

Adaptations of Desert Organisms

Edited by J.L. Cloudsley-Thompson

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Homeostasis in Desert Reptiles

With 62 Figures and 40 Tables



Springer

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Front cover illustration: The Ornate dragon lizard (*Ctenophorus ornatus*) from Western Australia whose ecology and physiology has been extensively studied, both in the field and the laboratory, over a period of three decades.

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To Felicity,
for her priceless gift
of truth and love . . .
dont la pureté m'aide à vivre

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Perth, December 1996

S.D. BRADSHAW

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Introduction

Deserts, whether hot or cold, are considered to be one of the most difficult environments for living systems, lacking the essential free water which accounts for approximately 60–70% of their body mass and more than 98% of their constituent atoms (Macfarlane 1978). Amongst vertebrates, reptiles are usually thought of as the animals most adapted or suited to such environments because of their diurnal habit, based on a need for external heat, and their ability to survive far from obvious sources of water. This impression is reinforced when one examines the composition of vertebrate faunae characteristic of deserts and arid zones: reptiles predominate and they are often the only vertebrates to be found in hyper-arid areas, such as some parts of the Sahara (Monod 1973).

I recently had occasion to examine this assumption carefully, however, and was led inexorably to the conclusion that reptiles represent a particularly successful desert group, not because of their evolution of superior adaptations, but because of their possession of a basic suite of behavioural and physiological characteristics that suit them uniquely to this very resource-limited environment (Bradshaw 1986a). These fundamental reptilian characteristics are:

1. their low rates of metabolism, compared with birds and mammals, which result in extremely low rates of resource utilisation and lead to considerable economy in the handling of water
2. their dependence upon external sources of heat for normal activity (ectothermy) and their inherent ability to thermoregulate by behavioural rather than more expensive, physiological, means
3. their ability to excrete the nitrogenous waste products of protein digestion in the form of highly insoluble uric acid, thereby conserving water that would otherwise be osmotically obligated to a substance such as urea
4. their ability to withstand, for long periods of time, marked perturbations of the *milieu intérieur* which would prove fatal for birds and mammals
5. their widespread utilisation of behavioural avoidance as an effective tactic promoting survival during periods when continued activity would be counterproductive.

To deny that these above characteristics are desert adaptations begs of course the question of what one means by an “adaptation”. Certainly desert

reptiles are adapted to their environment in the sense that they are constitutionally suited to it, but, as Medawar (1951) pointed out over 40 years ago, we employ the word “adaptation” in at least three quite different semantic situations. We employ it regularly as a noun to describe particular traits (an adaptation), as well as in the form of an intransitive verb when considering adaptation as a process (the process of becoming adapted), and we use the gerund and past participle forms to infer an attained state of being (to be adapted).

Not surprisingly, the literature on adaptation reflects to some extent this semantic confusion and definitions of the term fall for the main into two quite divergent categories. The “evolutionary” definition of an adaptation rests on the demonstration that the characteristic arose as a result of selection for the particular trait in a given environment, and thus includes an historical context (Burian 1983; Gould and Vrba 1982; Williams 1966), whereas the other group of essentially functional definitions implies no such constraint (Bock 1980; Gans 1993; Greene 1988). As an example of the second, non-historical, definition Stern (1970) describes an adaptation as “any characteristic of an organism (or population) that causes its possessor to be, on average, at a higher level of adaptation than would occur in its absence” (p. 41). Gans (1993) suggests that it is only necessary “to demonstrate that the trait currently improves the fitness of the organism” (p. 403) for it to be considered as an adaptation.

Burian (1983) draws an important distinction between the use of the term “adaptation”, which he employs in an historical sense and the terms “adapted” and “adaptedness” which are always employed in an ahistorical context. He points out that biologists have routinely confused realised fitness (or relative reproductive success) with that expected on the basis of design features. Williams (1966) was also at pains to restore the importance of design considerations in evolutionary theory and noted that “an effect should not be called a function unless it is clearly produced by design” (p. vii).

As Burian (1983) goes on to point out: “As soon as natural selection is characterised as differential reproduction rather than differential reproduction in consequence of systematic or of design differences, one is impaired, by one’s mistaken choice of definitions, from distinguishing between selective and random accidental cases of differential reproduction” (p. 307). Thus, when claiming that a trait is an adaptation, Burian (1983) implies that:

1. the trait in question is an optimal – or at least the relatively best – engineering solution to a real problem bearing on survival of the organism
2. the design features that yield the high engineering fitness of the trait have been produced by natural selection – i.e. by differential survival of organisms with high expected fitness.

This rigorous use of the term “adaptation” contrasts markedly with the common practice amongst biologists to assume that any distinctive feature of an organism that is associated with reproductive advantage (i.e. realised fitness) for its bearers is an adaptation in an engineering sense. It was this

propensity that was attacked with great effectiveness by Gould and Lewontin (1979) in their widely influential "Spandrels of San Marco" paper.

Gould and Vrba (1982) were conscious of the need to use the term adaptation judiciously and they specifically coined the term "exaptation" to account for situations in which an obvious adapted state appears not to have evolved in situ through the action of natural selection but to be the felicitous consequence of selection in another, quite separate, environment.

For Gans (1988, 1993), the constraint of natural selection renders the evolutionary definition of adaptation cumbersome, as it demands historical extrapolation, whereas the simple test of fitness has the advantage of being more operational. Greene (1988) uses the term adaptation "to describe a feature that promotes a performance advantage, relative to the next most ancestral condition, that was associated with the origin of that feature . . . and does not imply a particular process such as natural selection in the origin of an adaptation" (p. 24). However, as Williams (1992) points out, although the study of variation in performance is very valuable and informative, it is not a reliable way to demonstrate adaptation. The inadequacy of the approach is most apparent when findings are negative as it is always easy to maintain that extraneous factors have masked or negated the expected performance advantage. A more reliable way of demonstrating adaptation, according to Williams (1992), is by observed conformity to a priori design specifications.

To exclude natural selection from definitions of adaptation may be more convenient in an operational sense, but it is as well to remember that Marjorie Grene, in an important early article, argued, on purely philosophical grounds, that it was better to exclude genetics from the study of evolution as phylogenies based purely on morphological evidence led to identical conclusions (Grene 1959). Few biologists today would concur with such a decision, even on the grounds of parsimony.

I prefer to consider reptiles to be "exapted" to deserts, but not specifically adapted to them, since, so far as one has been able to ascertain, all non-desert species share the same suite of characteristics, listed above, that suit desert species to living in hot regions lacking in water.

By identifying these characteristics as being inherently reptilian, as well as acknowledging that they account for the success of those numerous species which inhabit deserts, I believe that we facilitate the process of analysis. It forces us to ask what led to the evolution of this particular suite of characteristics; are they the result, for example, of selective pressures over the period when reptiles first emerged on land, and does this explain their commonality? Nonetheless, most of what we know of the behaviour and physiology of reptiles is based on a relatively small number of lizards, and desert lizards at that, and it may well prove the case that the above generalisations do not apply to all chelonians, snakes and unusual groups such as the pygopodids (leg-less or "snake" lizards) and Amphisbaenians (worm lizards).

The list of fundamental reptilian characteristics outlined above highlights the regulation of the milieu intérieur or "internal environment" and specifi-

cally suggests that reptiles are able to abandon or modify this physiological contract in the interests of long-term survival. It is the purpose of this book to examine this question in some detail, particularly in the case of desert-living species, in order to know whether they conform generally as vertebrates to this dictum or whether natural selection has intervened to uncouple their absolute dependence on a tightly regulated physiology for survival.

We owe to the French physiologist Claude Bernard the concept of the *milieu intérieur* or “internal environment” and to the American Walter Cannon (Cannon 1929, 1939) the term “homeostasis” or “homeostasis” as it is more usually spelled. Both concepts underpin the study of physiology, and the notion of homeostasis as an automatic self-regulating system now has much wider ramifications in fields as diverse as engineering, aerodynamics, economics and computing.

Claude Bernard is remembered for his famous aphorism concerning the constancy of the *milieu intérieur*

“La fixité du milieu intérieur est la condition de la vie libre, indépendante”

(Bernard 1878; p. 113) which has been variously interpreted, or misinterpreted, over the years. He develops his concept of the *milieu intérieur* more fully on the previous page, however, and it is worth quoting this in full:

“Il en est ainsi, parce qu'en réalité le milieu intérieur qui enveloppe les organes, les tissus, les éléments des tissus, ne change pas; les variations atmosphériques s'arrêtent à lui, de sorte qu'il est vrai de dire que les conditions physique du milieu sont constantes pour l'animal supérieur; il est enveloppé dans un milieu invariable qui lui fait comme une atmosphère propre dans le milieu cosmique toujours changeant. Je crois avoir le premier insisté sur cette idée qu'il y a pour l'animal réellement deux milieux: un milieu extérieur dans lequel est placé l'organisme, et un milieu intérieur dans lequel vivent les éléments des tissus” (p. 112).

