role in thermoregulation (Kluger *et al.*, 1973; Berk and Heath, 1975). In the Australian blue-tongued skink, *Tiliqua scincoides*, it appears that some neurons within the hypothalamus respond to different temperature stimuli. A subset of these neurons fire when the hypothalamic region is heated (hot neurons), while other neurons respond only when the area is cooled (cool neurons) (Cabanac *et al.*, 1967). These results are consistent with the dual-set point model of thermoregulatory responses (Barber and Crawford, 1977, 1979). That is, once the tolerable thermal maximum has been reached, heat-sensitive neurons will fire and presumably trigger the initiation of cool-temperature seeking behaviors. The inverse should follow as hypothalamic temperatures approach the tolerable thermal minimum. An alternative model for thermoregulation suggests that body temperatures are regulated about a single set value which corresponds to the animal's average body temperature selected during activity. The selected or activity body temperature was further suggested to be a fixed and inherited trait (Bogert, 1949). However, studies have generally failed to support the single body temperature hypothesis as a controlling system for thermoregulation in reptiles (Heath, 1964; Berk and Heath, 1975; Barber and Crawford, 1979; Garrick, 1979). Some researchers suggest that the mechanistic basis of temperature regulation in reptiles is best understood as a negative feedback system (see review in Huey, 1982). Under this model, the animal monitors or anticipates changes in its body temperature and compares this deflection with some internal reference or range of "set points." The animal then responds with the appropriate physiological or behavioral adjustments necessary to maintain its body temperature within the reference range (Huey, 1982).

Finally, a reptile's body color has an influence on the animal's absorptance of short-wave radiation (Norris, 1967; Pearson, 1977; Bartholomew, 1982). Changes in color can increase the absorption of radiant energy by as much as 75% (Norris, 1967; Zug, 1993). Reptiles that live in cool environments such as *Liolaemus* lizards living at high elevations in the Andes, and some aquatic turtles, may have evolved a darker body coloration to increase their absorbance of solar radiation. Other reptiles may change color as a function of their body temperature. Color change from dark to light is controlled by dispersion or aggregation of pigments such as melanin in the melanophores.

Eastern Blue-tongued Skink, *Tiliqua scincoides*. Photo by Zoltan Takacs.

Thin Tree Lizard, *Liolaemus tenuis*. Photo by R. D. Bartlett.

Some squamate reptiles are able to alter their body coloration at different temperatures. Dark colors enhance absorbance of short-wave radiation, which increases the rate of heating (Pearson, 1977). Once the animal heats up, body coloration may lighten substantially. Lighter colors reflect more short-wave radiation and thereby reduce the radiant energy absorbed by the surface of the animal. However, color change for thermoregulatory purposes must be balanced with the need for crypsis and behaviorally communicated signals in some species.

BEHAVIORAL ASPECTS OF THERMOREGULATION

Solar radiation is the ultimate, but not necessarily the direct source of thermal energy used by living organisms. There are numerous pathways through which reptiles exchange energy with their environment (Tracy, 1982). The dynamics and direction of energy flow through each of these pathways is proportional to the differences in energetic states between the animal and its environment. For example, if a snake basking on a sun-warmed rock comes to the same temperature as the rock, no net exchange in thermal energy will result. However, the same snake would lose energy to the air if the air temperature is lower than the snake's surface temperature. To optimize these avenues of energy exchange, many reptiles **behaviorally thermoregulate** by altering their body posture and orientation with respect to thermal sources and sinks. These behavioral changes can alter the exchange of thermal energy (e.g., Norris, 1953; Heath, 1965; Heatwole, 1970; Brattstrom, 1971; Heatwole and Johnson, 1979, Autumn *et al.*, 1994).

In some environments, thermoregulatory behaviors may be subtle, while in others they may involve a complex repertoire of behaviors. These behaviors are likely to be familiar to anyone who has observed heliothermic reptiles in heterogeneous thermal environments. The behaviors (e.g., Heath, 1965; Riedesel *et al.*, 1971; Heatwole and Johnson, 1979) may include:

—posturing: flat on a rock (for rapid conductive heat exchange), or elevating the limbs (generally for convective cooling), flexing toes and raising the tail to avoid hot substrata

—orientation: to control the amount of bodily surface area exposed to the sun

—selection of the color of the substratum on which to bask (e.g., black rocks for rapid conductive heating)

—selecting a shaded crevice or burrow, or basking indirectly under or in a bush, or in full sun

—evaporative cooling by plunging into water, gaping, panting, salivating, or urinating.

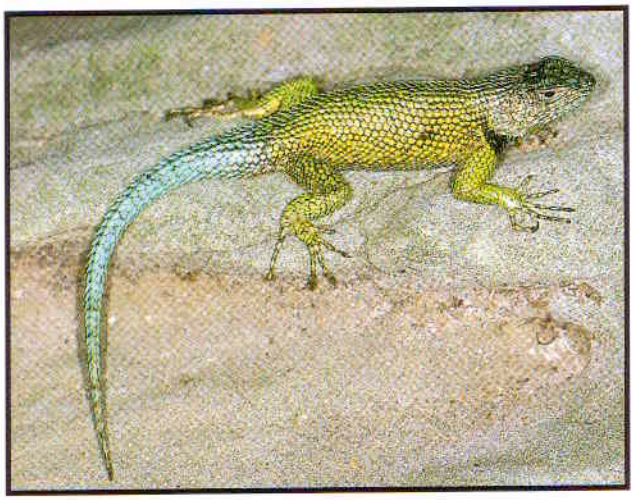
Red-bellied Black Snake, *Pseudechis porphyriacus*. Photo by John Coborn.

The Australian red-bellied black snake, *Pseudechis porphyriacus*, provides an ideal, yet extreme illustration of behavioral thermoregulation in heliothermic reptiles. When cool, these snakes flatten and tilt their bodies so that they are at a right angle—fully exposing themselves to the solar radiation (Heatwole and Johnson, 1979). Postural adjustments in this snake may even include propping the entire body off the cool substratum with the aid of the tail (Heatwole and Taylor, 1987). Generally, squamate reptiles—particularly smaller ones—have greater behavioral thermoregulatory capacities than do other reptiles because of their greater vagility (Bowker, 1984). Behavioral means of thermoregulation in turtles may be limited to movements between sun and shade and/or water due to their unique morphology. However, the shell of some turtles may provide an important thermal

Desert Tortoise, *Gopherus agassizii*. Photo by K. H. Switak.

shield. Under natural thermal conditions, the carapace of desert tortoises (*Gopherus agassizii*) may be 8-10 °C above core body temperatures (McGinnis and Voigt, 1971).

In some cases behavioral thermoregulation can be energetically and ecologically costly. This may be particularly apparent for reptiles living in thermally challenging environments. Time spent thermoregulating may be time lost for foraging, acquiring mates, defending territories, and may increase exposure to predators and parasites (Huey, 1974; Porter *et al.*, 1975; Huey and Slatkin, 1976).



Emerald Swift, *Sceloporus malachiticus*. Photo by Paul Freed.

PERVASIVENESS OF THERMAL EFFECTS ON REPTILE BIOLOGY

Temperature affects nearly all physical and biochemical processes associated with reptilian physiology and behavior. Consequently, in the absence of an appropriate thermal environment, many reptiles will not thrive. Anyone who has kept reptiles in captivity is aware that providing the appropriate thermal regime is often the most fundamental requirement for maintaining healthy animals (Regal, 1980). What constitutes an "appropriate thermal environment" for an individual of a given species depends upon:

—the genetically-based attributes resulting from evolutionary history

—environmental variables including season, daylength, macro-, meso-, and microclimate distribution and utilization

—attributes of the animal such as age, water balance, digestive state, reproductive status, and health

—interactions with other organisms, such as predators, prey, and parasites (Fig. 3).

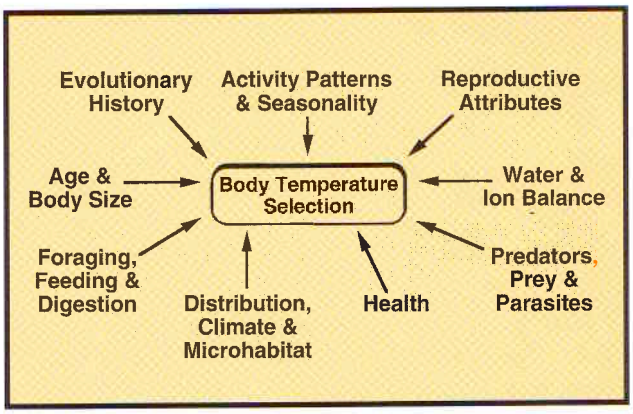


Figure 3.
Conceptual model of the abiotic and biotic variables that influence activity and selected body temperatures in reptiles. The relative importance of each variable is largely a function the individual animal.

The mechanisms by which body temperature affects these factors, and in some cases, how these factors may influence body temperature selection and maintenance, are discussed in the following sections.

EVOLUTIONARY HISTORY

The evolutionary history of a group or species provides the genetic foundation upon which all other characteristics are constructed. Thermal preferences tend to be relatively similar among species belonging to the same genus, often in spite of apparent differences in morphology, ecology, and behavior among the species within the group (Bogert, 1949; Brattstrom, 1965; Templeton, 1970; Avery, 1982; Heatwole and Taylor, 1987). For example, most spiny lizards in the genus *Sceloporus* maintain daytime activity body temperatures near 35°C (Brattstrom, 1965; references cited in Avery, 1982) despite the fact that they are distributed in a diverse array of habitats from British Columbia to Panama and from sea level to eleva-

Desert Grassland Whiptail, *Cnemidophorus uniparens*. Photo by R. D. Bartlett.

tions over 3500 m (Sites *et al.*, 1992). Apparent conservatism of activity body temperatures within a lineage has also been noted in some Chilean *Liolaemus* lizards (Fuentes and Jaksić, 1979), Australian skinks in the genus *Ctenotus* (Bennett and John-Alder, 1986), some whiptail lizards, *Cnemidophorus* (Schall, 1973, 1977), and among tortoises (family Testudinidae; Avery, 1982). Despite apparent conservatism within some reptilian clades, others may exhibit diversity within a single lineage. At the population level, differences in activity and selected body temperatures have been documented within and among populations of the northern European lizard (*Lacerta vivipara*) (Van Damme *et al.*, 1986).

DISTRIBUTION AND MICROHABITAT SELECTION

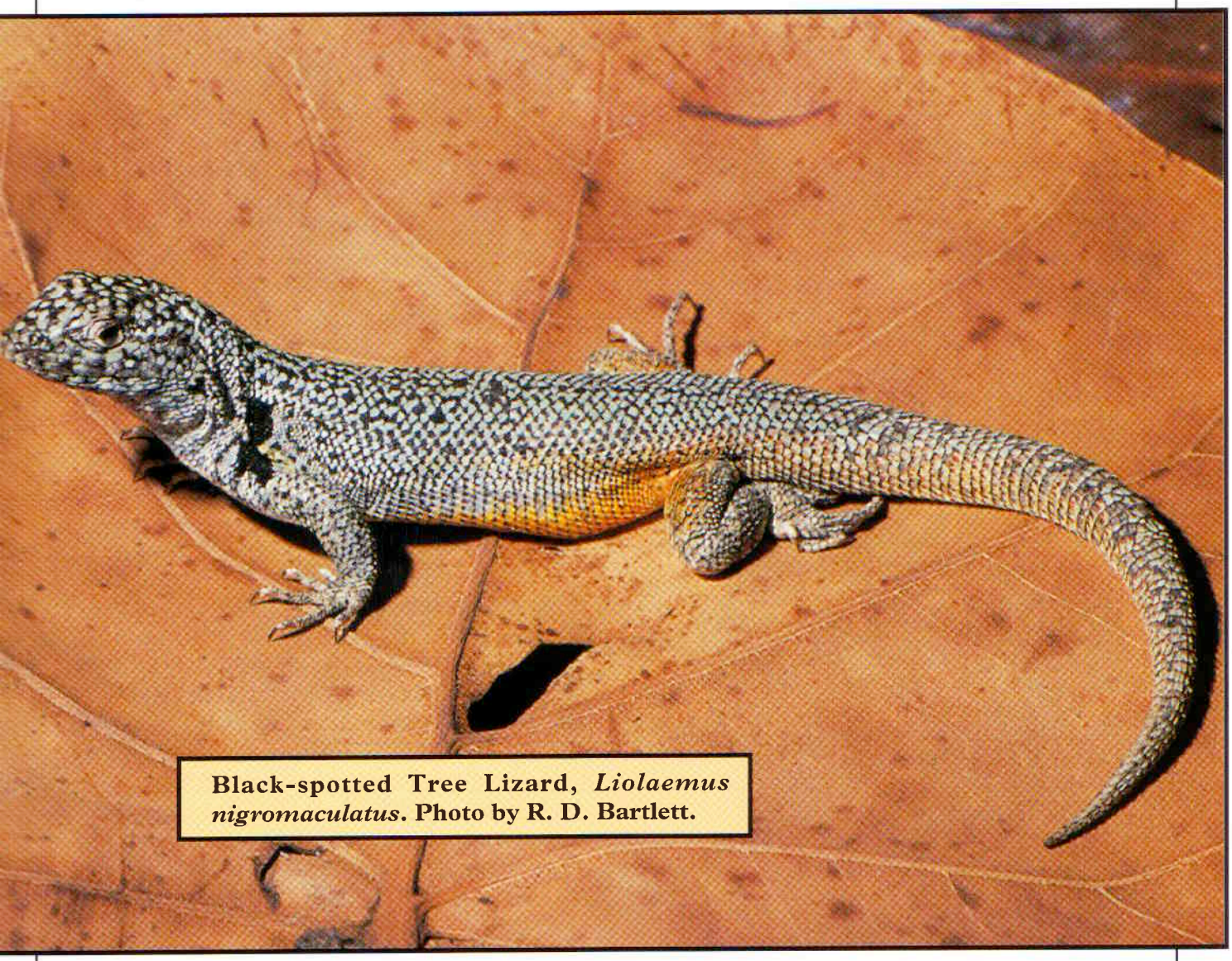
Sometimes geographic distribution, and the corresponding physical environments, can influence aspects of reptilian thermal biology. For example, some wide-ranging species (e.g., *Lacerta vivipara*) exhibit a gradient of activity temperatures across their latitudinal distribution (Avery, 1976). Caribbean anoles (*Anolis* spp.) from different latitudes have different thermoregulatory strategies (Clark and Kroll, 1974; Hertz, 1981; Huey, 1983). *Anolis carolinensis* from the southeastern United States exhibits a latitudinal gradient in critical thermal minimum with more northerly distributed populations exhibiting greater cold resistance (Wilson and Echternacht, 1987). Elevation has also been implicated in influencing activity temperatures of reptiles (Hertz and Huey, 1981; Avery, 1982). As elevation increases, environmental temperatures tend to decrease. Thus, reptiles living at particularly high elevations might be expected to possess morphological, physiological, and/or behavioral traits which are adaptive in these cooler environments. For example, Pearson (1954) studied *Liolaemus signifer* (= *multiformis*) at 4300 m in the Peruvian Andes. He found that these lizards were active when air temperatures were close to 0 °C. Despite low environmental temperatures, these lizards were able to maintain body temperatures in excess of 30 °C through careful selection of basking sites (dense clumps of bunch grasses), and by darkening their dorsal coloration (Pearson, 1954, 1977). Gorman and Hillman (1977) went as far to suggest that the geographic or elevational range limits of reptiles are generally a function of their thermal tolerances.

