CHAPTER 3

Metabolism

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I. Introduction

The reptiles are a particularly important group in considerations of comparative metabolism because of the phylogenetic and geographic diversity that they exhibit. This diversity is of interest from evolutionary, physiological, and ecological viewpoints. Some of the extant reptilian groups are of considerable antiquity (Romer, 1956) and occupy phylogenetic positions critical to our understanding of the physiological evolution of the vertebrates. The great variety of niches which reptiles currently occupy permits studies of the interrelations of organisms with their environments in a number of different habitats. In spite of the considerable interest in reptilian biology over the past three decades, the functional correlates of this diversity are only now beginning to be systematically explored and understood.

For example, even thermobiology, the most thoroughly investigated aspect of reptilian physiology, still presents difficulties in the elucidation of its adaptive patterns. Most reptiles, although nominally poikilothermous, thermoregulate rather precisely by behavioral means, confining body temperature to a narrow and species-specific range during activity (Cowles and Bogert, 1944; Brattstrom, 1965; Templeton, 1970; Cloudsley-Thompson, 1971). This thermoregulatory activity has led to an extensive search for correlations between physiological variables, including metabolic functions, and the preferred level of body temperature. This thermal level appears to be a sufficiently stable feature of particular species so that optimization of

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many physiological functions might be expected to have evolved in reference to it. On the other hand, reptiles, despite their regulatory capacities, must tolerate body temperatures departing widely from preferred levels in connection with daily or annual thermal cycles in the environment. This tolerance entails maintenance of functional capacities over two or three decades of degrees Celsius. Therefore, adjustments serving to reduce dependence of rate processes on body temperature and establish some degree of physiological homeostasis might also be expected. However, no definite pattern has yet emerged in reptilian physiology with respect to either preferred levels of body temperature or tolerance of daily and seasonal thermal cycles. Indeed, only a few instances of correlation of laboratory-determined physiological optima with level of preferred body temperature have thus far been detected (Dawson, 1967, 1975), and instances of thermal independence of rate functions such as metabolism are only now being analyzed.

Reptiles appear to be a key group for the analysis of the course of metabolic evolution. Hemmingsen (1960) recognizes only three metabolic groups in the Animal Kingdom: unicellular poikilotherms, metazoan poikilotherms, and homeotherms. Subsequent investigations have revealed significant endothermy during activity in some nominally poikilothermic forms. However, Hemmingsen's formulation is still adequate for describing the relations of standard metabolic rates among these groups. Reptilian metabolic rates are generally similar to those of metazoan invertebrates and anamniotic vertebrates of comparable body size and temperature. However, evolutionary lines within the class Reptilia have culminated in the two homeothermic classes, the birds and mammals. Homeothermy constitutes one of the major evolutionary developments in the vertebrates; the heightened demands it imposes for food and oxygen have required far-reaching morphological and physiological alterations of nearly all organ systems. Reconstruction of the evolutionary steps leading to the development of the homeothermic state requires understanding of the physiology of contemporary reptiles. These animals, of course, differ even from their own ancestors as well as from representatives of those groups from which the birds and mammals arose. However, many aspects of reptilian metabolic physiology, e.g., metabolic rate and capacities for oxygen transport, appear similar in all orders. It is therefore a reasonable assumption that such metabolic characteristics are indicative of the metabolic condition from which homeothermy arose. Although this problem has attracted considerable interest, its physiological and selective bases are still unresolved.

This report will include a summary of our current knowledge of many aspects of reptilian metabolism, and particular emphasis will be given to the considerations discussed above. Laboratory determinations of metabolic rate and of the effects on it of various factors, e.g., temperature, season, prior feeding, will be reviewed. The nature of metabolism in reptiles during activity

and the extent of their reliance on aerobiosis and anaerobiosis will be examined. Hormonal effects and the enzymatic bases of metabolism in reptiles will also be discussed. Some of these aspects have been reviewed previously. Benedict (1932) summarized early determinations of metabolic rates and respiratory quotients in his comprehensive monograph on the physiology of large reptiles. Dawson (1967) and Templeton (1970) considered measurements of oxygen consumption in resting and active animals and the effect of temperature on metabolic rate. A list of metabolic determinations for reptiles under various conditions has been compiled by Bennett and Dawson (1971).

II. General Considerations of Reptilian Metabolic Rates

A. Introduction

Regnault and Reiset (1849) were the first to report metabolic measurements on a reptile. Subsequently, their work has been followed by many studies concerning a large number of species (see Table I). The initial metabolic measurements on reptiles involved determination of rates of production of heat or carbon dioxide. Later estimates have generally depended on determination of rates of oxygen consumption, through use of manometric techniques or, more recently, paramagnetic oxygen analysis. The data amassed on metabolic rates have thus far permitted few generalizations because of variability in the results of different investigators, even on the same species. This variability must partially reflect such things as differences in activity level and sex among the experimental subjects. However, differences in other factors more amenable to experimental manipulation, e.g., season, nutritional state, state of acclimation, and time of observation, also are involved. The influence of each of these factors will be examined in later sections of this review. We feel that the variability thus far encountered in studies of reptilian metabolism would be reduced with better standardization of experimental conditions. Metabolism within a single organism is not necessarily highly variable, judging by Roberts' (1968a) results on the lizard *Uta stansburiana*. Measurements of standard metabolic rate on individuals of this species were repeatable within 10% on successive nights. Standard metabolic rate, which requires use of fasting animals resting in the dark in the inactive phase of their diurnal cycle, represents a highly reproducible function indicative of maintenance cost. Consequently, standard metabolic rate is the most meaningful measurement for comparison of fundamental metabolic levels between different animals. Unfortunately, very few studies have been conducted on reptiles under truly standard conditions (see Table I), and diurnal observations on animals resting in the dark have generally been used as the comparative base. The question posed by an investigator should, of course, determine the type of data required. However, any study should specify as much as

TABLE I

Measurements of reptilian energy metabolism

(O_2—Oxygen consumption, CO_2—Carbon dioxide production, DC—Direct calorimetry)

Species	Measurement	Status of animal	Reference
		Lizards	
Acanthodactylus pardalis	O_2	resting	Kayser, 1940
Amphibolurus barbatus	O_2	resting, active	Bartholomew and Tucker, 1963
	O_2	max. active	Wilson, 1971, 1974
A. ornatus	O_2	resting[a]	Dawson *et al.*, 1966
Amphisbaena alba	CO_2	active	Buytendijk, 1910
Anguis fragilis	CO_2		Vernon, 1897
	CO_2	active	Buytendijk, 1910
Anniella pulchra	O_2	resting	Vance ,1959
Anolis acutus	O_2	resting	McManus and Nellis, 1973
A. carolinensis	O_2		Clausen and Mofshin, 1939
	O_2	daily aver.	Dessauer, 1953
	O_2		Rahn, 1956
	O_2		Maher and Levedahl, 1959
	O_2	resting	Claussen, 1967
Callisaurus draconoides	O_2	resting	Vance, 1959
Cnemidophorus tigris	O_2	resting	Cook, 1949
	O_2	resting	Vance, 1959
	O_2	resting, max. active	Asplund, 1970
Coleonyx variegatus	O_2	resting	Cook, 1949
	O_2	resting	Vance, 1959
Crotaphytus collaris	O_2	resting	Dawson and Templeton, 1963
Dipsosaurus dorsalis	O_2	resting	Cook, 1949
	O_2	resting	Dawson and Bartholomew, 1958
	O_2	resting	Vance, 1959
	O_2	daily aver.	Moberly, 1963
	O_2		Boyer, 1966
	O_2	standard, max. active	Bennett and Dawson, 1972
Egernia cunninghami	O_2	resting, max. active	Wilson, 1971, 1974
Eremias arguta	O_2		Rodionov, 1938
Eumeces fasciatus	O_2	resting	Maher, 1965
E. obsoletus	O_2	resting	Dawson, 1960
Gerrhonotus multicarinatus	O_2	resting	Vance, 1959
	O_2	resting	Dawson and Templeton, 1966

Species	Measurement	Status of animal	Reference
Iguana iguana	CO_2	resting	Benedict, 1932
(*I. tuberculata*)	O_2	resting, max. active	Tucker, 1966
	O_2	resting	Bentley and Schmidt-Nielsen, 1966
	O_2	resting, max. active	Moberly, 1968a
Lacerta agilis	CO_2	resting	Pott, 1875
L. melisellensis galvagnii	O_2		Gelineo and Gelineo, 1955a
L. melisellensis kammereri	O_2		Gelineo and Gelineo, 1955b
L. melisellensis melisellensis	O_2		Gelineo and Gelineo, 1955a
L. muralis	O_2		Gelineo and Gelineo, 1955b
	O_2		Gelineo, 1967a
L. oxycephala	O_2		Gelineo, 1967a
L. sicula (*L. serpa*)	O_2	standard	Kramer, 1934
	O_2	standard	Kramer, 1935
	O_2		Gelineo and Gelineo, 1955b
	O_2		Gelineo, 1967a
	O_2		Gelineo, 1967b
L. trilineata	O_2	daily aver.	Regnault and Reiset, 1849
(*L. major*)	O_2	standard	Kramer, 1934
	O_2	standard	Kramer, 1935
L. viridis	DC		Krehl and Soetbeer, 1899
	CO_2	active	Buytendijk, 1910
	O_2	standard	Kramer, 1934
	O_2	standard	Kramer, 1935
	O_2		Gelineo and Gelineo, 1955b
	O_2	resting	Nielsen, 1961
	O_2, CO_2	resting	Nielsen, 1962
L. vivipara	CO_2		Weigmann, 1932
	O_2	active	Avery, 1971
Lizard	O_2	resting	Leichtentritt, 1919
Scincella lateralis	O_2	daily aver.	Hudson and Bertram, 1966
Phrynosoma cornutum	O_2, CO_2	daily aver.	Potter and Glass, 1931
	O_2		Prieto and Whitford, 1971
P. coronatum	O_2	resting	Vance, 1959
P. douglassii	O_2		Prieto and Whitford, 1971
P. mccalli	O_2	resting	Mayhew, 1965
P. platyrhinos	O_2	resting	Vance, 1959
Physignathus lesueurii	O_2	resting, max. active	Wilson, 1971, 1974
Sauromalus hispidus	O_2	standard, max. active	Bennett, 1972b

(*Table I continued page 132*)

Species	Measurement	Status of animal	Reference
S. obesus	O_2	resting	Vance, 1959
	O_2	resting	Bentley and Schmidt-Nielsen, 1966
	O_2	resting	Boyer, 1967
	O_2	resting	Crawford and Kampe, 1971
Sceloporus cyanogenys	O_2	resting[a]	Wilhoft, 1966
	O_2	resting	Wilhoft, 1966
	O_2	standard, resting	Songdahl and Hutchison, 1972
S. graciosus	O_2	resting	Vance, 1959
	O_2	resting	Mueller, 1969
S. occidentalis	O_2		Dawson and Bartholomew, 1956
	O_2	resting	Vance, 1959
	O_2		Francis and Brooks, 1970
Sphenomorphus labillardieri	O_2	resting	Dawson *et al.*, 1966
Tarentola mauritanica	O_2, CO_2	resting	Buytendijk, 1910
(*Platydactylus mauritanicus*)	O_2, CO_2	resting	Nielsen, 1962
Tiliqua scincoides after gigas[a]	CO_2		Martin, 1903
	O_2	resting, max. active	Bartholomew *et al.*, 1965
Trachydosaurus rugosus	O_2	resting, max. active	Wilson, 1971, 1974
Uma inornata	O_2	resting	Vance, 1959
U. notata	O_2	resting	Cook, 1949
Uromastyx acanthinurus	O_2	resting	Kayser, 1940
U. aegyptius[c]	DC		Krehl and Soetbeer, 1899
Urosaurus ornatus	O_2	resting	Vance, 1953
Uta mearnsi	O_2	resting,	Vance, 1959
	O_2	resting	Murrish and Vance, 1968
U. stansburiana	O_2		Dawson and Bartholomew, 1956
	O_2	resting	Vance, 1959
	O_2	resting	Claussen, 1967
	O_2	standard[a]	Roberts, 1968a
	O_2	standard	Roberts, 1968a
	O_2	resting	Halpern and Lowe, 1968
	O_2	resting, max. active	Alexander and Whitford, 1968
Varanus spp.	O_2	resting, max. active	Bartholomew and Tucker, 1964
V. gouldii	O_2	standard, max. active	Bennett, 1972b
Xantusia henshawi	O_2	resting	Vance, 1959

Species	Measurement	Status of animal	Reference
X. vigilis	O_2	resting	Cook, 1949
	O_2	resting	Vance, 1959
	O_2	resting	Snyder, 1971
		Snakes	
Boa constrictor	CO_2		Buytendijk, 1910
	CO_2	resting	Benedict, 1932
	O_2	resting	Galvão *et al.*, 1965
Cerastes cerastes	O_2	daily aver.[b]	Dmi'el, 1970
	O_2	resting, active	Dmi'el, 1972b
Chionactis occipitalis	O_2	resting	Norris and Kavanau, 1966
Chironius quadricarinatus	O_2	resting	Galvão *et al.*, 1965
Coluber constrictor[b]	O_2		Clark, 1953
C. ravergieri	O_2	resting, active	Dmi'el, 1972b
Coronella austriaca	O_2	resting	Galvão *et al.*, 1965
Crotalus atrox	CO_2	resting	Benedict, 1932
Crotalus spp.	CO_2	resting	Dammann, 1960
Cyclagras gigas (*Leiosophis gigas*)	O_2	resting	Galvão *et al.*, 1965
Diadophis punctatus arnyi	O_2	resting	Buikema and Armitage, 1969
Dipsas albifrons	O_2	resting	Galvão *et al.*, 1965
Drymarchon corais	CO_2	resting	Benedict, 1932
Echis coloratus	O_2	daily aver.[b]	Dmi'el, 1970
Epicrates angulifer	CO_2	resting	Benedict, 1932
Eunectes murinus	O_2	resting	Galvão *et al.*, 1965
E. notaeus	O_2	resting	Galvão *et al.*, 1965
Farancia abacura	O_2	resting	Belkin, 1965a
Lampropeltis getulus	O_2	daily aver.	Baldwin, 1928
Leimadophis poecilogyrus	O_2	resting	Galvão *et al.*, 1965
Liophis miliaris	O_2	resting	Galvão *et al.*, 1965
Mastigodryas bifossatus	O_2	resting	Galvão *et al.*, 1965
Natrix natrix[b]	CO_2		Bohr, 1903
	CO_2	active[a]	Bohr, 1903
	CO_2		Buytendijk, 1910
	DC	resting	Hill, 1911
	O_2	resting	Kayser, 1940
N. rhombifera	O_2		Jacobson and Whitford, 1970
N. taxispilota	O_2		Prange and Schmidt-Nielsen, 1969
N. tessellata[b]	O_2		Dmi'el, 1970

(*Table I continued page 134*)

Species	Measurement	Status of animal	Reference
N. tessellata	O_2	daily aver.[a]	Dmi'el, 1970
Opheodrys vernalis[b]	O_2		
	O_2	active[a]	Zarrow and Pomerat, 1937
Oxyrhopus trigeminus	O_2	resting	Gãlvo *et al.*, 1965
Philodryas olfersii	O_2	resting	Galvão *et al.*, 1965
P. patagoniensis	O_2	resting	Galvão *et al.*, 1965
P. serra	O_2	resting	Galvão *et al.*, 1965
Pituophis melanoleucus affinis	O_2		Prange and Schmidt-Nielsen, 1969
	O_2	resting, max. active	Greenwald, 1971
P. melanoleucus catenifer	O_2	resting	Licht and Bennett, 1972
P. melanoleucus sayi	O_2	daily aver.	Baldwin, 1928
	O_2		Boyer, 1966
Python curtus	O_2	resting	Vinegar *et al.*, 1970
P. molurus	O_2, CO_2	resting, active	Benedict, 1932
P. molurus bivittatus	O_2	resting, active[d]	Hutchison *et al.*, 1966
	O_2	resting, active[d]	Vinegar *et al.*, 1970
P. molurus molurus	O_2	resting, active[d]	Vinegar *et al.*, 1970
P. reticulatus	CO_2	resting	Benedict, 1932
	O_2	resting	Vinegar *et al.*, 1970
Salvadora hexalepis	O_2	resting	Jacobson and Whitford, 1970
Sibynomorphus mikanii	O_2	resting	Galvão *et al.*, 1965
Spalerosophis cliffordii[b]	O_2		Dmi'el, 1970
S. cliffordii	O_2	daily aver.[a]	Dmi'el, 1970
	O_2	resting, active	Dmi'el, and Borut 1972
	O_2	resting, active	Dmi'el, 1972b
Storeria dekayi	O_2		Clausen, 1936
Thamnodynastes strigatus	O_2	resting	Galvão *et al.*, 1965
Thamnophis dorsalis	O_2		Fleharty, 1963
T. elegans	O_2		Fleharty, 1963
T. ordinoides	O_2	resting	Stewart, 1965
T. proximus	O_2		Jacobson and Whitford, 1970
T. sirtalis	O_2	active	Chodrow and Taylor, 1973
T. sirtalis concinnus	O_2	resting	Stewart, 1965

Species	Measurement	Status of animal	Reference
T. sirtalis parietalis	O_2	resting	Aleksiuk, 1971a
Vipera palaestinae	O_2	resting, active	Dmi'el, 1972b
	O_2[b]		Dmi'el, 1970
	O_2	daily aver.[a]	Dmi'el, 1970
Xenodon guentheri	O_2	resting	Galvão *et al.*, 1965
X. merremii	O_2	resting	Galvão *et al.*, 1965
X. neuwiedii	O_2	resting	Galvão *et al.*, 1965
		Rhynchocephalians	
Sphenodon punctatus	O_2, CO_2	daily aver.	Milligan, 1924
	O_2	resting, max. active	Wilson and Lee, 1970
		Turtles	
Chelodina longicollis	CO_2		Buytendijk, 1910
Chelydra serpentina	O_2	resting, active	Baldwin, 1926
	O_2, CO_2	resting	Lüdicke, 1936
Ch. serpentina[a, b]	O_2		Lynn and von Brand, 1945
Chrysemys picta	CO_2	active	Buytendijk, 1910
	O_2		Rapatz and Mussacchia, 1957
Ch. picta[a, b]	O_2		Lynn and von Brand, 1945
Ch. picta marginata	O_2, CO_2	resting	Hall, 1924
	O_2	resting, active	Baldwin, 1926
Emys orbicularis	CO_2		Buytendijk, 1910
	O_2, CO_2	resting	Issekutz and Vegh, 1928
Geochelone denticulata	CO_2		Buytendijk, 1910
	O_2, CO_2	resting	Benedict, 1932
G. elephantopus	CO_2	resting	Benedict, 1932
G. gigantea elephantina	CO_2	resting	Benedict, 1932
	O_2, CO_2	resting, active	Hughes *et al.*, 1971
Gopherus polyphemus	CO_2	resting	Benedict, 1932
Kinosternon subrubrum[a, b]	O_2		Lynn and von Brand, 1945
Malaclemys terrapin centrata	O_2		McCutcheon, 1943
Pseudemys concinna mobilensis	O_2, CO_2	daily aver.	Chapman and Brubaker, 1891
	O_2		Hutton *et al.*, 1960
P. scripta	O_2, DC	resting, diving	Jackson and Schmidt-Nielsen, 1966
	DC	resting	Bentley and Schmidt-Nielsen, 1966
	O_2	resting, diving	Jackson, 1968

(*Table I continued page 136*)

Species	Measurement	Status of animal	Reference
	O_2	in air, diving	Belkin, 1968a
	O_2	standard, max. active	Gatten, 1973, 1974
P. scripta elegans	O_2		Jackson, 1971
Sternotherus minor	O_2	resting	Belkin, 1965a
	O_2	resting, active	Belkin, 1965b
	O_2	in air, diving	Belkin, 1968a
Terrapene carolina[b]	O_2		Lynn and von Brand, 1945
T. carolina	O_2		Altland and Parker, 1955
	O_2	resting	Bentley and Schmidt-Nielsen, 1966
T. ornata	O_2	standard, max. active	Gatten, 1973, 1974
Testudo graeca	CO_2		Buytendijk, 1910
	O_2, CO_2		Dontcheff and Kayser, 1937
	O_2	resting	Kayser, 1940
T. hermanni	O_2, CO_2	resting	Lüdicke, 1936
	O_2, CO_2	resting	Hughes *et al.*, 1971
Turtle	O_2, CO_2		Rubner, 1924
		Crocodilians	
Alligator mississippiensis	DC		Krehl and Soetbeer, 1899
	CO_2	active	Buytendijk, 1910
	CO_2	resting	Benedict, 1932
	O_2	resting	Hernandez and Coulson, 1952
	O_2		Andersen, 1961
	O_2	resting	Coulson and Hernandez, 1964
	O_2		Boyer, 1966
Caiman latirostris	O_2	resting	Hernandez and Coulson, 1952
C. crocodilus	CO_2	resting	Buytendijk, 1910
	O_2	resting	Bentley and Schmidt-Nielsen, 1966
	O_2	resting	Huggins *et al.*, 1971
Crocodile	O_2		Lüdicke, 1936
Crocodylus acutus	O_2	anesthetized	Dill and Edwards, 1931a
	O_2, CO_2	resting	Buchanan, 1909
C. porosus	CO_2	active	Buytendijk, 1910

Comments and Footnotes:
Status of animals: "standard"—animals fasting and resting in dark at night; "daily aver."—average of metabolic measurements extending over at least 24 h; "resting"—animals resting and presumably fasting during the day or unspecified period; "active"—some degree of spontaneous activity; "max. active"—animal stimulated to produce maximal metabolic rate for particular conditions.

[a]Juvenile [b]Embryo [c]Presumed identity [d]Female incubating eggs

possible of the following background information: age, sex, nutritional condition, state of thermal acclimation, and photoperiodic history of experimental animals; time of day; date; and light conditions during experiments. Metabolic data reported with this information can be used in other contexts than that of the particular study to which they pertain.

Subsequent sections of this review concern resting metabolic levels in the five surviving reptilian groups. Where sufficient data exist, we have calculated regression equations allowing metabolic comparisons among these groups and among reptiles and other vertebrate classes. These equations deal with the weight dependence of resting metabolic rate in adult animals and represent expressions of the allometric relation:

$$M = aW^b \tag{1}$$

or

$$M/W = aW^{(b-1)} \tag{2}$$

where M is metabolic rate (in cc O_2/h in this review), W is body weight (in grams in this review), and a and b are empirically determined constants representing the metabolic rate of a 1-g animal and the slope of the regression line for total metabolism (cc O_2/h) on a double logarithmic grid, respectively. Where several studies have been conducted on the same species, the lowest values reported have been used in our analyses. Data were excluded from consideration when any restlessness or activity on the part of the experimental animal was indicated. Only observations made at the specified temperature or interpolated from measurements within 5°C of that temperature were employed. Estimates involving the use of arbitrary values of Q_{10} have been employed in certain instances, but only to indicate approximate metabolic levels for species on which information was limited. The rates estimated in this manner were not used in the regression analyses.

B. Lizards

Dawson and Bartholomew (1956) were the first to formulate equations describing metabolic rate as a function of body size in lizards. At 30°C, metabolism of six species was described as

$$\text{cc } O_2/\text{h} = 1{\cdot}26\ \text{g}^{0{\cdot}54} \tag{3}$$

or

$$\text{cc } O_2/(\text{g} \times \text{h}) = 1{\cdot}26\ \text{g}^{-0{\cdot}46} \tag{4}$$

These expressions were unusual in the relatively low value specified for the exponent b. Bartholomew and Tucker (1964) added data for 13 species of lizards and presented revised equations for 30°C:

$$\text{cc } O_2/\text{h} = 0{\cdot}82\ \text{g}^{0{\cdot}62} \tag{5}$$

or

$$\text{cc } O_2/(\text{g} \times \text{h}) = 0{\cdot}82\ \text{g}^{-0{\cdot}38} \tag{6}$$

The 95% confidence limits of the exponent b are 0·54 and 0·70, which include the value indicating direct proportionality to surface area (0·67), but exclude those reported for mammals (Kleiber, 1961) and birds (Lasiewski and Dawson, 1967), 0·75 and 0·72, respectively. Such a fundamental metabolic difference between lizards and these homeotherms is surprising. Templeton (1970) plotted additional measurements on species of lizards and snakes at 30°C on the graph presented by Bartholomew and Tucker (1964), but did not calculate a new regression equation for this temperature. He did present the following expression for lizards at 37°C:

$$\text{cc } O_2/\text{h} = 1{\cdot}33\ \text{g}^{0{\cdot}65} \tag{7}$$

or

$$\text{cc } O_2/(\text{g} \times \text{h}) = 1{\cdot}33\ \text{g}^{-0{\cdot}35} \tag{8}$$

Equations (3)–(8) adequately describe metabolism for large lizards (>100 g), but the subsequent observations on species of smaller size have fallen consistently below predicted levels (Mayhew, 1965; Hudson and Bertram, 1966; Dawson and Templeton, 1966; Claussen, 1967; Mueller, 1969; Asplund, 1970; Snyder, 1971). A re-examination of the data on which Eqs (3)–(8) are based shows that almost all values for animals weighing less than 20 g are derived from the comparatively early studies of Dawson and Bartholomew (1956) on *Uta stansburiana* and *Sceloporus occidentalis* and of Gelineo and Gelineo (1955b) on several species of *Lacerta*. Several indications now exist that these metabolic values are well above levels characterizing resting lizards of the species. Rates reported for *Uta stansburiana* by Claussen (1967) and Alexander and Whitford (1968) are one-half those noted earlier. Roberts' determination (1968a) of standard metabolic rate in this species is 19–32% of those of Dawson and Bartholomew. Francis and Brooks (1970) found the metabolic rates of *Sceloporus occidentalis* to be one-third those reported previously. Gelineo and Gelineo's experimental procedures (1955a, b) for *Lacerta* are not reported, and activity may have influenced their results. Kramer's previous measurements (1934, 1935) of standard metabolism in *Lacerta* are only 10% of those of Gelineo and Gelineo. Metabolic measurements on active *Lacerta vivipara* (Avery, 1971) are similar to those reported by Gelineo and Gelineo (1955a, b).