“It is thus because, in reality, the internal environment which envelops the organs, tissues, and the elements within the tissues, does not change; atmospheric variations cease to have any influence at this point to such an extent that it is true to say that the conditions of the physical environment are constant in higher animals; they are enveloped in an unchanging environment which provides them with their own proper atmosphere in an ever-changing cosmic environment. I believe that I am the first to have proposed this idea that animals in reality possess two environments: an external environment in which the animal is situated and an internal environment in which are found the tissue elements” (my translations throughout).

It is important to note that Claude Bernard thought of the *milieu intérieur* as an environment composed of well-regulated physical elements and, although he never employed the term homeostasis in his writings (homéopathie was a common term but not homéostasie, and the word appears to have been coined by Cannon), he clearly envisaged a complex system of regulation to maintain the integrity and constancy of that same *milieu intérieur*. For example:

“La fixité du milieu suppose un perfectionnement de l'organisme tel que les variations externes soient à chaque instant compensées et équilibrées. Bien loin, par conséquent, que l'animal élevé soit indifférent au monde extérieur, il est au contraire dans une étroite et savante relation avec lui, de telle façon que son équilibre résulte d'une continuelle et délicate compensation établie comme par la plus sensibles des balances” (p. 113).

"The constancy of the internal environment implies a level of organisation of the organism such that external variations are continually being buffered and equilibrated. Even though it may appear as if the animal is quite independent from and insensitive to the external environment, this is far from the case as its state of equilibrium results from constant and delicate adjustments, as with the most sensitive of balances" (p. 113).

He also clearly enunciated the principle that "higher animals" benefit in their freedom over lower organisms through their possession and maintenance of a constant milieu intérieur, without which they would ever be at the mercy of the external environment:

"Ceci nous fait comprendre qu'il ne saurait y avoir de vie libre, indépendante, pour les êtres simples, dont les éléments constitutifs sont en contact direct avec le milieu cosmique, mais que cette forme de la vie est, au contraire, l'apanage exclusif des êtres parvenus au summum de la complication ou de la différenciation organique" (p. 113).

"This shows us that there is no such thing as a free or independent existence for simple organisms, whose constituent elements are in direct contact with the external environment, such an existence being reserved for those organisms that have reached the summit of organisation and biological differentiation" (p. 113).

Nowhere, however, does he expand on what he means precisely by "higher animals" although it has been taken by generations of physiologists to mean vertebrates, and with the emphasis clearly on humans and other mammals. Certainly, Claude Bernard's use of the term "êtres simples" (simple beings) in the above quotation would suggest that he was referring to invertebrates when condemning them to a life controlled by the exigencies of the external world.

Nor does he speculate on the origins of this complex system of regulation which is the key to the exploitation by vertebrates of such a diversity of habitats. He seems never to have seriously considered the question of evolution, even though writing some 20 years after the publication of Darwin's "On the Origin of Species", but this may reflect the fact that Darwin's views were not widely known or discussed in France at that time.

"Comme toutes les idées dont le sens s'est dégagé lentement, l'idée de l'évolution est énoncée partout et précisée nulpart" (p. 384).

"As with all ideas that have developed slowly, the concept of evolution is utilised everywhere, but never clarified" (p. 384).

Claude Bernard thus appears as perhaps the first true general physiologist – fundamentally mechanistic, opposed to vitalistic concepts and depending for his success upon the novel combination of vivisection aided by chemical analysis (Fرتون 1979). His influence on the development of the science of physiology was considerable, especially after moving from the Collège de France to the Muséum National d'Histoire Naturelle in 1868. It is perhaps difficult for us now to appreciate the impact of his discovery that the liver manufactures sugar, since at the time it was believed that only plants were capable of synthesising the sugar exploited by animals as a source of energy. This discovery came from his research with dogs, the aim of which was to uncover the cause of diabetes. Although the animals were fed on meat alone, they nonethe-

less had glucose circulating in their blood. This provided conclusive proof of the ability of the liver to manufacture carbohydrates – a virtual heresy at the time. He also made much of the fact that a study of anatomy alone was insufficient to discover the wider secretory capacity of the liver and hence the need for this new discipline of general physiology.

His concept of the *milieu intérieur* also had far wider implications in a philosophical sense than perhaps most physiologists today realise. Bernard's time was uniquely preoccupied with questions of vitalism versus determinism and his concept offered a way of resolving the two apparently opposed points of view (Dagognet 1984). It is only through the meticulous regulation of their internal state that "higher" organisms are able to achieve a large degree of independence from the constraints of their immediate environment. Their *liberté* or freedom is thus achieved through a tight and mindless control of their internal constituents. Might not such ideas have appealed to nineteenth century philosophers who were struggling to account for freedom of will in a world increasingly given to more and more mechanistic explanations of natural phenomena? One only has to generalise Claude Bernard's dictum to society in general to see its potential appeal and understand its ready acceptance by physiologists and the educated avant garde alike. At a time of great social upheaval in France, immediately following the Prussian war of 1870 and just prior to the commune, the idea that social harmony and peace can best be achieved by a strict control of the freedom of movement and expression of the lower elements in that society must have had considerable intrinsic appeal.

In just the same way that Darwin unwittingly provided Herbert Spenser with a rationale for an hereditarily structured class society in early capitalistic Victorian England – "nature red in tooth and claw" eliminating the unfit and ensuring the continuance of a lower class conditioned to its inevitable "place" in society – Claude Bernard's concept of the *milieu intérieur* offers a seductive model of how political stability and independence for the few may be achieved.

It is just because Claude Bernard's concept of the *milieu intérieur* has been so widely accepted and subjected to so little criticism or analysis since first enunciated over 120 years ago that we need to examine its general validity, especially in the case of "lower" vertebrates such as reptiles. Implicit in the concept is the notion of some normal or ideal state to which the physiology returns following significant perturbation, all other states being considered, by definition, pathological. Nowadays we would replace the idea of a normal resting state with that of a battery of set points, and Selye (1972) also pointed to situations in which the normal state is bypassed but all regulation is not lost. He coined the term "heterostasis" to account for the establishment and maintenance of balances in non-normal states. Mrosovsky (1990) has recently introduced the term "rheostasis" to describe "regulation around shifting set points" as, for example, with the case of fever in mammals, in which the body temperature is elevated above its normal set point, but regulated nonetheless.

By the use of the comparative method I should like to consider in some detail a series of specific propositions in the ensuing text:

1. that reptiles, in common with other vertebrates, share a common “normal state” that is maintained in the face of environmental challenges
2. that reptiles show evidence of homeostasis in the sense originally defined by Cannon as “the coordinated physiological processes which maintain most of the steady states in the organism”
3. that desert-living species of reptiles enhance their chances of survival during critical periods by abandoning or “loosening” basic homeostatic constraints, albeit at some cost.
4. that the purely physiological concept of homeostasis may be fruitfully extended to include behavioural adaptations as well as regulations that transcend the individual and operate instead at the level of the population.

I am conscious of the fact that the classical comparative methodology has recently come under attack from those who rightly point out that widely disparate groups of organisms cannot be simply compared without due regard for their phylogenetic affinities (Felsenstein 1985; Harvey and Pagel 1991; Harvey and Purvis 1991; Pagel and Harvey 1988). This is often far easier, however, to say than to do and to the extent that adequate phylogenies exist for the various reptilian groups, I have tried in the following to use the historical information inherent in the phylogeny to temper the conclusions offered by simple comparisons of physiological and other attributes.

The Osmotic Anatomy of the Reptiles

1.1

Evidence for Homeostasis

As we have seen, Claude Bernard's concept of a protected milieu intérieur referred to the physical elements within the tissues which are maintained at levels and concentrations different from those found in the external environment by the operation of homeostatic mechanisms. The notion of homeostatic mechanisms regulating the functional behaviour of machines is now a commonplace but it is important to note one fundamental difference when dealing with living organisms. Homeostasis in engineered artefacts results from inbuilt design constraints (aerodynamic stability in a flying object for example depends entirely on the location of the centre of gravity relative to the lift-generating surface) whereas that in animals is more often the result of purposive behaviour which may be modulated by specific chemicals secreted internally in the form of hormones. Evidence of homeostasis in animals may thus be sought at two levels: in the temporal stability of the chemical structure of the tissues themselves, and by the identification of hierarchical control systems impacting on the composition of the tissues through the maintenance of set points.

1.2

A Comparative Account

Bentley (1971) briefly reviewed the chemical composition of reptilian plasma and intracellular fluid in relation to other vertebrates and again, in more detail, in Bentley (1976). Table 1.1 draws together some of these data on chemical concentrations and suggests that plasma sodium is less than constant in lower vertebrates (fish, amphibians and reptiles).

Where there are data from more than a single season, or a single milieu, the variations for the fish, amphibians and reptiles listed fall in the range of 30–60%, whereas seasonal variations for the birds and mammals are much lower, of the order of 7%. This trend is not universal however as with the case of one desert lizard from Australia (*Ctenophorus nuchalis*) where the variation in plasma sodium concentration recorded between spring and summer was less than 1%.