Climate may also influence thermoregulatory responses. Generally, diurnal reptiles living in deserts have higher activity temperatures and tend to have higher critical thermal maxima than do diurnal reptiles from mesic or wet tropical environments (see e.g., Cowles and Bogert, 1944; Pianka, 1986; Heatwole and Taylor, 1987). Reptiles that select high body temperatures either live in warm areas (e.g., in the warm tropics) or they limit their activity periods in temperate regions to the warm times of the year.

Often reptiles from similar microhabitats tend to have similar thermoregulatory strategies and select similar body temperatures. Rock dwellers and species living on unconsolidated sand (e.g., beaches and sand dunes) tend to have higher average body temperatures than do most arboreal

Green Anole, *Anolis carolinensis*. Photo by Aaron Norman.

species (see data in Avery, 1982; Pianka, 1986; Heatwole and Taylor, 1987). This relationship is at least partly due to the shading associated with an arboreal lifestyle (Hertz, 1974), but may also be due to different thermoregulatory strategies. For example, thigmothermic reptiles generally have lower body temperatures than heliothermic species (Heatwole and Taylor, 1987). It is also the case that reptiles living in environments that do not provide opportunities for thermoregulation (e.g., leaf litter, forest understories, caves) or in



Black-spotted Tree Lizard, *Liolaemus nigromaculatus*. Photo by R. D. Bartlett.

those that act as thermal sinks (e.g., subterranean or aquatic environments) tend to be thermoconformers. For example, thermoconformity may be the best strategy in heavily-shaded forests where patches of sunlight would have to be "chased" throughout the day in order to thermoregulate. Following patches of light may increase apparency to predators and could account for a large portion of daily activity This evergy could be used to engage in other activities (e.g., feeding, finding mates, etc.). Although life in heat sinks may interfere or preclude thermoregulation in some species, the potential advantages associated with life in a thermally stable environment should not be neglected. However, even in thermally challenging situations, some reptiles are able to sustain temperatures above that of their environment. Some aquatic species, especially turtles, crocodilians, and sea snakes, bask in the warm surface layers of water which may be somewhat warmer due to solar heating. Many aquatic reptiles may partially or completely emerge and elevate their body temperatures by basking on vegetation, logs, and other floating or exposed areas.

Finally, some investigators have suggested that the variation in the morphology and number of scales exhibited by some squamate reptiles are the result of adaptations to the physical environment. For some species, selection seems to favor larger, overlapping scales in warmer climates (Soulé, 1966; Regal, 1975), which presumably provides a small, but nevertheless important shielding effect from solar radiation. In the cooler climates of the Chilean Andes, *Liolaemus* lizards tend to have a larger number of smaller, more narrowly arranged scales (Hellmich, 1951). These differences in squamation have been interpreted as adaptations for either thermoregulation or reducing water loss (Horton, 1972; Regal, 1975).

DAILY AND SEASONAL ACTIVITY AND BEHAVIOR

Selected body temperatures and thermoregulatory behaviors may vary temporally on both a daily and an annual basis. Some diurnal reptiles select warmer body temperatures by day and appear to voluntarily select cooler body temperatures at night or during periods of inactivity (Regal, 1967). Some

nocturnal species may not have the opportunity to achieve favorable body temperatures during periods of activity and may, therefore, thermoregulate by day (e.g., Bustard, 1967; Autumn *et al.*, 1994).

During the summer months, reptiles living in temperate deserts may experience differences between daytime and nighttime temperatures exceeding 50 °C. In these regions, the activity cycles of reptiles may be highly correlated with daily cycles in temperature. On summer days in the Australian deserts, the central netted dragon, *Ctenophorus nuchalis* (= *Amphibolurus inermis*), increases its perch height as ambient temperature rises, thereby avoiding the extreme temperatures nearer the ground surface (Heatwole, 1970). Similarly, box turtles (*Terrapene* spp.) avoid the extreme high temperatures of summer days by shifting their normally diurnal periods of activity to dawn and dusk, or may even adopt a nocturnal lifestyle (Avery, 1982).

Desert iguanas (*Dipsosaurus dorsalis*), which are distributed in the temperate deserts of southwestern North America, are inactive unless environmental temperatures permit them to achieve body temperatures above 38.5 °C (DeWitt, 1967). As a consequence, individuals of this species are only active during the warmest times of the day and of the year (Norris, 1953; DeWitt, 1967). Many temperate reptiles from hot regions also exhibit changes in activity as the warm season progresses. For example, activity is typically unimodal for the desert tortoise (*Gopherus agassizii*) in early spring when daytime temperatures do not exceed maximum tolerance levels. However, later in the summer, when environmental temperatures often exceed the lethal maximum by midmorning, desert tortoises adopt a bimodal activity cycle surfacing only early in the morning and after sunset (Auffenberg and Iverson, 1979). Changes in thermoregulatory behaviors, selected body temperatures, and activity may be coincident with seasonal changes in the environment (Case, 1976; Huey and Pianka, 1977; Moore, 1978; Patterson and Davies, 1978; Christian *et al.*, 1983; Van Damme *et al.*, 1987; Christian and Bedford, 1995), daylength (Rismiller and Heldmaier, 1982), and among different age classes (Paulissen, 1988). Additionally, some reptiles may only exhibit particular behaviors, such as foraging and displays of territorial defense, once they have achieved a specific body temperature (e.g., Cowles and Bogert, 1944; Bradshaw and Main, 1968; Brattstrom, 1971; Heatwole and Taylor, 1987).

In general, diurnal reptiles in thermally heterogeneous environments (i.e., those that are not heavily shaded) tend to be heliothermic or a combination of heliothermic and thigmothermic; whereas nocturnal species tend to be limited to thigmothermy for acquiring thermal energy. This explains why some nocturnal reptiles can be found on spring and summer nights on warm asphalt roads (Brattstrom, 1965). Although nocturnal species generally select and have cooler activity temperatures than do diurnal species (see e.g., Brattstrom, 1965; Avery, 1982; Pianka, 1986; Heatwole and Taylor, 1987), some evidence suggests that not all nocturnal reptiles are thermally passive. Bustard (1967) noted that the "nocturnal" Australian gecko *Gehyra variegata* actively thermoregulates within its diurnal retreat by day. These geckos live under bark on trees. By tracking the position of solar illumination on the tree, these lizards are able to select warm thermal microsites during their presumed "inactivity" period. Similarly, the frog-eyed gecko (*Teratoscincus przewalskii*) of China is largely a thermoconformer during nocturnal activity, but raises its body temperatures throughout the day by selecting warmer temperatures within its burrow (Autumn *et al.*, 1994). Thus partitioning some reptiles into discrete thermoregulatory categories can prove to be problematic.

Sensory perception, neurological response, and muscle reaction are the underlying physiological mechanisms of reptilian activity and behavior. Performance of many of these processes has been shown to be influenced by body temperature (Licht, 1964*a*,*b*, 1967*c*; Bennett and John-Alder, 1984; John-Alder and Bennett, 1987; Losos, 1988). Numerous ethological studies have corroborated the importance of temperature to behavior (e.g., Rand, 1964; Brattstrom, 1971; Bennett, 1980; Hertz *et al.*, 1982; Mautz *et al.*, 1992; see also Chapter 16 this volume), and temperature may even play a role in the process of learning (Krekorian *et al.*, 1968). In cooler environments, thermoregulation can be more challenging and, thus, thermoregulatory behaviors may preempt other activities. For example, it has been suggested that southern European lacertid lizards have more complex social behaviors than more northerly distributed species because the latter must spend more of their time engaged in thermoregulatory behaviors (Avery, 1976).

In some cases, temperature can influence interactions between reptiles and other organisms including predators (e.g., Porter *et al.*, 1975; Christian and Tracy, 1981). For example, some lizards exhibit temperature-dependent responses to **caudal autotomy**, or tail loss. Bustard (1965) found that side-blotched lizards, *Uta stansburiana,* may autotomize their tails more readily at higher body temperatures. However, studies on the Australian

Side-blotched Lizard, *Uta stansburiana*. Photo by R. D. Bartlett.

gecko, *Gehyra variegata,* showed a bimodal pattern to tail autotomy. That is, these lizards were most likely to autotomize their tails at low (4 °C) and high (19 °C), but not intermediate body temperatures (Bustard, 1968). This pattern may be interpreted as an adaptive strategy for balancing the cost of autotomy with that of would-be predation (Bustard, 1968). At low body temperatures, the geckos autotomized about 80% of their tails. At these body temperatures escape from predators would be difficult, and the writhing tail could provide a distraction. At higher body temperatures however, locomotion may be substantially improved, and only 20-25% of the tail is autotomized (Bustard, 1968). Thus, body temperature may influence the ability of these lizards to practice the "economy of caudal autotomy."

FEEDING, DIGESTION, AND DIET

Body temperature can influence the frequency of feeding, which can, in turn, influence the temperatures selected by reptiles. The efficiency of prey capture is also affected by body temperature. For example, strike accuracy and constriction in gopher snakes (*Pituophis melanoleucus*) are a function of body temperature (Greenwald, 1974).

Northern Pine Snake, *Pituophis melanoleucus melanoleucus*. Albino specimen. Photo by W. P. Mara.

Reptiles typically select warm microsites soon after ingesting a meal (Regal, 1966; Gatten, 1974; Lang, 1979; Sievert, 1989). This phenomenon is particularly evident in species that consume large prey items relative to their own body size. This is best illustrated in large snakes, such as boas and pythons, which can consume prey as large as 75% of their own body mass. Following ingestion, these snakes will almost immediately seek out a warm thermal environment where they can digest their meal. This behavior assures rapid and efficient digestion of the food item because most of the metabolic and enzymatic processes involved in digestion work faster at higher body temperatures. The inverse is also true, that is, reptiles experiencing even mild inanition may select cooler temperatures than satiated individuals (Gatten, 1974). Selecting lower body temperatures during periods of inanition may be a means of conserving energy.

Increasing body temperature also generally increases the rate at which digesta moves through the gut (MacKay, 1968; Throckmorton, 1973; Wilson and Lee, 1974; Diefenbach, 1975; Harwood, 1979; Naulleau, 1983; Waldschmidt *et al.*, 1986; Zimmerman and Tracy, 1989; van Marken Lichtenbelt, 1992) and may also increase the efficiency with which energy and nutrients are assimilated through the gut lining (Greenwald and Kanter, 1979; Harwood, 1979).

Green Turtle, *Chelonia mydas*. Photo by Zoltan Takacs.

Although most reptiles are carnivorous, some lizards and many turtle species are omnivorous. Strict herbivory is rare among reptiles but can be found in tortoises (Testudinidae), adult green turtles (*Chelonia* spp.), and within a few lineages of lizards (Pough, 1973; Zimmerman and Tracy, 1989; also see Table 1). Some evidence suggests that herbivorous reptiles are only able to process

their relatively low nutrient and high fiber diets at higher body temperatures (Harlow *et al.*, 1976; Troyer, 1987; Zimmerman and Tracy, 1989; van Marken Lichtenbelt, 1992). In nature, herbivorous lizards maintain relatively high body temperatures (Table 1), suggesting a correlation with digestion of plant matter. However, the underlying requirement for maintaining high body temperatures in herbivorous reptiles is unknown. One explanation for this phenomenon implicates the thermal needs of the symbiotic microbes (bacteria, protozoa, and nematodes) exploited by herbivores to digest the fibrous components of plant tissues. Perhaps herbivorous reptiles select higher body temperatures because their gut microfauna require a warm environment in which to ferment plant tissues (Schall and Dearing, 1994).

Table 1.
Mean body temperatures of herbivorous lizards in nature. Although many carnivorous/insectivorous reptiles also have high body temperatures, as a group herbivorous reptiles generally maintain body temperatures above 30°C when active. Taxonomy for iguanians follows Frost and Etheridge (1989).

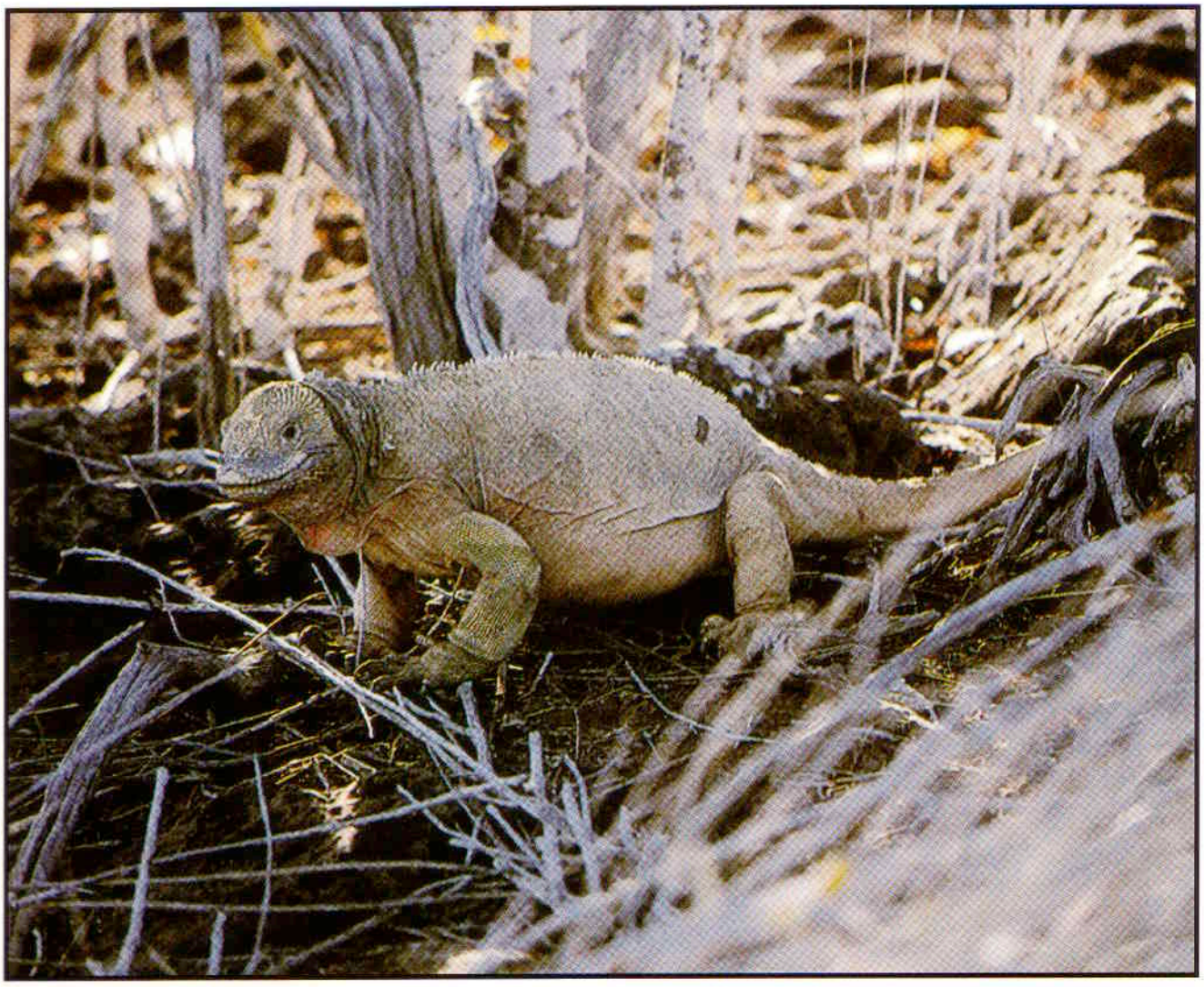
Taxon	Body Temperature (°C)	Source
Iguanidae		
Marine iguana (*Amblyrhynchus cristatus*)	36.0	1
Santa Fe land iguana (*Conolophus pallidus*)	36.6	4
Galápagos land iguana (*Conolophus subcristatus*)	32.0	2
Spiny-tailed iguana (*Ctenosaura hemilopha*)	37.1	14
Cuban iguana (*Cyclura nubila*)	38.6	5
Desert iguana (*Dipsosaurus dorsalis*)	40.0	10
Green iguana (*Iguana iguana*)	36.1	8
Spiny chuckwalla (*Sauromalus hispidus*)	35.8	3
Common chuckwalla (*Sauromalus obesus*)	38.3	9
Piebald chuckwalla (*Sauromalus varius*)	36.4	3
Leiolepidinae		
Egyptian spiny-tailed lizard (*Uromastyx aegyptius*)	39.9	6
Small-scaled dhabb (*Uromastyx microlepis*)	38.0	15
Tropiduridae		
Andean chuckwalla (*Phymaturus palluma*)	34.2	11
Scincidae		
Centralian blue-tongued skink (*Tiliqua multifasciata*)	34.3	10
Cordylidae		
Angolan dune lizard (*Angolosaurus skoogi*)	35.1	7
Teiidae		
Aruba Island whiptail (*Cnemidophorus arubensis*)	39.3	12
Bonaire Island whiptail (*Cnemidophorus murinus*)	38.5	13