These considerations have prompted us to recalculate equations describing the metabolic rate of lizards at 30°C and 37°C. An equation has also been calculated for 20°C to facilitate comparison of metabolism with other reptilian groups and lower vertebrate classes. The regressions for these three temperatures are illustrated in Figs 1, 2, and 3. The data used in their construction are given in Tables II, III, and IV. These data were chosen according to the criteria outlined in the introduction; consequently, the previously discussed

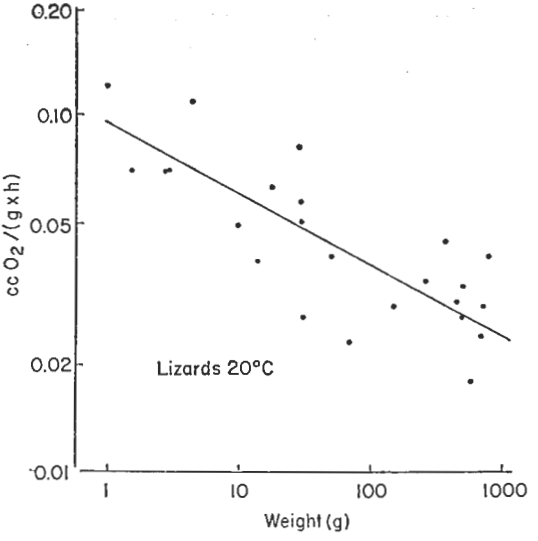

FIG. 1. The relation of weight-specific metabolic rate to body weight for lizards resting at 20°C. The data are plotted on a double logarithmic grid. The least squares regression line is described by the equation:

$$\log (\text{cc } O_2 \cdot g^{-1} \cdot h^{-1}) = \log 0{\cdot}096 - (0{\cdot}20)(\log g).$$

See Table II and Eq. (10) in text for further details.

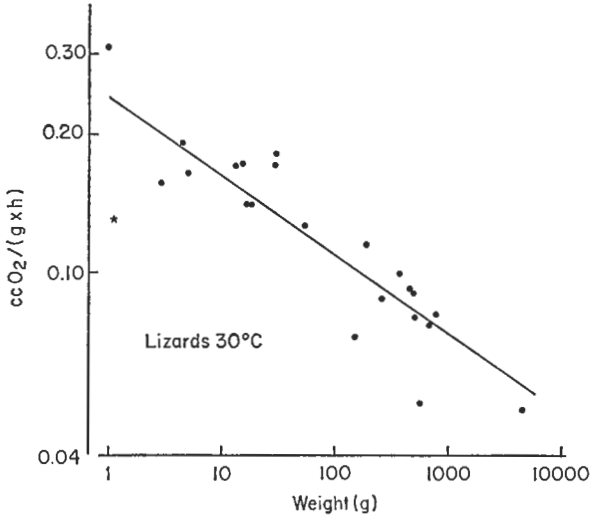

FIG. 2. The relation of weight-specific metabolic rate to body weight for lizards resting at 30°C. The data are plotted on a double logarithmic grid. The star indicates the point for *Xantusia vigilis*. The least squares regresssion line is described by the equation:

$$\log (\text{cc } O_2 \cdot g^{-1} \cdot h^{-1}) = \log 0{\cdot}240 - (0{\cdot}17)(\log g).$$

See Table III and Eq. (12) in text for further details.

measurements on *Lacerta*, *Sceloporus*, and *Uta* have been excluded. The least squares regression equation for metabolic rate of lizards at 20°C is

$$\text{cc } O_2/\text{h} = 0{\cdot}096\ \text{g}^{0{\cdot}80} \tag{9}$$

or

$$\text{cc } O_2/(\text{g} \times \text{h}) = 0{\cdot}096\ \text{g}^{-0{\cdot}20} \tag{10}$$

($n = 24$; correlation coefficient, $r = 0{\cdot}80$; 95% confidence limits for $b = 0{\cdot}73$ and $0{\cdot}87$).
That for 30°C is

$$\text{cc } O_2/\text{h} = 0{\cdot}240\ \text{g}^{0{\cdot}83} \tag{11}$$

or

$$\text{cc } O_2/(\text{g} \times \text{h}) = 0{\cdot}240\ \text{g}^{-0{\cdot}17} \tag{12}$$

($n = 24$; $r = 0{\cdot}86$; 95% c.l. for $b = 0{\cdot}79$ and $0{\cdot}87$). The metabolism-weight

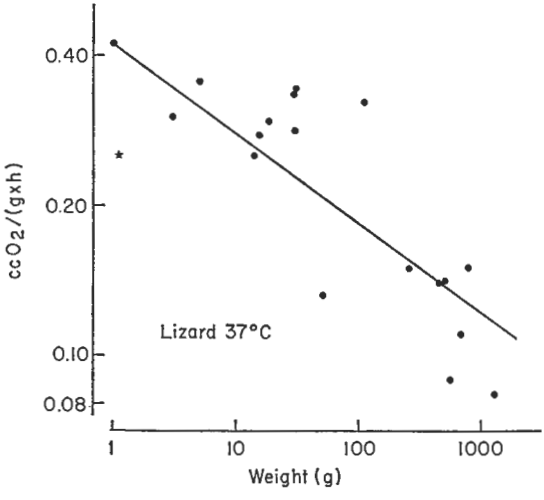

FIG. 3. The relation of weight-specific metabolic rate to body weight for lizards resting at 37°C. The data are plotted on a double logarithmic grid. The star indicates the point for *Xantusia vigilis*. The least squares regression line is described by the equation:

$$\log (\text{cc } O_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}) = \log 0{\cdot}424 - (0{\cdot}18)(\log \text{g}).$$

See Table IV and Eq. (14) in text for further details.

relation for lizards at 37°C is

$$\text{cc } O_2/\text{h} = 0{\cdot}424\ \text{g}^{0{\cdot}82} \tag{13}$$

or

$$\text{cc } O_2/(\text{g} \times \text{h}) = 0{\cdot}424\ \text{g}^{-0{\cdot}18} \tag{14}$$

($n = 19$; $r = 0{\cdot}82$; 95% c.l. for $b = 0{\cdot}75$ and $0{\cdot}89$). The values of b in Eqs (9)–(14) do not differ significantly from one another ($P = 0{\cdot}5$–$0{\cdot}8$), but all

are distinct from those previously reported by Bartholomew and Tucker (1964) and Templeton (1970). The confidence limits of the slopes in Eqs (9)–(14) include neither the value for surface-proportionality ($b = 0{\cdot}67$; $[b - 1] = -0{\cdot}33$) nor that for weight-proportionality ($b = 1{\cdot}0$; $[b - 1] = 0$). The values of b specified in Eqs (9), (11), and (13) are fairly close to those reported for mammals and birds, 0·72–0·75 (Kleiber, 1961; Lasiewski and Dawson, 1967).

TABLE II

Metabolic rates of lizards at 20°C

Species	Body weight g	Metabolic rate cc O_2/(g × h)	Reference
Amphibolurus barbatus	373	0·044	Bartholomew and Tucker, 1963
Anolis carolinensis	4·5[a]	0·110	Maher and Levedahl, 1959
Cnemidophorus tigris	18	0·062	Asplund, 1970
Crotaphytus collaris	30[a]	0·080	Dawson and Templeton, 1963
Dipsosaurus dorsalis	51·3	0·040	Moberly, 1963
Egernia cunninghami	261	0·034	Wilson, 1971, 1974
Eumeces obsoletus	30[a]	0·050	Dawson, 1960
Gerrhonotus multicarinatus	29·4	0·057	Dawson and Templeton, 1966
Iguana iguana	795[a]	0·040	Moberly, 1968a
Lacerta sicula	9·9	0·049	Kramer, 1934
L. trilineata	71	0·023	Kramer, 1934
L. viridis	30·5	0·027	Kramer, 1934
Phrynosoma mcalli	15·6	0·070	Mayhew, 1965
Physignathus lesueurii	504	0·033	Wilson, 1971, 1974
Sauromalus hispidus	574	0·018	Bennett, 1972b
S. obesus	150	0·029	Boyer, 1967
Scincella lateralis	1·0	0·122	Hudson and Bertram, 1966
Sphenomorphus labillardieri	2·8	0·070	Dawson *et al.*, 1966
Tiliqua scincoides	493	0·027	Bartholomew *et al.*, 1965
Trachydosaurus rugosus	461	0·030	Wilson, 1971, 1974
Uta mearnsi	14[a]	0·039	Murrish and Vance, 1968
U. stansburiana	3·0	0·070	Roberts, 1968a
Varanus spp.	714	0·029	Bartholomew and Tucker, 1964
Varanus gouldii	674	0·024	Bennett, 1972b

[a]Mid-point of weight range for animals studied

TABLE III

Metabolic rates of lizards at 30°C

Species	Body weight g	Metabolic rate cc O_2/(g × h)	Reference
Amphibolurus barbatus	373	0·098	Bartholomew and Tucker, 1963
Anolis carolinensis	4·5[a]	0·190	Maher and Levedahl, 1959
Cnemidophorus tigris	18	0·140	Asplund, 1970
Crotaphytus collaris	30[a]	0·180	Dawson and Templeton, 1963
Dipsosaurus dorsalis	51·3	0·090	Moberly, 1963
Egernia cunninghami	261	0·087	Wilson, 1971, 1974
Eumeces fasciatus	7[a]	0·240	Maher, 1965
E. obsoletus	30[a]	0·170	Dawson, 1960
Gerrhonotus multicarinatus	29·4	0·170	Dawson and Templeton, 1966
Iguana iguana	795[a]	0·081	Moberly, 1968a
Lacerta trilineata	54	0·124	Kramer, 1935
Phrynosoma mcalli	15·6	0·170	Mayhew, 1965
Physignathus lesueurii	504	0·080	Wilson, 1971, 1974
Sauromalus hispidus	574	0·052	Bennett, 1972b
S. obesus	150[a]	0·072	Boyer, 1956
Sceloporus graciosus	5·0	0·164	Mueller, 1969
Scincella lateralis	1·0	0·306	Hudson and Bertram, 1966
Tiliqua scincoides	493	0·090	Bartholomew *et al.*, 1965
Trachydosaurus rugosus	461	0·092	Wilson, 1971, 1974
Uta mearnsi	14[a]	0·170	Murrish and Vance, 1968
U. stansburiana	3·0	0·170	Roberts, 1968a
Varanus acanthurus	16·9	0·139	Bartholomew and Tucker 1964
V. gouldii	674	0·077	Bennett, 1972b
V. bengalensis	185	0·113	Bartholomew and Tucker, 1964
V. varius	4410	0·050	Bartholomew and Tucker, 1964
Xantusia vigilis	1·1	0·130	Snyder, 1971

[a]Mid-point of weight range for animals studied

Metabolism-weight relationships have been examined within several genera of lizards. The values of *b* reported vary considerably (Table V) and usually have wide confidence limits. However, they do not show any consistent relation to body temperature or phylogenetic position of the animals

involved (Vance, 1959). It is unclear whether these values reflect real differences among taxa, sampling errors, or artifacts of particular experimental designs. With regard to the last possibility, differential activity between large and small animals could influence the slope of the apparent metabolism-weight relation. In any case, the average of all the results cited in Table V are close to

TABLE IV

Metabolic rates of lizards at 37°C

Species	Body weight g	Metabolic rate cc O_2/(g × h)	Reference
Cnemidophorus tigris	18	0·270	Asplund, 1970
Crotaphytus collaris	30[a]	0·280	Dawson and Templeton, 1963
Dipsosaurus dorsalis	51·3	0·130	Moberly (1963)
Egernia cunninghami	261	0·150	Wilson, 1971, 1974
Eumeces obsoletus	30[a]	0·340	Dawson, 1960
Gerrhonotus multicarinatus	29·4	0·330	Dawson and Templeton, 1966
Iguana iguana	795[a]	0·150	Moberly, 1968a
Lacerta viridis	110	0·321	Krehl and Soetbeer, 1899
Phrynosoma mcalli	15·6	0·275	Mayhew, 1965
Physignathus lesueurii	504	0·140	Wilson, 1971, 1974
Sauromalus hispidus	574	0·088	Bennett, 1972b
Sceloporus graciosus	5·0	0·350	Mueller, 1969
Scincella lateralis	1·0	0·420	Hudson and Bertram, 1966
Trachydosaurus rugosus	461	0·140	Wilson, 1971, 1974
Uromastyx aegyptius	1250	0·083	Krehl and Soetbeer, 1899
Uta mearnsi	14[a]	0·250	Murrish and Vance, 1968
U. stansburiana	3·0	0·300	Roberts, 1968a
Varanus gouldii	674	0·111	Bennett, 1972b
Xantusia vigilis	1·1	0·250	Snyder, 1971

[a]Mid-point of weight range for animals measured

the value of b pertaining interspecifically in Eqs (9), (11), and (13). Vance (1959) obtained a composite b value of 0·87 at 35°C for 15 species of lizards.

Lizards appear to be a fairly homogeneous group with regard to metabolic level, despite the fact that some of the groups present today (e.g., the Iguanidae and Varanidae) already existed during the Cretaceous (Romer, 1956). However, some metabolic differences between groups may be obscured by the

variability of the available data. Xantusiid lizards represent the only notable departure from general saurian patterns of metabolism thus far detected. Vance (1959) reported metabolic rates for *Xantusia henshawi* and *X. vigilis*

TABLE V

Weight regression exponents (b) for lizards

Species	*b*	Reference
Callisaurus draconoides	0·72–0·86	Vance, 1959
Cnemidophorus tigris	0·98	Cook, 1949
Coleonyx variegatus	0·53–0·74	Vance, 1959
Dipsosaurus dorsalis	0·93	Cook, 1949
	0·81–0·95	Vance, 1959
Gerrhonotus multicarinatus	0·67–0·91	Vance, 1959
Lacerta spp.	0·70	Kramer, 1934
Phrynosoma coronatum	0·76	Vance, 1959
P. platyrhinos	0·88	Vance, 1959
Sauromalus obesus	0·95	Vance, 1959
Sceloporus graciosus	0·56–0·58	Vance, 1959
	0·76–0·85	Mueller, 1968
S. occidentalis	0·54–0·68	Dawson and Bartholomew, 1956
	0·47–0·83	Vance, 1959
Sincella lateralis	0·40–0·80	Hudson and Bertram, 1966
Uma inornata	0·65–1·07	Vance, 1959
U. notata	0·91	Cook, 1949
Urosaurus ornatus	0·67	Vance, 1953
Uta mearnsi	0·75–0·88	Vance, 1959
U. stansburiana	0·47–0·67	Dawson and Bartholomew, 1956
	0·88–1·09	Vance, 1959
	1·03[a]	Roberts, 1968a
	0·68[b]	Roberts, 1968a
	0·50[c]	Roberts, 1968a
Varanus spp.	0·82	Bartholomew and Tucker, 1964
Xantusia henshawi	0·55–0·69	Vance, 1959
X. vigilis	0·89	Cook, 1949
	0·57–0·88	Vance, 1959

[a]March–April
[b]Males, May–February
[c]Females, May–February

that are only 50% at 20°C and 35% at 30°C of the comparable levels predicted from Eqs (9) and (11). Snyder (1971) has also found relatively low rates in *X. vigilis*, the values he obtained being only 55–60% of those anticipated from the equations just mentioned. He regards this pattern as an adaptation facili-

tating water conservation. If this is the case, it is noteworthy that other species of xerophilous lizards do not show similarly low metabolism. Determination of the physiological basis of the low metabolic level in the Xantusiidae would be of great interest.

Initial observations on monitor lizards (*Varanus*) indicated that these animals had metabolic rates at high body temperatures (37°C) that were twice as great as comparable ones of other reptiles and approximately one-third the basal rates of mammals (Bartholomew and Tucker, 1964). However, subsequent measurements (Bennett, 1971, 1972b) showed the standard metabolic rate of *Varanus gouldii* to be virtually identical with those of other lizards of similar size at comparable temperatures (see Figs 2 and 3). Other instances of elevated metabolism among lizards thus far noted appear to involve failure of the animals to reach standard conditions in the course of experiments.

Metabolic physiology of saurians has been investigated primarily on iguanids, agamids, and skinks. Measurements currently are lacking or inadequate for several important groups of lizards: geckos, chameleons, pygopodids, lacertids, and teiids, as well as amphisbaenians. Concentration of research on representatives of these groups would be useful in determining whether the metabolic homogeneity apparent in currently available data is characteristic of saurians generally.

C. SNAKES

Greenwald (1971) compared metabolic values observed for snakes with estimates obtained from Bartholomew and Tucker's (1964) equation for lizards of similar weight. Although approximately half of these values for the snakes were substantially lower than the estimates, it was not possible to determine whether metabolic rates of ophidians are generally lower than those of saurians. Such a difference between closely related groups would be of considerable physiological interest.

We have drawn together the available information on metabolism of snakes and calculated equations describing the metabolism-weight relations for 20 and 30°C. Data for these temperatures are plotted in Figs. 4 and 5 and summarized in Tables VI and VII. At 20°C, the least squares regression of metabolic rate on body weight is

$$\text{cc } O_2/\text{h} = 0{\cdot}120\ \text{g}^{0{\cdot}77} \tag{15}$$

or

$$\text{cc } O_2/(\text{g} \times \text{h}) = 0{\cdot}120\ \text{g}^{-0{\cdot}23} \tag{16}$$

($n = 35$; $r = 0{\cdot}80$; 95% c.l. for $b = 0{\cdot}71$ and $0{\cdot}83$). The equation for 30°C is

$$\text{cc } O_2/\text{h} = 0{\cdot}280\ \text{g}^{0{\cdot}76} \tag{17}$$

or

$$\text{cc } O_2/(g \times h) = 0{\cdot}280\ g^{-0{\cdot}24} \tag{18}$$

($n = 13$; $r = 0{\cdot}91$; 95% c.l. for $b = 0{\cdot}69$ and $0{\cdot}83$). These values of b in Eqs (15) and (17) do not differ significantly from one another ($P = 0{\cdot}74$) or from those in the corresponding equations, (9) and (11), for lizards ($P = 0{\cdot}52$ at 20°C and $0{\cdot}07$ at 30°C). Analysis of covariance indicates no significant difference between Eqs (9) and (15) for 20°C ($P = 0{\cdot}41$), or between Eqs (11) and (17) for 30°C ($P = 0{\cdot}06$).

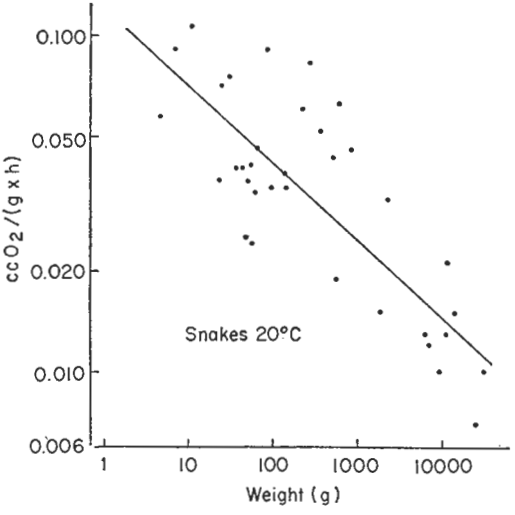

FIG. 4. The relation of weight-specific metabolic rate to body weight for snakes resting at 20°C. The data are plotted on a logarithmic grid. The least squares regression line is described by the equation:

$$\log (\text{cc } O_2 \cdot g^{-1} \cdot h^{-1}) = \log 0{\cdot}120 - (0{\cdot}14)(\log g).$$

See Table VI and Eq. (16) in text for further details.

Considerable controversy has surrounded the proper value of the exponent b in equations describing the relation of metabolic rate to body weight in snakes. Benedict's (1932) extensive observations on these animals led him to conclude that their metabolism varies in a manner directly proportional to surface area, b thus being $0{\cdot}67$. Galvão *et al.* (1965) measured metabolic rate at 20°C in 18 species of tropical snakes and obtained b values of $0{\cdot}98$ and $1{\cdot}09$ for representatives of the colubrids and boids, respectively. Neither of these exponents differed significantly from $1{\cdot}0$. Galvão *et al.*'s analysis of information on tropical boids from Benedict's (1932) study at 20°C yielded an exponent of $1{\cdot}12$. All these findings led the former authors to conclude that weight-specific metabolic rate is independent of body size in tropical snakes, a

condition differing from that in temperate species. This conclusion appears open to question on several counts. Galvão *et al.*'s (1965) statistical analysis of data for *both* boids and colubrids yields a *b* value of 0·86. Vinegar *et al.*'s (1970) results on three species of the former family at 28°C suggest a direct proportionality between metabolic rate and body surface area ($b = 0{\cdot}66$). Recalculation (Vinegar *et al.*, 1970) of Benedict's (1932) data on boids at 28°C indicated so much variability that a decision could not be made as to

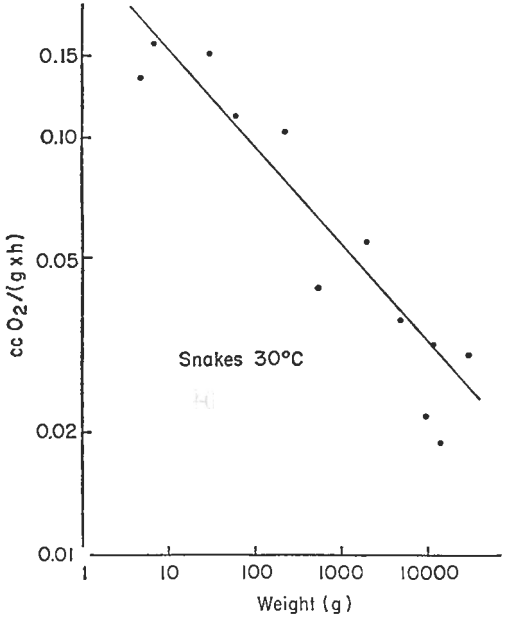

FIG. 5. The relation of weight-specific metabolic rate to body weight for snakes resting at 30°C. The data are plotted on a double logarithmic grid. The least squares regression line is described by the equation:

$$\log (\text{cc } O_2 \cdot g^{-1} \cdot h^{-1}) = \log 0{\cdot}280 - (0{\cdot}24)(\log g).$$

See Table VII and Eq. (18) in text for further details.

whether the metabolism of these animals was more accurately described by a *b* value of 1·0 or 0·67. The same situation resulted when Baldwin's (1928) data for the colubrid *Pituophis melanoleucus* were calculated, and Vinegar *et al.* (1970) therefore concluded that the weight regression coefficient *b* is temperature dependent in snakes. Buikema and Armitage's (1969) results suggest that such a conclusion may not be warranted for all species. These results indicated a high variation in the *b* values obtained for *Diadophis punctatus* at various temperatures, with none of these values differing significantly from the others. The mean value for the different temperatures was

TABLE VI

Metabolic rates of snakes at 20°C

Species	Body weight g	Metabolic rate cc O_2/(g × h)	Reference
Boa constrictor	9900	0·0102	Benedict, 1932
Chironius quadricarinatus	61	0·034	Galvão *et al.*, 1965
Crotalus atrox	5200	0·0132	Benedict, 1932
Cyclagras gigas	2680	0·032	Galvão *et al.*, 1965
Diadophis punctatus	4·7	0·057	Buikema and Armitage, 1969
Dipsas albifrons	22	0·037	Galvão *et al.*, 1965
Drymarchon corais	1920	0·0146	Benedict, 1932
Epicrates angulifer	12 400	0·0134	Benedict, 1932
Eunectes murinus	11 300	0·021	Galvão *et al.*, 1965
E. notaeus	14 400	0·015	Galvão *et al.*, 1965
Lampropeltis getulus	270[a]	0·081	Baldwin, 1928
Leimadophis poecilogyrus schottii	42	0·040	Galvão *et al.*, 1965
Liophis miliaris	55	0·024	Galvão *et al.*, 1965
Masticodryas bifossatus bifossatus	735	0·043	Galvão *et al.*, 1965
Natrix natrix	84	0·090	Hill, 1911
N. rhombifera	238	0·060	Jacobson and Whitford, 1970
Oxyrhopus trigeminus	98	0·035	Galvão *et al.*, 1965
Philodryas olfersii	176	0·039	Galvão *et al.*, 1965
P. patagoniensis	388	0·051	Galvão *et al.*, 1965
P. serra	145	0·035	Galvão *et al.*, 1965
Pituophis melanoleucus affinis	548	0·019	Greenwald, 1971
P. melanoleucus sayi	622	0·062	Baldwin, 1928
Python molurus	7000	0·0124	Benedict, 1932
P. m. molurus	25 600	0·065	Vinegar *et al.*, 1970
P. reticulatus	31 800	0·0096	Benedict, 1932
Salvadora hexalepis	65	0·046	Jacobson and Whitford, 1971
Sibynomorphus mikanii	11	0·113	Galvão *et al.*, 1965
Storeria dekayi	7·2	0·090[b]	Clausen, 1936
Thamnodynastes strigatus	55	0·041	Galvão *et al.*, 1965
Thamnophis proximus	31[a]	0·075	Jacobson and Whitford, 1970
T. sirtalis (temperate)	25[a]	0·070	Aleksiuk, 1971a
T. sirtalis (tropical)	38[a]	0·040	Aleksiuk, 1971a
Xenodon guentheri	50	0·025	Galvão *et al.*, 1965
X. merremii	502	0·043	Galvão *et al.*, 1965
X. neuwiedii	53	0·037	Galvão *et al.*, 1965

[a]Mid-point of weight range for animals measured
[b]Aggregated

1·03. Dmi'el and Borut (1972) obtained a b value of 0·62 at 30°C for *Spalerosophis cliffordii*; no confidence limits were reported for this exponent.