Table 1.1. Chemical composition of the extracellular and intracellular fluid compartments in representative vertebrates

Taxon ^a	Extracellular fluid (mmol l ⁻¹)					Intracellular fluid (mmol kg ⁻¹ H ₂ O)			
	Na ⁺	K ⁺	Cl ⁻	Urea	Osmol- ality	Na ⁺	K ⁺	Cl ⁻	Osmol- ality
Agnatha									
<i>Myxine glutinosa</i> ¹	549	11	563		1152	132	144	107	990
<i>Lampetra fluviatilis</i> ²	120	3	96		270				
Chondrichthyes									
<i>Raja clavata</i> ³	289	4	311	444	1050				
<i>Chimaera montrosa</i> ⁴	360	10	380	265					
Osteichthyes									
<i>Platichthyes flesus</i> ⁵									
Seawater	194	5	166		364	10	157	30	
Fresh water	157	5	114		304	15	158	42	
<i>Latimeria chalumnae</i> ⁶	181		199	335	1181				
<i>Protopterus aethiopicus</i> ⁷	99	8	44		238				
Amphibia									
<i>Bufo viridis</i> ⁸	113	5	99	16	279	30	95	17	
<i>Rana crancrivora</i> ⁹	252	14	227	350	830				
<i>Bufo marinus</i> ¹⁰									
Reptilia									
<i>Malaclemys terrapin</i> ²⁴									
Freshwater	130	3.1	90	22	300	48 ²⁵	102 ²⁵	32 ²⁵	
Seawater	174	3.8	140	115	459	52 ²⁵	108 ²⁵	43 ²⁵	
<i>Testudo hermanni</i> ²⁶									
Summer	105.2	4.8	94.7	3.9	290	52 ²⁷	76 ²⁷	35 ²⁷	
Winter	161.6	3.0	123.5	38.4	449				
<i>Tiliqua rugosa</i> ¹¹									
Winter	152	3.5							
Summer	196	4.6							
<i>Ctenophorus ornatus</i> ¹²									
Hydrated	150	5.0				28.5	123.8		
Drought	243	12.2				75.5	147.0		
<i>Ctenophorus nuchalis</i> ¹³									
Spring	170.4	5.1	128.6		328				
Summer	171.7	5.0	128.2		294				
<i>Pogona minor</i> ¹²									
Spring	157	5.6				67	99		
Summer	186	2.8				124	152		
<i>Varanus gouldii</i> ¹⁴									
Hydrated	130.2	4.5	122.5		236				
Dehydrated	154.5	3.95	141		312				
Salt-loaded	180.8	4.28	173.4		363				

Table 1.1 (Contd.)

Taxon ^a	Extracellular fluid (mmol l ⁻¹)					Intracellular fluid (mmol kg ⁻¹ H ₂ O)			
	Na ⁺	K ⁺	Cl ⁻	Urea	Osmol- ality	Na ⁺	K ⁺	Cl ⁻	Osmol- ality
<i>Dipsosaurus dorsalis</i> ²⁰									
Winter	131.0	3.44	91.5			42.4	117.0	29.9	
Spring	168.0	3.40	120.0			44.9	122.0	30.0	
Summer	163.0	3.36	120.0			40.5	126.0	25.9	
<i>Uma scoparia</i> ²⁸									
Hydrated	148	4.8	121			43	118	36	
Dehydrated	163	5.2	140			41	127	33	
<i>Natrix natrix</i> ²⁹									
Summer	156	5.1				72 ³⁰	102 ³⁰		
Winter	166	4.2							
Aves									
<i>Larus glaucescens</i> ¹⁵	154	4.0							
<i>Sericornis frontalis</i> ¹⁶									
Winter	139				356				
Summer	148				372				
<i>Zosterops lateralis</i> ²²									
Winter	144	5.5	111	1.0	310				
Summer	168	8.1	133	3.4	394				
Mammalia									
<i>Homo sapiens</i> ²³	150	4	111	7	290	27	135	74	
<i>Rattus norvegicus</i> ¹⁷	150	6	119	7	324	16	152	5	350
<i>Setonix brachyurus</i> ^{18,21}									
Water	142.7	5.32	89.4	10.9	279.8				
No water	150.4	5.08	95.9	13.25	301.3				
<i>Lagorhynchus conspicillatus</i> ¹⁹									
Dry	155.1	7.9	104.5	6.7	284.9				
Wet	142.2	7.2	104.7	7.2	286.6				

^aSuperscript numbers denote the following references:

¹Bellamy and Chester-Jones (1961); ²Robertson (1954); ³Murray and Potts (1961); ⁴⁻⁶Fänge and Fugelli (1962); ⁷Smith (1930); ⁸Gordon (1965); ⁹Gordon, et al. (1961); ¹⁰Shoemaker (1964); ¹¹Bentley (1959); ¹²Bradshaw (1970); ¹³Bradshaw (1978); ¹⁴Bradshaw (1981); ¹⁵Holmes, et al. (1961); ¹⁶Ambrose and Bradshaw (1988); ¹⁷Harris (1960); ¹⁸Miller and Bradshaw (1979); ¹⁹Bakker and Bradshaw (1989); ²⁰Minnich (1970a); ²¹Jones, et al. (1990); ²²Rooke, et al. (1986); ²³Ruch and Fulton (1960); ²⁴Gilles-Baillien (1970); Robinson and Dunson (1976); ²⁵Gilles-Baillien (1973); ²⁶Gilles-Baillien and Schoffeniels (1965); ²⁷Gilles-Baillien (1969); ²⁸Minnich and Shoemaker (1972); ²⁹Binyon and Twigg (1965); ³⁰Wright and Chester-Jones (1957).

1.3

Water and Electrolytes in Reptiles as a Group

Table 1.2 incorporates data on body water distribution as well as plasma electrolyte concentrations from a wide range of reptiles and I have attempted to document cases where the same species has been studied at different times, or in different parts of its range, so that some idea of the variability of the various parameters may be gauged. This is a crude way of investigating homeostasis but it does provide some idea of the extent to which different reptilian species maintain a constant milieu intérieur and whether this is linked in any way with the particular environment the species inhabits. I have also included some data from experimental situations which again bear on the particular species' capacity to maintain homeostasis.

1.4

Conclusions

Several features emerge from the above comparison and, despite the crudity of the data, there are quite a number of differences of statistical significance. Crocodiles, for example, would appear to differ from chelonians in having a higher total body water content (TBW) ($t_{27} = 4.08$, $P = 0.0004$ and Tukey-Kramer, $P < 0.05$), although the ANOVA for all groups is not quite significant with $F_{3,55} = 2.545$, $P = 0.0654$.

The extracellular fluid volume (ECFV) of lizards is significantly greater than that of crocodiles, at 27.98 ± 1.4 versus 15.0 ± 0.23 ml 100 g^{-1} ($F_{3,40} = 3.948$, $P = 0.0148$), and also Chelonians, at 22.1 ± 2.0 ml 100 g^{-1} (SNK test, $P < 0.05$). Plasma volume (PV) did not differ significantly between the different reptilian groups with $F_{3,38} = 2.822$, $P = 0.0517$ reflecting the disparity between crocodiles and turtles, but this falls just short of significance.

The intracellular fluid volume (ICFV) of lizards, at 41.7 ± 1.92 ml 100 g^{-1} , appears to be much smaller than that of the other reptilian groups which range from 46 to 58 ml 100 g^{-1} ($F_{3,29} = 5.628$, $P = 0.0036$) although the data are very limited and the only significant difference is between crocodiles and lizards (Tukey-Kramer, $P < 0.01$).

Plasma sodium concentrations (Na^+) of lizards, at 167.5 ± 3.2 mmol l^{-1} , are not significantly different from those of snakes but are much higher than in both crocodiles and chelonians (145.8 ± 2.8 and 144.1 ± 4.3 mmol l^{-1} , respectively; $F_{3,124} = 10.396$, $P < 0.0001$). Plasma potassium concentrations (K^+) are very much higher, at 6.5 ± 0.6 mmol l^{-1} , in snakes and significantly different from both lizards ($P < 0.01$) and crocodiles ($P < 0.01$, $F_{3,106} = 5.383$, $P = 0.0017$). Plasma potassium levels of Chelonians are also significantly higher than those of crocodiles (SNK, $P < 0.05$).