Sources: 1. Bartholomew, 1966; 2. Carpenter, 1969; 3. Case, 1982; 4. Christian *et al.*, 1983; 5. Christian *et al.*, 1986; 6. Foley *et al.*, 1992; 7. Hamilton and Coetzee, 1969; 8. McGinnis and Brown, 1966; 9. Muchlinski *et al.*, 1990; 10. Pianka, 1986; 11. Sage, 1974; 12. Schall, 1973; 13. Schall and Dearing, 1994; 14. Soulé, 1963; 15. Zari, 1991.

REPRODUCTION

Temperature can influence nearly every stage of the reptilian reproductive cycle including: gametogenesis, courtship and mating behavior, gestation, timing of incubation, hatchling gender and survival, and even reproductive modes (oviparous - egg producing, or viviparous - live bearing). Additionally, various stages of the reproductive cycle are known to influence patterns of thermoregulation and selected and activity body temperatures. (Refer to Chapters on reproduction and egg physiology for more in-depth information.)

The onset of the reproductive season for reptiles living in temperate regions is largely controlled by hormones which respond to abiotic cues, such as increases in daylength or environmental temperatures. For example, gametogenesis in the male green anole, *Anolis carolinensis*, is strongly correlated with daylength and temperature (Licht, 1967*a*,*b*, 1969).



Santa Fe Land Iguana, *Conolophus pallidus*. Photo by K. H. Switak.

Mate acquisition is influenced by numerous biotic variables, but temperature may also play an important role. For example, many reptiles exhibit species-specific courtship and reproductive behaviors (see review in Carpenter and Ferguson, 1977). Courtship displays typically involve both amplification of contrast and/or coloration, and physically communicated signals (e.g., "push-up" displays, head bobbing, body rubs, etc.). Performance of these stereotypic displays can be modified by body temperature (Bennett, 1980, 1982), but it is not completely understood how body temperatures of the individuals receiving the signs might influence the interpretation of the signal.

The thermal environment has substantial effects on eggs and developing reptiles. Nest incubation temperatures are known to influence hatchling viability and post-hatching performance. Warmer nest temperatures generally increase rates of development, but suboptimal incubation temperatures (i.e., too low or too high) can lead to developmental abnormalities (Beuchat, 1988; Packard and Packard, 1988) and, in extreme cases, death of the embryo (Licht and Moberly, 1965; Christian *et al.*, 1986; Packard and Packard, 1988). Temperature may also directly influence hatchling fitness. Christian and Tracy (1981) found that the ability of hatchling Santa Fe land iguanas (*Conolophus pallidus*) to avoid predators was temperature dependent. Successful dispersal from the nest sites was largely a function of a lizard's ability to achieve the high body temperatures necessary for efficient locomotory performance.

Nest temperatures not only affect rates of development, but in some cases may determine the gender of the hatchling. In some reptiles, the nest or incubating environment, not chromosomes, determine hatchling gender (see also chapters on sex determination and reproductive ecology in this volume). This phenomenon is generally known as **environmental sex determination** (ESD). In many cases temperature is the environmental variable responsible for gender determination. This type of ESD is known as **temperature-dependent sex determination**, or TSD. Nest temperatures may be affected by numerous factors including differences in season, nest depth, properties of the overlying nest material, nest moisture, com-

Incubation of python eggs. Photo by Isabelle Francais.

Leopard Gecko, *Eublepharis macularius*. Juvenile photo by R. D. Bartlett.

Northern Pacific Rattlesnake, *Crotalus viridis oreganus*. Photo by Ron Everhart.

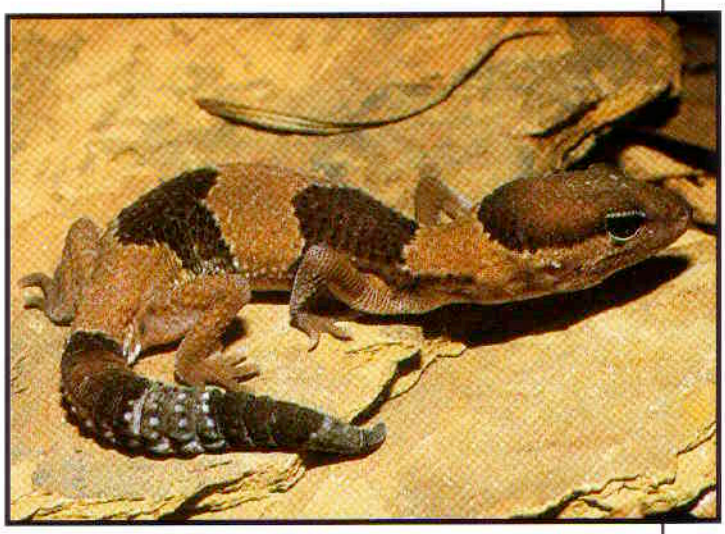
pass orientation, substratum type (including soil texture and structure), and other microclimatic factors. Thus, at the same general locality on a given year, some nests may produce only female offspring, while other nests produce only males (Janzen, 1994). When considered at a larger scale, TSD has the potential to effect population dynamics, demography, and long-term persistence. Although TSD is known to influence the sex ratios of individual nests (Bull and Vogt, 1979; Janzen, 1994), manypopulations of reptiles with TSD equal male:female gender ratios as adults (Ewert and Nelson, 1991).

Three general patterns of TSD have been characterized in reptiles (Bull, 1980). In some turtles, low temperatures (e.g., less than approximately 25-28 °C) produce all male offspring, and high incubation temperatures (e.g., greater than about 31-33 °C) produce all females (Vogt and Bull, 1982; Ewert and Nelson, 1991). At intermediate incubation temperatures both sexes are produced. In some lizards, higher incubation temperatures produce males and lower temperatures produce females. In crocodilians, some turtles, and some eublepharid geckos (e.g., leopard geckos, *Eublepharis macularius* and African fat-tailed geckos, *Hemitheconyx caudicinctus*), males are produced at intermediate temperatures and females are produced at higher and lower incubation temperatures (Webb and Cooper-Preston, 1989; Ewert and Nelson, 1991; Viets et al., 1993; Lang and Andrews, 1994).

Variable or cyclic nest temperatures generally have an effect that is dependent on the highest temperature reached in the cycle. Gender determination typically occurs over a narrow range of nest temperatures and within a short time frame - usually during the first to second third of the incubation period (Vogt and Bull, 1982). TSD is widespread among reptiles and found in some species of all major clades of extant reptiles, except the tuatara (*Sphenodon punctatus*) (see reviews in Bull, 1980; Janzen and Paukstis, 1991; Lang and Andrews, 1994; Viets *et al.*, 1994). Despite attempts by numerous investigators, a single ecologically adaptive or evolutionarily correlated mechanism has yet to be discovered to account for the distribution of TSD in all reptiles. There is however, some recent evidence which suggests that TSD may be correlated with shifts in sexual dimorphism in some lizards and turtles (Viets *et al.*, 1994), but there are many species which do not share this pattern, and many more species yet to be examined.

Among reptiles, parental care is generally rare (Graves and Duvall, 1995), although brooding behaviors have been noted in some squamate reptiles. Two particularly large snakes, the diamond python (*Morelia* [= *Python*] *spilotes spilotes*) and the Indian python (*Python molurus bivittatus*), encircle their eggs and brood them for several months until they hatch. During the egg-brooding cycle, the female python (males do not assist in brooding) rhythmically contracts the muscles along her coils and, as a result, her working muscles raise her body temperature as much as 7 °C above the ambient temperature (Hutchison *et al.*, 1966; Vinegar *et al.*, 1970; Harlow and Grigg, 1984). This phenomenon has been termed **shivering thermogenesis**, and is one of only a few examples of "facultative endothermy" found in reptiles. The retention of

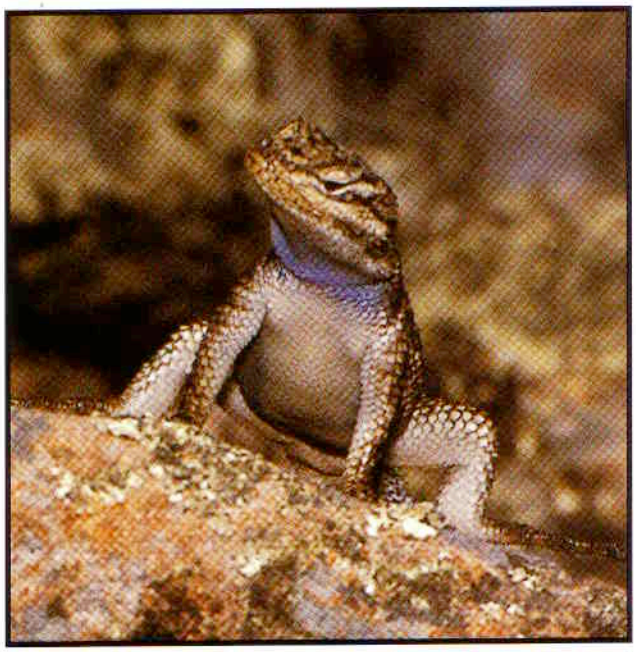
Diamond Python, *Morelia spilotes*. Photo by Aaron Norman.



Fat-tailed Gecko, *Hemitheconyx caudicinctus*. Photo by R. D. Bartlett.

the metabolic heat is undoubtedly facilitated by the large body size of these snakes and their tendency to coil around the egg mass, thereby reducing the total surface area exposed to the environment (Bennett and Dawson, 1976). During this period the brooding female may not feed or drink (Ellis and Chappell, 1987), although females of some species may leave their clutch to temporarily bask in the sun each day. Opportunistic thermoregulation may serve to conserve energy during incubation (Harlow and Grigg, 1984). Nevertheless, the energetic investment and protective behavior associated with brooding is costly, and thus the developing offspring must accrue a substantial benefit from this form of parental care for it to be adaptive. Indeed, the heat generated by the brooding mother warms the eggs and, thereby increases their rate of development (Harlow and Grigg, 1984).

Viviparity (bearing live young), has been proposed by some authorities to have evolved in squamate reptiles as an adaptive response to life in cool climates (Packard *et al.*, 1977; Shine and Bull, 1979; Shine, 1985; Guillette, 1992; see also the reproductive ecology chapter in this volume). The reasoning behind this hypothesis is simple: eggs that are deposited in nests are subject to the vagaries of the environment, whereas a pregnant female protects herself and, hence, her developing embryos, from such environmental threats. In cooler climates, the probability of eggs encountering lethally cold environments should lead to selection for shorter incubation periods (i.e., longer retention or gestation times), and under these conditions, oviparity may be evolutionarily "abandoned" altogether, and replaced by viviparity. Indeed, in many lineages of squamate reptiles, viviparous species are more frequently found in cooler environments (i.e., higher latitudes and elevations) than are oviparous species. Further sup-



Yarrow's Spiny Lizard, *Sceloporus jarrovi*. Photo by R. D. Bartlett.

port for the adaptive significance of viviparity in cooler climates is provided by groups of closely related lizards with dissimilar reproductive modes (e.g., *Liolaemus* and *Sceloporus*). Within these genera, viviparous species are typically associated with distributions at high latitude or elevation (Tinkle and Gibbons, 1977; Ramirez Pinilla, 1991, 1992).

In some cases, selection of particular body temperatures may be different for gestating females. Developing embryos of some species have different thermal requirements than do the adults. For some species, pregnant females select or maintain higher activity body temperatures (e.g., northern Pacific rattlesnake, *Crotalus viridis oreganus*; Gier *et al.*, 1989; ocellated skink, *Chalcides ocellatus*, Daut and Andrews, 1993), while other species maintain lower body temperatures (e.g., Yarrow's spiny lizard, *Sceloporus jarrovi*; Beuchat, 1986, 1988). Selection of higher body temperatures by gravid females should increase developmental rates of offspring, and therefore, shorten gestation periods. However, the thermal tolerances of developing offspring can be different from that of the adults and, in some cases, selection of high body temperatures during gestation can lead to developmental abnormalities and embryo death (Beuchat, 1988). Pregnant females of some viviparous species may also exhibit greater thermoregulatory precision than nonpregnant individuals (Stewart, 1984; Beuchat, 1986; Gier *et al.*, 1989). These embryos may be less tolerant of fluctuating temperatures, thermal extremes, and/or embryonic development is optimized over a small range of temperatures (Packard and Packard, 1988).