Dmi'el (1972a) has recently provided a further analysis of metabolism-weight relations in snakes. He has estimated the value of b for these animals at 30°C, using a Q_{10} of 2·5 to adjust selected values of other workers (principally Benedict, 1932; Galvão *et al.*, 1965; and Vinegar *et al.*, 1970) to that temperature. This estimate is 0·60, a figure differing considerably from that indicative of direct proportionality to body weight. Dmi'el believes that b is

TABLE VII

Metabolic rates of snakes at 30°C

Species	Body weight g	Metabolic rate cc O_2/(g × h)	Reference
Boa constrictor	9900	0·021	Benedict, 1932
Crotalus atrox	5200	0·035	Benedict, 1932
Diadophis punctatus	4·4	0·132	Buikema and Armitage, 1969
Drymarchon corais	2040		Benedict, 1932
Epicrates angulifer	12 400	0·031	Benedict, 1932
Natrix rhombifera	238	0·095	Jacobson and Whitford, 1970
Pituophis melanoleucus affinis	548	0·042	Greenwald, 1971
Python molurus	14 800	0·018	Vinegar *et al.*, 1970
P. reticulatus	30 200	0·029	Benedict, 1932
Salvadora hexalepis	65	0·107	Jacobson and Whitford, 1971
Spalerosophis cliffordii	351	0·136	Dmi'el and Borut, 1972
Storeria dekayi	7·2	0·167[b]	Clausen, 1936
Thamnophis proximus	31[a]	0·150	Jacobson and Whitford, 1970

[a]Mid-point of weight range for animals measured
[b]Aggregated

temperature dependent. We therefore question his adjustment of metabolic values to 30°C by use of an arbitrary Q_{10} for animals of all sizes; *a priori*, animals of different sizes would have to differ in their thermal sensitivities if b is to vary with temperature.

Our summary of the relevant metabolic measurements on snakes incorporates data from all the studies cited above and consequently provides a broader picture of the metabolism-weight relationship for this group than has previously been available. The values of b that we have obtained, 0·76–0·77—see Eqs (15)–(17)—differ significantly from both 0·67 (surface area proportionality) and 1·0 (weight proportionality), as well as from those obtained by

Galvão *et al.* (1965) for boids and colubrids, respectively. However, the confidence limits of our values overlap those for the other weight regression coefficients cited for snakes. Our statistical analysis of metabolic data for snakes at 20° and 30°C provides no support for the contention (Vinegar *et al.*, 1970; Dmi'el, 1972a) that b is temperature dependent in this group.

The metabolism-weight equations formulated by Galvão *et al.* (1965) predict that a 1-kg boa will have only half the metabolic rate of a colubrid of similar size. However, the size ranges of the representatives of the two families employed in their study barely overlap. Determinations on small

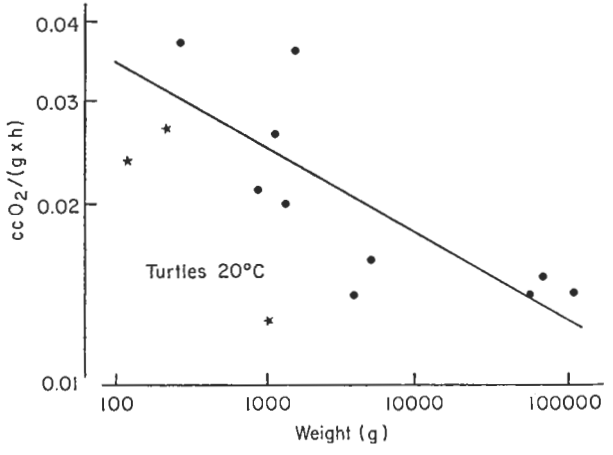

FIG. 6. The relation of weight-specific metabolic rate to body weight for turtles resting at 20°C. The data are plotted on a double logarithmic grid. The least squares regression line is described by the equation:

$$\log (\text{cc } O_2 \cdot g^{-1} \cdot h^{-1}) = \log 0{\cdot}066 - (0{\cdot}14)(\log g).$$

The values indicated by stars were not used in the determination of this equation. See Table VIII and Eq. (20) in text for further details.

boids and large colubrids would help to establish whether the differences in metabolic level suggested by Galvão *et al.*'s (1965) data are in fact real. Such an effort is of importance, for it is of interest to know whether phylogenetic position influences metabolic level in reptiles. Preliminary observations (Bennett and Dawson, unpublished data) on *Eryx tataricus*, a small boid, yielded a metabolic rate at 20°C indistinguishable from Galvão *et al.'s* (1965) colubrid values and twice that predicted from their equation for boid metabolism.

Data for representatives of families of snakes other than the boids and colubrids are exceedingly limited. Relatively few metabolic observations have been made on viperids (Benedict, 1932; Dmi'el, 1970, 1972b). Perhaps understandably, no data have been reported on elapids and hydrophids.

D. RHYNCHOCEPHALIANS

Measurements of several physiological functions, including metabolic rates for resting and active individuals, have been reported recently for the only surviving species of rhynchocephalian, *Sphenodon punctatus* (Wilson and Lee, 1970). The resting rates were 0·020 and 0·050 cc O_2/(g × h) at 20° and 30°C, respectively. These values are approximately two-thirds of

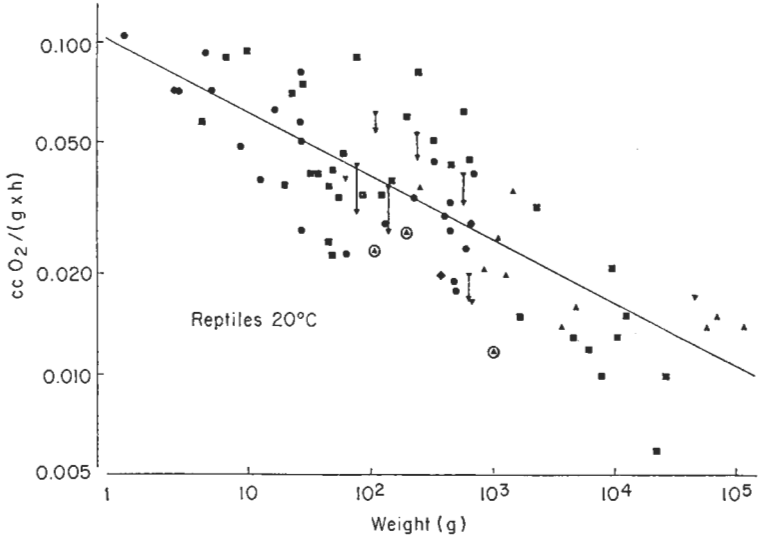

FIG. 7. The relation of weight-specific metabolic rate to body weight for reptiles resting at 20°C. The data are plotted on a double logarithmic grid. Representatives of the various groups are identified as follows: lizards, circles; snakes, squares; turtles at 20°C, triangles; turtles at 18–22°C, encircled triangles; crocodilians, inverted triangles; rhynchocephalian (*Sphenodon*), diamond. Metabolic estimates for crocodilians at 20°C made from data for other temperatures are indicated by inverted triangles connected by a vertical line. The higher estimate was obtained with a Q_{10} of 2; the lower, with a Q_{10} of 3. The values for turtles at 18–22°C and these estimates for crocodilians were not used in determining the least squares regression line. The equation for this line is:

$$\log (\text{cc } O_2 \cdot g^{-1} \cdot h^{-1}) = \log 0{\cdot}102 - (0{\cdot}20)(\log g).$$

See Tables II, VI, VIII, IX, the text, and Eq. (22) for further details.

comparable rates for other reptiles, but they do not fall outside the range of variability in reptilian metabolic data as a whole (see Figs 7 and 8).

E. TURTLES

The relation of metabolic rate at 20°C to body weight for 10 species of turtles is shown in Fig. 6. Data for representatives of three other species

measured near (±2°C) this temperature are also included in this figure, although excluded from the regression calculations. The data for these 13 species are also summarized in Table VIII. For turtles at 20°C:

$$\text{cc } O_2/\text{h} = 0{\cdot}066\ \text{g}^{0{\cdot}86} \tag{19}$$

or

$$\text{cc } O_2/(\text{g} \times \text{h}) = 0{\cdot}066\ \text{g}^{-0{\cdot}14} \tag{20}$$

($n = 10$; $r = 0{\cdot}78$; 95% c.l. for $b = 0{\cdot}77$ and $0{\cdot}95$). The value of the exponent b in Eq. (19) does not differ significantly from those for lizards ($P = 0{\cdot}32$)

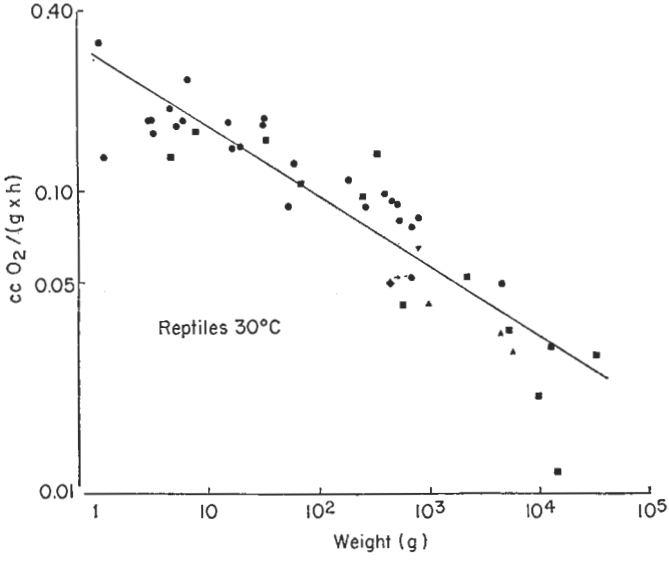

FIG. 8. The relation of weight-specific metabolic rate to body weight for reptiles resting at 30°C. The data are plotted on a double logarithmic grid. Representatives of the various groups are identified as follows: lizards, circles; snakes, squares; turtles, triangles; crocodilians, inverted triangles; rhynchocephalian (*Sphenodon*), diamond. The equation for the least squares regression line is:

$$\log (\text{cc } O_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}) = \log 0{\cdot}278 - (0{\cdot}23)(\log \text{g}).$$

See Tables III and VII, text, and Eq. (24) for further details.

or for snakes ($P = 0{\cdot}22$) at 20°C in Eqs (9) and (15), respectively. Analysis of covariance reveals no statistically significant difference between the regression for turtles and those for lizards ($P = 0{\cdot}83$) or snakes ($P = 0{\cdot}55$), or that for the two suborders combined ($P = 0{\cdot}61$). Recently reported standard metabolic rates for *Pseudemys scripta* and *Terrapene ornata* are only one-third the values predicted for these animals by Eq. (19) (Gatten, 1973). This evidently reflects a strong circadian component in testudinian metabolism (the data summarized

in Table VIII were mainly obtained in diurnal tests), which emphasizes the importance of careful stipulation of experimental design.

TABLE VIII
Metabolic rates of turtles near 20°C

Species	Body weight g	Metabolic rate cc O_2/(g × h)	Reference
	Observations at 20°C		
Chelydra serpentina	1488	0·0195	Baldwin, 1926
Chrysemys picta marginata	1281	0·026	Baldwin, 1926
Geochelone denticulata	4200	0·014	Benedict, 1932
G. elephantopus	69 000	0·0142	Benedict, 1932
	132 000	0·0139	Benedict, 1932
G. gigantea	80 000	0·0151	Benedict, 1932
Gopherus polyphemus	5450	0·0156	Benedict, 1932
Pseudemys concinna mobilensis	1700	0·0357	Chapman and Brubaker, 1891
P. scripta elegans	970	0·021	Hutton *et al.*, 1960
Turtle	285	0·037	Rubner, 1924
	Observations at 18–22°C		
Emys orbicularis (18°–20°C)	1100	0·0127	Issekutz and Vogh, 1928
Sternotherus minor (22°C)	121	0·0235	Belkin, 1968a
Testudo graeca (18°C)	225	0·0266	Dontcheff and Kayser, 1937

Insufficient data exist for definition of the metabolism-weight relation for turtles at 30°C. The available data pertain to only three species: *Geochelone* (*Testudo*) *denticulata*, 0·0346 cc O_2/(g × h) for a weight of 4200 g (Benedict, 1932); *Gopherus polyphemus*, 0·0298 cc O_2/(g × h) for a weight of 5430 g (Benedict, 1932), and *Pseudemys scripta elegans*, 0·042 cc O_2/(g × h) for a weight of 970 g (Hutton *et al.*, 1960). These values tend to fall below values for lizards of comparable size, but are not outside the scatter evident in the data for the various reptilian groups. Additional measurements are needed before a really meaningful definition can be made of the metabolic levels of turtles at 30°C.

The possession of shells by turtles has created uncertainty concerning the utility of weight-specific metabolic values for these animals and the validity of comparing such values with those for reptiles of other groups. The shell

has generally been assumed to be metabolically inert (Hall, 1924; Benedict, 1932; Hutton *et al.*, 1960; Hughes *et al.*, 1971). Inclusion of such inert material, which constitutes 15–30% of the bulk of the animal (Benedict, 1932; Hughes *et al.*, 1971), in the body weight could lead to underestimation of the metabolic rate of active tissue. This problem caused Benedict (1932) to consider calculation of weight-specific metabolic rates on a shell-free basis more useful than that based on gross body weight. However, our failure to detect any significant differences between regression equations for lizards, snakes, and turtles (see above) based on gross body weight—see Eqs (9), (15), and (19)—indicates either (1) that shell is not metabolically inert or (2) that the metabolic rate of the other tissues in turtles is just enough higher (20–40%) than that of other reptiles to compensate exactly for the inert character of the shell in the total metabolism. The former possibility appears more likely. Without experimental evidence, it is difficult to justify the exclusion of a tissue from metabolic calculations. At any rate, total body weight has the advantage of being an easily-determined, non-lethal measurement. Furthermore, all standards have potential objections, be they "metabolically active" tissue, dry weight, lean weight, etc.

Benedict (1932) and Hutton *et al.* (1960) found that the weight regression exponent b approximated 1·0 in turtles. On the other hand, Hughes *et al.* (1971) obtained a value of 0·82 for resting *Geochelone* (*Testudo*) *gigantea* over a wide range of body weight. They recalculated Hutton *et al.*'s (1960) data for *Pseudemys* and found a value of b that differed significantly from 1·0, but not from the exponent obtained for *Geochelone*. Our calculations dealing with all the species considered by these previous authors support Hughes *et al.*'s (1971) conclusions regarding the weight dependence of metabolism in turtles.

Studies on metabolic physiology of turtles have generally emphasized diving capacities (see section V), and measurements of metabolic rate are relatively few. The great range of size characterizing the Testudinidae has been exploited by several workers in metabolic studies, but comparable observations on other families are few (Chelydridae, Kinosternidae) or lacking (Chelidae, Cheloniidae, and Trionychidae).

F. Crocodilians

The paucity of data at any single body temperature prevents definition of a metabolism-weight relation for crocodiles and alligators. Available information on metabolic rates of these animals is summarized in Table IX. In instances where observations were made at other body temperatures, arbitrary Q_{10}'s of 2·0 and 3·0 have been used to estimate probable metabolic levels at 20°C. These estimates are included in Fig. 7, which illustrates the metabolism-weight relation for reptiles at 20°C. They appear indistinguishable

TABLE IX

Metabolic rates of crocodilians at 20°C

Species	Body weight g	Experimental temperature °C	Metabolic rate at 20°C cc O_2/(g × h)			Reference
			Observed	Estimated		
				$Q_{10} = 2$	$Q_{10} = 3$	
Alligator mississippiensis	750	20	0·0167			Coulson and Hernandez, 1964
	53 000	20	0·0073			Benedict, 1932
Crocodylus acutus	71	20	0·039			Buchanan, 1909
Alligator mississippiensis	87·7	28		0·042	0·031	Hernandez and Coulson, 1952
	650	25		0·040	0·033	Boyer, 1966
Caiman latirostris	161	28		0·037	0·027	Hernandez and Coulson, 1952
C. crocodilus	124	23		0·061	0·054	Bentley and Schmidt-Nielsen, 1966
	274·1	24		0·053	0·045	Huggins *et al.*, 1971a
	749	24		0·020	0·017	Huggins *et al.*, 1971b

from comparable values for representatives of other orders. Only one measurement has been made on a crocodilian at 30°C. This pertains to a 750-g *Alligator mississippiensis* and is 0·065 cc O_2/(g × h) (Coulson and Hernandez, 1964).

G. General Equations for Metabolism-Weight Relations

Despite the longstanding separation of the surviving reptilian lines and the ecological diversity apparent among their members, resting metabolic rate appears to have been a conservative function within them. Since this function does not seem to vary significantly at the ordinal or subordinal level, it is possible to define a reptilian grade of metabolism and to establish generalized metabolism-weight regressions for reptiles. We have calculated such an equation for 20°C, the temperature at which the greatest array of data is available (Fig. 7). Estimated values for crocodilians at 20°C and observations on turtles near that temperature are included for comparison in Fig. 7, but excluded in the regression formulation. The equation describing the general metabolism-weight relation for reptiles at 20°C is

$$\text{cc } O_2/\text{h} = 0{\cdot}102\ \text{g}^{0{\cdot}80} \tag{21}$$

or

$$\text{cc } O_2/(\text{g} \times \text{h}) = 0{\cdot}102\ \text{g}^{-0{\cdot}20} \tag{22}$$

(n = 73; r = 0·83; 95% c.l. for b = 0·77 and 0·83). The data for reptiles at 30°C are brought together in Fig. 8. The equation calculated from them is

$$\text{cc } O_2/\text{h} = 0{\cdot}278\ \text{g}^{0{\cdot}77} \tag{23}$$

or

$$\text{cc } O_2/(\text{g} \times \text{h}) = 0{\cdot}278\ \text{g}^{-0{\cdot}23} \tag{24}$$

(n = 44; r = 0·91; 95% c.l. for b = 0·74 and 0·80). The correlation coefficients for these equations indicate that 69% (20°C) and 83% (30°C) of the variance reported for metabolic measurements can be accounted for on the basis of variation in body weight alone. In view of the large assortment of techniques utilized in the measurement of these rates, the low residual variation due to extraneous factors is both surprising and gratifying. The regression exponents (b) in Eqs (21) and (23) do not differ significantly (P = 0·30). They indicate that metabolism for reptiles as a group is not directly proportional to either body weight or surface area. These exponents are both fairly close to 0·75, the exponent characterizing metabolism-weight relations for unicellular organisms, multicellular plants, and poikilothermic and homeothermic metazoans over wide ranges (Hemmingsen, 1960). As Hemmingsen (1960) concluded, real departures from this particular exponent may represent com-

promises within groups of limited phylogenetic range, but these departures do not extend beyond a few log units of body weight (measured in grams).

H. Comparison with Other Groups

Hemmingsen (1960) has assembled metabolic data obtained at 20°C for metazoan poikilotherms ranging in weight from 10 μg to 100 kg. The distribution of these measurements (Fig. 9) encompasses our regression for reptiles at

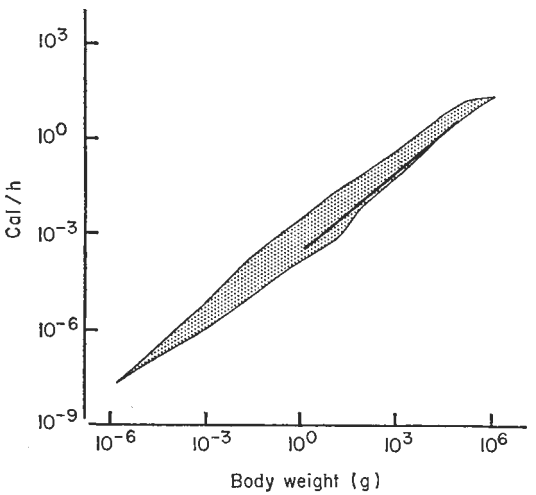

FIG. 9. Comparison of the relation of total metabolic rate to body weight for reptiles resting at 20°C (heavy line) with those presented by Hemmingsen (1960) for other groups of poikilothermic animals at this temperature. The dotted area contains the regression lines for these other groups. The regression line for the reptiles was obtained from Eq. (9) in the text, using a caloric equivalent of 4·8 Cal/l of O_2. The figure employs a double logarithmic grid.

20°C. The fact that the data we have summarized are indistinguishable from metabolic values for non-reptiles indicates that reptiles resemble other poikilothermic animals in general metabolic level. Benedict (1932) reached a similar conclusion through comparison of his measurements on members of this class with those of other authors on amphibians and fish.

Metabolic rates of resting reptiles are markedly below those of homeotherms of comparable size at similar body temperatures. For example, Benedict (1932) compared pythons and boas with mammals of similar size and found that the reptilian rates at 37°C were one-fifth and one-seventh, respectively, the basal rates of homeotherms. The ratio was one-eighth when surface-relative rates were employed. Benedict also found metabolic values

for curarized or pithed mammals at body temperatures near 20°C to be seven- to ten-fold greater than those of reptiles at the same temperature. The lizards *Uta stansburiana* and *Sceloporus occidentalis* were subsequently shown (Dawson and Bartholomew, 1956) to have metabolic rates at 37°C that were one-tenth the values reported for normothermic hummingbirds and shrews. Studies of the lizards *Dipsosaurus dorsalis* (Dawson and Bartholomew, 1958), *Amphibolurus barbatus* (Bartholomew and Tucker, 1963), and *Varanus gouldii* (Bennett, 1972b) at 37°C place their resting metabolic rates at one-fifth

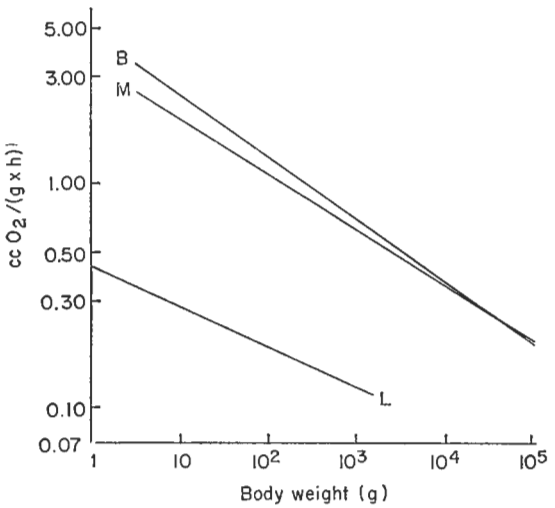

FIG. 10. Comparison of the relation of weight-specific metabolic rate to body weight for lizards resting at 37°C with those of basal metabolic rate to body weight for birds and mammals. The line for lizards (L) was obtained from Eq. (14) in the text. The line for birds (B) is based on the equation of Lasiewski and Dawson (1967) for non-passerine birds. That for mammals (M) is based on the equation of Kleiber (1961) for eutherian mammals.

to one-seventh the basal metabolic rate of homeothermic animals of similar size.