Focusing on each group of reptiles we may conclude that the data in the literature suggest that the following physiological differences exist between different reptilian groups:

Table 1.2. Variation in fluid distribution and plasma electrolyte concentrations reported in reptiles

		Body fluid compartments (ml 100 g ⁻¹)				Plasma electrolytes (mmol l ⁻¹)	
Taxon and treatment ^a	Habitat	TBW	ECFV	PV	ICFV	Na ⁺	K ⁺
Crocodilia							
<i>Caiman crocodilus</i> ¹	Freshwater	73.0	14.9	3.5	58.1	134 ⁹	3.8 ⁹
Freshwater							
Seawater (24 h)						160 ⁹	4.6 ⁹
<i>Alligator mississippiensis</i> ¹³	Freshwater	79.3				141	3.8
Freshwater		72.9 ¹				170 ¹⁸	3.9 ¹⁸
						134 ²¹	3.6 ²¹
						139 ²²	2.5 ²²
<i>Crocodylus moreleti</i> ¹	Freshwater	73.1	14.6	3.4	58.5		
<i>Crocodylus acutus</i> ¹	Estuarine	72.9	15.4	3.6	57.5	129 ¹⁶	
Freshwater						148 ¹⁷	
Seawater						169 ¹⁸	
						157 ¹⁷	4.8 ¹⁸
						137 ¹⁸	3.0 ¹⁸
						110 ¹⁸	8.3 ¹⁸
						157 ¹⁸	
Laboratory ⁴¹						134	4.2
<i>Crocodylus niloticus</i> ¹⁵	Freshwater					152.8	4.6
Freshwater						150 ¹⁹	4.9 ¹⁹
Seawater (6 days)						143 ¹⁹	3.9 ¹⁹
						171.5	4.6
<i>Crocodylus porosus</i> ²	Estuarine	81.1				141	4.2
Freshwater	Marine	75.7				159	4.4
Seawater		76.9				136	4.1
		76.9				157	4.1
						157	4.8
						135	3.7
						132	3.5
						130	3.8
<i>Crocodylus palustris</i> ²⁰	Freshwater					154	4.3
Mean ± SE (CV%)		75.5 ± 0.9 (4.0)	14.9 ± 0.2 (2.7)	3.5 ± 0.06 (1.6)	58.0 ± 0.3 (0.9)	145.8 ± 2.9 (10.0)	4.2 ± 0.22 (24.9)
Testudinae							
<i>Chelydra serpentina</i> ¹	Freshwater	72.9	14.9	3.3	58.0		
Summer ⁵⁸		71.4		6.7		141.2	3.5
Winter		75.2		6.5		129.1	3.0
<i>Graptomys geographica</i> ⁵⁸	Freshwater	66.9		10.7		139.6	3.8
Summer							
Winter		70.9		7.8		129.9	3.7
				9.0 ⁵⁹			
				10.4			
				7.5			
				6.9			
<i>Trionyx spiniferus</i> ²³	Freshwater					140	
Fasting						126 ²⁴	4.8 ²⁴
<i>Pseudemys scripta</i> ²⁴	Freshwater					126	4.8
Fasting							
Seawater (24 h)						143	4.3
Freshwater ⁶⁰			40.2				
<i>Chrysemys picta</i> ²⁶	Freshwater					112	6.3
Laboratory ⁵²						174	
<i>Chelodina rugosa</i> ⁷¹	Freshwater					123.4	4.2
Aestivating						133	3.9

Table 1.2 (Contd.)

Taxon and treatment ^a	Habitat	Body fluid compartments (ml 100 g ⁻¹)				Plasma electrolytes (mmol l ⁻¹)	
		TBW	ECFV	PV	ICFV	Na ⁺	K ⁺
<i>Malaclemys terrapin</i> ¹	Estuarine	64.9	21.9	4.4	43.0	164 ²⁵	6.3 ²⁵
Freshwater (6 weeks)						142 ²⁵	10 ²⁵
Seawater (6 weeks)						154 ²⁵	8.8 ²⁵
Freshwater ⁵⁷		61.6	18.6	5.8		131	
Seawater ⁵⁷		59.9	16.4	3.5	43.5	184	
Freshwater + Salt-loaded ⁵⁷		66.4	26.6	7.6	39.8	201	
<i>Chelonia mydas</i> ¹	Marine	64.9	19.1	4.4	45.8	158 ⁵⁵	1.5 ⁵⁵
<i>Lepidochelys kemp</i> ¹	Marine	64.1	18.9	4.4	45.2		
<i>Lepidochelys olivacea</i> ¹	Marine	66.0	18.7	4.4	47.3		
<i>Caretta caretta</i> ¹	Marine	64.0	19.3	4.4	44.7		
<i>Gopherus polyphemus</i> ¹	Terrestrial	69.9	16.8	4.1	54.1		
<i>Gopherus agassizii</i> ³	Desert	74.0				136	7.6
Spring							
Summer		74.8				174	15.5
Autumn		74.0				140	8.5
Summer ³⁵		67.8	24.5			122	5.3
Dehydrated ³⁶		66.8	32.2			155	3.8
Laboratory ³⁹						116	
<i>Testudo hermannii</i> ⁷⁰	Terrestrial					154.8	6.0
Mean ± SE (CV%)		67.7 ± 1.3 (8.2)	22.2 ± 2.0 (32.4)	6.2 ± 0.5 (36.9)	46.8 ± 1.9 (12.1)	144.2 ± 4.3 (15.0)	5.8 ± 0.7 (54.2)
Rhynchocephalia							
<i>Sphenodon punctatus</i> ⁴⁷						135	5.7
Lacertilia							
<i>Tropidurus</i> sp. ⁴⁰	Tropical-arid					163	
<i>Hemidactylus</i> sp. ⁴⁰	Tropical-moist					149	
<i>Amblyrhynchus cristatus</i> ¹⁰	Marine	71.0				203	6.2
<i>Iguana iguana</i> ¹	Tropical	70.8	16.8	4.2	54.0		
<i>Tiliqua rugosa</i> ²⁹	Mesic					151.9	3.5
Winter							
Summer						195.9	4.6
Water-loaded ⁵¹						112.2	3.5
Salt-loaded						138.7	3.7
<i>Lacerta viridis</i> ³⁷	Mesic	65.6				182	
Summer							
Spring ³⁸		74.8				167	
Autumn		68.6				190	
<i>Pogona minor</i> ⁵	Mesic	75.5	26.4	4.0	49.1	157	5.6
Spring							
Summer		75.1	33.7	7.3	41.4	186	2.8
<i>Pogona minimus</i> ⁵	Mesic	76.0	23.4	5.9	52.6	204	6.8
Winter							
Summer		72.6	26.0	6.1	46.6	163	5.1
<i>Ctenophorus ornatus</i> ⁴	Semi-arid	73.5	25.5	5.1	48.0	150	5.0
Winter							
Early-summer		73.6	25.7	5.4	47.9	155	5.5
Mid-summer		73.8	33.0	7.1	41.2	172	5.7

Table 1.2 (Contd.)

Taxon and treatment ^a	Habitat	Body fluid compartments (ml 100 g ⁻¹)				Plasma electrolytes (mmol l ⁻¹)	
		TBW	ECFV	PV	ICFV	Na ⁺	K ⁺
Drought ⁵		74.3	17.5	7.0	27.9	243	12.2
Post-rain (10 hr) ⁵		78.3				166	5.6
<i>Ctenophorus nuchalis</i> ⁵	Desert	75.2	27.7	5.8	47.5	168	4.3
Spring (1963)							
Summer		55.4	21.1	4.1	34.3	186	5.8
Spring ³⁸		82.1				170.4	5.1
Summer (1977)		74.7				171.7	5.0
Autumn ³⁰		73.6				153	4.6
Spring ³⁰		85.6				149	5.6
Summer (1982) ³⁰		61.3				151	4.4
<i>Ctenophorus caudicinctus</i> ⁵	Desert	75.1	44.9	6.6	30.2	192	5.7
Summer (1963)							
Autumn						169	4.2
<i>Phrynosoma cornutum</i> ⁴⁰	Desert					163	
<i>Dipsosaurus dorsalis</i> ⁶	Desert					168	3.4
Spring							
Summer						163	3.4
Winter						131	3.4
Spring ³¹		71.5	30.6	4.8	40.6		
Summer		74.7	29.0	5.1	45.7		
Laboratory ⁴⁸						164	2.3
Laboratory ^{49,56}		77.9				158	2.5
<i>Sauromalus obesus</i> ⁷	Desert	76.3	35.1	7.0	36.3	178	4.6
Spring							
Autumn		73.0	32.9	6.1	40.0	188	3.9
Autumn, Expressed as % Initial mass ³³		40.2	18.1	3.4	22.0		
Laboratory ⁶²						169	4.9
<i>Sauromalus hispidus</i> ³⁴	Desert	74.5	38.9			171	6.9
Summer							
Autumn		71.4				150	5.5
<i>Uromastix acanthinurus</i> ⁸	Desert	75.6	28.6	5.2	47.0	170	4.1
Spring							
Autumn		71.6	31.5	6.0	40.1	199	5.5
Dehydrated		45.6	22.4	4.0	23.2	197	3.4
<i>Varanus griseus</i> ^{41,12}	Desert	77.3				140	3.2
Spring							
Summer						202	6.0
<i>Varanus gouldii</i> ³²	Desert					146.6	4.8
Summer							
Water-loaded						135.9	4.3
Salt-loaded						176.1	5.4
Dehydrated						156.3	4.8
Laboratory ⁴⁵						151	3.7
Laboratory ³³						183.0	4.6
Salt-loaded							
<i>Sceloporus cyanogenys</i> ⁴⁴	Desert					145	3.3
<i>Agama stellio</i> ⁵⁰	Desert					138	4.6
Mean \pm SE (CV)		71.5 \pm 1.8 (13.3)	27.9 \pm 1.4 (24.4)	5.6 \pm 0.3 (19.4)	41.8 \pm 1.9 (20.0)	167.5 \pm 3.2 (13.7)	4.8 \pm 0.2 (32.8)
Ophidia							
<i>Boa constrictor</i> ¹	Tropical	71.0	16.8	4.0	54.2		

Table 1.2 (Contd.)