INFECTION AND WATER BALANCE

Body temperature may play an important role in fighting disease in ectotherms by shortening the initiation of the immune response (Tait, 1969). When humans become infected with certain pathogenic microbes, the immune system responds by increasing body temperature (i.e., creating a fever) to make the body a less hospitable environment for the pathogen. In vertebrates, fever may be induced by adjusting the internal thermostat, or the voluntary minimum and maximum temperatures. Endotherms accomplish this by increasing metabolic heat production (Kluger, 1979), whereas some reptiles do so by behaviorally selecting warmer thermal environments than they would normally prefer. In controlled laboratory experiments, desert iguanas (*Dipsosaurus dorsalis*) infected with the fever-inducing bacterium, *Aeromonas hydrophila*, behaviorally selected higher body temperatures than did uninfected lizards (Vaughn *et al.*, 1974). In subsequent studies, infected lizards were subjected to temperatures ranging from 34-42 °C. Lizards maintained at cooler temperatures died sooner than did those maintained at higher temperatures (Kluger *et al.*, 1975). Presumably, the survival rates of the lizards maintained at higher temperatures increased because of reduced bacterial growth (Kluger *et al.*, 1975; Kluger, 1979), or as a result of an enhanced immune response. However, like behavioral thermoregulation, "behavioral fever" thermoregulation may not be ubiquitous in reptiles. For instance, researchers working with the leopard tortoise (*Geochelone pardalis*) failed to demonstrate a febrile response despite subjecting the tortoises to several species of known fever-inducing microbes (Zurovsky *et al.*, 1987). Because this phenomenon has been studied in so few reptiles, it is premature to suggest any general explanations for the distribution of this behavior.

Water and ion balance may influence the regulation of body temperature in some reptiles. Following periods of dehydration, desert lizards such as the bearded dragon, *Pogona barbata* (= *Amphibolurus barbatus*) and the desert iguana, *Dipsosaurus dorsalis*, will only initiate panting at higher body temperatures (Parmenter and Heatwole, 1975; Dupré and Crawford, 1985, 1986), presumably as a water conservation mechanism. However, the precise mechanism(s) responsible for elevating the panting threshold have not been identified and may include a reduction in body fluid volume, plasma osmolality or volume, or an increase in plasma ion concentration (Dupré and Crawford, 1986). Similarly, artificially increasing ionic loads (e.g., NaCl, KCl) may increase the panting threshold and the average temperature selected by some reptiles (Dupré and Crawford, 1985; and see review in Bradshaw, 1986).

Bearded Dragon, *Pogona barbata*. Photo by R. G. Sprackland.

METABOLISM

GENERAL REMARKS AND TERMINOLOGY

Metabolism is the general term that embraces the processes associated with energy consumption and utilization by all living organisms. Metabolizable energy and other materials are acquired from the biochemical processes that convert foods into their molecular constituents. These products are used to support maintenance of normal activities, growth and repair, reproduction, and/or may be stored for later use.

Metabolism of energy can be performed through two pathways depending upon the rate of demand for oxygen and for energy production:

—**aerobic** metabolism, which is used during normal sustainable activities

—**anaerobic** metabolism, which is employed during "fight or flight" responses, such as sprinting to capture mobile prey or to avoid predation.

Unlike the aerobic pathway, anaerobic metabolism does not require an immediate source of oxygen to produce work. The distinction between, and the relative importance of, these two metabolic pathways are discussed in the forthcoming section on *Activity and Locomotion*.

ESTIMATES OF METABOLIC RATES

Metabolic rates of reptiles were first studied under controlled conditions in the laboratory. An animal's metabolic rate is often measured from the rate of consumption of materials used in metabolism. Oxygen is the most frequently measured material and metabolic rate is often expressed on a per unit body mass basis (e.g., ml O_2/(g*h)). Numerous laboratory studies have examined the metabolic rates of fasted reptiles at rest. The oxygen consumption value acquired under these conditions is termed the **standard metabolic rate** (SMR), and is assumed to be the energetic costs of "maintenance" at a specified temperature.

Recent advances using isotopically-labeled water have provided physiological ecologists with the opportunity to study reptilian energetics under natural field conditions (e.g., Bennett and Nagy, 1977; Nagy *et al.*, 1984; Christian and Conley, 1994). **Field metabolic rates** (FMRs) can provide information on changes in energy expenditure resulting from changes in season and over the reproductive cycle. Moreover, FMRs can be used to compare the activity metabolism of reptiles with different ecological attributes (e.g., herbivores vs. carnivores; terrestrial vs. aquatic, etc.).

Although metabolic rates have been measured in many reptiles, most of what we know about reptilian energetics is a product of research on squamate reptiles, and lizards in particular. Andrews and Pough (1985) developed a model for predicting the metabolic rate for squamate reptiles based on their body mass. They found that the metabolic rates (SMRs) of these reptiles were generally 10-20% that of a similarly-sized endotherm. Specifically, oxygen consumption by most squamates fell below 0.25 ml per gram of animal per hour and never exceeded 0.5 ml per gram of animal per hour. Their data show that the metabolic rates of squamate reptiles generally scale to the 0.8 power with body masses (on a log-log basis) over their normal range of activity temperatures. However, it is important to note that a single relationship based on body mass may lead to erroneous estimations of metabolism for some squamates because some evolutionary and ecological factors also explain much of the variation. For example, diurnal predators have significantly higher metabolic rates than do reclusive predators (Andrews and Pough, 1985).

In addition to differences among species in metabolic rates, there can be appreciable variation in metabolism within individuals as a function of the time of day and season of the year. The mechanisms thought to be responsible for the daily and seasonal differences in activity and metabolic rate include differences in age, gender, reproductive condition, elevational distribution, and resource availability (e.g., Bennett and Dawson, 1976; Bennett, 1982; Christian and Conley, 1994; Christian and Green, 1994; see also Chapter 10 this volume).

INFLUENCE OF BODY TEMPERATURE

In most ectotherms, temperature and metabolism are tightly coupled. Generally, metabolic rate increases exponentially with an increase in body temperature. Under aerobic conditions, a 10 °C increase in temperature will typically result in a two- to three-fold increase in the rate or function of a particular physiological process (Bennett and Dawson, 1976; Bennett, 1982). For example, digestive efficiency for a given reptile may increase two-fold over a body temperature span of 25-35°C. A few lizards and snakes have effectively decoupled this effect over a small range of body temperatures. For these reptiles, including the tuatara (*Sphenodon punctatus*) and several species of lizards and snakes, "metabolic plateaus" are observed over the range of their activity body temperatures, or during hibernation when body temperatures stabilize at lower levels (see reviews in Bennett and Dawson, 1976; Bennett, 1982).

INFLUENCE OF BODY SIZE

Body size greatly influences rates of energy exchange between reptiles and their environment. Smaller animals have higher metabolic rates per unit body mass than do larger individuals (see reviews in Bennett and Dawson, 1976; Bennett, 1982; Andrews and Pough, 1985). This relationship is generally expressed by the allometric equation

$\boldsymbol{MR = am^b}$, or $\boldsymbol{\log MR = (b \log m) + \log a}$ (Fig. 4)

where: MR = standard metabolic rate;
log a = y intercept of the regression (constant);
m = body mass of the animal (g); and
b = slope of the regression (constant).

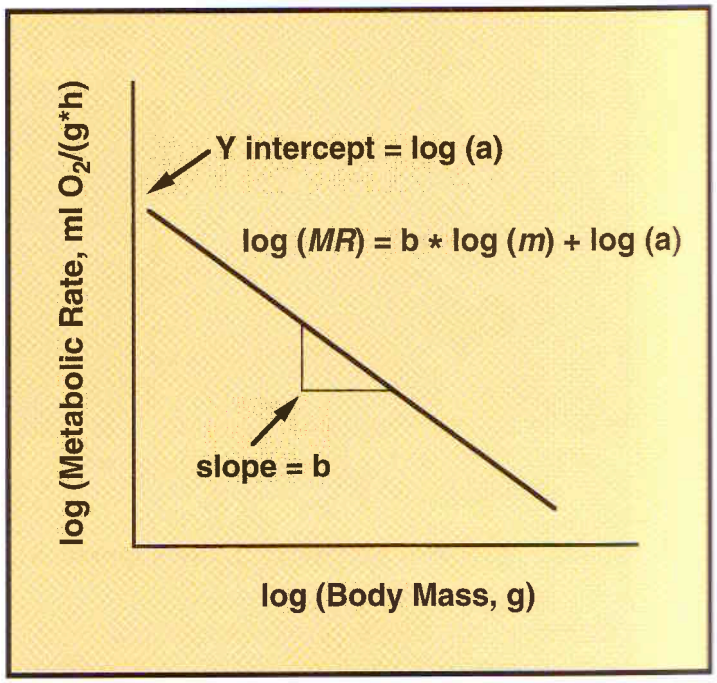


Figure 4.
General relationship for the effect of body mass on metabolic rate in reptiles

Among reptiles, metabolism increases in proportion to body mass raised to the 0.600.88 power. Because the value of the exponent is less than one, larger reptiles expend less energy per unit mass of body tissue than do smaller individuals. The variance in the exponent term b may be a function of body temperature, and/or it may be related to various ecological and/or evolutionary attributes (see Andrews and Pough, 1985).

EVOLUTIONARY HISTORY

Some reptiles have extremely low metabolic rates, while others process energy much more rapidly. Genetic constraints may account for some of the variation in energy use among reptilian lineages. The tuatara (*Sphenodon punctatus*) has a resting metabolic rate approximately two-thirds that of other reptiles, however this value does not fall

Nile Monitor, *Varanus niloticus*. Photo by K. H. Switak.

outside of the range exhibited by reptiles as a group (Bennett and Dawson, 1976). The night lizards (family Xantusiidae) have metabolic rates as low as one half that of other lizards of similar body sizes and temperatures (Mautz, 1979). By contrast, many lizards in the family Teiidae are considered "hyperactive" (e.g., *Ameiva* spp., *Cnemidophorus* spp., *Teius* spp., *Tupinambis* spp.), and indeed some of these species have high metabolic rates (Anderson and Karasov, 1981). Monitor lizards (*Varanus* spp.) also have high metabolic capacities and are generally considered to be a highly active group (Pough, 1973; Bartholomew, 1982; Andrews and Pough, 1985). However, some varanids have extended periods of inactivity over which FMRs can be substantially suppressed. Thus, as a group, monitors may be as physiologically diverse as other lizards (Christian and Conley, 1994). Generally, snakes and lizards exhibit similar metabolic rates on a mass-specific basis, though several snake lineages have not been studied. Among squamates, boas and pythons tend to have lower metabolic rates; however, these rates are statistically indistinguishable from even the high rates recorded for monitor lizards (Andrews and Pough, 1985). Fewer studies have examined the metabolic

Boa Constrictor, *Boa constrictor*. Photo by R. D. Bartlett.

rates of turtles and crocodilians, but the values for species studies in these groups fall within the range found for squamate reptiles (Bennett and Dawson, 1976; Andrews and Pough, 1985).

FORAGING, FEEDING, AND DIGESTION

Foraging behaviors vary widely among reptiles. Some reptiles, known as **sit-and-wait predators**, remain relatively motionless until prey are within striking range and then suddenly lunge out for their meal. **Active** or **widely-foraging predators** move through their environment, digging, scratching, browsing, or engaging in similar activities associated with finding prey. Not surprisingly, sit-and-wait predators have lower resting metabolic rates than do active foragers (Anderson and Karasov, 1981; Nagy *et al.*, 1984; Secor and Diamond, 1995). Generally, the cost of capturing and subduing prey for small reptiles is insignificant relative to the energy acquired from the meal, and under most circumstances, prey capture is accomplished via aerobic metabolism (Pough and Andrews, 1985; Preest, 1991).

In most cases, the energy acquired from a herbivorous diet is less than that obtained from a carnivorous diet. This is because most plant tissues contain less energy on a gram-by-gram basis than do animal tissues, and it is compounded by the fact that herbivorous reptiles digest a smaller proportion of the their diets than do carnivores. For example, digestive efficiencies for herbivorous reptiles range from 30-85%, whereas carnivorous species have efficiencies on the order of 70-95% (Throckmorton, 1973; Harwood, 1979; Ruppert, 1980; Iverson, 1982; Waldschmidt *et al.*, 1986; Zimmerman and Tracy, 1989; Davenport *et al.*, 1992; Foley *et al.*, 1992; van Marken Lichtenbelt, 1992; Barboza, 1995). However, herbivores typically expend only a small amount of time and energy acquiring their food and, thus, the "inefficiency" they experience in digestion may be offset by the low costs required for foraging (Pough, 1973; Iverson, 1982).

Recent comparative studies suggest that significant metabolic costs may be incurred when digestive structures and functions are activated to accommodate increases in food intake. Interestingly, the cost of these changes may be strikingly greater for sit-and-wait predators than for active foragers. Within 24 hours of ingestion, sit-and-wait predatory snakes, such as pythons (*Python* spp.), boas (*Boa constrictor*), and sidewinders (*Crotalus cerastes*), experience as much as a 17-fold increase in metabolic rate (Secor *et al.*, 1994; Secor and Diamond, 1995 *a,b*). Post-feeding metabolic rates of actively foraging species, such as coachwhip snakes (*Masticophis* spp.), king snakes (*Lampropeltis* spp.) and gopher

Gray-banded Kingsnake, *Lampropeltis alterna*. Photo by R. G. Markel.

snakes (*Pituophis* spp.), also significantly increase, but not as dramatically as the sit-and-wait species. These substantial differences in metabolic costs of digestion are interpreted as adaptive strategies resulting from the frequency of feeding (Secor *et al.*, 1994; Secor and Diamond, 1995*a,b*). Because sit-and-wait foragers may go for months between feeding bouts, maintaining digestive structures at their functionally operating levels is not energetically cost effective. By contrast, active foragers, which may feed daily, are expected to maintain their gut functions closer to operating levels instead of continuously turning on and off their digestive systems.

ACTIVITY AND LOCOMOTION

Activity patterns in reptiles range from sedentary species that remain virtually motionless for hours or days, to those that are nearly continuously active. Thus, for some reptiles, the energy expended in activity and locomotion can account for a substantial proportion of the total energy budget. This is particularly true for actively foraging species which spend a significant proportion of their activity period seeking prey (Bennett and Gleeson, 1979; Anderson and Karasov, 1981; Secor and Nagy, 1994). Yet for sit-and-wait reptiles, locomotion is limited to short-distance bursts used to capture prey or to avoid predation and, therefore, may not impose a significant cost relative to other behaviors (Anderson and Karasov, 1981; Secor and Nagy, 1994). Most reptiles rely on aerobic metabolism for normal locomotory activities such as foraging, migration, finding mates, dispersal, and similar behaviors. Anaerobic metabolism may be required for exertion such as sprinting, diving, or intense interactions with conspecifics and predators. Although anaerobiosis can generate energy at rates five to 10 times greater than that produced by aerobic metabolism, the ability to sustain anaerobic metabolism rapidly degrades during such activities (Bennett and Dawson, 1976; Bennett, 1982). Moreover, recovery from anaerobic locomotion may take from hours to days depending on the intensity and duration of the activity, and body temperature (Bennett and Dawson, 1976; Wagner and Gleeson, 1996). Although the oxygen debt and lactic acid may be returned to normal levels relatively quickly, it may take longer to replace the energy consumed as a result of anaerobic metabolism because of the inefficiency with which the energy is used relative to aerobic metabolism. Indeed, anaerobic metabolism may require as much as 10 times the equivalent food energy to accomplish the same work under aerobic conditions (Zug, 1993). Interestingly, anaerobic activity is relatively independent of body temperature over much of the thermal activity range for most of the reptiles that have been examined (Bennett and Dawson, 1976). Decoupling temperature from anaerobic locomotion may permit rapid escape responses in times of need.