From consideration of Eq. (7) for the metabolism-weight relation of lizards at 37°C, Templeton (1970) concluded that 10-g and 10-kg representatives of these animals metabolize at approximately 29% and 14%, respectively, the basal rates of normothermic mammals of comparable weight. This percentage is much less size-dependent if our equation (13) for 37°C is used in making the comparisons. This results from the similarity noted previously between the *b* values in Eq. (13) and Kleiber's (1961) equation for the metabolism-weight relation of eutherian mammals. The value of *b* that we obtained for lizards is likewise not far above that for birds (Lasiewski and Dawson, 1967). A compari-

son of metabolic levels between lizards and homeotherms yields the following results if based on Eq. (13) and the equations of Kleiber (1961) and Lasiewski and Dawson (1967) for eutherian mammals and non-passerine birds, respectively. For 1-g animals, the saurian level of metabolism represents 9% and 13% of avian and mammalian levels, respectively; for 1-kg animals, the saurian level represents 18 and 20% of these respective homeothermic levels. If the fact that the body temperatures of the birds tend to exceed 37°C were taken into account, the percentages in the lizard to non-passerine comparisons would probably be slightly larger. Estimates for lizards have been used in the above comparisons, because of the relative paucity of information on other groups at 37°C. We feel that these comparisons reflect the situation for reptiles generally (Fig. 10).

The basis of the differential in metabolic level between reptiles and homeotherms is becoming more clearly understood. Benedict (1932) dismissed the assertion that it involved the presence of a greater proportion of metabolically inert material, e.g., water or bone, in these poikilotherms than in the birds and mammals. The differential in metabolic level is simply too great, and the proportion of water and inert material quite similar in all these animals. Heath (1968) has linked the greater metabolic expenditures of homeotherms to the alteration of limb suspension from the reptilian pattern. Erect posture in mammals is postulated to involve increased muscle tonus requiring more energy and, thus, more heat production. Bennett (1972a) finds that the specific activity of mitochondrial (aerobic) enzymes is one-fourth to one-sixth as great in lizards as in rats. A similar differential exists in the concentration of mitochondria in these animals. Both these ratios resemble that between the metabolic rates of reptiles and homeotherms (see above). The similarity among these ratios suggests that specific activity of mitochondrial enzymes has not changed greatly during the evolution of homeothermy, but that the concentration of mitochondria has. Presumably, this entailed a relatively simple morphological alteration at the cellular level, once it became selectively advantageous.

III. Some Factors Influencing Resting Metabolic Rate

A. Temperature

The regression equations presented in the previous section permit examination of the general thermal dependence of metabolism in lizards and snakes. In the case of the former, Eqs (9)–(13) indicate that metabolic rate does not have a constant thermal dependence between 20 and 37°C. Instead, Q_{10} for values of this function estimated for a 100-g lizard declines from 2·87 between 20 and 30°C to 2·12 between 30 and 37°C. The thermal dependence estimated from Eqs (15)–(18) for the metabolism in a 100-g snake between

20 and 30°C is less pronounced ($Q_{10} = 2{\cdot}23$) than for the lizard in this temperature interval.

The decline in Q_{10} with increasing temperature indicated by the equations describing the metabolism-weight relations of lizards contrasts with the situation observed in many individual species, in which this temperature coefficient remains constant over a wide thermal range, thus conforming to the standard model for thermal dependence of biological rate processes. These species include, among many others, *Sphenodon* (Wilson and Lee, 1970), several large snakes (Benedict, 1932), and several lizards—*Amphibolurus barbatus* (Bartholomew and Tucker, 1963), *Eumeces obsoletus* (Dawson, 1960), *Gerrhonotus multicarinatus* (Dawson and Templeton, 1966), *Lacerta* sp. (Kramer, 1935), *Phrynosoma cornutum* (Prieto and Whitford, 1971), *Sauromalus hispidus* (Bennett, 1972b), *Tiliqua scincoides* (Bartholomew *et al.*, 1965), *Uta stansburiana* (Roberts, 1968a), and *Xantusia vigilis* (Snyder, 1971). However, many instances of departure from this strict thermal dependence have been observed in reptiles. These involve a continuously decreasing Q_{10} with increasing temperature or the presence of metabolic plateaus where metabolic rate is essentially stable over a range of several degrees Celsius (i.e., Q_{10} falls to near 1·0). Such temperature responses have been reported in several species of snakes: a single *Boa constrictor* (Benedict, 1932), *Diadophis punctatus* (Buikema and Armitage, 1969), *Natrix rhombifera* and *Thamnophis proximus* (Jacobson and Whitford 1970), and *Thamnophis sirtalis* (Aleksiuk, 1971a). They have also been observed in several lizards: *Cnemidophorus tigris*, *Uma notata*, *Xantusia vigilis* (Cook, 1949), *Crotaphytus collaris* (Dawson and Templeton, 1963), *Scincella lateralis* (Hudson and Bertram, 1966), *Phrynosoma douglassii* (Prieto and Whitford, 1971), *P. mcalli* (Mayhew, 1965), and *Varanus gouldii* (Bennett, 1972b). The Q_{10} for *in vitro* metabolism of *Lacerta* liver also decreases with increasing temperature (Locker, 1958). A biphasic relationship between oxygen consumption and temperature has been detected with *in vitro* measurements on cardiac and skeletal muscle and liver of *Thamnophis sirtalis* (Hoskins and Aleksiuk, 1973a). The metabolic rates of these tissues at temperatures above 20°C have a significantly lower thermal dependence ($Q_{10} \simeq 2{\cdot}4$) than those between 4 and 20°C ($Q_{10} \simeq 5{\cdot}8$). A high thermal dependence of metabolism at temperatures below the range normally associated with activity might well produce considerable conservation of energy for reptiles during inactivity in cool surroundings.

Metabolic plateaus have been observed in hibernating individuals of *Dipsosaurus dorsalis* (Moberly, 1963) and *Phrynosoma mcalli* (Mayhew, 1965). In a number of cases, such plateaus occur in non-hibernating reptiles in thermal ranges over which the animals are normally active in nature. These ranges do not include injuriously high temperatures and are, therefore, not

due to thermal inactivation of metabolic enzymes. Aleksiuk (1971b) has correlated the metabolic plateaus evident in *Thamnophis sirtalis* with a compensatory shift in the activity of lactate dehydrogenase, which probably results from differential isoenzyme activity at different temperatures.

The possession of a thermally independent metabolism would free an organism from metabolic fluctuations with minor changes in body temperature. This "perhaps . . . indicates a tendency toward homeostasis in these species" (Dawson and Bartholomew, 1956). Many intertidal invertebrates subjected to rapid temperature fluctuations also have metabolic rates which seem essentially temperature independent (Newell, 1969). However, no obvious differences in thermal preferenda, ecology, or phylogeny exist among reptiles possessing such metabolic independence and those lacking it. The cellular bases and selective advantages of the thermal patterns of metabolism merit investigation.

A fundamental question in the thermobiology of reptiles asks whether metabolism has undergone any compensatory adjustment to preferred body temperature. The relation between thermal sensitivity of metabolism and thermal preferenda in lizards has been reviewed by Dawson (1967) and Templeton (1970). The former author concluded that most values of Q_{10} for individual species lie between 1·5 and 3·1 and that no correlation is apparent between the size of this temperature coefficient and extent of thermophily. However, metabolic rates of cold-tolerant species undergo relatively less retardation at 5–15°C than those of heat-tolerant ones (Vance, 1959; Dawson, 1967). Dawson (1967) and Templeton (1970) have cited studies of the lizards *Dipsosaurus dorsalis*, *Crotaphytus collaris*, *Eumeces obsoletus*, and *Gerrhonotus multicarinatus*, indicating that certain species with high thermal preferenda tend to have lower metabolic rates at high temperatures than those with low preferenda. With the larger array of metabolic data now available on lizards, it is possible to determine the extent of this tendency within this suborder. We have assembled diurnal metabolic measurements on representatives of 19 species of lizards resting at their respective preferred body temperatures or at temperatures observed in individuals active in nature (Table X). If resting metabolism were compensated for preferred body temperature, the rates should approximate one another, after appropriate adjustment for differences in body weight among the animals considered. Thus resting metabolic rate at the thermal preferendum would be essentially independent of temperature. This condition would be analogous to complete temperature compensation in individual organisms. On the other hand, if no metabolic adjustment to preferred body temperature has occurred, a significant thermal dependence of metabolic rate with a Q_{10} approaching those reported for lizards as a group should exist. An intermediate condition would indicate partial compensation. Metabolic rate divided by (body weight)$^{0·82}$ [0·82 representing the

TABLE X

Metabolic rates of lizards at their preferred body temperatures (PBT[a])

Species	Body weight g	PBT[a] °C	Metabolic rate cc O_2/(g × h)	Reference
Amphibolurus barbatus	373	35	0·120	Bartholomew and Tucker, 1963
Anolis carolinensis	4·5[b]	31	0·190	Maher and Levedahl, 1959
Cnemidophorus tigris	18	40	0·350	Asplund, 1970
Crotaphytus collaris	30[b]	38	0·300	Dawson and Templeton, 1963
Dipsosaurus dorsalis	70[b]	40	0·200	Dawson and Bartholomew, 1958
Egernia cunninghami	261	33	0·110	Wilson, 1971, 1974
Eumeces obsoletus	30[b]	34	0·240	Dawson, 1960
Gerrhonotus multicarinatus	29·4	21	0·060	Dawson and Templeton, 1966
Iguana iguana	795[b]	36	0·140	Moberly, 1968a
Phrynosoma mcalli	15·6	38	0·275	Mayhew, 1965
Physignathus lesueurii	504	30	0·080	Wilson, 1971, 1974
Sceloporus cyanogenys	51·5	32	0·116	Wilhoft, 1966
S. graciosus	5·0	31	0·190	Mueller, 1969
S. occidentalis	16·0	35	0·180	Francis and Brooks, 1970
Scincella laterale	1·0	29	0·280	Hudson and Bertram, 1966
Trachydosaurus rugosus	461	33	0·113	Wilson, 1971, 1974
Uta mearnsi	14[b]	36	0·240	Murrish and Vance, 1968
U. stansburiana	4·0	35	0·340	Alexander and Whitford, 1968
Xantusia vigilis	1·1	30	0·130	Snyder, 1971

[a]PBT usually defined from measurements of animals in experimental thermal gradients. However, some of the values presented here have been inferred from thermal observations on animals active in nature

[b]Mid-point of weight range

approximate value of b in Eqs (9), (11), and (13)] is illustrated as a function of preferred body temperature in Fig. 11. The least squares regression for this relation is described by the equation:

$$\log [\text{cc } O_2/(g^{0\cdot82} \times h)] = -1\cdot771 + 0\cdot038T_b \qquad (25)$$

where T_b is in degrees Celsius ($n = 19$; $r = 0\cdot89$; 95% c.l. of slope = 0·028 and 0·048). The slope of this regression is highly significant ($P < 10^{-6}$) and corresponds to a Q_{10} of 2·40. Since this value lies between the Q_{10}'s indicated by Eqs (9), (11), and (13) for 20–37°C, it appears that little if any adjustment

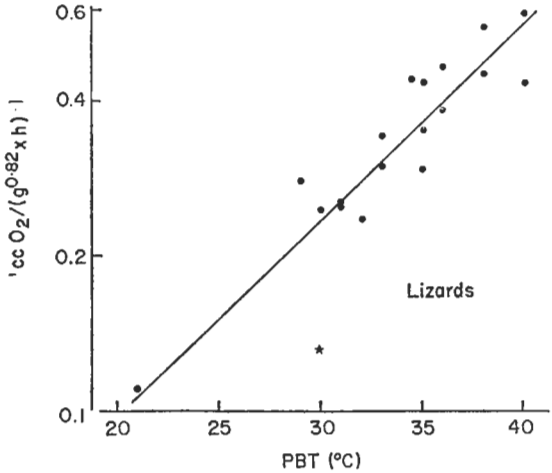

FIG. 11. Metabolic rates of lizards at their respective preferred body temperatures (PBT). The use of the 0·82 power of body weight in the computation of these rates serves to minimize variation due to differences in body size among the species considered. These data are plotted on a semilogarithmic grid. The value for *Xantusia vigilis* is indicated by a star. The equation for the least squares regression line is:

$$\log (\text{cc } O_2 \cdot g^{-0\cdot82} \cdot h^{-1}) = -1\cdot771 + 0\cdot038T_b,$$

where T_b refers to PBT in degrees Celsius. See Eq. (25) and Table X for further details.

of resting metabolic rate to preferred levels of body temperature has occurred in these lizards. In retrospect, this conclusion is not surprising, since metabolic rate at any single temperature is primarily a function of body weight. The fact that resting metabolic rate has not been adjusted to preferred body temperature does not preclude thermal compensation of other metabolic functions (see section IV).

B. THERMAL ACCLIMATION

Many poikilotherms demonstrate metabolic adjustments to their thermal regime. When one of these animals is transferred from one temperature to

another, its metabolic rate changes according to the normal Van't Hoff effect. However, compensation for temperature may occur with continued exposure to the new environment. The metabolic rate (and other physiological processes as well) may return toward the level that prevailed at the previous temperature. Such a process is termed thermal acclimation. If metabolic rate returns to the former level, acclimation is complete; incomplete return is termed partial acclimation.

Prolonged exposure to a given temperature has been shown to produce metabolic acclimation in reptiles under laboratory conditions. Correlation of metabolic rate with acclimation temperature has been reported in the follow-animals: *Urosaurus ornatus* (Vance, 1953), *Sceloporus occidentalis* (Dawson and Bartholomew, 1956), *Lacerta* spp. (Gelineo and Gelineo, 1955a, b; Gelineo, 1967a, b), *Anolis carolinensis* (Maher and Levedahl, 1959), *Thamnophis* spp. (Stewart, 1965; Jacobson and Whitford, 1970), *Uta mearnsi* (Murrish and Vance, 1968), *Diadophis punctatus* (Buikema and Armitage, 1969), *Natrix rhombifera* (Jacobson and Whitford, 1970), and *Python molurus* (Vinegar *et al.*, 1970). These findings contrast with the apparent absence of thermal acclimation in *Phrynosoma mcalli* (Mayhew, 1965), *Python reticulatus* (Vinegar *et al.*, 1970), and *Sceloporus occidentalis* (Bartlett, 1970), despite changes in the thermal environment. Extensive acclimation of metabolism to temperature is possible in reptiles, but is generally incomplete. Gelineo (1967a) and Gelineo and Gelineo (1955a, b) have investigated differences in ability to acclimate within the genus *Lacerta*. After two or three weeks, these investigators found partial (40–50%) metabolic compensation (i.e., metabolic rate returned approximately half-way toward the level prevailing at the previous acclimation temperature) in *L. muralis* and *L. sicula*, and complete metabolic compensation in *L. melisellensis* and *L. oxycephala*. Complete acclimation has not been observed in any other species of reptile, and it appears desirable to examine further the situation in these latter representatives of *Lacerta*. Representatives of *Anolis carolinensis* undergo partial metabolic compensation (50%) within three weeks at a new temperature (Maher and Levedahl, 1959). A specimen of *Python molurus* showed 57% acclimation within two weeks (Vinegar *et al.*, 1970).

The effects of acclimation on tissue metabolism in the garter snakes *Thamnophis sirtalis parietalis* and *T. s. concinnus*, cold- and warm-temperature forms respectively, have been investigated by Hoskins and Aleksiuk (1973a). In *T. s. parietalis*, cold acclimation increases the metabolic rate of cardiac muscle and decreases that of liver at low temperatures. The metabolic rate of skeletal muscle in this subspecies is increased by cold acclimation during summer, but not during winter. In *T. s. concinnus*, cold acclimation causes a decrease in metabolic rates of skeletal muscle and liver.

Thermal tolerances of reptiles also can undergo laboratory acclimation in

a manner that may indicate basic metabolic alterations. Critical thermal maxima or minima (temperature levels at which locomotor coordination fails) can be influenced by thermal acclimation in *Urosaurus ornatus* (Lowe and Vance, 1955), *Sceloporus occidentalis* (Larson, 1961), *Amphibolurus barbatus* (Bradshaw and Main, 1968), *Anolis carolinensis* (Licht, 1968), *Uta mearnsi* (Murrish and Vance, 1968), *Natrix rhombifera* (Jacobson and Whitford, 1970), and *Thamnophis sauritus proximus* (Jacobson and Whitford, 1970). Laboratory acclimation to high temperatures decreases the thermal preferendum of *Sceloporus occidentalis* (Wilhoft and Anderson, 1960), but that of *Anolis carolinensis* remains stable with changes in acclimation state (Licht, 1968).

Although acclimation of rates of oxygen consumption to temperature appears to require approximately two weeks, changes in preferred body temperature and critical thermal maximum (a measure of heat tolerance) may be complete within a day or two after transfer of the animals to new conditions (Ballinger and Schrank, 1970; Mayhew and Weintraub, 1971). The functional bases of these compensatory phenomena are completely unstudied in reptiles, but may involve shifts in isozymic patterns, as Hochachka has found in fish (see Fry and Hochachka, 1970).

The available information affords convincing proof that reptiles in the laboratory possess a suite of acclimation responses to temperature, which resembles that noted in other groups of animals. However, the nature and extent of thermal acclimation by these vertebrates in the field remains largely undetermined. In this connection, relatively little is understood about the factors involved in the production of seasonal differences in reptiles in the field. It is known that the ability of various tissues of *Thamnophis sirtalis* to acclimate metabolically varies seasonally (Hoskins and Aleksiuk, 1973a). In addition, Mayhew (1965) has linked low body temperature and seasonal depression of metabolic rate in hibernating *Phrynosoma mcalli* (hibernation and seasonal metabolic changes that may depend on a combination of factors are considered in section III.D.). Such a linkage appears unusual, for, as Roberts (1966) points out, lowering of metabolic levels in reponse to reduced body temperature in winter is quite the reverse of the usual acclimation response; when measured under identical conditions, an animal acclimated to a lower temperature normally has a metabolic rate exceeding that of one acclimated to a higher temperature. *Uta stansburiana* is the only reptile thus far demonstrated to have a higher level of metabolism at a given temperature in winter than in summer (Roberts, 1968a), as described in more detail in section III.D. This situation contrasts with the results of an earlier study (Roberts, 1966) in which metabolic level remained stable between winter and summer.

A principle criterion for thermal acclimation in reptiles in the field has been the demonstration of seasonal alteration of body temperatures occurring

during activity (Roberts, 1966). However, body temperatures measured over the portion of the year in which a species is active tend to remain remarkably constant, seasonal changes in body temperatures employed during activity having been demonstrated in relatively few reptiles. These include the lizards *Sceloporus orcutti* (Mayhew, 1963; Mayhew and Weintraub, 1971), *Trachydosaurus rugosus* (Warburg, 1965), *Sceloporus occidentalis* (McGinnis, 1966), and *Uta stansburiana* (Roberts, 1966). In all these cases, body temperature is lower during winter or early spring than during the rest of the year. In contrast to Roberts' (1966) results, Halpern and Lowe (1968) detected no seasonal difference in body temperatures of active *Uta stansburiana*. Seasonal differences in critical thermal limits have been observed in *Sceloporus occidentalis* (Larson, 1961) and *S. graciosus* (Mueller, 1969) and in preferred body temperatures in *S. undulatus* (Ballinger *et al.*, 1969), *S. graciosus* (Mueller, 1969), and *S. orcutti* (Mayhew and Weintraub, 1971). No seasonal difference in preferred body temperature has been found in *Sceloporus occidentalis* (McGinnis, 1966).

Seasonal alteration or stability of body temperatures utilized during activity, of preferred body temperatures, or of critical thermal maxima cannot be regarded as conclusive evidence for the presence or absence of metabolic acclimation to temperature in reptiles. An animal might undergo such acclimation in response to other things, e.g., temperatures prevailing during the inactive phase of its daily cycle, and still maintain these other thermal characteristics constant. Conversely, change in these characteristics may not have a significant influence on the state of metabolic acclimation to temperature. More direct studies of this form of acclimation are needed for reptiles under field conditions.

C. Circadian Oscillations of Metabolism

Circadian patterns in activity have been reported for reptiles (see, for example, Heath, 1962; Evans, 1966; Saint Girons, 1971), but their metabolic correlates have received relatively little attention. Kramer (1934) reported that stable, low metabolic rates in *Lacerta* occurred only at night; measurement of the animals in darkened chambers during the day did not produce minimal readings. Dmi'el (1970) detected a possible circadian rhythm in the metabolism of snake embryos. Roberts (1968a) noted that *Uta stansburiana* has nocturnal metabolic rates one-half to one-third of diurnal ones measured under identical conditions of darkness and fasting. Nocturnal measurements of *Uta* were also considerably less variable than diurnal ones. Metabolic rate of *Sauromalus hispidus* decreases approximately 50% at night (Bennett, unpublished data). Circadian fluctuations in metabolism have also been demonstrated in *Sceloporus cyanogenys* (Songdahl and Hutchison, 1972).

Metabolism in this lizard is higher during the light phase and during light–dark transitions than during the nocturnal phase of the daily cycle. Animals on short photoperiods have higher levels of oxygen consumption than those on longer ones. Parietalectomy and blinding do not affect these differences. *Xantusia henshawi* also has circadian metabolic rhythms, and nocturnal metabolism reaches as little as 30% of diurnal values (Mautz and Case, 1974). Circadian oscillations of metabolism in reptiles appear to have quite large amplitudes and these may allow significant conservation of energy during the inactive phase of the animals' daily cycles. Further research on circadian fluctuations of metabolism in members of this class is needed.

D. Seasonal Metabolic Changes and Hibernation

The nature and extent of seasonal fluctations in metabolic rates of reptiles have not been comprehensively analyzed. In certain species, such fluctuations appear to be small or lacking. For example, metabolism does not differ between spring and fall in *Pituophis melanoleucus sayi* (Baldwin, 1928). Measurements have not been obtained for this species in winter. Metabolic rate does not vary seasonally in *Lacerta oxycephala*, a lizard inhabiting the islands in the Adriatic Sea (Gelineo, 1967a). Whether this species hibernates (see below) is not recorded, but other insular species of closely related *Lacerta* do not (Gelineo and Gelineo, 1963). Metabolic level does not differ in *Sceloporus occidentalis* between winter and summer, either in populations where hibernation occurs or in ones where it is absent (Bartlett, 1970). Metabolism also remains stable or undergoes relatively little seasonal variation in reptiles living in the tropics or subtropics. Seasonal metabolic rhythms appear to be absent in *Alligator* and *Caiman* (Hernandez and Coulson, 1952). *Anolis carolinensis* does show a lower metabolic rate during spring than at other seasons, but the reduction amounts to only 10% (Dessauer, 1953).

In contrast to the metabolic stability evident in the species just cited, certain temperate zone reptiles do show seasonally labile levels of metabolism. One example of this lability is provided by *Uta stansburiana*, a non-hibernating desert lizard that, at 25–35°C, has metabolic rates during winter that are 20% higher than the comparable ones during summer (Roberts, 1968a); curiously, seasonal variation is not apparent in the rates obtained for this species at −5°C to + 5°C (Halpern and Lowe, 1968). Other documented instances of seasonal variation in reptilian metabolic levels involve temperate zone species that appear to hibernate. In contrast to the seasonal shift noted in *Uta stansburiana*, these animals typically show reduced metabolic rates in winter. Thus, *Lacerta sicula* (Gelineo, 1967b) and *L. vivipara* (Weigmann, 1932) have rates of oxygen consumption during winter that are only half those

recorded at identical temperatures between 14 and 29°C during summer. The metabolic rates of hibernating *Dipsosaurus dorsalis* (Moberly, 1963) and *Phrynosoma mcalli* (Mayhew, 1965) subjected to temperatures of 30–40°C are only 50–60% of the comparable ones observed in non-hibernating controls. Oxygen consumption of *Xantusia henshawi* during February is significantly lower than during April through July (Mautz and Case, 1974). Similarly, the metabolic rate of the snake *Storeria dekayi* is 27% lower at 30°C in winter than in spring (Clausen, 1936). An indication of seasonal metabolic variation has also been obtained under *in vitro* conditions. Oxygen consumption by isolated heart mitochondria from *Chrysemys picta* is lowest in late fall and winter and highest in summer (Privitera and Mersmann, 1966). However, activity of liver succinoxidase from the skink *Egernia cunninghami* remains stable seasonally (Barwick and Bryant, 1966).

The reductions in metabolic rate referred to above may act to conserve the energy resources of the reptiles during winter inactivity, when minimal maintenance is presumably all that is required. However, it should be noted that these reductions can be highly temperature specific (similar thermal specificity exists in the seasonal shift of metabolic rate described above for *Uta stansburiana*). Thus, unlike the situation at 30–40°C, *Dipsosaurus dorsalis* and *Phrynosoma mcalli* have metabolic rates at 15–25°C that match those of non-hibernating controls (Moberly, 1963; Mayhew, 1965). Likewise, the rates for *Storeria dekayi* at 10 or 20°C are similar between winter and spring, in contrast to the situation pertaining at 30°C (Clausen, 1936).