Taxon and treatment ^a	Habitat	Body fluid compartments (ml 100 g ⁻¹)				Plasma electrolytes (mmol l ⁻¹)	
		TBW	ECFV	PV	ICFV	Na ⁺	K ⁺
<i>Natrix natrix</i> ⁶⁴	Freshwater					156	5.1
Summer							
Winter						166	4.2
<i>Natrix (Nerodia?) sipedon</i> ¹⁴	Freshwater					159	3.9
Laboratory ⁴³						144	4.9
<i>Natrix (Nerodia?) cyclopion</i> ¹⁶						134	5.9
<i>Nerodia fasciata clarki</i> ⁶⁵	Estuarine					134	12.0
Freshwater							
Seawater						174	10.7
<i>Nerodia fasciata compressicauda</i> ⁶⁵	Estuarine					148–181	5.6–7.6
<i>Nerodia valida</i> ⁶⁵	Estuarine					226	
Seawater							
<i>Vipera aspis</i> ³⁷	Mesic	71.6				157	4.8
<i>Vipera aspis</i> ⁶⁶						152	5.5
Spring							
Summer						172	7.2
<i>Pituophis melanoleucus</i> ¹	Desert	70.0	16.7	4.1	53.3	167 ⁴³	4.6 ⁴³
<i>Aipysurus laevis</i> ²⁷	Marine					178.5	3.9
Hydrated						177.0	3.5
Seawater-loaded						191.0	3.9
<i>Hydrophis cyanocinctus</i> ⁵⁴	Marine					150	4.3
<i>Laticauda semifasciata</i> ⁶⁷	Marine					159	
<i>Pelamis platurus</i> ⁶⁵						264?	11?
<i>Pelamis platurus</i> ⁶⁸						210	8.1
<i>Elaphe obsoleta</i> ⁶¹			42.2				
<i>Acrochordus granulatus</i> ⁶¹			48.8				
<i>Chersydrus (?) granulatus</i> ⁶⁹	Marine					162	9.2
Sea water							
Freshwater						128	10.0
<i>Crotalus viridis</i> ⁶¹	Terrestrial		41.9				
Mean ± SE (CV)		70.9 ± 0.5 (1.1)	31.1 ± 8.4 (54.0)	4.1 ± 0.1 (1.7)	53.8 ± 0.5 (1.2)	169.1 ± 6.5 (19.4)	6.5 ± 0.6 (41.5)

^aSuperscript numbers denote the following references:

¹Thorson (1968); ²Taplin (1984), Grigg (1981), Taplin (1988); ³Nagy and Medica (1986); ⁴Bradshaw and Shoemaker (1967); ⁵Bradshaw (1970); ⁶Minnich (1970a); ⁷Nagy (1972); ⁸Lemire et al. (1982); ⁹Bentley and Schmidt-Nielsen (1965); ¹⁰Shoemaker and Nagy (1984); ¹¹Vernet et al. (1988); ¹²Vernot, et al. (1988); ¹³Coulson and Hernandez (1964); ¹⁴Dantzler (1967, 1970); ¹⁵Balment and Loveridge (1993); ¹⁶Evans and Ellis (1977); ¹⁷Ellis (1981); ¹⁸Dunson (1982); ¹⁹Taplin and Loveridge (1988); ²⁰Taplin (1988); ²¹Ellis and Evans (1984); ²²Lauren (1985); ²³Dunson and Weymouth (1965); ²⁴Bentley (1976); ²⁵Dunson (1970); ²⁶Trobec and Stanley (1971); ²⁷Yokota, Benyajati and Dantzler (1985); ²⁸Bradshaw (1978a); ²⁹Bentley (1959); ³⁰Nagy and Bradshaw (1995); ³¹Minnich and Shoemaker (1970); ³²Rice (1982); ³³Bradshaw (1986a); ³⁴Smits (1985, 1986); ³⁵Minnich (1977); ³⁶Minnich and Ziegler (1976); ³⁷Bradshaw, et al. (1987); ³⁸Bradshaw, et al. (1991b); ³⁹Dantzler and Schmidt-Nielsen (1966); ⁴⁰Roberts and Schmidt-Nielsen (1966); ⁴¹Schmidt-Nielsen and Skadhauge (1967); ⁴²Davis and Schmidt-Nielsen (1967); ⁴³Komadina and Solomon (1970); ⁴⁴Stolte et al. (1977); ⁴⁵Green (1972a); ⁴⁶Elizondo and LeBrie (1969), LeBrie and Elizondo (1969); ⁴⁷Schmidt-Nielsen and Schmidt (1973); ⁴⁸Bradshaw, et al. (1972); ⁴⁹Chan, et al. (1970); ⁵⁰Skadhauge and Duvedvani (1977); ⁵¹Bradshaw and Grenot (1976); ⁵²Butler (1972), Butler and Knox (1970); ⁵³Rice (1982); ⁵⁴Duggan and Lofts (1978), Duggan and Lofts (1979); ⁵⁵Holmes and McBean (1964); ⁵⁶Templeton (1972); ⁵⁷Robinson and Dunson (1976); ⁵⁸Semple, et al. (1969, 1970); ⁵⁹Stitt et al. (1970); ⁶⁰Smits and Kozubowski (1985); ⁶¹Smits and Lillywhite (1985); ⁶²Templeton (1964); ⁶³Dunson (1968); ⁶⁴Binyon and Twigg (1965); ⁶⁵Dunson (1980); ⁶⁶Izard, Detrait and Bouquet (1961); ⁶⁷Dunson and Taub (1967); ⁶⁸Dunson et al. (1971); ⁶⁹Dunson and Dunson (1973); ⁷⁰Gilles-Ballien and Schoffeniels (1965); ⁷¹Grigg et al. (1986).

Crocodiles have high TBW and an ICFV expanded at the expense of the ECFV and PV. This effect is evident in both freshwater and terrestrial species and plasma electrolyte levels are also similar in both. These differences are shown diagrammatically in Fig. 1.1.

Chelonians have more “normal” fluid volumes but high and quite variable plasma K^+ concentrations, with a coefficient of variation (CV) of 54.2%. Plasma electrolyte concentrations show a similar trend in both freshwater, estuarine and terrestrial species. Relative potassium levels are shown in Fig. 1.2.

Lizards have a high ECFV and PV that is expanded at the expense of the ICFV when compared with the three other groups of reptiles: their plasma Na^+ is very significantly higher than that of both crocodiles and chelonians, but not different from that of snakes. Lizards also appear to have quite variable plasma K^+ concentrations, with a CV of 32.8%. Plasma sodium concentrations for all reptiles are shown in Fig. 1.3.

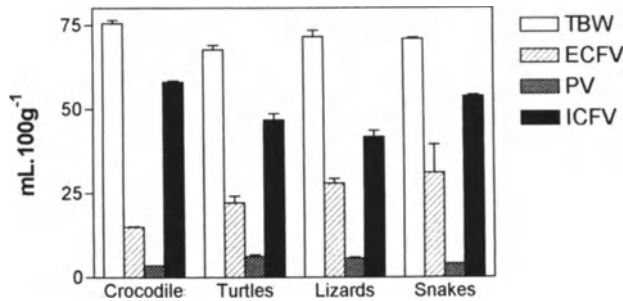


Fig. 1.1. Compartmental distribution of water in the various reptilian groups. *TBW*, total body water content; *ECFV*, extracellular fluid volume; *PV*, plasma volume; *ICFV*, intracellular fluid volume. (Data derived from Table 1.2)

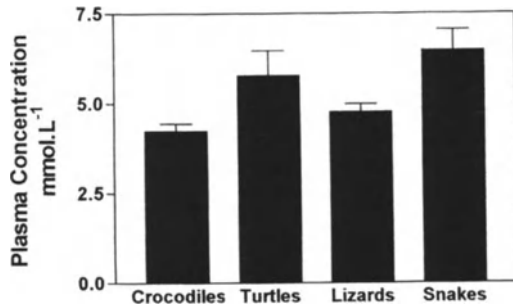


Fig. 1.2. Variation in mean plasma potassium concentration in the major reptilian group. (Data derived from Table 1.2)

Snakes appear to be normal so far as fluid volumes are concerned but they have high plasma sodium concentrations and very high potassium levels. The CV of the potassium levels in snakes is also high at 41.5%, reflecting the influence of data from the marine snakes.