Numerous studies have quantified the cost of locomotion in reptiles at maximal levels, but fewer have addressed sustainable exercise. **Aerobic scope** is a measure of an animal's ability to do work without relying on anaerobiosis. Aerobic scope is measured as the difference between an animal's maximal aerobic capacity and its SMR, and is often associated with the locomotory and behavioral characteristics of the animal. A corollary of aerobic scope is locomotory endurance or stamina. Garland (1994) measured the endurance capacity of 57 lizard taxa on a treadmill and found that roughly half of the variation in endurance was attributable to body mass and temperature. Specifically, warmer and larger lizards tend to have greater endurance capacities. However, evolutionary history and various ecological attributes were also suggested to have important correlates with locomotory performance. For instance, some lineages of lizards exhibit relatively greater locomotory stamina, such as some Scincidae (skinks), Lacertidae (*Lacerta* spp.), Teiidae (whiptail lizards), Helodermatidae (Gila monster and Mexican beaded lizards), Varanidae (*Varanus* spp.), while other groups, including most of the Iguanian lineages and the Gekkota, have lower endurance capacities. Not surprisingly, the latter two groups are sit-and-wait predators, whereas the majority of the others are active foragers.

REPRODUCTION

Reproduction is a key determinant of organismal fitness, but can also be one of the most energetically costly activities. In many reptiles, mate acquisition can involve a substantial energetic investment which may be associated with costly migra-

Gila Monster, *Heloderma suspectum*. Photo by Karl H. Switak.

tions, complex behaviors and courtship displays, competition among conspecifics for mates and/or nest sites, excavating nest sites, fasting, incubation, nest guarding, gestation, and in a few exceptional cases, parental care (see Chapter 6 this volume).

Female reptiles of viviparous species might be expected to accrue the greatest metabolic costs of reproduction. Metabolic rate increases sigmoidally over the course of pregnancy in Yarrow's spiny lizard (*Sceloporus jarrovi*), and plateaus just prior to parturition (DeMarco, 1993). Litter metabolism is lowest during early pregnancy, when the litter mass consists mostly of metabolically inert yolk (DeMarco, 1993). Thus the cost of early pregnancy in this viviparous lizard is likely to closely approximate the value expected for a gravid oviparous species. However, metabolic rates substantially increase later in pregnancy, and may significantly exceed that incurred by oviparous species (DeMarco, 1993). Additionally, despite the fact that viviparous species tend to produce fewer offspring per clutch than do oviparous species, maternal investments may still be equal to or greater than that for viviparous species because the period of gestation is typically twice as long (Shine, 1985). Longer periods of pregnancy may impose additional energetic costs and may lower fitness due to an increase in total body mass which, in turn, may hamper agility, locomotory performance, and the ability to acquire prey and avoid predators.

As discussed previously, some brooding pythons produce heat via rhythmic contractions of skeletal muscles, or shivering thermogenesis. This form of incubation can be metabolically costly, because the animal's muscles may continuously twitch for more than two months. In fact, depending upon the heat differential between the mother and the environment, brooding pythons can expend anywhere from 2-22 times more energy than similarly-sized nonbrooding individuals (Vinegar *et al.*, 1970; Harlow and Grigg, 1984). Although other species of pythons brood their eggs, shivering thermogenesis has only been recorded in the larger species (e.g., Ellis and Chappell, 1987).

HIBERNATION

GENERAL REMARKS AND TERMINOLOGY

Reptiles have been remarkably successful at invading the hot climates of the world; however, they have not experienced a similar degree of success in cooler environments. As we have discussed previously, cold temperatures, such as those associated with temperate zone winters, impose challenging or even intolerable conditions for many reptiles. **Hibernation** may be the only option available to some reptiles to avoid the unfavorable conditions of cold and limited food availability during winter. Although not all reptiles hibernate, all major reptilian clades have some hibernators. Examples are the tuatara (*Sphenodon punctatus*); most temperate and some subtropical sea turtles;

American Alligator, *Alligator mississippiensis*. Photo by R. T. Zappalorti.

alligators (*Alligator mississippiensis* and *A. sinensis*), and the Nile crocodile (*Crocodylus niloticus*); and many temperate and some subtropical squamates (Gregory, 1982).

For the purposes of this discussion, we define hibernation broadly as a state of dormancy coinciding with the cold of winter (but see Gregory, 1982 for a review of alternative definitions). Hibernation is a period of quiescence: normal activities cease, body temperature regulation may be abandoned, feeding and excretion are uncommon, and metabolism may be greatly reduced. **Brumation** was used by Mayhew (1965) to describe obligatory hibernation first seen in flat-tailed horned lizards (*Phrynosoma mcalli*). Unlike most other hibernating reptiles, *P. mcalli*, will enter and remain in a inactive state even if photoperiod and temperature are artificially increased to levels that

are typical of the activity season (Mayhew, 1965). Mayhew (1965) further suggested that the term brumation be adopted to describe reptilian hibernation generally, but perhaps due to its specific definition, the term has failed to receive wide acceptance or usage (Gregory, 1982). **Estivation**, like hibernation, is a strategy to avoid harsh environments and sparse resources, but estivation generally occurs during the challenging months of summer. Like hibernation, estivation includes a reduction in activity, but unlike hibernation, estivation is generally thought to be more a strategy for conserving body water. Estivation has been commonly reported in turtles and squamate reptiles living in the hot deserts of the world.

INDUCTION AND TERMINATION OF HIBERNATION

Hibernation can be partitioned into several components or stages: fasting; entering the hibernaculum; dormancy; and metabolic depression (Gregory, 1982). The induction into each of these stages probably results from a suite of interacting exogenous and endogenous cues (Licht, 1972).

ENDOGENOUS CUES

Reptiles that hibernate in response to cues received from exogenous sources are often termed **facultative hibernators.** For most temperate reptiles, hibernation is coincident with the declining temperatures of fall and early winter. However, few studies have gone beyond simply correlating the onset of hibernation with these lower ambient temperatures. Nevertheless, the fact that some reptiles emerge on unseasonably warm days during winter suggests that temperature is an important cue. Because lower body temperatures generally inhibit appetite in reptiles (Gatten, 1974), the lower temperatures associated with seasonal cooling may also provide an exogenous cue for the initiation of fasting in hibernating reptiles (Gregory, 1982). Day length also may function as an important exogenous cue, but it is difficult to separate true day length responses from other correlated seasonal changes (Licht, 1972). Furthermore, because many reptiles hibernate in environments where they do not receive light cues, it is unlikely that photoperiod alone could serve as a controlling factor for emergence.

ENDOGENOUS CUES

Reptiles that hibernate as a result of cues received from endogenous sources are termed **obligatory hibernators**, and are probably less common than are facultative hibernators. Some investigators have suggested that the underlying hormonal mechanisms in reptiles are similar to those found in mammals (see reviews in Gilles-Baillien, 1974; Firth and Turner, 1982); however, few studies have investigated this directly. Hibernating reptiles exhibit seasonal cycles in hormone, amino acid, and neurotransmitter titers, which may play a key role in the regulation of reptilian hibernation (Firth and Turner, 1982). Several of these hormones (e.g., melatonin, serotonin, and others) are influenced by circadian and seasonal rhythms and, in reciprocal fashion, are themselves altered by daily and annual cycles. However, the mechanisms associated with these relationships are not well understood. Reproductive hormones also cycle in a similar manner, and may serve to induce reproduction upon emergence.

DURATION OF HIBERNATION

The length of the dormancy period depends upon numerous abiotic and biotic factors, including latitudinal and elevational distribution, climate, age, gender, and prehibernation condition (e.g., energy reserves) (Bennett and Dawson, 1976; Gregory, 1982). Reptiles living at high latitudes or elevations may experience longer periods of dormancy than activity (e.g., Pearson, 1954; Gregory, 1982). Different species of reptiles living in identical environments may exhibit remarkably different periods of dormancy, or hibernation strategies. Thus, the duration of dormancy is best considered a continuum spanning a few days, to longer periods interrupted by intermittent emergence, to continuous dormancy for several months (Gregory, 1982). In most reptiles, males emerge from hibernation before females. Because male reptiles can potentially mate more than once in a given reproductive season, early emergence may facilitate the establishment of breeding territories and dominance prior to female emergence, and thus enhance the probability of reproduction (Gregory, 1982).

Generally reptiles experience a substantial metabolic depression during hibernation. In most cases, metabolic rates of hibernating reptiles are lower than would be expected on the basis of the reduction in body temperature alone, and is typically accompanied by a significant reduction in cardiovascular function (Gregory, 1982; Ultsch, 1989). Some reptiles may also experience various changes in body composition during hibernation such as reductions in body fat, and water, though there is no clear pattern to these changes both among and within species and among individuals within a species (see review in Gregory, 1982). Lipid reserves are generally thought to provide the needed energy during the hibernation, but lipid metabolism may be greater before or soon after hibernation rather than during hibernation period itself, and stores generally far exceed that needed to sustain continuos hibernation (Gregory, 1982). Some hi-

bernators may rely on these lipid reserves rather than feed during intermittent periods of activity (Derickson, 1976).

SELECTION OF THE HIBERNACULUM

Hibernacula, or overwintering sites, can function to insulate and shield the hibernator from extremes in temperature, and in some cases, predation. Selection of the hibernaculum may vary among species, populations, and individuals. Hibernacula take many forms, ranging from a pile of leaf litter, soil, or snow, to an ant or termite nest, to deep burrows or caves. Interestingly, some reptiles even hibernate under water. This strategy is well documented in fresh water turtles and alligators, some of which hibernate at the bottom of streams, ponds, or in wallows constructed especially for overwintering. Water provides a stable thermal environment for the hibernator, and because water is most dense at 4 °C, temperatures at the bottom of deeper bodies of water will typically remain above freezing. Fresh water turtles seem to be the best-adapted reptiles for submerged hibernation because they can remain under water for several months (Ultsch and Jackson, 1982*a,b*; Ultsch, 1989). However, sometimes oxygen is unavailable in these environments. To avoid anoxia, some aquatic hibernators do not bury in the mud or rocks, but simply rest on the bottom. This form of exposure may facilitate extrapulmonary respiration, such as that which can occur through the skin, which may be sufficient to meet the metabolic demands during hibernation (Bennett and Dawson, 1976; Ultsch and Jackson, 1982*a,b*; Costanzo, 1989). Nevertheless, some submerged hibernators may experience anoxic conditions which results in the accumulation of lactic acid in their tissues due to their reliance on anaerobic metabolism. For these reptiles, flushing of lactic acid may be accomplished by periodically shuttling to normoxic waters, or by breaching the surface to breathe (Ultsch, 1989).

Some reptiles overwinter in large aggregations in a common hibernaculum known as a **communal den**. This behavior is especially well documented in some temperate zone snakes (Gregory, 1984). In some cases, several different species may share a communal den. Communal denning may provide an adaptive advantage to snakes hibernating in large groups because rates of water loss can be lower than for snakes hibernating individually (Gregory, 1982). However, there is no evidence to suggest that denning clusters of snakes have a survival advantage over those that hibernate individually within the same den environment (Gregory, 1982). Nevertheless, individual snakes may return to the same den site year after year, though the factors responsible for inducing migration towards these dens have not been examined. Communal denning may also improve the probability of finding a mate upon emergence. This may be especially important for reptiles that have short activity seasons such as those living at high latitude or elevation.

FREEZE AVOIDANCE, TOLERANCE, AND SUPERCOOLING

Most temperate zone reptiles can withstand brief periods of subzero temperatures (Lowe *et al.*, 1971; Gregory, 1982; Ultsch, 1989; Costanzo *et al.*, 1993; Packard *et al.*, 1993; Packard and Packard, 1995). Survival from extremely low temperatures is achieved by one or a combination of three strategies:

—freeze avoidance
—freeze tolerance
—supercooling.

Freeze avoidance can be accomplished via a simplistic form of behavioral thermoregulation. For example, some hibernating snakes move periodically in an effort to find the warmest microenvironments within their hibernaculum (Sexton and Hunt, 1980). Similarly, some box turtles (*Terrapene* spp.) begin hibernation near the surface and bury deeper as the cold of winter progressively lowers the frost line. As spring approaches and ground temperatures increase, these turtles slowly "migrate" to the surface (Legler, 1960). As discussed above, some reptiles hibernate on the bottom of deeper ponds and streams, or in mud, which generally do not freeze.

Freeze tolerance may be an important adaptive strategy some reptiles use to survive the cold

Wood Frog, *Rana sylvatica*. Photo by David Green.

of winter. Two primary adaptations are thought to promote freeze tolerance in reptiles; however, these responses were developed from research on frogs (primarily the wood frog, *Rana sylvatica*), and have only been examined in a small number of reptiles. First, as the periphery of the animal begins to freeze, glucose is rapidly mobilized from glycogen stores in the liver and is carried via blood vessels to other tissues (Storey, 1990). The concentrated glucose serves as a cryoprotectant by inhibiting freeze damage to cells and tissues (Costanzo *et al.*, 1991). The second adaptation involves a redistribution of visceral and tissue water into the coelomic and subdermal spaces (Costanzo *et al.*, 1993). Reducing the concentration of water in the organs reduces the likelihood of ice-crystal formation within the tissues and may, therefore, reduce the chance of cell rupture associated with freezing (Lee *et al.*, 1990, 1992). Glucose distribution and tissue dehydration are further facilitated by a persistence of cardiac function during the onset of freezing (Costanzo *et al.*, 1993). If these mechanisms fail, the animal will die upon thawing as a result of cellular disfunction due to dehydration or mechanical rupturing of their cells resulting from ice crystal formation.

Eastern Painted Turtle, *Chrysemys picta picta*. Aaron Norman.

Some turtles (e.g., eastern box turtles, *Terrapene carolina* and painted turtles, *Chrysemys picta*) may tolerate freezing of extracellular fluids, while other reptiles are intolerant of freezing, but can withstand the formation of ice in a portion of their body fluids (e.g., Costanzo, 1988; Storey *et al.*, 1988; Costanzo and Lee, 1990; Costanzo *et al.*, 1993; Packard *et al.*, 1993). For example, hatchling painted turtles (*Chrysemys picta*) overwinter in their nests and commonly experience subzero temperatures which may freeze their extracellular fluids (Packard *et.al.*, 1989). Similarly, American alligators (*Alligator mississippiensis*) may regularly experience and survive freezing temperatures at the northern edge of their range (Hagan *et al.*, 1983).

Supercooling occurs when an animal's body temperature falls below freezing, but the animal does not freeze because ice nuclei fail to form within the body. Hatchling painted turtles (*Chrysemys picta*) may avoid nucleation from ice and subsequent freezing, which is generally lethal at high subzero temperatures, by avoiding contact with water and by withdrawing the head and appendages into the shell during hibernation (Packard and Packard, 1995). Supercooling has been examined in only a few species of reptiles (e.g., Lowe *et al.*, 1971; Claussen *et al.*, 1990; Claussen and Zani, 1991; Packard and Packard, 1995), so little is known about the range of conditions under which this strategy is possible in nature (Packard and Packard, 1995), or the ubiquity of this phenomenon among hibernating reptiles generally.