Hibernation in reptiles appears to involve several complex physiological modifications, particularly of factors related to metabolism. Consequently, this state does not, contrary to Hock's (1958) suggestion, represent merely a condition of cold-induced torpor. For this reason, Mayhew (1965) has proposed the term "brumation" to describe winter dormancy in ectothermic vertebrates. Although no difference in metabolic rate of hibernating field and non-hibernating captive *Storeria dekayi* was reported (Clausen, 1936), the more common finding is a metabolic depression in hibernating animals (*Phrynosoma cornutum*, Potter and Glass, 1931; *Dipsosaurus dorsalis*, Moberly, 1963; *Phrynosoma mcalli*, Mayhew, 1965). Preparation for hibernation begins well before winter. *Lacerta sicula* develops an insensitivity of metabolic rate to changes of body temperature in mid-autumn (i.e., Q_{10} for this function declines); the condition precedes a decrease in general levels of metabolism during the winter (Gelineo, 1967b). Hibernation may involve alterations in metabolic pathways and enzymatic activities. During existence in this state by the agamid lizard *Uromastyx hardwickii*, activities of liver succinic dehydrogenase and glucose-6-phosphate dehydrogenase decrease significantly, while that of lactate dehydrogenase increases (Hasnain and Ramwani, 1972).

Mayhew's work on *Phrynosoma mcalli* (1965) is the most detailed study

of reptilian hibernation. He characterized this animal as an "obligatory" hibernator because in winter it ceases to eat and becomes dormant even in the laboratory where food and high temperatures are available. This contrasts with the performance of "facultative" hibernators such as *Dipsosaurus* and *Uma* under these conditions. Dormancy and depression of metabolic rate are independently controlled in *Phrynosoma*, the former developing in response to decreased photoperiod and the latter, to reduced temperature. Some over-riding circannian sense must also exist, however, since alterations of light and temperature are only effective during the proper season. Loss of appetite occurs at the same time each year, independent of light and temperature conditions. Hoskins and Aleksiuk's (1973a) examination of the metabolic characteristics of *Thamnophis sirtalis* under hibernating conditions in the laboratory also serves to illustrate the complex basis of this phenomenon in reptiles. The rates of oxygen consumption by tissues of this snake were found to be influenced by a complex interaction of several factors: an inherent seasonal rhythm, state of thermal acclimation, temperature, and photoperiod.

Mayhew (1965) believes that the depression of metabolism at high temperatures in hibernating iguanids constitutes a significant economy, since the temperature of the soil in which these animals burrow sometimes reaches high levels during late fall and winter when they are dormant. Hibernation has received far less study in reptiles than in homeotherms. More extensive observations are required to ascertain the nature and extent of this process and its controlling factors in these poikilothermic vertebrates.

E. Food, Food Consumption, and Respiratory Quotients

The effects of feeding and starvation on reptilian metabolism have received only limited study. Benedict (1932) found that metabolic rate in large snakes (*Python*, *Boa*, and *Drymarchon*) increased three- to seven-fold within one or two days after a meal of small mammals. Metabolism returned to preingestion levels within a week after food intake. A meal of carbohydrates eaten by *Testudo* generally produced a doubling of the metabolic rate within a few hours, and the feeding increment disappeared within two days. Roberts (1968a) reported that metabolism increased 32% in *Uta stansburiana* after a meal of mealworm larvae and that one day was sufficient for the disappearance of this specific dynamic effect. Therefore, one or two days of fasting appear to be sufficient to obtain a post-absorptive condition for metabolic determinations, except in large, carnivorous reptiles. Short-term starvation appears not to alter resting metabolic rate, for weight-specific metabolism after feeding remains constant over at least ten days in *Gopherus* and *Testudo* (Benedict, 1932) and over at least two weeks in *Uta* (Roberts, 1968a). Prolonged fasting

(for more than 100 days) is accompanied by a decrease in metabolic rate equivalent to one-third in *Python* (Benedict, 1932) and one-half in *Sternotherus* (Belkin, 1965b).

Specific dynamic effects (ratio of calories expended over resting metabolic levels to calories of foodstuff assimilated) appear fairly low in snakes. Benedict (1932) obtained the following estimates for protein ingestion: 32% in *Python*, 9–19% in *Boa*; and 26% in *Drymarchon*. The specific dynamic effect of protein in mammals usually ranges between 30 and 40%.

Gross assimilation efficiency, the ratio of the calories assimilated to the total calories ingested in a meal, varies with diet in reptiles, as would be anticipated. Insectivorous lizards have high assimilation efficiencies: *Anolis carolinensis*, 54–89% (Licht and Jones, 1967) and 70% (Kitchell and Windell, 1972); *Sceloporus graciosus* and *S. occidentalis*, 83% (Mueller, 1970); *Lacerta vivipara*, 89% (Avery, 1971). The assimilation efficiency of juvenal *Natrix* for fish is also high, 80% (Gehrmann, 1971). The herbivorous lizards *Sauromalus obesus* and *Dipsosaurus dorsalis* extract 50–55% of the total caloric content of natural plant material ingested (Nagy, 1971). This relatively low assimilation is associated with an apparent inability to digest cellulose. The percentages for these herbivores contrast with assimilation efficiencies of 71% and 64% in cattle and rabbits, respectively, organisms having symbionts in their guts that facilitate digestion of cellulose (Brody, 1945). The relatively high efficiency (82%) of the herbivorous lizard *Ctenosaura pectinata* on a diet of sweet potatoes (Throckmorton, 1971) is thought by Pough (1973) to be linked with the low cellulose content of these tubers.

Rates of food consumption have been measured in or estimated for relatively few species of reptiles, all of them lizards. These values are compiled in Table XI. Avery (1971) used several methods to estimate energy expenditure by *Lacerta vivipara* in the field: determination of fecal production or nitrogen excretion by animals captured in nature, and of food consumption, oxygen consumption, and assimilation of food or growth by captive individuals. He found close agreement among these methods, except that concerned with measurement of growth, and concluded that the one dealing with fecal production was the simplest. The energetic impact of lizards upon the ecosystems of which they are part appears to be relatively small, but these animals may be important consumers of the productivity of certain species of the community. For example the insectivore *Uta stansburiana* dissipates only about 0·1% of the primary productivity of a creosote bush (*Larrea*) community (Alexander and Whitford, 1968). The herbivore *Sauromalus obesus* consumes 0·5% of the total primary production rate of the desert community of which it is a member, but this represents nearly 30% of the productivity of herbaceous annuals (Nagy, 1971).

Several attempts have been made to correlate diet and metabolic functions

TABLE XI

Energy consumption by lizards

Species	Body weight g	Energy (cal/[g × day]) consumed	assimilated	Basis[a]	Reference
Anolis carolinensis	5	81		LFC[b]	Dessauer, 1955
	4	85–103	76–92	LFC	Licht and Jones, 1967
	4	36–73	25–50	LFC	Kitchell and Windell, 1972
Cnemidophorus tigris	22		71	SC	Johnson, 1966
Lacerta vivipara	3·5	71	63	LFC	Avery, 1971
Sauromalus obesus	92·8	50	28	LFC	Nagy, 1971
Sceloporus graciosus	4·1	88–106	73–88	LFC	Mueller, 1970
S. magister	30		72	SC	Johnson, 1966
S. occidentalis	19		59	O_2	McNab, 1963
	13·3	43	36	LFC	Mueller, 1970
S. undulatus	15		55	SC	Johnon, 1966
Uta stansburiana	4		40	O_2	Alexander and Whitford,1968

[a]LFC—determined from food consumption in laboratory; SC—estimated from analysis of stomach contents; O_2—estimated from rates of oxygen consumption

[b]June

in reptiles. Bennett (1971, 1972b) in an investigation of respiratory metabolism in a carnivorous (*Varanus gouldii*, and in an herbivorous (*Sauromalus hispidus*) lizard found that the former has greater stamina and superior physiological capacities for supporting aerobic activity. Pough (1971, 1973) has suggested that, among other factors, metabolic rate is an important determinant of diet in members of several lizard families, particularly the Agamidae, Gerrhosauridae, Iguanidae, and Scincidae. In all these groups, smaller animals (less than 50–100 g) are generally carnivorous (insectivorous), whereas larger (more than 300 g) animals, even of the same species, are herbivorous. Although smaller animals have a higher weight-specific metabolic rate than larger animals, their total metabolic rate is lower. Energetic demands in smaller animals can thus be met with a diet of insects. Larger animals must switch to more abundant vegetable matter, which does not require as much energy to harvest, to meet their higher total caloric demands. Large carnivorous lizards of various families (Anguidae, Chamaeleonidae, Helodermatidae, Teiidae, Varanidae) possess morphological or physiological specializations for the acquisition of larger prey.

The stoichiometric ratio of carbon dioxide evolved to oxygen consumed, the respiratory quotient (R.Q.), can yield information on foodstuffs being catabolized by an animal. Values for R.Q.'s of reptiles are summarized in Table XII. Resting and fasting reptiles generally have R.Q.'s approximating 0·7. These values have been commonly accepted as indications of fat catabolism. However, Roberts (1968b) has pointed out that the R.Q. for protein catabolism also approximates 0·7 in uricotelic animals. Both fat and protein are catabolized in fasting *Uta stansburiana* having an R.Q. of 0·71 (Roberts, 1968b). For accurate determination of the nature of the foodstuffs oxidized, measurements of gas exchange should be accompanied by determinations of urinary nitrogen excretion, so that protein catabolism and non-protein R.Q.'s can be calculated.

Fluctuations of body temperature represent an important complication in the accurate determination of R.Q. in reptiles. Values for this ratio of less than 0·7 have repeatedly been reported in animals maintained at low temperatures (Hall, 1924; Potter and Glass, 1931; Benedict, 1932; Lüdicke, 1936; Dontcheff and Kayser, 1937; Kayser, 1940; Cook, 1949). Some of these anomalous ratios are as low as 0·4–0·5, figures that do not correspond to the catabolism of any known foodstuff. These low ratios persist for days or weeks, long after the animals have come to thermal equilibrium. With longer term exposure to low temperatures, the R.Q. returns to 0·7 (Potter and Glass, 1931; Lüdicke, 1936; Dontcheff and Kayser, 1937; Kayser, 1940). Complicated schemes of fat conversion to carbohydrate or incomplete oxidation of foodstuffs have been devised to explain these low values. However, they can be accounted for by retention of carbon dioxide in the blood at low

Respiratory quotients (R.Q.) of reptiles

Species	R.Q.	Remarks	Reference
Anguis fragilis	0·72	T_b[a] 6°–30°C	Vernon, 1897
Anolis carolinensis	0·91	T_b 28°C; 4-day fast	Dessauer, 1953
Chelydra serpentina	0·69	T_b 25°C	Hall, 1924
	0·7	T_b 20°C	Lüdicke, 1936
Chrysemys picta	0·81	T_b 22°C; fed control	Rapatz and Mussachia, 1957
	0·72	T_b 22°C; fasting	
	0·74	T_b 4°C; torpid	
Boa constrictor	1·46	T_b 20°C; acclimated 2 weeks	Rebach, 1973
	1·17	T_b 32°C; acclimated 2 weeks	
Emys sp.	0·98	T_b ca. 20°C	Issekutz and Vegh, 1928
Geochelone denticulata	1·47	after eating a banana	Benedict, 1932
	0·7	after long fast	
Geochelone gigantea elephantina	1·02	T_b 25°C	Hughes *et al.*, 1971
Lacerta major	0·65	T_b ca. 20°C	Kramer, 1934
L. sicula	0·70	T_b ca. 20°C	Kramer, 1934
L. viridis	0·70	T_b ca. 20°C	Kramer, 1934
	0·85	T_b 10°–35°C; 1-day fast	Nielsen, 1961
Natrix natrix	0·91	egg at 15°C	Bohr, 1903
	0·88	T_b 15°C; juvenile	
Phrynosoma cornutum	0·72	T_b 10°C; hibernating	Potter and Glass, 1931
	0·68	T_b 32°–35°C; summer	
Python molurus	0·93	T_b 33°C; non-incubating	Hutchison *et al.*, 1966
	0·90	T_b 33°C; incubating	
Sphenodon punctatus	0·70	T_a[b] 12°–14°C; fasting	Milligan, 1924
Terrapene carolina	0·93	T_a 35°–38°C	Altland and Parker, 1955
	7·9	T_a 35°–38°C; hypoxic environment (3–5% O_2)	
Testudo graeca	0·73	at all T_b's tested	Kayser, 1940
T. hermanni	0·7	T_b 20°C	Lüdicke, 1936
	0·91	T_b 25°C	Hughes *et al.*, 1971
Uta stansburiana	0·71	fasting	Roberts, 1968b
Lizards of five species	0·71	T_b 36°C	Cook, 1947

[a]Animals had body temperatures (T_b) that were stable at the levels indicated or at levels within the thermal ranges specified
[b]Ambient temperature

temperatures, as postulated by Hall (1924), and demonstrated by Dontcheff and Kayser (1937) and Kayser (1940). The bicarbonate concentration (alkaline reserve) in reptilian blood is temperature dependent, with an increased concentration at low temperature (Kayser, 1940). When an animal is placed at a lower temperature, a portion of the metabolically produced carbon dioxide that ordinarily would be expired is retained in the blood until a new equilibrium is established. When this occurs, R.Q. values return to the normal range. All of the deficit in the anticipated production of carbon dioxide can be accounted for by the increase of bicarbonate concentration in the blood (Dontcheff and Kayser, 1937). Carbon dioxide stored in the form of this ion is released upon warming of the animal. This effect is particularly pronounced in turtles, which normally have relatively high concentrations of bicarbonate in the blood, as well as low metabolic rates. It should be possible to obtain relatively high R.Q.'s in reptiles by warming the animals. This may account for some of the values between 0·9 and 1·0 reported in Table XII. Reptiles apparently must remain at a test temperature for several weeks prior to measurement, if a true R.Q. is desired.

F. Age

It is of interest to determine if any metabolic increment is associated with immaturity in reptiles, as is the case in other groups, e.g., mammals (Brody, 1945). This can be accomplished by comparing the metabolic rates of juveniles with estimates for adult reptiles of similar body size (Eqs [21] and [23]). Juvenal *Amphibolurus ornatus* (Dawson *et al.*, 1966) and *Sceloporus cyanogenys* (Wilhoft, 1966) have metabolic rates 10% below predicted levels for adult lizards of similar size. In March and April, juvenal *Uta stansburiana* are at metabolic levels similar to those that would be anticipated for adults of similar size (Roberts, 1968a). However, the rates of these juveniles during July are erratic and generally average about 28% greater than those of their adult counterparts. Dmi'el (1970) measured metabolism of hatchlings of five species of snakes. The metabolic rates of these young exceeded values predicted from Eq. (17) by an average of 11% (range: −14% to +48%). Measurements of hatchling turtles, *Chrysemys picta* and *Chelydra serpentina* (Lynn and von Brand, 1945), were 145% and 17%, respectively, greater than predicted for adult turtles of comparable size by Eq. (19). It is often difficult to determine the contribution of activity to these increments (see additional measurements on active hatchlings by Bohr, 1903, and Zarrow and Pomerat, 1937); small animals tend to be more restless in metabolic chambers than adults. Even so, most of these observations, except for juvenal *Chrysemys*, fall within the natural scatter of data about the regression lines. Therefore, no

well defined metabolic increment can be attributed to the juvenal condition in reptiles.

Little information is available on metabolism or growth by reptilian embryos. Metabolic measurements have been made on embryonic snakes (Bohr, 1903; Zarrow and Pomerat, 1937; Clark, 1953; Dmi'el, 1970) and turtles (Lynn and von Brand, 1945). Dmi'el (1970) reported that the lowest rates of increase in metabolism and growth during development occur in desert species of snakes. Lynn and von Brand (1945) found close agreement in metabolic measurements of embryonic *Terrapene*, *Chrysemys*, and *Kinosternon*; *Chelydra* embryos were larger and consumed oxygen more rapidly. Oxygen consumption increased exponentially until 10–20 days before hatching. It then stabilized at the level found for hatchling animals. The highest metabolic rates were reported during the process of hatching and those presumably reflect the exertion associated with emergence from the egg.

G. Sex

Most metabolic studies of reptiles do not allow determination of whether differences in rate exist between sexes, either because of small sample sizes or failure of the investigators to specify the gender of their experimental animals. In those cases where adequate data are available, females generally have been found to have the lower metabolic rates. For example, in *Storeria dekayi*, a small viviparous colubrid, metabolism of non-gravid females averages only 70% that of males from 10° to 30°C (Clausen, 1936). Rates of gravid females remain higher than those of non-gravid ones in this snake, being double at the beginning of the gestation period. Adult females of the lizard *Urosaurus ornatus* have metabolic rates equivalent to 60–80% those of adult males (calculated from Vance, 1953). Similarly, metabolic rates of female *Uta stansburiana* are only 75% those of males throughout the year (Roberts, 1968a). Perhaps much of the variation in the metabolic data for individual species of reptiles results from combining data for the two sexes. The basis of the different metabolic levels between males and females is both physiologically and ecologically interesting. Is the differential due to higher levels of activity in the males or is it a reflection of fundamentally higher metabolic levels in their tissues? Is it under hormonal control? These questions merit further examination.

H. Aggregation

Clausen (1936) has reported the only study dealing explicitly with the effects of aggregation on metabolic rate of reptiles. This concerned the brown

snake (*Storeria dekayi*), a species that normally aggregates in nature. During the initial three hours of measurement, metabolism of these animals in groups was only one-half to two-thirds that of isolated individuals. This situation was reversed with longer measurements. These results suggest that the metabolic differential may stem from activity. The metabolism of aggregated brown snakes is closer to that predicted by the general equations for resting metabolic rate in snakes—Eqs (15) and (17)—than is that of isolated animals (100% vs. 192% of the predicted value at 30°C). Creation of synthetic aggregations in which single brown snakes were tested in the presence of artificial snakes significantly reduced but did not abolish this differential.

White and Lasiewski (1971) have presented a hypothesis concerning the significance of the winter aggregations observed in several species of rattlesnakes that den at this season. These authors believe that denning behavior may keep these animals appreciably warmer than their surroundings by facilitating the retention of metabolic heat through reduction of the total area of body surfaces directly exposed to the air. Presumably, this would act to maintain metabolism at a relatively high level, owing to the relatively warm body temperatures. Evaluation of this hypothesis awaits physiological observations on the rattlesnakes in their dens.

IV. Metabolic Correlates of Activity

A. Aerobic Metabolism

The metabolism of reptiles has received much less attention during controlled activity than during rest (see Table I). This is understandable, since metabolic measurements of active animals are more difficult technically. Activity patterns of reptiles generally involve bouts of exertion interspersed with long quiescent periods. These animals seldom can be trained in the laboratory to exercise on treadmills or activity wheels. Determination of metabolic rate during periods of exertion has usually necessitated the fitting of the experimental subject with a head mask to minimize the lag in respirometer response. The subject is also restrained and electrical stimulation is usually required to elicit maximal struggling and metabolic rate. All these considerations markedly complicate the determination of the metabolism of reptiles during activity.

Bartholomew and Tucker (1963) reported the first systematic observations on the oxygen consumption of reptiles during physical exertion, using spontaneously active *Amphibolurus barbatus*. Representatives of more than a dozen additional species have subsequently been examined, with particular emphasis being placed on determination of their maximum rates of oxygen consumption at various temperatures. Several important generalizations have emerged from these studies. Spontaneous struggling does not appear to produce

maximal rates of oxygen consumption. If such rates are desired, electrical or mechanical stimulation should be employed. Electrical stimulation at body temperatures normally prevailing during activity produces rates of oxygen consumption in *Amphibolurus barbatus* two- or three-times higher than those observed during spontaneous exertion (compare Bartholomew and Tucker, 1963, and Wilson, 1974). Electrically stimulated *Uta stansburiana* consume oxygen at twice the rate noted in spontaneously active individuals of this

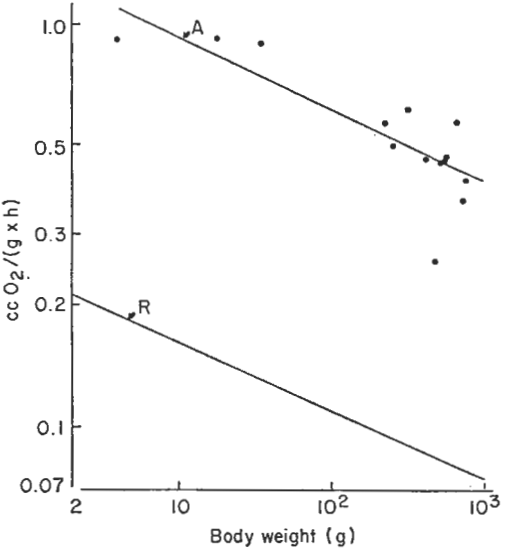

FIG. 12. The relation of weight-specific metabolic rate to body weight for reptiles during maximal activity at 30°C. The data are plotted on a double logarithmic grid. The equation of the least squares regression line for this relation (A) is described by the equation:

$$\log (\text{cc } O_2 \cdot g^{-1} \cdot h^{-1}) = \log 1{\cdot}40 - (0{\cdot}18)(\log g).$$

The line (R) illustrating the comparable metabolism–weight relation for reptiles resting at 30°C (see Fig. 2) is also plotted. See Eq. (27) in text and Table XIII for further details.

species (Alexander and Whitford, 1968; L. A. Roberts, personal communication). Spontaneous struggling by the turtles *Pseudemys scripta* and *Terrapene ornata* only occasionally produced aerobic metabolic rates as high as those observed during electrical stimulation (Gatten, 1973).

Maximal metabolic rates for 14 species of reptiles during activity at 30°C are assembled in Table XIII and illustrated in Fig. 12. The best least squares regression describing these data is

$$\text{cc } O_2/h = 1{\cdot}40\ g^{0{\cdot}82} \tag{26}$$

or

$$\text{cc } O_2/(g \times h) = 1{\cdot}40\ g^{-0{\cdot}18} \tag{27}$$

(n = 14; r = 0·81; 95% c.l. for b = 0·74, 0·90). The similarity of the exponent b in Eq. (26) to those observed in the equations describing metabolism-weight relations for reptiles resting at 30°C is of interest, for it indicates that the ratio

TABLE XIII

Maximum rates of oxygen consumption ($\dot{V}O_2$)[a] during activity by reptiles at 30°C

Species	Body weight g	Maximum $\dot{V}O_2$ cc O_2/(g × h)	Reference
Amphibolurus barbatus	239	0·553	Wilson, 1971, 1974
Cnemidophorus tigris	18	0·90	Asplund, 1970
Dipsosaurus dorsalis	35	0·89	Bennett and Dawson, 1972
Egernia cunninghami	260	0·496	Wilson, 1971, 1974
Iguana iguana	795[b]	0·40	Moberly, 1968a
Physignathus lesueurii	585	0·459	Wilson, 1971, 1974
Pituophis melanoleucus affinis	548	0·461	Greenwald, 1971
Pseudemys scripta	325	0·60	Gatten, 1973, 1974
Sauromalus hispidus	574	0·450	Bennett, 1972b
Tiliqua scincoides	493	0·252	Bartholomew *et al.*, 1965
Trachydosaurus rugosus	424	0·451	Wilson, 1971, 1974
Uta stansburiana	4	0·90[c]	Alexander and Whitford, 1968
Varanus gouldii	674	0·568	Bennett, 1972b
Varanus spp.	714	0·366	Bartholomew and Tucker, 1964

[a]Maximal rates of oxygen consumption obtained by direct (mechanical or electrical) stimulation of experimental subjects
[b]Mid-point of weight range for experimental animals
[c]Estimated from measurements at 25 and 35°C

of resting to maximal oxygen consumption is independent of body size at this temperature. According to Eq. (27), smaller reptiles can achieve higher weight-specific rates of oxygen consumption during activity than larger ones. A similar relationship has been found for active animals of other groups (Hemmingsen, 1960).

Maximal oxygen consumption of lizards usually has a pronounced thermal dependence below preferred body temperature (Q_{10} = 2 to 4), coupled with a metabolic plateau or decline in oxygen consumption at body temperatures above the preferendum. This is a valid description for all species examined in detail except *Varanus* spp., in which oxygen consumption during maximal

activity continues to increase with temperature above the preferred level (Bartholomew and Tucker, 1964; Bennett, 1972b). Determination of the applicability of this description to *Cnemidophorus tigris*, *Tiliqua scincoides*, and *Uta stansburiana* (Table I) awaits further observations on their oxygen consumption during maximal activity at various temperatures.

Aerobic metabolism of active snakes has received relatively little study to date. The only species thus far examined (*Pituophis melanoleucus*, Greenwald, 1971; *Spalerosophis cliffordic*, Dmi'el and Borut, 1972) have no plateau evident in their oxygen consumption during activity at high body temperatures. However, the activity of *Spalerosophis* during metabolic tests was not induced by direct stimulation. The rates of metabolism reported by Dmi'el (1972b) for four species of snakes during activity are not maximal and presumably constitute measures of oxygen debt.

The relationship between resting and maximal metabolic rates has been discussed by Fry (1947). He formulated the concept of metabolic scope, in which the differential between resting and maximal metabolic rates is an index of capacity for activity. The difference in maximal and resting rates of oxygen consumption has been measured and analyzed in several species of reptiles. As Moberly (1964, 1968a) pointed out, it is important to note that this represents only *aerobic* scope. Reptilian activity also depends to a considerable extent on anaerobic processes (see section IV.B.). Other assumptions in the concept of metabolic scope specify that maintenance processes are not temporarily abandoned during activity (Moberly, 1968a) and that the efficiency of muscular work is similar at different body temperatures (Bartholomew and Tucker, 1963). The latter was verified by Moberly (1968b) for *Iguana iguana*.