When attempting to search for habitat correlations to account for the above differences, one is confounded by the fact that virtually all the lizards that have been studied are desert species, with only five species coming from mesic habitats and three from tropical environments. Even so, plasma electrolyte concentrations differ only slightly from those of desert species and only the fluid volumes in *Iguana iguana* appear to be atypical of the group as a whole.

Another obvious conclusion from this literature comparison is just how few species of snakes have been studied from this point of view, regardless of their origins and habitat. The statistically significant differences listed above thus may reflect genuine differences, or simply be the result of the vagaries of the literature, with its inherent sampling errors due to different techniques employed, and variations due to factors such as season and sex ratio.

The fact that crocodiles have a high TBW content and ICFV relative to other reptiles may be related to their aquatic habit, although a similar trend is not obvious in those few species of aquatic turtles in which fluid distributions have been measured. Minnich (1982) suggested that TBW is lower in turtles than in crocodiles because the volume is expressed relative to total mass in the former, which includes their extensive bony shell. In fact the TBW of turtles measured in this way is no different from that of lizards and snakes. This suggests that they must have an extremely high water content if one corrects for shell mass, which is normally taken to represent about 30% of total body mass in turtles, but which may in fact vary enormously with size (Dunson and Heatwole 1986). If a figure of 30% is taken, then their measured TBW of $70 \text{ ml } 100 \text{ g}^{-1}$ would increase to 100%, which is clearly impossible, and better data are clearly needed on water distribution in the body tissues of turtles. Patterson (1977), for example, found that shell mass as a percentage of total mass varied between

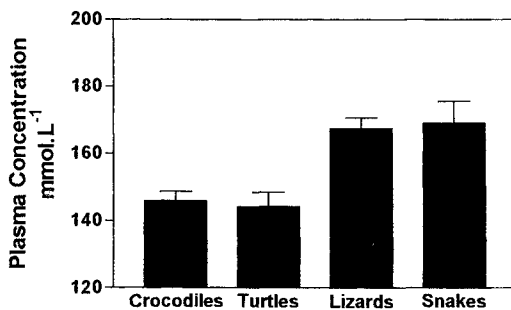


Fig. 1.3. Variation in mean plasma sodium concentration in the major reptilian groups. (Data derived from Table 1.2)

7 and 25% with increasing carapace length in the desert tortoise *Gopherus agassizii*.

The relatively expanded ECFV and PV of lizards may reflect the common incidence of dehydration in their daily existence and we will have occasion to examine the ways in which different species cope with this problem. High and variable plasma potassium concentrations in chelonians may relate to the incidence of herbivory in this group of reptiles and it is known that the cephalic salt glands are important osmoregulatory organs in turtles. Both lizards and snakes have relatively high plasma sodium concentrations when compared with turtles and crocodiles. This may be a reflection of the fact that they are virtually the only desert species to have been studied in detail.

Despite the lack of any obvious solutions to the above problems, it is clear that reptiles as a group are not homogeneous as to the composition of their milieu intérieur and they may differ quite markedly from what is considered the "typical" vertebrate model. Significant differences also exist within reptiles as a group, and in the next chapter I will attempt to review what is known of the control mechanisms that apparently maintain these different stable states. This will involve a consideration of both laboratory and field data and the emphasis will be on the inherent stability of the milieu intérieur as evidenced in both sets of data.

Water and Electrolyte Homeostasis

2.1

Basic Concepts

One needs to appreciate that the milieu intérieur is a dynamic concept and that the observed steady state is in effect the resultant of the continual influx and efflux of those essential elements of which the body is composed. Measuring, or more often estimating, these essential fluxes is as important a part of the study of the maintenance of the milieu intérieur as is the measurement of the changes in those control mechanisms which ultimately moderate these fluxes. Radioactive and stable isotopes are used routinely to estimate these fluxes and there now exists a large body of literature on the subject, especially for reptiles which are ideal subjects for such a study (Nagy 1988). Theoretical considerations demand that the injected or ingested isotopes do not diffuse from the body and that their specific activity be only reduced by the influx of nonlabelled isotope. This limitation renders the technique less than useful with groups such as amphibians and fish in which there is a constant high rate of interchange of elements between the animal's body and the external environment. In such cases the high loss rate of the isotope may be used to measure the permeability of external membranes, but overall influx via such routes is much greater than the influx of say, water, by feeding and the technique thus cannot be used to estimate feeding rates as in the case of a terrestrial animal such as a lizard.

Variations in appetitive behaviour are an important means by which reptiles may vary influxes (e.g. drinking, salt appetite, increased food intake) and hormones such as angiotensin II and corticosterone also have a direct effect on water and food intake respectively. Behaviour may to some extent exert an effect on effluxes, but to a much lesser degree (an animal may reduce evaporative water loss by selecting cool or moist environments) and effluxes are modified primarily by physiological processes involved in excretion.

The kidney is the major site of such excretion and it is important to note that in reptiles the work of the kidney is aided and completed through the activity of a number of extrarenal or postrenal excretory sites which include the cloaca, colon and cephalic salt-secreting glands. One of the difficulties which will become apparent when attempting to interpret excretory processes in reptiles is that much of the physiological information in the literature

pertains to the kidney alone and much less is known of the activity of these extrarenal sites and their control. In many cases all that is clear is that the animal would die in a short space of time if it were to excrete unmodified the urine that can be collected from the ureters (Bradshaw 1975).

Pituitary and adrenal hormones are traditionally implicated in the regulation and maintenance of the milieu intérieur and information is gradually accumulating on their effects in reptiles. It was long thought that the reptilian adrenal gland is not under the control of the pituitary gland (see for example, Macchi and Phillips 1966; Nothstine et al. 1971). This curious state of affairs came about through a general ignorance of the biology of reptiles by the physiologists who chose to study them in the 1960s. Briefly, when the adrenals of fish and amphibians are incubated in vitro with either pituitary extracts or mammalian adrenocorticotrophic hormone (ACTH), they respond with a net increase in the rate of corticosteroidogenesis. This was not the case with reptiles, however, and hence the conclusion that they did not possess an ACTH. One needs to know, however, that reptilian tissues, and that of other lower vertebrates, were traditionally incubated at room temperature – because they are “cold blooded” and in the case of fish and amphibians their operant temperatures are sufficiently close to 20°C for ACTH to have an effect. In the case of lizards and other reptiles, however, with preferred body temperatures usually in excess of 30°C, it is not surprising that the response of their adrenal enzymes to exogenous ACTH was sluggish if not nonexistent. It was not until levels of adrenal corticosteroids could be measured in the small volumes of plasma that can be collected from reptiles that the problem was resolved, with the demonstration that the adrenal is indeed under direct control by the pituitary gland and that a negative feedback of steroids on ACTH secretion exists, as in other vertebrates (Licht and Bradshaw 1969; Bradshaw 1972, 1986a; Bradshaw and Grenot 1976). Another interesting by-product of this same piece of research was the discovery that the γ -cell in the rostral pars distalis, responsible for secreting ACTH in the reptilian pituitary (the corticotroph), had long been mis-identified as a gonadotroph secreting luteinizing hormone (LH) by cytologists, who had been led to believe that reptiles did not possess an ACTH (Saint Girons and Bradshaw 1981). Amazingly, a quite recent paper on the turtle *Pseudemys scripta* by authors who are clearly neither herpetologists nor comparative endocrinologists attempts to revive this long-discredited shibboleth of the lack of an ACTH in reptiles (Sanford and Stephens 1988).

A thorough understanding of the biology of an animal and an appreciation of the restraints of its natural existence are always essential in designing any experiment that is meant to illuminate complex systems such as hormonal and glandular hierarchies, and negative results always need to be treated with caution. As we shall see, reptiles differ homeostatically in many fundamental ways from birds and mammals and this needs to be borne carefully in mind when designing and interpreting experiments which themselves are meant to reveal evolutionary relationships. The essential elements of the

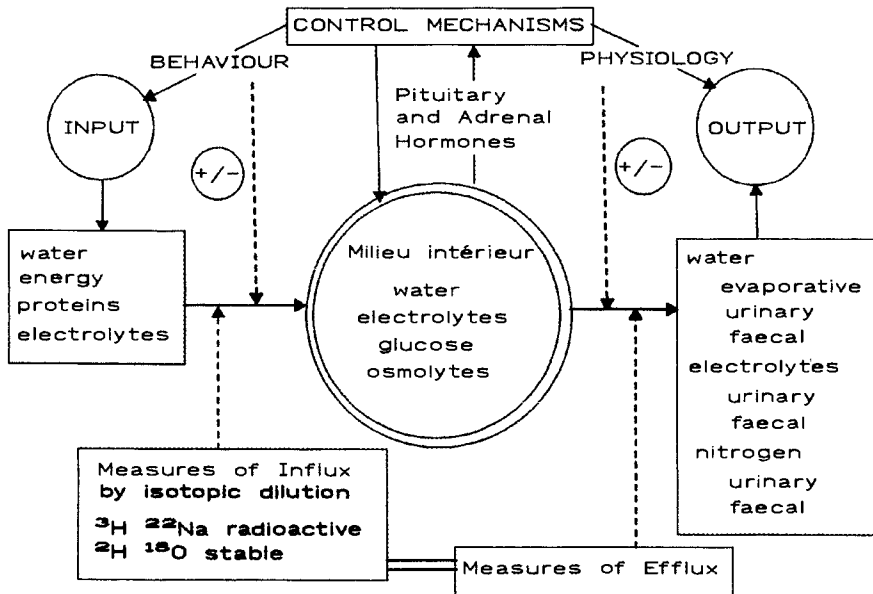


Fig. 2.1. The essential elements of vertebrate homeostasis. The control of inputs and outputs by behaviour and physiology and the measurement of essential fluxes using stable and radioactive isotopes are shown

process of homeostasis may be represented somewhat schematically as shown in Fig. 2.1.