SUMMARY

THERMAL BIOLOGY

The thermal environment plays a critical role in the lives of most reptiles. Even reptiles that do not actively thermoregulate must adhere to the countless temperature-dependent physical and biochemical processes that sustain their lives. Studies on the thermal biology of reptiles have historically focused on lizards, but many important aspects of the thermal biology of most other major groups of reptiles have been examined. Many reptiles have evolved morphological, physiological, and behavioral specializations that can be used to either enhance or reduce exchanges of thermal energy between them and their environments. The specific thermal strategies and activity body temperatures maintained or selected by an individual reptile can be strongly influenced by abiotic factors (such as distribution, climate, and microhabitat selection) as well as biotic factors (such as genetic constraints, health and reproductive status, seasonal and daily patterns of activity, and interactions with other organisms).

METABOLISM

Metabolism is the physiological process of consuming energy and is therefore useful as a tool for comparing energy utilization strategies among reptiles. Metabolism can be either aerobic or anaerobic. Aerobic metabolism is generally used for sustained activities, and is energetically more efficient; however, anaerobic metabolism can be an effective means of delivering energy during brief bursts of activity. Metabolic rate generally increases with increased body temperature, though some reptiles

may have decoupled metabolism from temperature over the range of their activity body temperatures. Body size and shape also influence metabolic rates. Larger animals have lower surface-to-volume ratios and thus have lower mass-specific metabolic rates than do smaller animals. Genetic constraints may also explain some of the variation in energy use among reptiles. Indeed, some lineages are comprised of species that exhibit relatively high rates of metabolism when active, while others have remarkably low rates of energy expenditure. Metabolic rate is typically measured indirectly as the amount of oxygen consumed over a specified period of time, and can now be closely estimated on reptiles in nature as well as in the laboratory. Generally, reptilian metabolism scales to the 0.8 power with body mass; however, not all reptiles conform to this predicted value, and those that do may increase or decrease energy expenditure under certain circumstances. Numerous biotic factors, such as activity, acquiring and processing food, and reproduction, may impose important energetic demands.

HIBERNATION

Hibernation is a period of dormancy that coincides with the cold of winter and is an effective strategy for avoiding reductions in energy and other resources. Most temperately distributed reptiles hibernate, though the timing and duration of hibernation may vary widely among taxa and even among individuals at a single locality. The induction and termination of hibernation are controlled by both exogenous and endogenous cues, though the precise mechanisms are not well understood. Reptiles hibernate in a variety of sites ranging from those constructed specifically for that purpose, to more opportunistically selected sites. Some squamates and tortoises hibernate in communal dens and may return to these sites each year. Some hibernating reptiles can survive short periods at subfreezing temperatures. Survival is achieved by one or a combination of three strategies: freeze avoidance, tolerance, and supercooling.

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REFERENCES AND RECOMMENDED READING

—Anderson, RA; Karasov, WH:
Contrasts in energy intake and energy expenditure in sit-and-wait and widely foraging lizards. Oecologia, 1981; 49: 67-72.

—Andrews, RM; Pough FH:
Metabolism of squamate reptiles: allometric and ecological relationships. Physiological Zoology, 1985; 58: 214-231.

—Auffenberg, W; Iverson, JB:
Demography of terrestrial turtles. In, Turtles: Perspectives and Research, N Harless; H Morlock (Eds). Wiley and Sons, New York, 1979, pp. 541-569.

—Autumn, K; Weinstein, RB; Full, RJ:
Low cost of locomotion increases performance at low temperature in a nocturnal lizard. Physiological Zoology, 1994; 67: 238-262.

—Avery, RA:
Thermoregulation, metabolism, and social behaviour in Lacertidae. In, Morphology and Biology of Reptiles, A d'A Bellairs; CB Cox (Eds). Academic Press, London, 1976, pp. 245-259.

—Avery, RA:
Field studies of body temperature and thermoregulation. In, Biology of the Reptilia, C Gans; FH Pough, (Eds). Academic Press, New York, 1982, 12: 93-166.

—Barber, BJ; Crawford, EC Jr:
A stochastic dual-limit hypothesis for behavioral thermoregulation in lizards. Physiological Zoology, 1977; 50: 53-60.

—Barber, BJ; Crawford, EC Jr:
Dual threshold control for peripheral temperature in the lizard *Dipsosaurus dorsalis*. Physiological Zoology, 1979; 52: 250-263.

—**Barboza, PS:**
Digesta passage rate and functional anatomy of the digestive tract in the desert tortoise (*Xerobates agassizii*). *Journal of Comparative Physiology* B, 1995; 165: 193-202.
—**Bartholomew, GA:**
A field study of temperature relations in the Galapagos marine iguana. Copeia, 1966; 1966: 241-250.
—**Bartholomew, GA:**
Physiological control of body temperature. In, Biology of the Reptilia, C Gans; FH Pough, (Eds). Academic Press, New York, 1982, 12: 167-211.
—**Bennett, AF:**
Thermal dependence of lizard behavior. Animal Behaviour, 1980; 28: 752-762.
—**Bennett, AF:**
The energetics of reptilian activity. In, Biology of the Reptilia, C Gans; FH Pough (Eds). Academic Press, New York, 1982, 13: 155-199.
—**Bennett, AF; Dawson, WR:**
Metabolism. In, Biology of the Reptilia, C Gans; WR Dawson (Eds). Academic Press, New York, 1976, 5: 127-223.
—**Bennett, AF; Nagy, KA:**
Energy expenditure in free-ranging lizards. Ecology, 1977; 58: 697-700.
—**Bennett, AF; John-Alder, HB:**
The effect of body temperature on the locomotory energetics of lizards. Journal of Comparative Physiology B, 1984; 155: 21-27.
—**Bennett, AF; John-Alder, HB:**
Thermal relations of some Australian skinks (Sauria: Scincidae). Copeia, 1986; 1986: 57-64.
—**Berk, ML; Heath, JE:**
An analysis of behavioural thermoregulation in the lizard *Dipsosaurus dorsalis*. Journal of Thermal Biology, 1975; 1: 15-22.
—**Beuchat, CA:**
Reproductive influences on the thermoregulatory behavior of a live-bearing lizard. Copeia, 1986; 1986: 971-979.
—**Beuchat, CA:**
Temperature effects during gestation in a viviparous lizard. Journal of Thermal Biology, 1988; 13: 135-142.
—**Bligh, J; Johnson, KG:**
Glossary of terms for thermal physiology. Journal of Applied Physiology, 1973; 35: 941-961.
—**Bogert, CM:**
Thermoregulation in reptiles, a factor in evolution. Evolution, 1949; 3: 195-211.
—**Bowker, RG:**
Precision of thermoregulation of some African lizards. Physiological Zoology, 1984; 57: 401-412.
—**Bradshaw, SD:**
Ecophysiology of Desert Reptiles. Academic Press, NSW, Australia, 1986, 324 pp.
—**Bradshaw, SD; Main, AR:**
Behavioral attitudes and regulation of temperature in *Amphibolurus* lizards. Journal of Zoology, 1968; 154: 193-221.
—**Brattstrom, BH:**
Body temperatures of reptiles. American Midland Naturalist, 1965; 73: 376-422.
—**Brattstrom, BH:**
Social and thermoregulatory behavior of the bearded dragon, *Amphibolurus barbatus*. Copeia, 1971; 1971: 484-497.
—**Bull, JJ:**
Sex determination in reptiles. Quarterly Review of Biology, 1980; 55: 13-21.
—**Bustard, HR:**
Activity cycle and thermoregulation in the Australian gecko *Gehyra variegata*. Copeia, 1967; 1967: 753-758.
—**Bustard, HR:**
Temperature-dependent tail autonomy mechanism in gekkonid lizards. Herpetologica, 1968; 24: 127-130.
—**Cabanac, M; Hammel, T; Hardy, JD:**
Tiliqua scincoides: temperature sensitive units in lizard brain. Science, 1967; 158: 1050-1051.
—**Carpenter, CC; Ferguson, GW:**
Variation and evolution of stereotyped behaviors in reptiles. In, Biology of the Reptilia, C Gans; DW Tinkle (Eds). Academic Press, New York, 1977, 7: 335-354.
—**Case, TJ:**
Seasonal aspects of thermoregulatory behavior in the chuckawalla, *Sauromalus obesus* (Reptilia, Lacertilia, Iguanidae). Journal of Herpetology, 1976; 10: 85-95.
—**Case, TJ:**
Ecology and evolution of the insular gigantic chuckawallas, *Sauromalus hispidus* and *Sauromalus varius*. In, Iguanas of the World, GM Burghardt; AS Rand (Eds). Noyes Publications, Park Ridge, NJ, 1982, pp. 184-212.
—**Christian, KA; Tracy, CR:**
The effect of the thermal environment on the ability of hatchling Galapagos land iguanas to avoid predation during dispersal. Oecologia, 1981; 49: 218-223.
—**Christian, KA; Tracy, CR; Porter, WP:**
Seasonal shifts in body temperature and use of microhabitats by Galapagos land iguanas

(*Conolophus pallidus*). Ecology, 1983; 64: 463-468.

—Christian, KA; Tracy, CR; Porter, WP:
The effect of cold exposure during incubation of *Sceloporus undulatus* eggs. Copeia, 1986; 1986: 1012-1014.

—Christian, KA; Clavijo, IE; Cordero-Lopez, N; Elias-Maldonado, EE; Franco, MA; Lugo-Ramirez, MV; Marengo, M:
Thermoregulation and energetics of a population of Cuban iguanas (*Cyclura nubila*) on Isla Magueyes, Puerto Rico. Copeia, 1986; 1986: 65-69.

—Christian, KA; Conley, KE:
Activity and resting metabolism of varanid lizards compared with 'typical' lizards. Australian Journal of Zoology, 1994; 42: 185-193.

—Christian, KA; Green, B:
Seasonal energetics and water turnover of the frillneck lizard, *Chlamydosaurus kingii*, in the wet-dry tropics of Australia. Herpetologica, 1994; 50: 274-281.

—Christian, KA; Bedford, GS:
Seasonal changes in thermoregulation by the frillneck lizard, *Chlamydosaurus kingii*, in tropical Australia. Ecology, 1995; 76: 124-132.

—Clark, DR; Kroll, JC:
Thermal ecology of anoline lizards: temperate versus tropical strategies. Southwestern Naturalist, 1974; 19: 9-19.

—Claussen, DL; Art, GR:
Heating and cooling rates in *Anolis carolinensis* and comparisons with other lizards. Comparative Biochemistry and Physiology, 1981; 69A: 23-29.

—Claussen, DL; Townsley, MD; Bausch, RG:
Supercooling and freeze-tolerance in the European wall lizard, *Podarcis muralis*, with a revisional history of the discovery of freeze-tolerance in vertebrates. Journal of Comparative Physiology, 1990; 160B: 137-143.

—Claussen, DL; Zani, PA:
Allometry of cooling, supercooling, and freezing in the freeze-tolerant turtle *Chrysemys picta*. American Journal of Physiology, 1991; 261: R626-R632.

—Costanzo, JP:
Recovery from ice-entombment in garter snakes. Herpetological Review, 1988; 19: 76-77.

—Costanzo, JP:
A physiological basis for prolonged submergence in hibernating garter snakes *Thamnophis sirtalis*: evidence for an energy-sparing adaptation. Physiological Zoology, 1989; 62: 580-592.

—Costanzo, JP; Lee, RE Jr:
Natural freeze tolerance in the terrestrial turtle, *Terrapene carolina*. Journal of Experimental Zoology, 1990; 254: 228-232.

—Costanzo, JP; Lee, RE Jr; Wright, MF:
Glucose loading prevents freezing injury in rapidly-cooled wood frogs. American Journal of Physiology, 1991; 261: R1346-R1350.

—Costanzo, JP; Lee, RE Jr; Wright, MF:
Physiological responses to freezing in the turtle *Terrapene carolina*. Journal of Herpetology, 1993; 27: 117-120.

—Cowles, RB:
Semantics in biothermal studies. Science, 1962; 135: 670.

—Cowles, RB; CM Bogert:
A preliminary study of the thermal requirements of desert reptiles. Bulletin of the American Museum of Natural History, 1944; 83: 261-296.

—Daut, EF; Andrews, RM:
The effect of pregnancy on thermoregulatory behavior of the viviparous lizard *Chalcides ocellatus*. Journal of Herpetology, 1993; 27: 6-13.

—Davenport, J; Andrews, TJ; Hudson, G:
Assimilation of energy, protein and fatty acids by the spectacled caiman *Caiman crocodilus crocodilus* L. Herpetological Journal, 1992; 2: 72-76.

—Dawson, WR:
On the physiological significance of the preferred body temperatures of reptiles. In, Perspectives of Biophysical Ecology, DM Gates; RB Schmerl (Eds). Springer-Verlag, New York, 1975, pp. 443-473.

—DeMarco, V:
Metabolic rates of female viviparous lizards (*Sceloporus jarrovi*) throughout the reproductive cycle: do pregnant lizards adhere to standard allometry? Physiological Zoology, 1993; 66: 166-180.

—Derickson, WK:
Lipid storage and utilization in reptiles. American Zoologist, 1976; 16: 711-723.

—DeWitt, CB:
Precision of thermoregulation and its relation to environmental factors in the desert iguana, *Dipsosaurus dorsalis*. Physiological Zoology, 1967; 40: 49-66.

—DeWitt, CB; Friedman, RM:
Significance of skewness in ectotherm thermoregulation. American Zoologist, 1979; 19: 195-209.

—Diefenbach, CO daC:
Gastric function in *Caiman crocodilus* (Crocodylia: Reptilia)-I. Rate of gastric di-

gestion and gastric motility as a function of temperature. Comparative Biochemistry and Physiology, 1975; 51A: 259-265.

—**Dupré, RK; Crawford, EC Jr:**
Behavioral thermoregulation during dehydration and osmotic loading of the desert iguana. Physiological Zoology, 1985; 58: 357-363.

—**Dupré, RK; Crawford, EC:**
Elevation of the panting threshold of the desert iguana, *Dipsosaurus dorsalis*, during dehydration: potential roles of changes in plasma osmolality and body fluid volume. Journal of Comparative Physiology B, 1986; 156: 377-381.

—**Ellis, TM; Chappell, MA:**
Metabolism, temperature relations, maternal behavior, and reproductive energetics in the ball python (*Python regius*). Journal of Comparative Physiology B, 1987; 157: 393-402.

—**Ewert, MA; Nelson, CE:**
Sex determination in turtles: diverse patterns and some possible adaptive values. Copeia, 1991; 1991: 50-69.

—**Firth, BT; Turner, JS:**
Sensory, neural, and hormonal aspects of thermoregulation. In, Biology of the Reptilia, C Gans; FH Pough (Eds). Academic Press, New York, 1982, 12: 214-274.

—**Foley, WJ; Bouskila, A; Shkolnik, A; Choshniak, I:**
Microbial digestion in the herbivorous lizard *Uromastyx aegyptius* (Agamidae). Journal of Zoology, 1992; 226: 387-398.