Fry's concept of metabolic scope (1947) is valid in general terms for reptiles; the slower, more sluggish animals, e.g. *Sphenodon* and *Tiliqua*, have smaller maximal aerobic scopes than do more active ones, e.g., *Amphibolurus* and *Varanus* (see Table XIII for references). However, since both resting and active oxygen consumption are size dependent, differences in aerobic scope can reflect differences in body size. Thus the relatively large weight-specific scopes of *Cnemidophorus tigris* (Asplund, 1970) and *Dipsosaurus dorsalis* (Bennett and Dawson, 1972) primarily reflect relatively small body size rather than specialized aerobic powers. On the basis of information on just a few species, Tucker (1967) postulated that lizards with aerobic scopes below 0·2 cc O_2/(g × h) usually engage in static defense and threat posturing rather than flight when threatened. Although subsequent investigations have shown that very few reptiles have scopes this low (see Table XIII for references), the linkage of comparatively limited abilities to mobilize energy aerobically and reliance on static defense seems generally valid.

Until recently, it has been impossible to determine any relation between

preferred thermal levels and the temperature for maximal aerobic scope (Dawson, 1967; Tucker, 1967; Templeton, 1970). This is rather surprising, since it would be anticipated that the capacity for activity should be greatest at body temperatures prevailing during normal activity. A recent analysis by Wilson (1971, 1974), based on more complete information than previously available, has indicated a good correlation between the temperature range over which aerobic scope is maximal and preferred body temperature (Table XIV). Aerobic scope does appear to be maximal near the preferred levels of body temperature in all animals examined (primarily lizards), except varanid lizards.

Comparison of Eqs (23) and (26) indicates a general increment of five- to six-fold between rates of oxygen consumption for reptiles at rest and during maximal activity at 30°C. At preferred body temperature, metabolic rate during maximal activity generally reaches three- to six-fold above resting levels in most species of lizards and in *Sphenodon* (Bartholomew *et al.*, 1965; Moberly, 1968a; Alexander and Whitford, 1968; Wilson and Lee, 1970; Asplund, 1970; Wilson, 1971, 1974; Bennett, 1972b). However, an increment of seventeen-fold has been measured in *Dipsosaurus* (Bennett and Dawson, 1972). The factorial increment can be highly temperature dependent, e.g., *Varanus* is able to increase its oxygen consumption 24-fold at 15°C, but only eight-fold at 40°C (Bennett, 1972b). Six- to nine-fold increments have been reported during spontaneous activity in *Python* (Benedict, 1932; Hutchison *et al.*, 1966; Vinegar *et al.*, 1970). *Pituophis melanoleucus* increases oxygen utilization twelve-fold during maximal activity (Greenwald, 1971). A three- to six-fold increment during spontaneous activity has been reported for turtles (Benedict, 1932; Hughes *et al.*, 1971). Increments of over twenty-fold during maximal activity have been observed in *Pseudemys scripta* and *Terrapene ornata* (Gatten, 1973, 1974). A twelve-fold increment was observed in spontaneously active *Alligator* (Benedict, 1932). These measurements suggest that snakes, turtles, and crocodilians have a relative greater capacity for mobilizing aerobic metabolism during activity than do most lizards. However, precise comparisons will have to await more extensive study of aerobic scope in the non-saurians; as noted previously, observations of spontaneously active animals generally do not yield maximal rates of oxygen consumption. Aerobic scope has thus far been adequately defined for only one snake, *Pituophis melanoleucus* (Greenwald, 1971), and two turtles, *Pseudemys scripta* and *Terrapene ornata* (Gatten, 1973, 1974). In these turtles the maximal value for this function occurs at 40°C. No data are available on scope in crocodilians.

Moberly (1968) has reported the most extensive study assessing the energetic cost of controlled, sub-maximal activity in reptiles. He found that the cost of walking in comparison to resting is high in *Iguana iguana*; the rate of oxygen consumption by this lizard at 35°C triples at a walking speed

TABLE XIV

Preferred body temperatures (PBT)[a] *and temperatures for maximal aerobic scope (modified from Wilson*, 1971, 1974)

Species	PBT (°C)	Approximate temp. for max. aerobic scope (°C)	Reference for aerobic scope
Sphenodon punctatus	18–19 or 25[c]	25·5	Wilson and Lee, 1970
Amphibolurus barbatus	35·7	35·0	Wilson, 1971, 1974
Cnemidophorus tigris	40·4	40·0[b]	Asplund, 1970
Dipsosaurus dorsalis	40	40	Bennett and Dawson, 1972
Egernia cunninghami	32·5	34·5	Wilson, 1971, 1974
Iguana iguana	33·4	32·5	Moberly, 1968a
Physignathus lesueurii	30·1	30·0	Wilson, 1971, 1974
Pituophis melanoleucus	26·7 or 30[c]	30·0	Greenwald, 1971
Sauromalus hispidus	37·1	38·0	Bennett, 1972b
Spalerosophis cliffordii	30	30–35	Dmi'el and Borut, 1972
Tiliqua scincoides	32·6	40·0[b]	Bartholomew *et al.*, 1965
Trachydosaurus rugosus	32·6	33·0	Wilson, 1971, 1974
Uta stansburiana	35·4	35·0[b]	Alexander and Whitford, 1968
Varanus gouldii	37·5	40·0	Bennett, 1972b
Varanus spp.	35·5	40·0	Bartholomew and Tucker, 1964

[a]Preferred body temperatures determined by observation of animals in experimental thermal gradients or by inference from thermal records for individuals active in nature

[b]More detailed observations of aerobic scope appear desirable in this species

[c]This higher temperature more accurately reflects the PBT of this species, according to Wilson (1971)

of only 2·2 m/min. The increment of oxygen consumption for walking at any given speed is independent of temperature in this animal. Efficiency of walking (distance travelled/calories expended) is greater at higher speeds. Moberly (1968b) found that walking speeds of *Iguana* could be divided into two categories: slower speeds (2·2–6·2m /min) that the lizards could sustain for over an hour with little accumulation of lactate in the blood, and higher speeds that they could only sustain for shorter periods in which considerable anaerobiosis occurred and exhaustion ensued (see Fig. 13). The maximal speed

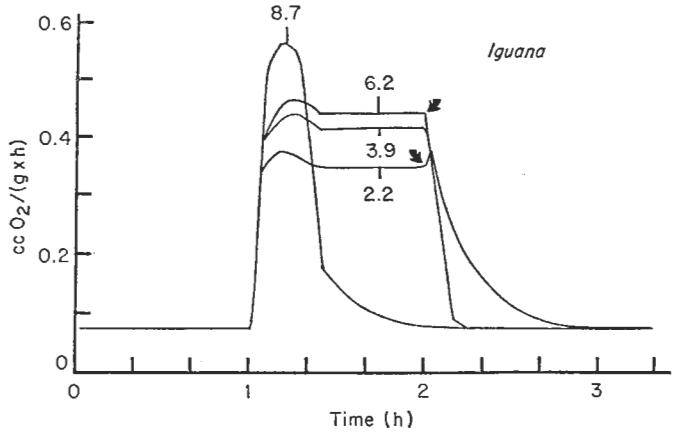

FIG. 13. Representative results concerning metabolic rates of an *Iguana iguana* exercising on a treadmill at 35°C (after Moberly, 1968b). The horizontal line extending over the first hour indicates the metabolic level prior to the onset of activity. The treadmill was started at the end of this period and kept in operation for the next hour, unless exhaustion occurred sooner. The number above each curve indicates walking rate in meters/min. The arrows indicate the point at which the treadmill was stopped in tests with animals walking at 2·2–6·2 m/min. The lizard became exhausted after a 17-min period of walking at 8·7 m/min.

sustainable by aerobiosis in *Iguana* is temperature dependent and highest at 35°C, a temperature close to that at which aerobic scope is greatest in this animal. At faster walking speeds, where reliance on anaerobiosis is extensive, a greater amount of activity could be sustained at 35°C than at other body temperatures (Fig. 14). These observations support Fry's (1947) assertion that aerobic scope is a valid measurement of the capacity for activity.

Bakker (1972a) reports that the cost of submaximal activity in lizards running on a treadmill is approximately 1·0 cc O_2/(g × km). Thus an increment of 1·0 cc O_2/(g × h) is required for every 1·0 km/h increment in running speed. This cost varies with body sizes in such a manner that b equals 0·67—see Eq. (1). This energetic cost for locomotion is approximately equal to or slightly less than that for mammals of comparable size moving at similar speeds. Therefore, the "sprawling" gait of lizards is judged to be no less

efficient than the "upright" locomotion of mammals. However, the latter can sustain much higher speeds because of their greater aerobic capacities. Preliminary metabolic measurements of active snakes (*Thamnophis*) suggest that limbless, crawling locomotion is more efficient energetically than the running of lizards (Chodrow and Taylor, 1973).

B. Anaerobic Metabolism

During periods of high energy demand, aerobic animals may supplement the catabolism of foodstuffs with oxygen via the mitochondrial enzymes with anaerobic metabolism. The only form of the latter known to be of significance for energy generation in such animals is the degradation of glycogen or glucose to lactic acid. A recent report (Hochachka, 1973) indicates that green sea turtles (*Chelonia mydas*) form succinate and alanine through amino acid catabolism during the anaerobiosis associated with diving. Whether these products appear during non-diving activity in other reptiles is unknown. The energy yield per molecule catabolized anaerobically is much less than in the aerobic scheme, and the accumulation of lactic acid may cause serious physiological disruptions of the blood equilibria. Some animals, particularly homeotherms, tolerate anaerobic conditions poorly. However, reptiles, with their limited capacities for oxygen transport, appear extremely reliant on and tolerant of energy generation by lactate production. The fact that such generation can be extremely rapid and independent of factors external to the metabolizing tissue make its consideration of particular importance in connection with activity. A further consideration of anaerobiosis is included in a subsequent portion of this review (see section V) dealing with metabolism in hypoxic environments.

During strenuous activity, most reptiles produce considerable quantities of lactic acid. This has been documented for *Pseudemys scripta*, *Terrapene ornata* (Gatten, 1973), *Alligator mississippiensis* (Austin *et al.*, 1927; Dill and Edwards, 1935; Coulson and Hernandez, 1964), *Crocodylus acutus* (Dill and Edwards, 1931b), *Iguana iguana* (Moberly, 1968a, b), *Sauromalus hispidus* (Bennett, 1971, 1973b), *Amphibolurus barbatus*, *Egernia cunninghami*, *Physignathus lesueurii*, *Trachydosaurus rugosus*, *Tiliqua scincoides* (Wilson, 1971), *Anolid carolinensis*, *Dipsosaurus dorsalis*, *Scincellz lateralis*, *Phrynosoma platyrhinos*, *Uta stansburiana*, and *Xantusia vigilis* (Bennett and Licht, 1972). The diffusion of this lactate into the blood causes a marked decrease in pH (Bennett, 1971, 1973b; Wilson, 1971; Gatten, 1973) and can significantly impair oxygen transport through the Bohr effect on the hemoglobin (Bennett, 1971, 1973b). Anaerobic metabolism during activity thus becomes self-reinforcing: lactate production decreases oxygen uptake and thereby increases reliance on anaerobiosis.

Varanus gouldii, a large carnivorous lizard, is a conspicuous exception to the general dependence of reptiles on anaerobic metabolism during vigorous exertion. It has an aerobic scope about twice that of other lizards of similar size, a characteristic linked with its possession of high myoglobin concentrations and of complex lungs with large surface area for gas exchange. Its lack of dependence upon lactate production during activity and highly effective proteinaceous blood buffers prevent the marked decrease in blood pH noted in other active lizards (Bennett, 1971, 1972b, 1973a, b).

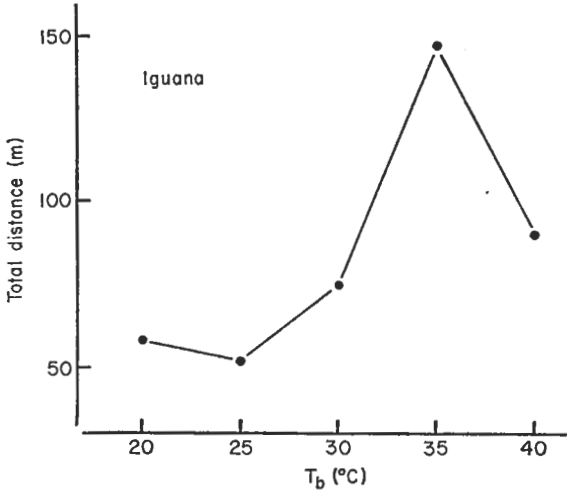

FIG. 14. The thermal dependence of total distance travelled by *Iguana iguana* before exhaustion, when walking at speeds in excess of those that can be sustained by aerobiosis alone. (Based on data from Moberly, 1968b.)

Anaerobic metabolism is generally detected by measurements of blood lactate. Levels of blood lactate normally range between 4–20 mg% in resting reptiles (Dill *et al.*, 1935; Edwards and Dill, 1935; Coulson and Hernandez, 1964; Berkson, 1966; Moberly, 1968a; Bennett, 1971; Wilson, 1971; Bennett, and Licht, 1972). Moderate activity, which can be sustained for considerable periods and supported aerobically, produces blood lactate levels of approximately 30–80 mg%. Moberly (1968b) found that iguanas attained blood concentrations of 28–48 mg% during walking at slow speeds. *Varanus gouldii* reaches blood lactate levels of 59 mg% during maximal activity (Bennett, 1971, 1973b). Prolonged or vigorous activity by other lizards leads to the rapid establishment of blood lactate concentrations in excess of 100 mg% and subsequent exhaustion (Dill and Edwards, 1931b; Moberly, 1968a, b; Bennett, 1971, 1973b; Wilson, 1971; Bennett and Licht, 1972).

Despite the attention devoted to determination of levels of lactate in the blood of active reptiles, these levels alone cannot be used to estimate the total amount of energy obtained anaerobically, owing to the dynamic and compartmentalized nature of the production and catabolism of lactate. This difficulty has been circumvented by assay of total lactate production during activity in reptiles (Bennett and Licht, 1972). The total amount generated

TABLE XV

Anaerobic capacity and anaerobic scope in several small lizards (after Bennett and Licht, 1972)

Species	Temperature °C	Anaerobic capacity[a] mg lactate/g	Anaerobic scope[b] mg lactate/(g × min)
Anolis carolinensis	20	1·02	1·24
	30	1·07	1·34
	37	1·19	1·54
Dipsosaurus dorsalis	37	1·56[c]	1·70
Phrynosoma platyrhinos	37	1·16	1·00
Scincella lateralis	12	1·13	—
	20	0·94	—
	30	0·88	—
Uta stansburiana	20	1·12	1·16
	37	1·12	1·78
Xantusia vigilis	12	1·15	0·54
	20	1·19	1·32
	30	1·32	1·54

[a]Total lactate produced during activity to exhaustion
[b]Rate of lactate formation during first 30 sec of activity
[c]After 10 min of activity

during activity to exhaustion varies little among species of small lizards (approximately 1·0 mg lactate/g of body weight) and is thermally independent (Table XV). The extremely thermophilic lizard *Dipsosaurus dorsalis* is an exception to these generalizations. Maximal lactate levels generated by this lizard (1·8 mg/g) are significantly higher than those observed in other species and only develop near the preferred body temperature (Bennett and Dawson, 1972). The rate of lactate production by lizards is maximal during the first half-minute of activity, the period in which struggling is most vigorous in response to electrical stimulation.

C. Comparison of Aerobiosis and Anaerobiosis during Activity

The partitioning of total energy expenditure into its aerobic and anaerobic components has not been widely attempted for reptiles. Oxygen consumption and lactate production can both be expressed in terms of the associated production of adenosine triphosphate, and thus compared. In such a comparison Moberly (1968a) estimated that at least 77% of the total energy utilized by *Iguana iguana* in 5 min of activity is derived from anaerobiosis. He did not

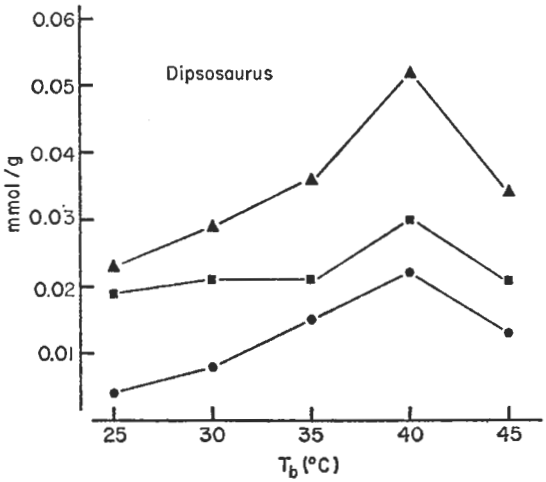

FIG. 15. Estimated weight-specific production of ATP (in mmol/g of body weight) by *Dipsosaurus dorsalis* during maximum activity produced by 2-min periods of electrical stimulation at various temperatures. Circles: ATP resulting from aerobic metabolism; squares: ATP resulting from anaerobic metabolism; triangles: total ATP resulting from both aerobic and anaerobic metabolism. (After Bennett and Dawson, 1972.)

take into account the presence of lactate in resting animals and a more precise estimate from his data is 64% (see Bennett and Licht, 1972). On the basis of measurements of total lactate production and estimates of aerobic scope, Bennett and Licht (1972) calculated that more than 80–90% of the total energy expended by a number of lizards during the first half-minute of activity is associated with lactate formation. Anaerobic and aerobic components of energy generation were simultaneously determined in *Dipsosaurus dorsalis* during a 2 min burst of activity (Bennett and Dawson, 1972). These measurements (Fig. 15) represent the first determination of total energy expenditure during activity. Anaerobiosis accounts for at least 58–83% of this expenditure, depending on the temperature. Both aerobic scope and lactate

production are greatest in *Dipsosaurus* near 40°C. Consequently, total energy expenditure is also greatest at this temperature, which is in the range normally associated with activity by this lizard in nature. The errors inherent in determination of the total expenditure favor exaggeration of the contribution of aerobic metabolism. Consequently, the percentages specified above for *Dipsosaurus* should be regarded as conservative estimates of the importance of anaerobic metabolism during activity. Over half the total energy utilization during 2 min bouts of activity by the turtles *Pseudemys scripta* and *Terrapene ornata* is derived from anaerobic pathways (Gatten, 1973, 1974). It appears that most of the energy for activity, particularly in its crucial initial phases, is derived from anaerobic glycolysis except in varanid lizards (see section IV.B). The low thermal dependence of anaerobiosis makes it an ideal system for energy mobilization in poikilotherms, in contrast to aerobiosis, which is strongly temperature dependent. The former is a metabolic system that operates only on demand and does not require large expenditures of energy for its maintenance. The disadvantages of large accumulations of lactate appear to be outweighed by the rapid responses in activity which the system permits (see Bennett and Licht, 1972).

D. Recovery

Recovery from activity can be monitored by determining either the repayment of the oxygen debt (the amount of oxygen consumed in excess of resting levels after a bout of activity) or the elimination of the lactate formed during the period of physical exertion. The former method measures both the alactacid (replenishment of oxygen stores and resynthesis of creatine phosphate) and the lactacid aspects of recovery. Measurement of lactate elimination permits independent consideration of the anaerobic debt. The only measurements of oxygen debt in reptiles are those of Bennett (1972b) for the lizards *Sauromalus hispidus* and *Varanus gouldii*. The former animal relies on anaerobic mobilization of energy during activity to a much greater extent than the latter (Bennett, 1971). Accordingly, its total oxygen debt can become much larger, particularly at high body temperatures. *Sauromalus* recovers from vigorous exertion most rapidly at 25–30°C; recovery is slower at 40° than at 20°C. In contrast, *Varanus* recovers most rapidly at 40°C. Its recovery at this temperature proceeds at three times the rate noted in *Sauromalus*. The extent of the oxygen debts developed with activity and the time courses of their repayment should provide useful insights concerning the nature of energy mobilization during vigorous exertion and the time required for recovery in reptiles.

Reptiles will only gradually eliminate the lactate formed during activity. This is indicated by the fact that the amounts of blood lactate produced in

Alligator mississippiensis with injections of adrenaline required nearly a day for total elimination (Coulson and Hernandez, 1964). Sea turtles (*Chelonia mydas*) require five hours to eliminate half the lactate burden acquired during a one-hour dive (Berkson, 1966). Only half the maximum amount of blood lactate had been removed an hour after activity in *Iguana iguana* at most body temperatures; however, this did not occur over two hours at 20°C (Moberly, 1968a). The recovery of *Iguana* progressed most rapidly at 35°C, near the preferred body temperature for this species. The rate at 40°C is intermediate to those at 30 and 25°C. Bennett (1972b) separated the lactacid and alactacid facets of the oxygen debt in *Sauromalus*. The former followed the same thermal pattern of clearance evident in *Iguana*, being most rapid at 35°C, near the preferred level of body temperature, and slower at 40 than at 30°C. The estimated rates of lactate removal were nearly twice as rapid in *Sauromalus* as those reported in *Iguana*. Bennett and Licht (1972) determined the rate of disappearance of total lactate following activity in *Anolis carolinensis*. The amount of this substance did not decline significantly in the first hour following the termination of exercise at 20°C. The initial rate of lactate elimination was most rapid at 30°C, near the preferred body temperature for *Anolis*, but total recovery occurred most rapidly at 37°C. Elimination of blood lactate was found to be a relatively poor indicator of total lactate clearance in this lizard. The elimination of the lactate formed during vigorous exertion by reptiles appears to be slow in comparison with its rapid formation and this appears to be an impediment to sustained activity.

E. Thermogenic Capacities

Metabolic rates in reptiles are so low and thermal conductances so high that thermogenesis is considered an insignificant factor in the heat economy of these animals (Beckman *et al.*, 1971). During activity, metabolic heat gains tend to be offset by increased heat loss through increased evaporation (Beckman *et al.*, 1971). However, an increase in body temperature during exercise has been noted in several large reptiles (see Benedict, 1932). Bartholomew and Tucker (1963, 1964) found individual increments as high as 1·8–2·0°C above ambient levels in large (>200 g) representatives of the lizards *Amphibolurus barbatus* and *Varanus* spp.; an increment of 1·0°C could be maintained for more than an hour by an intermittently struggling animal. An increment as high as 0·8°C above ambient is reported by Asplund (1970) for large (> 50 g) *Cnemidophorus maximus* at 37°C. Average increments of 0·4°C for *Sauromalus hispidus* (maximum, 1·5°C) and 0·2°C for *Varanus gouldii* (maximum, 1·3°C) were observed during activity (Bennett, 1972b). However, the body temperature of the latter species during activity is not significantly higher than that during rest.

An increase of body temperature during aggressive display has been reported in *Sceloporus occidentalis* (Engbretson and Livezy, 1972), a much smaller lizard than those just mentioned. Whether this increment results from thermogenesis or gain of heat from the environment is undetermined. Physical exertion can influence the body temperature of snakes (see below); Dmi'el and Borut (1972) report that representatives of *Spalerosophis cliffordii* became 1–3°C warmer during struggling. Preliminary observations indicate

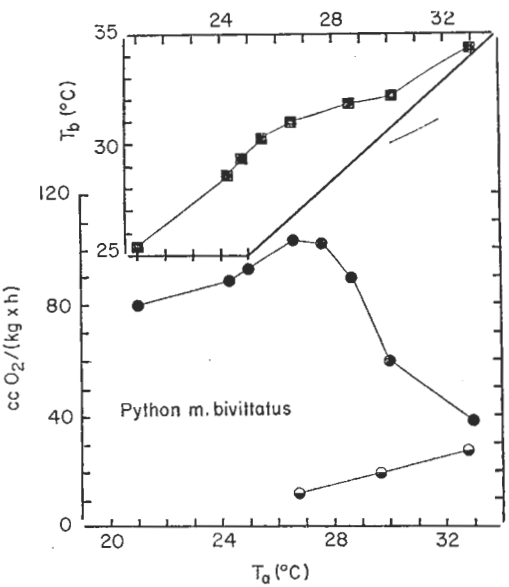

FIG. 16. Relation of body temperature (squares in upper graph) and metabolic rate (shaded circles in lower graph) to ambient temperature during incubation in the female Indian python (*Python molurus bivittatus*). The diagonal line marking the righthand boundary of the upper graph is the isothermal line ($T_b = T_a$). Metabolic rates in the absence of incubation are indicated by the half-shaded circles in the lower graph. (After Hutchison *et al.*, 1966.)

that muscular thermogenesis may also affect body temperature of leatherback sea turtles (*Dermochelys coriacea*). Thus these animals may be able to maintain themselves appreciably warmer than the surrounding water by this process (Friar *et al.*, 1972).