2.2

The Maintenance of Homeostasis

Obviously one may detect the presence and operation of homeostatic mechanisms through the temporal constancy of the milieu intérieur but what degree of tolerance should we expect, 1, 5 or even 15%, and what degree of variation would we consider to be inconsistent with the concept of homeostasis? Plasma sodium concentrations, for example, may reach levels of 300 mmol l^{-1} in some individuals of the lizard *Ctenophorus ornatus* during prolonged periods of drought (Bradshaw 1970) whereas a level of 175 mmol l^{-1} is close to lethal for a mammal (Knowles 1956). Does this indicate that the lizards have abandoned all efforts at homeostasis, or is their level of regulation much less precise than that of mammals because of their obviously greater tolerance to hypernatraemia?

Bartholomew (1964) in an early article stressed the variety of ways in which desert animals survive the exigencies of their environment and tried to extend the concept of homeostasis to include hyperthermia and behavioural avoidance of extremes. I believe it is important, however, to distinguish between

Table 2.1. Hierarchical nature of regulatory interactions between an organism and its immediate environment. (Modified from Bradshaw 1986a)

Level of hierarchy	Nature of change	Example
Primary	Perturbation	Water deficit
Secondary	Stimulus	Increased plasma osmolality
Tertiary	Regulatory response	Release of ADH
Quaternary	Effector response	Decreased urine production
Pentary	Resultant state	Regulation of body water

animals that survive in a particularly difficult environment such as the desert because of their capacities for physiological regulation, in contrast to those that persist simply because of their capacity to endure perturbations of the milieu intérieur. The end result may be the same (survival) but the mechanisms are clearly different and this begs the question of their separate evolution.

Inherent in any notion of homeostasis is an hierarchical set of regulatory interactions between the environment and an organism, operating through a stimulus and an effector to maintain a steady state. In the very simple example shown in Table 2.1, five distinct operational levels may be distinguished starting with an environmental perturbation (lack of water), which entrains an increase in plasma osmolality, which then operates as the stimulus for increased secretion of antidiuretic hormone (ADH) from the *pars nervosa* of the pituitary gland. This in turn operates on the kidney as effector organ to reduce water loss and, by this means, body water is conserved. The parameter under homeostatic control in this example is not plasma osmolality, nor circulating levels of ADH, nor even the rate of urine production, but the overall water content of the body which must remain within rather narrow limits if the animal is to survive.

2.2.1

Regulatory Responses

Central to the above scheme is the release of a hormone into the circulation which brings about a response at a remote site, in this case the kidney. It follows that we should also be able to discern the existence of homeostatic states in animals through changes in levels of things such as regulatory hormones, as well as by observing the relative constancy of the milieu intérieur. If we suspect that a particular attribute of an animal, such as body temperature or water content, is under homeostatic control we should theoretically be able to identify regulatory responses that are initiated whenever environmental conditions threaten the stability of this parameter. These regulatory responses will obviously be able to maintain the milieu intérieur between desirable limits, depending upon the extent of the environmental perturbation and the condi-

tion of the animal at the time. By measuring the extent to which regulatory processes are activated by a change in the environment, one should thus be able to assess the extent of the animal's homeostatic response. In the case of an extreme challenge, the animal's ability to maintain homeostasis would be surpassed and the milieu intérieur modified significantly as a result.

2.2.2

The Concept of Stress

We thus have the elements not only for detecting the existence of homeostatic mechanisms (the presence of associated regulatory systems) but also for measuring the incidence of stress in animals, which we may consider as the physiological consequences of demands that exceed an animal's regulatory capacities (Bradshaw 1992a,b). A stressed individual would thus be one showing evidence of an activated, but inadequate, regulatory response to an environmental change. It should typically be characterised by the coupling of maximally stimulated regulatory responses (be these hormonal or otherwise) with a significant alteration of the milieu intérieur from whatever is considered to be its "normal" state. Taking our example above, an animal with very high levels of ADH in the plasma would only be considered to be stressed if also experiencing a significant level of desiccation. In the case of temperature regulation in a lizard, stress would be indicated by the association of high-temperature avoidance behaviour patterns with a body temperature significantly elevated above the preferred.

Stress is thus perceived as a temporary and maladapted state existing between homeostasis and pathology. Little attention has been given to the question of whether desert animals experience significant levels of stress during their normal existence, but the question is of some importance, especially as it has been argued that stress is of critical significance in the evolution of novel genetic adaptations (Bradshaw 1988; McDonald 1983; Slobodkin and Rapaport 1974).

2.3

Effector Systems

Osmoregulation may be defined as

"the processes by which the amounts of water and specific solutes within the body of an organism are maintained constant, or within tolerable limits"

(Shoemaker and Nagy 1977) and the kidneys are the major organs involved in controlling rates of loss of water and solutes from the body. As mentioned above, however, reptiles differ from mammals in having extensive post- and extrarenal sites which complement and complete the osmotic work of the kidney. These include the bladder, when present, the cloacal-colonic complex and the various cephalic salt-secreting glands, which are quite diverse in rep-

tiles. The skin, respiratory and digestive tracts are also important sites for loss of water in reptiles, although the extent to which their rates can be modified is not well known, and they are thus not normally thought of as effector systems *sensu stricto*.

2.3.1

Kidney Morphology

The structure of the reptilian nephron has been reviewed a number of times (Dantzler 1976, 1980, 1989a; Dantzler and Braun 1980; Fox 1976), but always in fairly general terms and usually referring to the same few primary sources (e.g. Cordier 1928). The shape of the kidneys varies considerably between the various orders. In lizards the two kidneys extend into the pelvic girdle and are fused at the mediocaudal margin (Regamey 1936); the number of glomeruli is also smaller than in birds and mammals. Yokota et al. (1985) have derived an allometric equation describing variation in number of glomeruli with body mass in 11 species of reptiles: $N = 330x^{0.803}$, where N is the number of glomeruli and x is the body mass in grams ($r^2 = 0.95$, mass range 3 g–1 kg). This equation needs to be treated with some caution, however, as it predicts roughly 45 500 glomeruli in a 500 g reptile, which compares with an actual figure of 2300 per kidney for the skink *Tiliqua rugosa* (Bentley 1959), weighing about 500 g, and over 3600 for a 20 g reptile, which compares with a figure of 400–600 recently measured in the agamid lizard *Ctenophorus ornatus* by O'Shea et al. (1993). Figures of 1000 and 800 glomeruli per kidney were also reported for the small lizards *Sceloporus cyanogenys* and *Platydictylas mauritanicus* by Davis et al. (1976) and Zarnick (1910) respectively.

The nephron in reptiles opens into a short ciliated neck segment which is followed by a long proximal convoluted tubule (PCT), a short ciliated intermediate segment (IS) of much narrower diameter, and then a broader distal convoluted tubule (DCT) emptying into the much wider collecting ducts (CDs). It is often emphasised that in lower vertebrates such as reptiles the DCT always enters the CDs at right-angles but this is clearly not the case in the lizard *C. ornatus*, as shown in Plate 2.1 (O'Shea et al. 1993). The CDs in this species can be seen to branch extensively and run directly into the terminal segment of the DCT without any abrupt change in direction, as in mammals.