—**Frair, W; Gackman, R; Mrosovsky, N:**
Body temperature of *Dermochelys coriacea*: warm turtle from cold water. Science, 1972; 177: 791-793.

—**Fraser, S; Grigg, GC:**
Control of thermal conductance is insignificant to thermoregulation in small reptiles. Physiological Zoology, 1984; 57: 392-400.

—**Frost, DR; Etheridge, R:**
A phylogenetic analysis and taxonomy of iguanian lizards (Reptilia: Squamata). Occasional Papers of the Museum of Natural History, University of Kansas, 1989; 81: 1-65.

—**Fuentes, ER; Jaksić, FM:**
Activity temperatures of eight *Liolaemus* (Iguanidae) in central Chile. Copeia, 1979; 1979: 546-548.

—**Gans, C; Pough, FH:**
The vocabulary of reptilian thermoregulation. In, Biology of the Reptilia, C Gans; FH Pough (Eds). Academic Press, New York, 1982, 12: 17-23.

—**Garland, T Jr:**
Phylogenetic analyses of lizard endurance capacity in relation to body size and body temperature. In, Lizard Ecology: Historical and Experimental Perspectives, LJ Vitt; ER Pianka (Eds). Princeton University Press, Princeton, New Jersey, 1994, pp. 237-259.

—**Garrick, LD:**
Lizard thermoregulation: operant responses for heat at different thermal intensities. Copeia, 1979; 1979: 258-266.

—**Gatten, RE Jr:**
Effect of nutritional status on the preferred body temperature of the turtles *Pseudemys scripta* and *Terrapene ornata*. Copeia, 1974; 1974: 912-917.

—**Gier, PJ; Wallace, RL; Ingermann, RL:**
Influence of pregnancy on behavioral thermoregulation in the northern Pacific rattlesnake. Journal of Experimental Biology, 1989; 145: 465-469.

—**Gilles-Baillien, M:**
Seasonal variation in reptiles. In, Chemical Zoology. M Florkin; BT Sheer (Eds). Academic Press, London, 1974, 13: 353-376.

—**Gorman, GC; Hillman, S:**
Physiological basis for climatic niche partitioning in two species of Puerto Rican *Anolis* (Reptilia, Lacertilia, Iguanidae). Journal of Herpetology, 1977; 11: 337-340.

—**Graves, BM; Duvall, D:**
Aggregation of squamate reptiles associated with gestation, oviposition, and parturition. Herpetological Monographs, 1995; 9: 102-119.

—**Greenwald, OE:**
Thermal dependence of striking and prey capture by gopher snakes Copeia, 1974; 1974: 141-148.

—**Greenwald, OE; Kanter, ME:**
The effects of temperature and behavioral thermoregulation on digestive efficiency and rate in corn snakes (*Elaphe guttata guttata*). Physiological Zoology, 1979; 52: 398-408.

—**Greer, AE; Lazell, JD; Wright, RM:**
Anatomical evidence for a counter-current heat exchanger in the leatherback turtle (*Dermochelys coriacea*). Nature, 1973; 244: 181.

—**Gregory, PT:**
Reptilian hibernation. In, Biology of the Reptilia, C Gans; FH Pough (Eds). Academic Press, New York, 1982, 13: 53-154.

—**Gregory, PT:**
Communal denning in snakes. In, Vertebrate Ecology and Systematics: A Tribute to Henry S. Fitch, RA Seigel; LE Hunt; JL Night; L Maralet; NL Zuschlag (Eds). Special Publications in Natural History, University of Kansas, Lawrence, 1984, pp. 57-75.

—**Guillette, LJ Jr:**
The evolution of viviparity in lizards. Bioscience, 1993; 43: 742-751.
—**Hagan, JM; Smithson, PC; Doerr, PD:**
Behavioral response of the American alligator to freezing weather. Journal of Herpetology, 1983; 17: 402-404.
—**Hamilton, WJ; Coetzee, CG:**
Thermoregulatory behaviour of the vegetarian lizard *Angolosaurus skoogi* on the vegetationless northern Namib Desert dunes. Scientific Papers of the Namib Desert Research Station, 1969; 47: 95-103.
—**Harlow, JJ; Hillman, SS; Hoffman, M:**
The effect of temperature on digestive efficiency in the herbivorous lizard *Dipsosaurus dorsalis*. Journal of Comparative Physiology, 1976; 111: 1-6.
—**Harlow, P; Grigg, G:**
Shivering thermogenesis in a brooding diamond python, *Python spilotes spilotes*. Copeia, 1984; 1984: 959-965.
—**Harwood, RH:**
The effect of temperature on the digestive efficiency of three species of lizards, *Cnemidophorus tigris*, *Gerrhonotus multicarinatus* and *Sceloporus occidentalis*. Comparative Biochemistry and Physiology, 1979; 63A: 417-433.
—**Heath, JE:**
Reptilian thermoregulation: evaluation of field studies. Science, 1964; 146: 784.
—**Heath, JE:**
Temperature regulation and diurnal activity in horned lizards. University of California Publications in Zoology, 1965; 64: 97-136.
—**Heatwole, H:**
Thermal ecology of the desert dragon *Amphibolurus inermis*. Ecological Monographs, 1970; 40: 425-457.
—**Heatwole, H; Johnson, CR:**
Thermoregulation in the red-bellied blacksnake, *Pseudechis porphyriacus* (Elapidae). Zoological Journal of the Linnean Society, 1979; 65: 83-101.
—**Heatwole, H; Taylor, J:**
Ecology of Reptiles. Surrey Beatty & Sons, Chipping Norton, NSW, 1987, 325 pp.
—**Hellmich, WC:**
On ecotypic and autotypic characters, a contribution to the knowledge of the evolution of the genus *Liolaemus* (Iguanidae). Evolution, 1951; 5: 359-369.
—**Hertz, PE:**
Thermal passivity of a tropical forest lizard, *Anolis polylepis*. Journal of Herpetology, 1974; 8: 823-827.
—**Hertz, PE; Huey, RB:**
Compensation for altitudinal changes in the thermal environment by some *Anolis* lizards on Hispaniola. Ecology, 1981; 62: 515-521.
—**Hertz, PE; Huey, RB; Nevo, E:**
Flight versus flight: body temperature influences defensive responses of lizards. Animal Behaviour, 1982; 30: 676-679.
—**Horton, DR:**
Lizard scales and adaptation. Systematic Zoology, 1972; 21: 441-443.
—**Huey, RB:**
Behavioral thermoregulation in lizards: importance of associated costs. Science, 1974; 184: 1001-1003.
—**Huey, RB:**
Temperature, physiology, and the ecology of reptiles. In, Biology of the Reptilia, C Gans; FH Pough (Eds). Academic Press, New York, 1982, 12: 25-91.
—**Huey, RB; Slatkin, M:**
Costs and benefits of thermoregulation. Quarterly Review of Biology, 1976; 51: 363-384.
—**Huey, RB; Pianka, ER:**
Seasonal variation in thermoregulatory behavior and body temperature of diurnal Kalahari lizards. Ecology, 1977; 58: 1066-1075.
—**Huey, RB; Stevenson, RD:**
Integrating thermal physiology and ecology of ectotherms: a discussion of approaches. American Zoologist, 1979; 19: 357-366.
—**Huey, RB; Bennett, AF:**
Phylogenetic studies of coadaptation: preferred temperatures versus optimal performance temperatures of lizards. Evolution, 1987; 41: 1098-1115.
—**Hutchison, VH; Dowling, HG; Vinegar, A:**
Thermoregulation in a brooding female Indian python, *Python molurus bivittatus*. Science, 1966; 151: 694-696.
—**Hutchison, VH; Dupré, RK:**
Thermoregulation. In, Environmental Physiology of the Amphibians, ME Feder; WW Burggren (Eds). University of Chicago Press, Chicago, 1992, pp. 206-249.
—**Iverson, JB:**
Adaptations to herbivory in iguanine lizards. In, Iguanas of the World, GM Burghardt; AS Rand, (Eds). Noyes Publications, Park Ridge, NJ, 1982, pp. 60-76.
—**Janzen, FJ:**
Vegetational cover predicts the sex ratio of hatchling turtles in natural nests. Ecology, 1994; 75: 1593-1599.

—**Janzen, FJ; Paukstis, GL:**
Environmental sex determination in reptiles: ecology, evolution, and experimental design. Quarterly Review of Biology, 1991; 66: 149-179.

—**John-Alder, HB; Bennett, AF:**
Thermal adaptation in lizard muscle function. Journal of Comparative Physiology B, 1987; 157: 241-252.

—**Kingsbury, BA:**
Thermoregulatory set points of the eurythermic lizard *Elgaria multicarinata*. Journal of Herpetology, 1993; 27: 241-247.

—**Kluger, MJ:**
Fever in ectotherms: evolutionary implications. American Zoologist, 1979; 19: 295-304.

—**Kluger, MJ; Ringler, DH; Anver, MR:**
Fever and survival. Science, 1975; 188: 166-168.

—**Lang, JW:**
Thermophilic responses of the American alligator and the American crocodile to feeding. Copeia, 1979; 1979: 48-59.

—**Lang, JW; Andrews, HV:**
Temperature-dependent sex determination in crocodilians. Journal of Experimental Zoology, 1994; 270: 28-44.

—**Lee, RE Jr; Layne, JR Jr; Costanzo, JP;** Davidson, EC: Systemic and organismal responses to freezing in vertebrates. Cryobiology, 1990; 27: 643-644.

—**Lee, RE Jr; Costanzo, JP; Davidson, EC; Layne, JR Jr:**
Dynamics of body water during freezing and thawing in a freeze-tolerant frog (*Rana sylvatica*). Journal of Thermal Biology, 1992; 17: 263-266.

—**Legler, JM:**
Natural history of the ornate box turtle (*Terrepene o. ornata*) Agassiz. University of Kansas Publications of the Museum of Natural History, 1960; 11: 527-669.

—**Licht, P:**
The temperature dependence of myosin-adenosinetriphosphatase and alkaline phosphatase in lizards. Comparative Biochemistry and Physiology, 1964*a*; 12: 331-340.

—**Licht, P:**
A comparative study of the thermal dependence of contractility in saurian skeletal muscle. Comparative Biochemistry and Physiology, 1964*b*; 13: 27-34.

—**Licht, P:**
Environmental control of annual testicular cycles in the lizard *Anolis carolinensis*. I. Interaction of light and temperature in the initiation of testicular recrudescence. Journal of Experimental Zoology, 1967*a*; 165: 505-561.

—**Licht, P:**
Environmental control of annual testicular cycles in the lizard *Anolis carolinensis*. II. Seasonal variations in effects of photoperiod and temperature on testicular recrudescence. Journal of Experimental Zoology, 1967*b*; 166: 243-253.

—**Licht, P:**
Thermal adaptation in the enzymes of lizards in relation to preferred body temperatures. In, Molecular Mechanisms of Temperature Adaptation. American Association for the Advancement of Science, Washington, DC, 1967*c*, pp. 131-145.

—**Licht, P:**
Environmental control of annual testicular cycles in the lizard *Anolis carolinensis*. I. Interaction of light and temperature in the initiation of testicular recrudescence. Journal of Experimental Zoology, 1969; 165: 505-561.

—**Licht, P:**
Problems in experimentation on timing mechanisms for annual physiological cycles in reptiles. In, Hibernation and Hypothermia, Perspectives and Challenges, TE South; JP Hannon; JR Willis; ET Pengelley; NR Alpert (Eds). Elsevier, Amsterdam, 1972, pp. 681-710.

—**Licht, P; Moberly, WR:**
Thermal requirements for embryonic development in the tropical lizard *Iguana iguana*. Copeia, 1965; 1965: 515-517.

—**Losos, JB:**
Thermoregulatory correlates of escape behavior by a desert lizard, *Ctenophorus isolepis*. Journal of Herpetology, 1988; 22: 353-356.

—**Lowe, CH; Lardner, PJ; Halpern, EA:**
Supercooling in reptiles and other vertebrates. Comparative Biochemistry and Physiology, 1971; 39A: 125-135.

—**MacKay, RS:**
Observations on peristaltic activity versus temperature and circadian rhythms in undisturbed *Varanus flavescens* and *Ctenosaura pectinata*. Copeia, 1968; 1968: 252-259.

—**Mautz, WJ:**
The metabolism of reclusive lizards, the Xantusiidae. Copeia, 1979; 1979: 577-584.

—**Mautz, WJ; Daniels, CB; Bennett, AF:**
Thermal dependence of locomotion and aggression in a xantusiid lizard. Herpetologica, 1992; 48: 271-279.

—**McGinnis, SM; Brown, CW:**
Thermal behavior of the green iguana, *Iguana*

iguana. Herpetologica, 1966; 22: 189-199.
—**McGinnis, SM; Voigt, WG:**
Thermoregulation in the desert tortoise, *Gopherus agassizii*. Comparative Biochemistry and Physiology, 1971; 40A: 119-126.
—**Moore, RG:**
Seasonal and daily activity patterns and thermoregulation in the southwestern speckled rattlesnake (*Crotalus mitchelli pyrrhus*) and the Colorado Desert sidewinder (*Crotalus cerastes laterorepens*). Copeia, 1978; 1978: 439-442.
—**Mrosovsky, N:**
Sex ratios of sea turtles. Journal of Experimental Zoology, 1994; 270: 16-27.
—**Mrosovsky, N; Pritchard, PCH:**
Body temperatures of *Dermochelys coriacea* and other sea turtles. Copeia, 1971; 1971: 624-631.
—**Muchlinski, AE; Hogan, JM; Stoutenburgh, RJ:**
Body temperature regulation in a desert lizard, *Sauromalus obesus*, under undisturbed field conditions. Comparative Biochemistry and Physiology, 1990; 95A: 579-583.
—**Nagy, KA; Huey, RB; Bennett, AF:**
Field energetics and foraging mode of Kalahari lacertid lizards. Ecology, 1984; 65: 588-596.
—**Norris, KS:**
The ecology of the desert iguana *Dipsosaurus dorsalis*. Ecology, 1953; 34: 265-287.
—**Norris, KS:**
Color adaptation in desert reptiles and its thermal relationships. In, Lizard Ecology: A Symposium, WW Milstead (Ed). University Press of Missouri, Columbia, MO, 1967, pp. 162-229.
—**Naulleau, G:**
The effect of temperature on digestion in *Vipera aspis*. Journal of Herpetology, 1983; 17: 166-170.
—**Packard, GC; Tracy, CR; Roth, JJ:**
The physiological ecology of reptilian eggs and embryos, and the evolution of viviparity within the class Reptilia. Biological Reviews, 1977; 52: 71-105.
—**Packard, GC; Packard, MJ:**
The physiological ecology of reptilian eggs and embryos. In, Biology of the Reptilia, C Gans; RB Huey (Eds). Alan R Liss, Inc., New York, 1988, 16: 523-605.
—**Packard, GC; Packard, MJ; McDaniel, PL; McDaniel, LL:**
Tolerance of hatchling painted turtles to subzero temperatures. Canadian Journal of Zoology, 1989; 67: 828-830.
—**Packard, GC; Ruble, KA; Packard, MJ:**
Hatchling snapping turtles overwintering in natural nests are inoculated by ice in frozen soil. Journal of Thermal Biology, 1993; 18: 185-188.
—**Packard, GC; Packard, MJ:**
The basis for cold tolerance in hatchling painted turtles (*Chrysemys picta*). Physiological Zoology, 1995; 68: 129-148.
—**Parmenter, CJ; Heatwole, H:**
Panting thresholds of lizards. IV. The effect of dehydration on the panting threshold of *Amphibolurus barbatus* and *Amphibolurus muricatus*. Journal of Experimental Zoology, 1975; 191: 327-332.
—**Patterson, JW; Davies, PMC:**
Preferred body temperature: seasonal and sexual differences in the lizard *Lacerta vivipara*. Journal of Thermal Biology, 1978; 3: 39-41.
—**Paulissen, MA:**
Ontogenetic comparisons of body temperature selection and thermal tolerance of *Cnemidophorus sexlineatus*. Journal of Herpetology, 1988; 22: 473-476.
—**Pearson, OP:**
Habits of the lizard, *Liolaemus multiformis multiformis* at high altitudes in southern Peru. Copeia, 1954; 1954: 111-116.
—**Pearson, OP:**
The effect of substrate and of skin color on thermoregulation of a lizard. Comparative Biochemistry and Physiology, 1977; 58A: 353-358.
—**Pianka, ER:**
Ecology and Natural History of Desert Lizards. Princeton University Press, Princeton, NJ, 1986, 208 pp.
—**Porter, WP; Mitchell, JW; Beckman, WA; Tracy, CR:**
Environmental constraints on some predator-prey interactions. In, Perspectives of Biophysical Ecology, DM Gates; RB Schmerl (Eds). Springer-Verlag, New York, 1975, pp. 347-364.
—**Pough, FH:**
Lizard energetics and diet. Ecology, 1973; 54: 837-844.
—**Pough, FH:**
The advantages of ectothermy for tetrapods. American Naturalist, 1980; 115: 92-112.
—**Pough, FH:**
Amphibians and reptiles as low energy systems. In, Behavioral Energetics, WP Aspey; S Lustick (Eds). Ohio State University Press, Ohio, 1983, pp. 141-188.
—**Pough, FH; Andrews, RM:**
Energy costs of subduing and swallowing prey for a lizard. Ecology, 1985; 66: 1525-1533.