The importance of the thermal increments cited above in the natural thermal economies of the animals concerned is difficult to evaluate. Many of these measurements were made in confining metabolic chambers housed in temperature cabinets. The rate of heat loss under these conditions will be highly dependent on the thermal characteristics of the chamber and the rate

of air movement over the animal. The significance of metabolic heat generation during activity probably must ultimately be determined in field animals by use of telemetric methods.

The most spectacular instance of thermogenesis in reptiles, which concerns some incubating female pythons, requires special comment. Incubation of eggs within the genus *Python* has long been known (see Benedict, 1932), but the importance of the thermogenesis involved has only recently been quantified in *P. molurus bivittatus* (Hutchison *et al.*, 1966; Vinegar *et al.*, 1970). A female of this species will coil about her eggs and initiate spasmodic muscular contractions. This muscular activity can maintain the temperature of the snake and the eggs as much as 7·3°C warmer than the environment. Heat production is directly proportional to the frequency of the contractions. This frequency is adjusted in a manner serving to maintain body temperature between 30 and 35°C at ambient temperatures of 25–33°C; below 25°C the temperature of the egg mass falls markedly despite the female's continuing to produce heat at an elevated rate (see Fig. 16). Oxygen consumption of incubating *P. molurus bivittatus* at 27°C reaches approximately nine times the resting level for this temperature (Fig. 16). Indications of effective incubation behavior have also been found in other pythons: *P. m. molurus*, *P. curtus*, and *Chondropthon viridis*. However, *Python reticulatus* and *P. sebae* seem not to regulate the temperature of their egg masses by metabolic means (Vinegar *et al.*, 1970). *Python molurus* has a wider and more northerly distribution in Asia than does *P. reticulatus*, and Vinegar *et al.* (1970) believe that the capacity of the former for active thermoregulation of the eggs is a significant factor in its broader range. The thermostatic performance of incubating pythons seems to be unique among reptiles, and the mechanisms on which it depends must have evolved quite independently from those involved in the muscular thermogenesis of birds and mammals. The retention of the metabolic heat by these snakes is undoubtedly facilitated by their large body size and by their tendency to coil about the egg mass, which serves to reduce the effective area of body surface for heat loss to the environment.

There has been considerable speculation that the thermogenic capacities of dinosaurs exceeded those of modern reptiles, and some workers (Bakker, 1971, 1972; Ricqlès, 1972a, b, c) have maintained that members of this group were homeothermic. Several types of indirect evidence have been advanced to support this view, since it cannot be tested directly. First, it has been proposed (Bakker, 1971, 1972) that the fully erect posture exhibited by dinosaurs is evidence of activity levels and metabolic rates substantially surpassing those of modern reptiles. This interpretation has been challenged (Bennett and Dalzell, 1973; Feduccia, 1973) on the grounds that no logical association exists between these factors and that erect posture may have served other functions (e.g., support of a massive body). Second, it has been

concluded that predator/prey ratios among the fossil remains of dinosaurs resemble more closely those of communities of homeotherms than those of poikilotherms (Bakker, 1972). Resulting inferences concerning feeding rates and standing crop ratios in these groups have been challenged (Thulborn, 1973), and the enormously large size of the herbivores is bound to distort these ratios, ignoring for a moment the vagaries of fossilization. A third line of evidence, the most promising of all, involves the differential histological structure of bone in ectotherms and endotherms. Bone in the former is relatively poorly organized ("lamellaires-zonaires"), having few Haversian canals and very little secondary reorganization of spongy bone, in contrast to bone from endotherms ("fibro-lamellaires"), which is a metabolically active tissue with extensive reworking and well-developed Haversian systems (Ricqlès, 1972a, c). Bone from dinosaurs appears to have an organization very similar to that of modern endotherms. Whether these associations should be accepted as *de facto* evidence of homeothermy is at present unclear; it might be argued that the more active nature of dinosaur bone is the result of high, stable body temperatures (not necessarily metabolically maintained) or of the stress of supporting such a large body. However, the fact that tunas also possess fibro-lamellar bone (Ricqles, 1972a) lends support to a direct association between bone structure and endothermy.

It is difficult to imagine why dinosaurs might have controlled body temperature primarily by regulation of heat production. Bartholomew and Tucker (1964) calculated that no significant temperature differential between the body and the environment could be maintained by metabolic levels characteristic of ectotherms, since conductance is so high in reptiles. Therefore, an expensive increment in metabolic rate would have been necessary. However, bulk alone is sufficient to retard the dissipation of environmentally-acquired heat (Colbert *et al.*, 1946; Spotila *et al.*, 1973), and a thermally stable condition would have existed in large dinosaurs, even with low metabolic rates (Spotila *et al.*, 1973). If dinosaurs did possess an elevated metabolism, it may have been evolved in response to factors involved in activity metabolism, rather than in thermoregulation.

V. Metabolism and Survival in Hypoxic Environments

A. Survival under Anoxia; Critical Oxygen Tensions

Reptiles can survive for considerable periods in atmospheres of low oxygen content (Johlin and Moreland, 1933; Belkin, 1962, 1963, 1968b; Dodge and Folk, 1963; Jackson and Schmidt-Nielsen, 1966; Meyer, 1967; Boyer, 1967). Belkin (1963) has measured survival time by members of several different reptilian groups in atmospheres of pure nitrogen (Table XVI). Survival times of lizards, snakes, and crocodilians all approximate 30 min. Turtles can survive

exposures of from several hours to over a day in some cases (Johlin and Moreland, 1933; Belkin, 1963). Survival time in nitrogen is inversely correlated with temperature in the lizard *Holbrookia maculata* (Meyer, 1967).

TABLE XVI

Tolerance of anoxia in various families of reptiles (after Belkin, 1963)

Family	No. of species tested	Tolerance times (mean and range of means for species) (min)
	Turtles	
Kinosternidae	5	836 (480–1140)
Chelydridae	1	1050
Testudinidae	14	945 (495–1980)
Cheloniidae	2	120 (114–126)
Trionychidae	7	546
Pelomedusidae	2	980 (738–1218)
Chelidae	2	465 (360–570)
	Lizards	
Iguanidae	6	57 (22–79)
Gekkonidae	1	31
Teiidae	1	22
Scincidae	4	25 (20–30)
Anguidae	1	29
	Snakes	
Boidae	3	59 (41–61)
Colubridae	22	42 (25–84)
Viperidae	3	95 (64–118)
Elapidae	1	33
	Crocodilians	
Crocodylidae	1	33

The physiological effects of prolonged exposure to anoxia have been examined extensively in the turtle *Pseudemys scripta*. Isolated hearts remain beating in a completely anoxic medium, and, although heart rate decreases slightly, mechanical performance is unaffected (Reeves, 1963). Glycolysis can supply all the energy required by the anoxic tissue and levels of ATP remain intact (Reeves, 1963; Penny and Shmerdiak, 1973). Intact turtles are less tolerant of anoxia than are their isolated tissues (Clark and Miller, 1973;

Lai and Miller, 1973). During existence of these animals under anoxic conditions, extensive lactate production is accompanied by decreases in glycogen content, intracellular pH, and the ratio of NAD to $NADH^+$ in liver, brain, and heart tissue. Levels of ATP and creatine phosphate decrease even during periods of high glycolytic activity, and this suggests that this process is not efficient enough to generate the requisite energy for the intact animal. Death may result from cardiac failure.

Maintenance of cardiovascular function is essential for extended survival of turtles in nitrogen, suggesting that maintenance of a supply of substrates for glycolysis in the central nervous system is important in these periods (Belkin, 1968b). Reptiles produce considerable amounts of lactate during exposure to pure nitrogen, tolerating concentrations as high as 985 mg% in the blood (Johlin and Moreland, 1933). Survival appears to depend on a capacity for sustained anaerobic energy mobilization and, at least in turtles, a depression of metabolic rate (Jackson and Schmidt-Nielsen, 1966).

Differences in critical oxygen tension—i.e., the partial pressure of oxygen below which normal resting levels of oxygen consumption cannot be maintained—parallel those in survival time in the various reptilian groups (cf. Tables XVI and XVII). Lizards, snakes, and crocodilians have critical oxygen tensions of about 70 mmHg; turtles may maintain normal rates of oxygen consumption down to 8–15 mmHg O_2. In line with Fry's suggestion (1947), capacity for activity in lizards is strongly curtailed at oxygen concentrations below the critical tensions (Nielsen, 1962; Meyer, 1967). Nielsen noted reduced activity in *Lacerta* and *Tarentola* even at Po_2's as high as 114–137 mmHg.

B. High Altitude

The observations on critical oxygen tensions call attention to the interesting problem of reptilian survival under the chronic conditions of hypoxia prevailing at high altitudes. The only study on reptilian oxygen consumption as a function of altitude is the measurement of standard metabolism in highland and lowland forms of *Sceloporus malachiticus* (1200–3100 m = 3937–10 171 ft) and *S. occidentalis* (400–2400 m = 1312–7874 ft) (Bartlett, 1970). Minimal oxygen consumption at night is 30–45% higher in montane than in lowland populations of both species, when both are tested at low altitude. The physiological basis of this increment is unknown. Bartlett (1970) believes the metabolic differences are genetic and represent metabolic compensation for the lower activity temperatures and thermal preferenda of the montane lizards. The aerobic capacity for activity in species residing at high altitudes has not been studied and is of considerable interest, since a low partial pressure of oxygen might restrict aerobic scope (Fry, 1947; Nielsen, 1962).

TABLE XVII

Critical oxygen tensions for reptiles

Species	Temperature °C	Critical O_2 tension mm Hg	Reference
		Turtles	
Chelydra serpentina	25	<15	Boyer, 1963
	25	<18	Boyer, 1966
Pseudemys scripta	22	ca. 8	Belkin, 1965a
	24	38	Jackson and Schmidt-Nielsen, 1966
Sternotherus minor	22	8	Belkin, 1965a
Terrapene carolina	20–23, 35–38	>23–37	Altland and Parker, 1955
		Lizards	
Dipsosaurus dorsalis	25	74	Boyer, 1966
Lacerta viridis	20	72	Nielsen, 1961
Sauromalus obesus	15–40	>74	Boyer, 1967
Sceloporus occidentalis	15	<112	Bartlett, 1970
Tarentola mauritanica	20	72	Nielsen, 1961
		Snakes	
Farancia abacura	22	40	Belkin, 1965a
Pituophis melanoleucus sayi	25	ca. 74	Boyer, 1966
		Crocodilians	
Alligator mississippiensis	25	74	Boyer, 1966

Montane reptiles potentially have many problems in oxygen acquisition, particularly with regard to the transport of this gas by the blood. Even in lowland reptiles, the oxygen carrying capacity (Dawson and Poulson, 1962), oxygen affinity (Dill and Edwards, 1931b, 1935; Dill *et al.*, 1935; Edwards and Dill, 1935; Pough, 1969) and pulmonary oxygen saturation (Steggerda and Essex, 1957; White, 1959; Andersen, 1961; Tucker, 1966; Frankel *et al.*, 1966) are quite low. Mammals and birds exposed to high altitudes normally demonstrate compensatory increments in erythropoiesis and hemoglobin concentration. However, the evidence for similar responses by reptiles is, at best, ambiguous. In laboratory-simulated high altitude exposures, increased erythropoiesis does not occur in turtles exposed to simulated altitudes as great as 13 700 m (44 950 ft) (Sokolov, 1941; Altland and Parker, 1955); however, exposure of the lowland lizard *Dipsosaurus dorsalis* to a simulated altitude of 5500 m (18 040 ft) produces a 20% increase in hematocrit and hemoglobin concentration (Weathers and McGrath, 1972). Considerable information has been gathered on hematological variables in natural populations of highland sceloporine lizards, but the results are confusing. Highland populations of *Sceloporus jarrovii* have been reported to have a greater hemoglobin concentration than lowland forms (Vinegar and Hillyard, 1972), but another study showed no altitudinal trend in oxygen capacity of the blood in this species (Dawson and Poulson, 1962). An increment in oxygen capacity with increasing altitude is reported for *Sceloporus occidentalis* (Vinegar and Hillyard, 1972). Other studies on this species have found an increased hematocrit but no increment in hemoglobin content of the blood at high elevations (Weathers and White, 1972) and no altitudinal trend in blood oxygen affinity (Pough, 1969). Still other studies have reported increments in red blood cell counts in *Lacerta vivipara* (Richter, 1933) and in hemoglobin concentration in *Uta stansburiana* (Hadley and Burns, 1968) with increasing altitude. Some of the data summarized here are clearly contradictory, and a definitive statement about the role of alteration of hemoglobin concentrations in reptilian responses to high altitude is not possible at this time. In any case, the functional significance of any of these factors of oxygen transport in high altitude forms has not been analyzed. Reptiles, with poor systems for oxygen uptake to begin with, are liable to demonstrate entirely different patterns of adaptation to high elevation than are homeotherms.

A study of stamina and anaerobic metabolism during maximal activity by sceloporine lizards failed to reveal any altitudinal adaptation (Bennett and Ruben, 1975). The duration of activity did not differ significantly between groups of lowland *Sceloporus occidentalis* exercised at 61 and 3109 m, respectively. Moreover, the durations for these groups were similar to those noted for *S. occidentalis* and *S. graciosus* resident at high altitude. Lactic acid production and tolerance were also similar among all the groups. Bennett and Ruben

(1975) concluded that the basically anaerobic activity patterns of small lizards constitute a sufficient protoadaptation to permit colonization of montane situations involving altitudes of at least 3100 m, since these animals are largely independent of external oxygen supplies during maximal activity.

C. Diving

Diving is another natural activity in which oxygen is severely limited to that secured in body stores or that which can be extracted from the water (see section V.D). All groups of reptiles examined produce large amounts of lactate during diving: alligators (Andersen, 1961), snakes (Murdaugh and Jackson, 1962), turtles (Robin *et al.*, 1964; Berkson, 1966; Altman and Robin, 1969; Penny, 1974), and lizards (Moberly, 1968b). A recent report (Hochachka, 1973) indicates that green turtles (*Chelonia mydas*) also form succinate and alanine from amino acid metabolism during diving. As in activity metabolism in air, virtually all of the anaerobically derived energy is obtained from lactate formation. Although levels of succinate increases significantly in the blood of green turtles and in the liver of *Pseudemys scripta* during diving, the energetic contribution is only about 1% that for lactate formation (Hochachka, 1973, pers. comm.; Penny, 1974). As in diving mammals, lactate does not appear in high concentrations in the blood until after the termination of the dive (Andersen, 1961; Murdaugh and Jackson, 1962; Berkson, 1966). This is probably the result of curtailed perfusion of the skeletal musculature with blood during diving. Such curtailment would minimize the physiologically disruptive effects of lactate production by the muscles. The alligators, lizards, and snakes used in the studies cited above generally remained submerged 30–90 min. Turtles are capable of more prolonged diving; *Pseudemys scripta* withstand submergence for over five days (Robin *et al.*, 1964; Altman and Robin, 1969). The ability to mobilize and tolerate the production of energy through anaerobic glycolysis is the major factor responsible for these long dives; injection of iodoacetate, an inhibitor of glycolysis, reduces the tolerance by turtles of submergence to about an hour and causes death by drowning (Belkin, 1962; Jackson, 1968). Jackson (1968) and Jackson and Schmidt-Nielsen (1966) have measured by direct calorimetry the total metabolism of *Pseudemys scripta* during diving (see Fig. 17). Heat production during the first half-hour is maintained at pre-diving levels. This phase is accompanied by the rapid depletion of oxygen in the blood and lungs (see also Wilson, 1939). Metabolic rate declines over the next half-hour to approximately 20% of its original level. This reduced rate, which may persist for hours, represents completely anaerobic metabolism. Thus reptilian diving involves an impressive capacity for sustained anaerobiosis.

D. AQUATIC RESPIRATION

Extrapulmonary uptake of oxygen during diving has been demonstrated in several species of turtles. These include members of the Trionychidae (Gage and Gage, 1886; Dunson, 1960; Girgis, 1961) and Kinosternidae (Root, 1949; Belkin, 1968a). Very limited uptake also occurs in *Pseudemys scripta* (Jackson and Schmidt-Nielsen, 1966), but this does not significantly prolong survival time during submersion (Belkin, 1968a). Root (1949) found that approximately one-third of the aquatic oxygen uptake occurs in the buccopharyngeal region in *Sternotherus odoratus*. Pharyngeal uptake of oxygen in

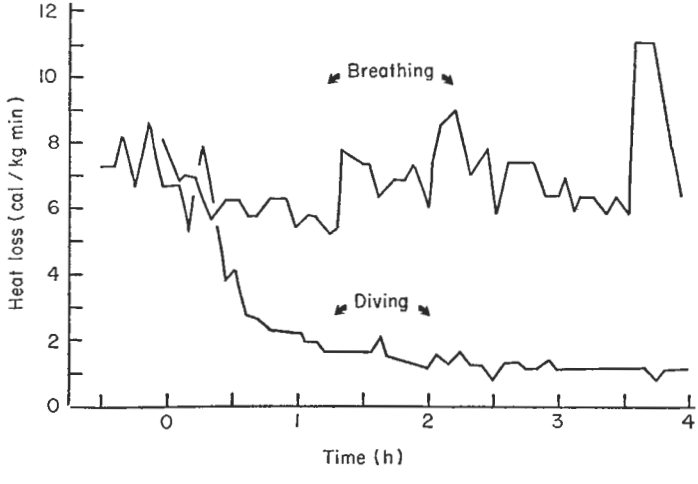

FIG. 17. Heat loss of a turtle (*Pseudemys scripta elegans*) while breathing (upper line) and during diving (lower line). A portion of the prediving record is included for the latter. (After Jackson, 1968.)

Trionyx spiniferus can reach higher levels than that occurring through either the skin or cloaca (Dunson, 1960). Girgis (1961) found that 30% of the oxygen consumption by submerged *Trionyx triunguis* is buccopharyngeal. Extraction of oxygen from water by members of the Trionychidae may be facilitated by the filiform projections present in the buccopharyngeal region.

The importance of the uptake of oxygen from water by turtles has been questioned (Root, 1949). The rate of oxygen consumption observed in submerged animals is only a fraction of that in air: 4–6% in *Pseudemys scripta* (Jackson and Schmidt-Nielsen, 1966; Belkin, 1968a) and 13–32% in *Sternotherus odoratus* (Root, 1949; Belkin, 1968a). However, total metabolism of the animals during diving is markedly reduced, judging by direct calorimetric measurements. As noted previously, these measurements indicate that

metabolic rate of diving *Pseudemys scripta* falls to 20% of pre-diving levels (Jackson and Schmidt-Nielsen, 1966). Consequently, aquatic oxygen uptake might well assume a major energetic role during quiet dives in kinosternids and trionychids. This view is supported by the fact that *Sternotherus odoratus* can survive much longer in water equilibrated with air than in that equilibrated with nitrogen. Representatives of this species can survive indefinitely if submerged in water saturated with oxygen (Belkin, 1968a).

A recent study (Graham, 1973) indicates that the sea snake *Pelamis platurus* can also obtain oxygen aquatically. Underwater survival time for this animal is directly proportional to the oxygen tension of the water. The site of this oxygen uptake is unknown at present.

VI. Effects of Hormones on Reptilian Metabolism

Thyroid hormone appears to have the same function in the maintenance and stimulation of metabolic rate in reptiles that it does in mammals (Lynn, 1970). Injection of thyroxine has been shown to produce a substantial rise in metabolism in the following lizards: *Anolis carolinensis* (Maher and Levedahl, 1959), *Lacerta muralis* (Maher, 1961), *Eumeces fasciatus* (Maher, 1965), and *Sceloporus cyanogenys* (Wilhoft, 1966). Thyroxine injections increase metabolism in brain, heart, kidney, liver, and lung (Maher, 1964). In all the above mentioned species, thyroxine was only effective in increasing metabolism when body temperatures were near preferred thermal levels (30°C or above), having no significant effect at lower body temperatures (20°C or below). Increased environmental temperature causes a rise in secretory activity by saurian thyroids (Eggert, 1936). This pronounced thermal dependence may be responsible for the lack of metabolic stimulation by thyroxine reported for a turtle (Drexler and Issekutz, 1935). Dried pituitary powder, but not thyroid powder, causes a rise in metabolic rate in alligators at 28°C (Coulson and Hernandez, 1964).

Thyroidectomy, either surgical or chemical, causes a decrease of 18–43% in resting metabolic rate of lizards at 30°C (Maher and Levedahl, 1959; Maher, 1965; Wilhoft, 1966). This reduction is similar to that reported for individual tissues from thyroidectomized rats (Barker, 1964). It thus appears that reptiles are not simply "mammals with hypothyroidism", but that the thyroid gland is actively involved in metabolism of these lower vertebrates to approximately the same extent that it is in mammals.

The role of epinephrine in reptilian metabolism during activity has not been extensively examined. This hormone is released during excitation and exposure to hypoxia in *Anolis carolinensis* (Rahn, 1956). Injection of adrenaline (the synthetic counterpart of epinephrine) immediately stimulates glycolysis and lactate formation in *Alligator* (Coulson and Hernandez, 1964). Blood

glucose levels also rise in response to these injections, but it takes 24 hours to achieve maximal concentrations. The effect of adrenaline appears to be temperature dependent in *Alligator*. Coulson and Hernandez (1964) concluded that the principal role of epinephrine release during activity would be stimulation of the breakdown of glycogen to lactate. Injections of noradrenaline increase the concentration of glucose in the blood of the turtle *Emys orbicularis* (Farkas, 1969). Moberly (1966) found an instantaneous rise of blood glucose in *Iguana iguana* at 30°C with injection of adrenaline. This involved a change from 60 mg% to over 250 mg%. This high level appeared to be maintained for up to 12 hours, after which a return toward resting levels commenced. Blood lactate also rose to peak concentrations within the first half-hour after injection, increasing from approximately 4 to 60 mg%. This elevated concentration persisted for about 8 h, after which it rapidly declined to resting levels. These results contrast with observations on iguanas exercising under conditions that would presumably foster the release of epinephrine (Moberly, 1968a). Blood glucose levels usually did not change appreciably in these lizards with activity. The effects of epinephrine in physiological concentrations are thus debatable at present.

Unlike the situation in mammals, nor-adrenaline does not stimulate the release of free fatty acids either *in vivo* in *Emys orbicularis* (Farkas, 1969) or *in vitro* from fat deposits in *Emys*, *Natrix natrix* (Farkas, 1969), *Sphenodon*, and the skink *Leiolopisma* (Nye and Buchanan, 1969). Perhaps this indicates that reptiles, unlike mammals, do not use free fatty acids as a source of energy during activity (see Drummond, 1971).