—Preest, MR:
Energetic costs of prey ingestion in a scincid lizard, *Scincella lateralis*. Journal of Comparative Physiology B, 1991; 161: 327-332.

–Ramírez Pinilla, MP:
Estudio histologico de los tractos reproductivos y actividad ciclica anual reproductiva de machos y hembras de dos especies del género *Liolaemus* (Reptilia: Sauria: Iguanidae). Unpublished PhD dissertation, Universidad Nacional de Tucumán, Argentina, 1991, 208 pp.

—Ramírez Pinilla, MP:
Actividad reproductiva en tres especies simpatricas del género *Liolaemus* (Reptilia: Sauria: Tropiduridae). Caldesia, 1992; 17: 67-74.

—Rand, AS:
Inverse relationship between temperature and shyness in the lizard *Anolis lineatopus*. Ecology, 1964; 45: 863-864.

—Regal, PJ:
Thermophilic responses following feeding in certain reptiles. Copeia, 1966; 1966: 588-590.

—Regal, PJ:
Voluntary hypothermia in reptiles. Science, 1967; 155: 1551-1553.

—Regal, PJ:
The evolutionary origin of feathers. Quarterly Review of Biology, 1975; 50: 35-66.

—Regal, PJ:
Temperature and light requirements of captive reptiles. In, Reproductive Biology and Diseases of Captive Reptiles, JB Murphy; JT Collins (Eds). Society for the Study of Amphibians and Reptiles, Contributions to Herpetology, 1980, 1: 79-89.

—Riedesel, ML; Cloudsley-Thompson, JL;
Cloudsley-Thompson, JA: Evaporative thermoregulation in turtles. Physiological Zoology, 1971; 44: 28-32.

—Rismiller, PD; Heldmaier, G:
The effect of photoperiod on temperature selection in the European green lizard, *Lacerta viridis*. Oecologia, 1982; 53: 222-226.

—Ruppert, RM:
Comparative assimilation efficiencies of two lizards. Comparative Biochemistry and Physiology, 1980; 67A: 491-496.

—Sage, RD:
The structure of lizard faunas: comparative biologies of lizards in two Argentina deserts. Unpublished PhD dissertation, University of Texas, Austin, 1974, 341 pp.

—Saint-Girons, H:
Thermoregulation in reptiles with special reference to the tuatara and its ecophysiology. Tuatara, 1980; 24: 59-80.

—Schall, JJ:
Relations among three macroteiid lizards on Aruba Island. Journal of Herpetology, 1973; 7: 289-295.

—Schall, JJ:
Thermal ecology of five sympatric species of *Cnemidophorus* (Sauria: Teiidae). Herpetologica, 1977; 33: 261-272.

—Schall, JJ;
Dearing, MD: Body temperature of the herbivorous Bonaire Island whiptail lizard (*Cnemidophorus murinus*). Journal of Herpetology, 1994; 28: 526-528.

—Secor, SM:
Ecological aspects of foraging mode for the snakes *Crotalus cerastes* and *Masticophis flagellum*. Herpetological Monographs, 1995; 9: 169-186.

—Secor, SM; Nagy, KA:
Energetic correlates of foraging mode of the snakes *Crotalus cerastes* and *Masticophis flagellum*. Ecology, 1994; 75: 1600-1614.

—Secor, SM; Stein, ED; Diamond, J:
Rapid upregulation of snake intestine in response to feeding: a new model in intestinal adaptation. Amercian Journal of Physiology, 1994; 266: G695-G705.

—Secor, SM; Diamond, J:
Evolution of the digestive response in snakes. Abstract # 340. Joint meeting of the American Society of Ichthyologists and Herpetologists and the Herpetologists League, University of Alberta, Edmonton, Canada, 1995.

—Secor, SM; Diamond, J:
Adaptive responses to feeding Burmese pythons: pay before pumping. Journal of Experimental Biology, 1995*b*; 198: 1313-1325.

—Sexton, OJ; Hunt, SR:
Temperature relationships and movements of snakes (*Elaphe obsoleta, Coluber constrictor*) in a cave hibernaculum. Herpetologica, 1980; 36: 20-26.

—Shine, R:
The evolution of viviparity in reptiles: an ecological analysis. In, Biology of the Reptilia, C Gans; F Billet (Eds). Academic Press, New York, 1985, 15: 605-694.

—Shine, R; Bull, JJ:
The evolution of live-bearing in lizards and snakes. American Naturalist, 1979; 113: 905-923.

—Shine, R; Madsen, T:
Is thermoregulation unimportant for most reptiles? An example using water pythons

(*Liasis fuscus*) in tropical Australia. Physiological Zoology, 1996; 69: 252-269.

—Sievert, LM:
Postprandial temperature selection in *Crotaphytus collaris*. Copeia, 1989; 1989: 983-989.

—Sites, JW, Jr; Archie, JW; Cole, CJ; Flores Villela, O:
A review of phylogenetic hypotheses for lizards of the genus *Sceloporus* (Phrynosomatidae): implications for ecological and evolutionary studies. Bulletin of the American Museum of Natural History, 1992; 213: 1-110.

—Soulé, M:
Aspects of thermoregulation in nine species of lizards from Baja California. Copeia, 1963; 1963: 107-115.

—Soulé, M:
Trends in the insular radiation of a lizard. American Naturalist, 1966; 100: 47-64.

—Spellerberg, IF:
Critical minimum temperatures of reptiles. In, Effects of Temperature on Ectothermic Organisms, W Weiser (Ed). Springer-Verlag, Berlin, 1973, pp. 239-247.

—Spotila, JR; Lommen, PW; Bakken, GS; Gates, DM:
A mathematical model for body temperatures of large reptiles. Implications for dinosaurian ecology. American Naturalist, 1973; 107: 391-404.

—Stebbins, RC:
An experimental study of the "third eye" of the tuatara. Copeia, 1958; 1958: 183-190.

—Stevenson, RD:
Body size and limits to the daily range of body temperature in terrestrial ectotherms. American Naturalist, 1985; 125: 102-117.

—Stewart, JR:
Thermal biology of the live bearing lizard *Gerrhonotus coeruleus*. Herpetologica, 1984; 40: 349-355.

—Storey, KB:
Life in a frozen state: adaptive strategies for natural freeze tolerance in amphibians and reptiles. American Journal of Physiology, 1990; 258: R559-R568.

—Storey, KB; Storey, JM; Brooks, SPJ; Churchill, TA; Brooks, RJ:
Hatchling turtles survive freezing during winter hibernation. Proceedings of the National Academy of Sciences, 1988; 85: 8350-8354.

—Storey, KB; Storey, JM:
Natural freeze tolerance in ectothermic vertebrates. Annual Review of Physiology, 1992; 54: 619-637.

—Swingland, IR; Frazier, JG:
The conflict between feeding and overheating in the Aldabran giant tortoise. In, A Handbook of Biotelemetry and Radio Tracking, CJ Amlaner; DW McDonald (Eds). Pergamon Press, Oxford and New York, 1980, pp. 611-615.

—Tait, NN:
The effect of temperature on the immune response in cold-blooded vertebrates. Physiological Zoology, 1969; 42: 29-35.

—Templeton, JR:
Reptiles. In, The Comparative Physiology of Thermoregulation, GC Whittow (Ed). Academic Press, New York and London, 1970, 1: 167-221.

—Throckmorton, G:
Digestive efficiency in the herbivorous lizard *Ctenosaura pectinata*. Copeia, 1973; 1973: 431-435.

—Tinkle, DW; Gibbons, JW:
The distribution and evolution of viviparity in reptiles. Miscellaneous Publications of the University of Michigan, 1977; 154: 1-55.

—Tracy, CR:
Biophysical modeling in reptilian physiology and ecology. In, Biology of the Reptilia, C Gans; FH Pough (Eds). Academic Press, New York, 1982, 12: 275-321.

—Troyer, K:
Small differences in daytime body temperature effect digestion of natural food in a herbivorous lizard (*Iguana iguana*). Comparative Biochemistry and Physiology, 1987; 87A: 623-626.

—Turner, JS:
The cardiovascular control of heat exchange: consequences of body size. American Zoologist, 1987; 27: 69-79.

—Turner, JS; Tracy, CR:
Blood flow to appendages and the control of heat exchange in American alligators. Physiological Zoology, 1983; 56: 195-200.

—Turner, JS; Tracy, CR:
Body size and the control of heat exchange in alligators. Journal of Thermal Biology, 1985; 10: 9-11.

—Ultsch, GR:
Ecology and physiology of hibernation and overwintering among freshwater fishes, turtles, and snakes. Biological Reviews 1989; 64: 435-516.

—Ultsch, GR; Jackson, DC:
Long-term submergence at 3 °C of the turtle *Chrysemys picta bellii* in normoxic and severely hypoxic water. I. Survival, gas exchange, and

acid-base balance. Journal of Experimental Zoology, 1982*a*; 96: 11-28.

—Ultsch, GR; Jackson, DC:
Long-term submergence at 3 °C of the turtle *Chrysemys picta bellii* in normoxic and severely hypoxic water. III. Effects of changes in ambient PO_2 and subsequent air-breathing. Journal of Experimental Zoology, 1982*b*; 97: 87-99.

—Van Damme, R; Bauwens, D; Verheyen, RF:
Selected body temperatures in the lizard *Lacerta vivipara*: variation within and between populations. Journal of Thermal Biology, 1986; 2: 219-222.

—Van Damme, R; Bauwens, D; Verheyen, RF:
Thermoregulatory responses to environmental seasonality by the lizard *Lacerta vivipara*. Herpetologica, 1987; 43: 405-415.

—van Marken Lichtenbelt, WD:
Digestion in an ectothermic herbivore, the green iguana (*Iguana iguana*): effect of food composition and body temperature. Physiological Zoology, 1992; 65: 649-673.

—Vaughn, LK; Bernheim, HA; Kluger, MJ:
Fever in the lizard *Dipsosaurus dorsalis*. Nature, 1974; 252: 473-474.

—Viets, BE; Ewert, MA; Talent, LG; Nelson, CE:
Sex-determining mechanisms in squamate reptiles. Journal of Experimental Zoology, 1994; 270: 45-65.

—Viets, BE; Tousignant, A; Ewert, MA; Nelson, CE; Crews, D:
Temperature-dependent sex determination in the leopard gecko, *Eublepharis macularius*. Journal of Experimental Zoology, 1993; 265: 679-683.

—Vinegar, A; Hutchison, VH; Dowling, HG:
Metabolism, energetics, and thermoregulation during brooding of snakes of the genus *Python*. Zoologica, 1970; 55: 19-48.

—Vogt, RC; Bull, JJ:
Temperature controlled sex-determination in turtles: ecological and behavioral aspects. Herpetologica, 1982; 38: 156-164.

—Wagner, EL; Gleeson, TT:
Low temperature and exercise recovery in the desert iguana. Physiological Zoology, 1996; 69: 168-190.

—Waldschmidt, SR; Jones, SM; Porter, WP:
The effect of body temperature and feeding regime on activity, passage time, and digestive coefficient in the lizard *Uta stansburiana*. Physiological Zoology, 1986; 59: 376-383.

—Webb, GJG; Cooper-Preston, H:
Effects of incubation temperature on crocodiles and the evolution of reptilian oviparity. American Zoologist, 1989; 29: 953-971.

—Werner, YL:
Temperature effects on the inner-ear sensitivity in six species of iguanid lizards. Journal of Herpetology, 1972; 6: 147-177.

—Werner, YL:
Optimal temperatures for inner-ear performance in gekkonid lizards. Journal of Experimental Zoology, 1976; 195: 319-352.

—Wilson, KJ; Lee, AK:
Energy expenditure of a large herbivorous lizard. Copeia, 1974; 1974: 338-348.

—Wilson, MA; Echternacht, AC:
Geographic variation in the critical thermal minimum of the green anole, *Anolis carolinensis* (Sauria: Iguanidae), along a latitudinal gradient. Comparative Biochemistry and Physiology, 1987, 87A: 757-760.

—White, FN:
Circulation. In, Biology of the Reptilia, C Gans; WR Dawson (Eds). Academic Press, London, 1976, 5: 275-334.

—Zari, TA:
The influence of body mass and temperature on the standard metabolic rate of the herbivorous desert lizard, *Uromastyx microlepis*. Journal of Thermal Biology, 1991; 16: 129-133.

—Zimmerman, LC; Tracy, CR:
Interactions between the environment and ectothermy and herbivory in reptiles. Physiological Zoology, 1989; 62: 374-409.

—Zug, GR:
Herpetology. Academic Press, San Diego, 1993, 527 pp.

—Zurovsky, Y; Mitchell, D; Laburn, H:
Pyrogens fail to produce fever in the leopard tortoise *Geochelone pardalis*. Comparative Biochemistry and Physiology, 1987; 87A: 467-469.