VII. The Enzymatic Bases of Metabolism

A. Presence of Metabolically Important Enzymes

The metabolically important enzymes of reptiles have received relatively little attention in comparison with those of some of the other classes of vertebrates. However, enzymes from all the principal energy-yielding pathways (glycolysis and gluconeogenesis, tricarboxylic acid cycle, electron transport system, and pentose shunt) have been identified in reptilian tissue (Table XVIII). Although activities may differ, reptiles exhibit a similar general pattern of enzymatic distribution as do the other vertebrate classes. Moreover, enzymatic assays developed for mammalian tissues appear effective for reptilian preparations. Extensive studies on the metabolism of intermediate compounds of glycolysis and the tricarboxylic acid cycle in *Alligator mississippiensis* (Coulson and Hernandez, 1964), *Chrysemys picta* (Mersmann and Privitera, 1964), *Egernia cunninghami* (Barwick and Bryant, 1966), *Pseudemys scripta* (Reeves, 1966), and *Uromastyx hardwickii* (Beloff-Chain and Rookledge, 1970) have all indicated that these animals employ metabolic pathways identical to those

TABLE XVIII

Identification of metabolically important enzymes of reptiles

Enzyme (Enzyme commission number)	Species	Source	Observation[a]	Reference
Adenosine triphosphatase (E.C. 3.6.1.4)	*Chrysemys picta*	cardiac muscle	A	Rotermund and Privitera, 1970
Adenylate kinase (E.C. 2.7.4.3)	*Chrysemys picta*	cardiac muscle	A	Kane and Privitera, 1968
Aldolase (E.C. 4.1.2.7)	*Lacerta agilis*	liver	A	Heinz and Weiner, 1969
	Natrix natrix	liver	A	Heinz and Weiner, 1969
	Pseudemys scripta	cardiac muscle	A	Reeves, 1966
	Testudo hermanni	liver	A	Heinz and Weiner, 1969
Citrate synthetase (E.C. 4.1.3.7)	*Lacerta* spp.	brain	A	Wegener and Zebe, 1971
Cytochrome oxidase (E.C. 1.9.3.1)	*Chelydra serpentina*	cardiac muscle	PS	Chan *et al.*, 1966
		liver	A	Morgan and Singh, 1969
	Crotalus adamanteus	cardiac muscle	PS	Bahl and Smith, 1965
	Dipsosaurus dorsalis	skel. muscle and liver	A	Bennett, 1972a
	Kinosternon subrubrum	liver	A	Morgan and Singh, 1969
	Pseudemys scripta	cardiac and skel. muscle	A	Robin and Simon, 1970
		liver	A	Morgan and Singh, 1969
	Sauromalus hispidus	skel. muscle and liver	A	Bennett, 1972a
	Terrapene carolina	liver	A	Morgan and Singh, 1969
	Varanus gouldii	skel. muscle and liver	A	Bennett, 1972a
	Xenochrophis piscator	skel. muscle	H	Talesara, 1972
Enolase (E.C. 4.2.1.11)	*Pseudemys scripta*	cardiac muscle	A	Reeves, 1966
Fructose diphosphatase (E.C. 3.1.3.1)	*Pseudemys scripta*	liver, cardiac and skel. muscle, kidney	A	Papademas and Penny, 1973
Glucose-6-phosphate dehydrogenase (E.C. 1.1.1.49)	*Lacerta* spp.	brain	A	Wegener and Zebe, 1971
	Mabuya carinata	tail	H	Shah and Ramachandran, 1973

	Uromastyx hardwickii	liver and kidney	A	Hasnain and Ramwani, 1972
Glucose-6-phosphatase (E.C. 3.1.3.9)	*Pseudemys scripta*	liver, cardiac and skel. muscle, kidney	A	Papademas and Penny, 1973
Glucose phosphate isomerase (E.C. 5.3.1.9)	*Pseudemys scripta*	cardiac muscle	A	Reeves, 1966
Glutamate dehydrogenase (E.C. 1.4.1.2)	*Agkistrodon halys*	skel. muscle	H	Ogata and Mori, 1964
	Eumeces latiscutatus	skel. muscle	H	Ogata and Mori, 1964
	Gekko japonicus	skel. muscle	H	Ogata and Mori, 1964
	Trionyx sinensis	skel. muscle	H	Ogata and Mori, 1964
Glyceraldehyde phosphate dehydrogenase (E.C. 1.2.1.12)	*Lacerta* spp.	brain	A	Wegener and Zebe, 1971
	Pseudemys scripta	cardiac muscle	A	Reeves, 1966
	Testudo horsfieldii	cardiac muscle	A	Bass *et al.*, 1973
Glycerin-1-phosphatoxidase (E.C. 1.1.99.5)	*Lacerta* spp.	brain	A	Wegener and Zebe, 1971
α-Glycerophosphate dehydrogenase (E.C. 1.1.1.8)	*Agkistrodon halys*	skel. muscle	H	Ogata and Mori, 1964
	Eumeces latiscutatus	skel. muscle	H	Ogata and Mori, 1964
	Gekko japonicus	skel. muscle	H	Ogata and Mori, 1964
	Lacerta spp.	brain	A	Wegener and Zebe, 1971
	Testudo horsfieldii	cardiac muscle	A	Bass *et al.*, 1973
	Trionyx sinensis	skel. muscle	H	Ogata and Mori, 1964
	Xenochrophis piscator	skel. muscle	H	Talesara, 1972
Glycogen phosphorylase (E.C. 2.4.1.1)	*Chrysemys picta*	cardiac muscle	A	McNeill *et al.*, 1971
	Emydoidea blandingii	cardiac muscle	A	Reeves, 1964
	Pseudemys scripta	cardiac muscle	A	McNeill *et al.*, 1971
		cardiac muscle	A	Reeves, 1964
Hexokinase (E.C. 2.7.1.1)	*Pseudemys scripta*	cardiac muscle	A	Reeves, 1966
	Testudo horsfieldii	cardiac muscle	A	Bass *et al.*, 1973
3-Hydroxyacyl-co-A dehydrogenase (E.C. 1.1.1.35)	*Lacerta* spp.	brain	A	Wegener and Zebe, 1971

(*Table XVIII continued page* 202)

Enzyme (Enzyme commission number)	Species	Source	Observation[a]	Reference
α-Hydroxybutyrate dehydrogenase (E.C. 1.1.1.30)	*Agkistrodon halys*	skel. muscle	H	Ogata and Mori, 1964
	Chrysemys picta	cardiac muscle	A	Mersmann and Privitera, 1964
	Eumeces latiscutatus	skel. muscle	H	Ogata and Mori, 1964
	Gekko japonicus	skel. muscle	H	Ogata and Mori, 1964
	Trionyx sinensis	skel. muscle	H	Ogata and Mori, 1964
Isocitrate dehydrogenase (NAD) (E.C. 1.1.1.41)	*Chrysemys picta*	cardiac muscle	A	Mersmann and Privitera, 1964
	Dipsosaurus dorsalis	skel. muscle and liver	A	Bennett, 1972a
	Sauromalus hispidus	skel. muscle and liver	A	Bennett, 1972a
	Varanus gouldii	skel. muscle and liver	A	Bennett, 1972a
Isocitrate dehydrogenase (NADP) (E.C. 1.1.1.42)	*Chrysemys picta*	liver, kidney, cardiac and skel. muscle	A	Klicka and Mahmoud, 1970
	Dipsosaurus dorsalis	skel. muscle and liver	A	Bennett, 1972a
	Sauromalus hispidus	skel. muscle and liver	A	Bennett, 1972a
	Sternotherus odoratus	liver, kidney, cardiac and skel. muscle	A	Klicka and Mahmoud, 1970
	Terrapene carolina	liver, kidney, cardiac and skel. muscle	A	Klicka and Mahmoud, 1970
	Varanus gouldii	skel. muscle and liver	A	Bennett, 1972a
α-Ketoglutarate dehydrogenase (E.C. 1.2.4.2)	*Chrysemys picta*	cardiac muscle	A	Mersmann and Privitera, 1964
Lactate dehydrogenase (E.C. 1.1.1.27)	all orders of reptiles	plasma	EI	Gorman *et al.*, 1971
	13 spp. of snakes	skel. and cardiac muscle, liver, lung, eye	E	Schwantes, 1973
	Agkistrodon halys	skel. muscle	H	Ogata and Mori, 1964
	Chelydra serpentina	skel. muscle	E	Mahmoud and Klicka, 1971
	Dipsosaurus dorsalis	skel. muscle and liver	A	Bennett, 1972a
	Eumeces latiscutatus	skel. muscle	H	Ogata and Mori, 1964

	Gekko japonicus	skel. muscle	H	Ogata and Mori, 1964
	Lacerta spp.	brain	A	Wegener and Zebe, 1971
	Pseudemys scripta	serum, brain, lung, kidney, liver, cardiac and skel. muscle	AE	Altman and Robin, 1969
		cardiac muscle	A	Reeves, 1966
	P. scripta elegans	cardiac and skel. muscle	A	Miller and Hale, 1968
	Sauromalus hispidus	skel. muscle and liver	A	Bennett, 1972a
	Testudo horsfieldii	cardiac muscle	A	Bass *et al.*, 1973
	Thamnophis sirtalis	skel. muscle	AE	Aleksiuk, 1971b
	Trionyx sinensis	skel. muscle	H	Ogata and Mori, 1964
	Varanus gouldii	skel. muscle and liver	A	Bennett, 1972a
	Uromastyx hardwickii	liver and kidney	A	Hasnain and Ramwani, 1972
	Xenochrophis piscator	skel. muscle	H	Talesara, 1972
Malate dehydrogenase (E.C. 1.1.1.37)	*Agkistrodon halys*	skel. muscle	H	Ogata and Mori, 1964
	Chrysemys picta	cardiac muscle	A	Mersmann and Privitera, 1964
		liver, kidney, cardiac and skel. muscle	A	Klicka and Mahmoud, 1970
	Eumeces latiscutatus	skel. muscle	H	Ogata and Mori, 1964
	Gekko japonicus	skel. muscle	H	Ogata and Mori, 1964
	Pseudemys scripta	cardiac muscle and liver	A	Penny and Kornecki, 1972
		cardiac and skel. muscle, liver	A	Penny and Kornecki, 1973
	Sternotherus odoratus	liver, kidney, cardiac and skel. muscle	A	Klicka and Mahmoud, 1970
	Terrapene carolina	liver, kidney, cardiac and skel. muscle	A	Klicka and Mahmoud, 1970
	Testudo horsfieldii	cardiac muscle	A	Bass *et al.*, 1973
	Thamnophis sirtalis parietalis	liver	AE	Hoskins and Aleksiuk, 1973b

(*Table XVIII continued page* 204)

Enzyme (Enzyme commission number)	Species	Source	Observation[a]	Reference
Malate dehydrogenase (E.C. 1.1.1.37)	*Trionyx sinensis*	skel. muscle	H	Ogata and Mori, 1964
	Xenochrophis piscator	skel. muscle	H	Talesara, 1972
Malic enzyme (NADP) (E.C. 1.1.1.40)	*Mabuya carinata*	tail	H	Shah and Ramachandran, 1973
Myosin adenosinetriphosphatase (E.C. 3.6.1.3)	*Amphibolurus ornatus*	skel. muscle	A	Licht, 1964
	Dipsosaurus dorsalis	skel. muscle	A	Licht, 1964
	Egernia carinata	skel. muscle	A	Licht, 1964
	Eumeces obsoletus	skel. muscle	A	Licht, 1964
	Gerrhonotus multicarinatus	skel. muscle	A	Licht, 1964
	Gymnodactylus milii (*Phyllurus milii*)	skel. muscle	A	Licht, 1964
	Sceloporus undulatus	skel. muscle	A	Licht, 1964
	Testudo horsfieldii	cardiac muscle	A	Bass *et al.*, 1973
	Uma notata	skel. muscle	A	Licht, 1964
Phosphoenolpyruvate carboxykinase (E.C. 4.1.1.32)	*Pseudemys scripta*	cardiac muscle and liver	A	Penny and Kornecki, 1972
		cardiac and skel. muscle, liver	A	Penny and Kornecki, 1973
Phosphofructokinase (E.C. 2.7.1.11)	*Dipsosaurus dorsalis*	skel. muscle and liver	A	Bennett, 1972a
	Pseudemys scripta	cardiac muscle	A	Reeves, 1966
		cardiac muscle	A	Penny and Shemerdiak, 1973
		cardiac muscle	A	Lobes and Penny, 1973
	Sauromalus hispidus	skel. muscle and liver	A	Bennett, 1972a
	Varanus gouldii	skel. muscle and liver	A	Bennett, 1972a
Phosphoglucoisomerase (E.C. 5.3.1.9)	*Pseudemys scripta*	cardiac muscle	A	Reeves, 1966
Phosphoglycerate kinase (E.C. 2.7.2.3)	*Pseudemys scripta*	cardiac muscle	A	Reeves, 1966

Phosphoglycerate mutase (E.C. 2.7.5.3)	*Pseudemys scripta*	cardiac muscle	A	Reeves, 1966
Phosphoglucomutase (E.C. 2.7.5.1)	*Pseudemys scripta*	liver, cardiac and skel. muscle, kidney	A	Papademas and Penny, 1973
Pyruvate kinase (E.C. 3.7.1.40)	*Dipsosaurus dorsalis*	skel. muscle and liver	A	Bennett, 1972a
	Pseudemys scripta	cardiac muscle	A	Reeves, 1966
		cardiac muscle and liver	A	Penny and Kornecki, 1972
		cardiac and skel. muscle, liver	A	Penny and Kornecki, 1973
	Sauromalus hispidus	skel. muscle and liver	A	Bennett, 1972a
	Varanus gouldii	skel. muscle and liver	A	Bennett, 1972a
Succinic dehydrogenase (E.C. 1.3.99.1)	*Agkistrodon halys*	skel. muscle	H	Ogata and Mori, 1964
	Chelydra serpentina	liver	A	Morgan and Singh, 1969
	Chrysemys picta	cardiac muscle	A	Mersmann and Privitera, 1964
	Dipsosaurus dorsalis	skel. muscle and liver	A	Bennett, 1972a
	Eumeces latiscutatus	skel. muscle	H	Ogata and Mori, 1964
	Gekko japonicus	skel. muscle	H	Ogata and Mori, 1964
	Lacerta spp.	brain	A	Wegener and Zebe, 1971
	Kinosternon subrubrum	liver	A	Morgan and Singh, 1969
	Pseudemys elegans	liver	A	Morgan and Singh, 1969
	Sauromalus hispidus	skel. muscle and liver	A	Bennett, 1972a
	Terrapene carolina	liver	A	Morgan and Singh, 1969
	Trionyx sinensis	skel. muscle	H	Ogata and Mori, 1964
	Varanus gouldii	skel. muscle	A	Bennett, 1972a
	Uromastyx hardwickii	liver and kidney	A	Hasnain and Ramwani, 1972
	Xenochrophis piscator	skel. muscle	H	Talesara, 1972
Triose phosphate isomerase (E.C. 5.3.1.1)	*Pseudemys scripta*	cardiac muscle	A	Reeves, 1966

[a]Methods used in making the observations are as follows: A, activity determination; E, electrophoresis; PS, purification and sequence determination; H, histochemical staining; I, immunological reaction

of mammals. Typical P/O ratios (3·0) are obtained for isolated heart mitochondria from turtles (Mersmann and Privitera, 1964; Privitera and Mersmann, 1966). The only major difference is an absence of detectable activity of ketohexokinase (E.C. 2.7.1.3) in reptilian liver (Heinz and Weiner, 1969). This is the principal enzyme involved in the entry of fructose into the glycolytic pathway in the liver of homeotherms. Fish and amphibians also lack hepatic ketohexokinase activity, and its presence in mammals and birds appears to be a new evolutionary development. The only reptile investigated, *Pseudemys scripta*, does not conform to the "constant proportion group" ratio of certain glycolytic enzymes found in different mammalian species (Reeves, 1966). Some aspects of gluconeogenesis may also differ between reptiles and homeotherms; several amino acids capable of stimulating carbohydrate formation in mammalian and avian tissues are ineffective in saurian liver and kidney slices (Zain-ul-Abedin and Katorski, 1967). Pathways of amino acid formation and interconversion in reptiles are similar to those reported for mammals (Coulson and Hernandez, 1965, 1968; Barwick and Bryant, 1966), although additional, previously undocumented interconversions have been reported in a lizard (Herbert, 1973). Fat catabolism may play a distinctly smaller role in energy metabolism of reptiles than in that of homeotherms (see section VI).

B. Enzymatic Activities

Enzymatic activities are notorious for their sensitivity to conditions of preparation and analysis and cannot readily be compared among different studies. Few comparative investigations involving reptilian material have been undertaken. These suggest that the distribution of enzymatic activities in different organs is similar to that in mammals. The protein-specific activities of mitochondrial (aerobic) enzymes are much higher in cardiac muscle than in liver, kidney, or skeletal muscle (Privitera and Mersmann, 1961; Klicka and Mahmoud, 1970) and higher in liver than in skeletal muscle (Bennett, 1972a). Glycolytic enzymes have higher protein-specific activities in skeletal muscle than in liver (Bennett, 1972a). Lactate dehydrogenase activity in skeletal muscle is higher than that in cardiac muscle or brain (Miller and Hale, 1968).

The considerable capacities for anaerobiosis in reptiles are reflected at the enzymatic level. *Dipsosaurus dorsalis*, a lizard with a very high anaerobic capacity (Bennett and Dawson, 1972), has a correspondingly high level of phosphofructokinase activity in skeletal muscle (Bennett, 1972a). The latter enzyme controls the rate-limiting step of glycolysis and a high activity indicates capacity for rapid anaerobiosis. The activity of lactate dehydrogenase in skeletal muscle and liver of *Dipsosaurus* is also high (Bennett, 1972a). The blood plasma of this species contains three-times the level of this enzyme noted in most other lizards examined and ten- to twenty-times that in mammals (H. Pough, personal communication). Turtles also show enzymatic

adaptations to the prolonged anaerobiosis occurring during diving. Activity of cytochrome oxidase, the terminal enzyme in the aerobic pathway, is considerably depressed during diving (Robin and Simon, 1970), whereas that of phosphofructokinase is increased two- to six-fold during anoxia (Penny and Shemerdiak, 1973). Both the aerobic (H) and anaerobic (M) subunits constituting the lactate dehydrogenase molecule are remarkably convergent

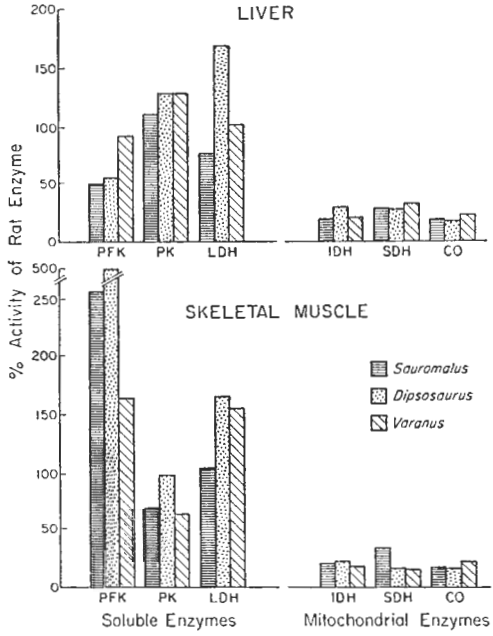

FIG. 18. Protein-specific activities of metabolic enzymes from the lizards *Sauromalus hispidus*, *Dipsosaurus dorsalis*, and *Varanus gouldii*, expressed as a percentage of the activity of the corresponding enzyme measured in tissue from laboratory rats. Abbreviations: PFK, phosphofructokinase; PK, pyruvate kinase; LDH, lactate dehydrogenase; IDH, NAD-linked isocitrate dehydrogenase; SDH, succinic dehydrogenase; CO, cytochrome oxidase. (From Bennett, A. F. *Comp. Biochem. Physiol.* **42B**, 637–647, 1972; reprinted with permission of the Editor.)

in the high degree of anaerobic tolerance they exhibit as well as in their molecular structure. Neither form is inhibited by high concentrations of pyruvate and both can continue to function in lactate production even during a prolonged dive (Miller and Hale, 1968; Altman and Robin, 1969; Beall and Privitera, 1973).

In a comparison of the activities of glycolytic enzymes and aerobic, mitochondrial enzymes in lizards and rats, Bennett (1972a) found that the former

have approximately equal protein-specific activities in the two kinds of animals. On the other hand, the activities of reptilian mitochondrial enzymes are only about a fifth those of the corresponding mammalian ones (see Fig. 18). A similar differential exists in the concentrations of mitochondria present in members of the two classes of vertebrates. These differentials correspond closely with that for resting metabolic rates between reptiles and mammals. Bennett (1972a) attributed the higher metabolic rate of mammals to a greater concentration of mitochondria rather than to increased activity of aerobic enzymes *per se*, since isolated reptilian and mammalian mitochondria show equal enzymatic activities (Mersmann and Privitera, 1964; Cassuto, 1971). The pattern of high glycolytic activity but low aerobic activity in reptiles has generally been supported by other comparative studies (Hack and Helmy, 1964; Ogata and Mori, 1964; Miller and Hale, 1968; Heinz and Weiner, 1969; Robin and Simon, 1970). Wegener and Zebe (1971) found approximately equal protein-specific activities of mitochondrial enzymes in brain tissue of *Lacerta* spp. and mammals and birds, but a general increase in the activity of aerobic enzymes between the lower and higher vertebrates. Bennett (1972a) postulated that an increase in mitochondrial concentration might have been the significant factor in the increased metabolic capacity associated with the evolution of homeothermy.

C. Thermal Dependence of Activity of Metabolic Enzymes

The paucity of work on the thermal dependence of enzymatic function in reptiles is surprising, considering the emphasis placed on thermobiology in physiological studies of these animals. Several investigations, particularly those of Russian workers, have dealt with denaturation temperatures and thermostability of reptilian enzymes. Consideration of this material is beyond the scope of this review (see Ushakov, 1964; Precht, 1968; Vinogradova, 1970), as differences in thermostability do not necessarily reflect the nature of differences in enzymatic function within the normal physiological range of temperature (Licht, 1967). Licht (1964) has examined intestinal alkaline phosphatase and myosin ATPase from several species of lizards. Activity of the former reaches a maximum at 42°C in all these animals, regardless of differences in their preferred levels of body temperature. On the other hand, the temperature range in which myosin ATPase attains maximal activity varies interspecifically and correlates well with these preferred levels of body temperature. These results strongly support the conclusion of Coulson and Hernandez (1964) that different enzymes have different thermal sensitivities. Thermal dependence of function by enzymes regulating activity in particular metabolic pathways, e.g., phosphofructokinase, pyruvate kinase, isocitrate dehydrogenase (NAD), is especially important. This requires investigation

before any meaningful assessment can be made of enzymatic adaptation of metabolism in reptiles.

The effect of temperature on activity of lactate dehydrogenase (LDH) has been examined in some reptiles. Maximal activity of plasma LDH is attained at distinctly lower temperatures in the lizard *Gerrhonotus multicarinatus* than in more thermophilic saurians (H. Pough, personal communciation). Aleksiuk (1971b) has measured the activity of this enzyme in skeletal muscle from northern and southern forms of the garter snake *Thamnophis sirtalis*. The enzyme from the northern animals displays a compensatory shift below 20°C which involves an increased affinity for the substrate. That from the southern animals shows a similar shift below 28°C, which in this case is caused by a decrease in activation energy at low temperatures. Since the M and H subunits of the lactate dehydrogenase molecule have different thermal sensitivities (H is more active at low temperatures), Aleksiuk (1971b) believes that the thermal shifts in total LDH activity are due to differing subunit activities. An increased affinity between enzyme and substrate with decreasing temperature has also been demonstrated for cardiac lactate dehydrogenase in *Chrysemys picta* (Beall and Privitera, 1973). Such relationships tend to counteract thermal effects on velocity, resulting in relatively stable rates of enzymatic catalysis over a wide thermal range (see Hochachka and Somero, 1973).

Hepatic malate dehydrogenase in *Thamnophis sirtalis* shows compensatory increments in enzyme substrate affinity (i.e., decreased K_m values) at low temperatures (Hoskins and Aleksiuk, 1973b). This increased affinity is responsible for the low thermal dependence ($Q_{10} \simeq 1{\cdot}7$) of the *in vitro* reaction rate at non-saturating concentrations of substrate. This enzyme also exists in two isozymes of differing thermal sensitivities. Differential isozymic activities and substrate affinities may serve to stabilize *in vivo* enzymatic rates over a broad thermal range and lead to a degree of homeostasis in poikilothermic animals (Fry and Hochachka, 1970; Aleksiuk, 1971a, b; Hoskins and Aleksiuk, 1973b).

VIII. Conclusion

Extensive investigations of a great variety of reptiles have revealed little diversity in resting metabolic rates within or among extant groups. Standard metabolic rate in these animals is fundamentally determined by body temperature and body size. The only notable exceptions thus far detected are xantusiid lizards and the rhynchocephalian *Sphenodon punctatus*, both of which possess far lower standard metabolic rates than would be predicted from general equations relating metabolic rate to body size in reptiles. The metabolic homogeneity evident in reptiles contrasts with the diversity of basal metabolic levels evident among different groups of mammals (see Kleiber, 1961, and Dawson and Hulbert, 1970) and birds (see Lasiewski and Dawson, 1967; Zar,

1968). It appears that the cost of maintenance has been a conservative parameter during reptilian evolution. This suggests that the primitive metabolic condition of this group was similar to that observed in its modern representatives. Any differentials in energy expenditure by present day reptiles result primarily from differences in thermal preferenda, size, and activity, since maintenance costs are otherwise equal.

In contrast to the physiological homogeneity apparent in resting metabolism, considerable accommodation to preferred thermal level and specific behavioral patterns is apparent in metabolic parameters involved in activity. These parameters include aerobic scope, heart rate increment, increment in oxygen pulse during activity, maximum sustainable walking speed, rate of blood lactate clearance, and plasma lactate dehydrogenase activity. These parameters are mainly concerned with oxygen procurement during activity and rapid repayment of oxygen debts. The ability to obtain energy anaerobically has been found to be thermally independent in all species investigated except *Dipsosaurus dorsalis*. This thermal independence permits rapid activity over a wide range of body temperatures. It appears that selection has maximized aerobic and recovery factors at preferred thermal levels, while establishing a broad anaerobic competence over a wide thermal range. Reptilian activity is primarily supported by anaerobic means, supplemented by aerobic systems. The latter were elaborated and became of greatly increased importance in the birds and mammals.

Although a considerable amount of information is currently available on metabolic rates of resting and active animals, little attention has been directed to the functional correlates of these factors or to more ecologically relevant aspects of reptilian metabolism. The physiological bases of such diverse aspects as sexual, circadian, and seasonal differences remain to be investigated. Reptilian enzymology and metabolic endocrinology are virtually unexplored. The formulation of energy budgets for reptiles in nature and the partitioning of the costs of various types of activity have only begun. Potentially, the utilization of reptilian material has a large contribution to make to both cellular biology and ecology, and the future of reptilian comparative physiology should be linked closely with these areas.

IX. Acknowledgements

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X. Dedication

We dedicate this review to the memory of Dr. Walter R. Moberly, our friend and colleague. His untimely death in 1969 prevented full realization of his exceptional promise as a student of reptilian metabolic physiology. Even so, a number of lines of investigation discussed here were significantly influenced by his work (see Moberly, 1963, 1964, 1966, 1968a, 1968b).

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