Another important aspect of the reptilian kidney which is little emphasised in reviews is the renal-portal system, and this is obviously because little is known of its functional significance. The recent study of O'Shea et al. (1993), however, shows just how important this vascular system may be in relation to the arterial supply. *C. ornatus*, which is an agamid lizard inhabiting semi-arid regions in western Australia, has only two small renal arteries supplying the kidneys and the renal-portal system is clearly of much greater significance in irrigating the nephrons in this species. Even more surprising, O'Shea et al. (1993) described the presence of aglomerular tubules in this species which appear to be vascularised uniquely via the renal-portal system. Aglomerular

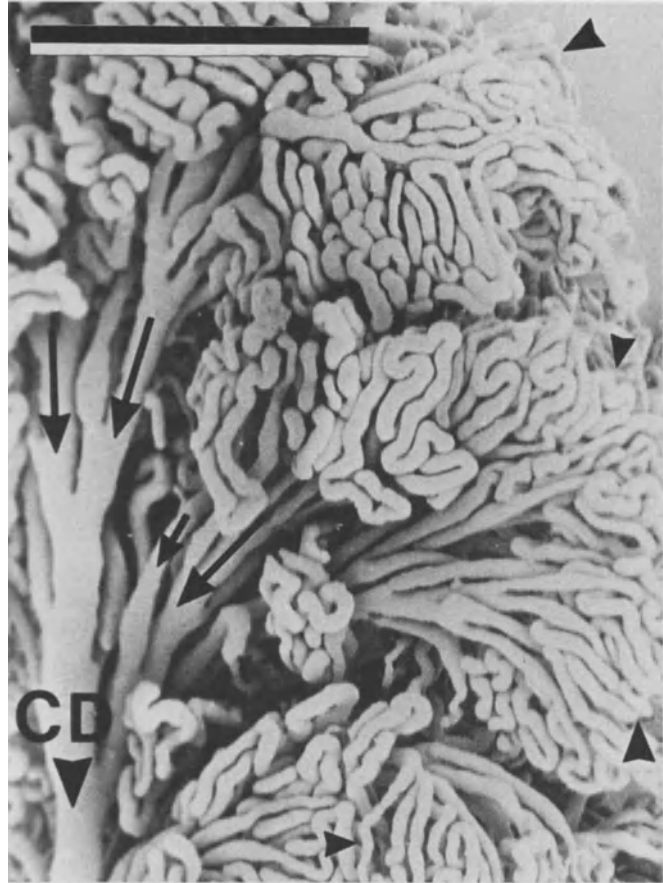


Plate 2.1. Corrosion cast of the kidney of the Australian agamid lizard *Ctenophorus ornatus* showing the distribution and orientation of the peripherally placed nephric tubules (arrows) and the collecting ducts (CD). Bar = 100 μm . (Adapted from O'Shea et al. 1993)

tubules have been described previously in the early literature on snake kidneys (Regaud and Policard 1903), but are usually thought to be restricted to marine fish (Dantzler 1989a).

Another aspect to emerge from the study of O'Shea et al. (1993) is the relationship of the DCT to the glomerulus. In birds and mammals the DCT comes into close contact with the glomerulus and its afferent arteriole, forming the renin-secreting juxtaglomerular apparatus and associated macula densa. Although juxtaglomerular cells, juxtaglomerular granules and renin have been identified in reptilian kidneys (Peek and McMillan 1979a,b) a macula densa is thought not to occur and it is usually stated in reviews that a juxtaglomerular apparatus does not exist in reptiles (e.g. Sokabe and Ogawa 1974). In *C. ornatus*, however, the DCT clearly comes into close proximity with the glom-

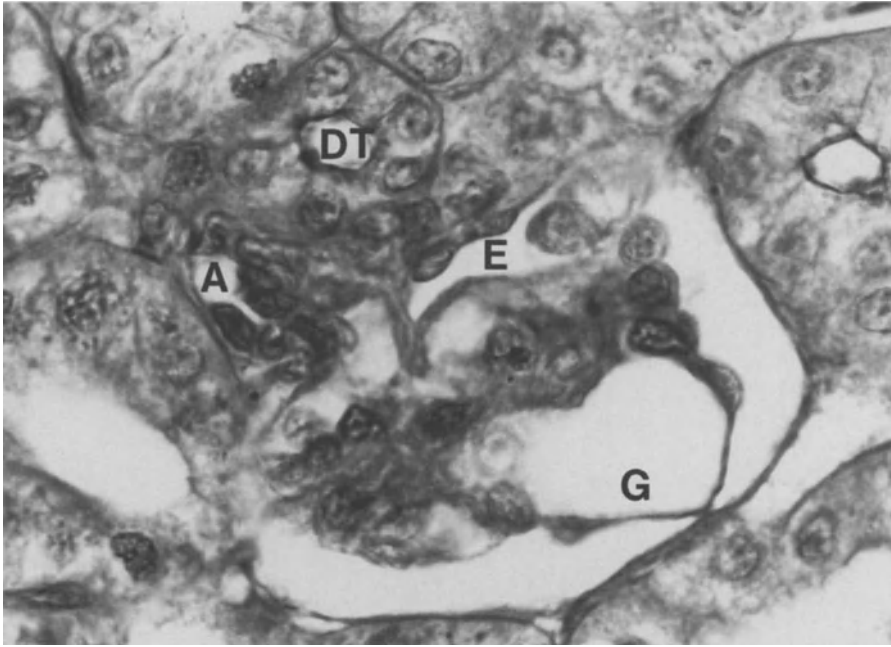


Plate 2.2. Section at the level of the glomerulus (G) showing the juxtaglomerular apparatus of the agamid lizard *Ctenophorus ornatus*, with the afferent (A) and efferent arterioles (E) lying in close association with the distal tubule (DT). (Adapted from O'Shea et al. 1993)

erulus and its afferent and efferent arterioles, as shown in Plate 2.2, forming an incipient juxtaglomerular apparatus. Dantzler (Dantzler and Braun 1980; Dantzler 1989a) makes a similar observation as concerns the snake kidney and the question clearly needs more careful examination in reptiles.

2.3.2

Derivation of Renal Parameters

The kidney and associated post- and extrarenal sites of water and electrolyte exchange are clearly of major importance in assuring homeostasis in reptiles and it is important to have an appreciation of the methods used to interrogate their activity. Renal function is classically studied by clearance techniques and some of the basic concepts and formulae, which are well-understood by renal physiologists but rarely explained in scientific publications, are listed as follows:

The basic clearance formula describes the removal or “clearance” of a substance (X) from the plasma over a finite period of time (t) by the process of ultrafiltration through the glomerulus. Clearance has the dimensions of volume per unit time and is measured by the quantity of the substance that

is ultimately voided in the urine. It is thus the resultant of the processes of filtration followed by any reabsorption and secretion of substance X that may occur in the kidney tubule. The formula is:

$$C_X = U_X/P_X \cdot V$$

where C_X is the clearance in ml/ $t_1 - t_0$ of substance X; U_X is the concentration of X in urine at time $t_0 - t_1$; P_X is the concentration of X in plasma at time $t_0 - t_1$; and V is the rate of urine production from $t_1 - t_0$.

The glomerular filtration rate (GFR) is a special case in which advantage is taken of a substance such as inulin (IN), a plant polysaccharide that is filtered but neither reabsorbed nor secreted subsequently in the tubule. Thus, the amount of inulin collected in the urine over the time period $t_1 - t_0$ must equal the amount that was filtered through the glomerulus over that same time period and:

$$U_{IN} \cdot V = P_{IN} \cdot C_{IN}$$

The clearance of inulin (C_{IN}) or GFR is thus:

$$C_{IN} = U_{IN}/P_{IN} \cdot V$$

and equals the volume of plasma cleared of inulin over the time interval $t_1 - t_0$; C_{IN} has the same dimensions as V , i.e. volume/time and is thus a rate.

The fractional reabsorption of filtrate (or water) is that fraction of the filtrate that is not excreted but reabsorbed in the tubules and is expressed as:

$$\begin{aligned} FR_{H_2O} &= (C_{IN} - V)/C_{IN} \cdot 100\% = (U/P_{IN} \cdot V - V)/U/P_{IN} \cdot V \\ &= (U/P_{IN} - 1)/U/P_{IN} \cdot 100\% \end{aligned}$$

The filtered load (FL) is the quantity of a solute X filtered per unit time. Thus:

$$FL = C_{IN} \cdot P_X$$

The excreted load (EL) is the quantity of a solute X excreted per unit time. Thus:

$$EL = V \cdot U_X$$

The fractional reabsorption (FR_X) of a substance X is the difference between the filtered load for X and the final amount of X excreted in the urine, expressed as a percentage. Thus:

$$\begin{aligned} FR_X &= (FL_X - EL_X)/FL_X \cdot 100\% \\ &= (C_{IN} \cdot P_X - V \cdot U_X)/C_{IN} \cdot P_X \\ &= (C_{IN} \cdot P_X - C_X \cdot P_X)/C_{IN} \cdot P_X \\ &= (C_{IN} - C_X)/C_{IN} \cdot 100\% \end{aligned}$$

The urine excreted is made up of both osmolytes which may be considered to be contained in an isosmotic solution plus, in the case of urine that is hypo-osmotic to the plasma, a certain quantity of free water which has been "added"

to dilute the urine. If the urine is hyper-osmotic to the plasma, then the amount of free water is a negative quantity and equals that abstracted from the filtrate in the process of rendering it concentrated. Thus:

$$V = C_{\text{OSM}} + C_{\text{H}_2\text{O}}$$

where C_{OSM} and $C_{\text{H}_2\text{O}}$ are osmolar and free water clearances respectively.

Free water clearance ($C_{\text{H}_2\text{O}}$) is thus calculated as:

$$C_{\text{H}_2\text{O}} = V - C_{\text{OSM}}$$

The clearance ratio (CR_X) of a substance X is its clearance relative to that of inulin or the GFR and equals that fraction of X filtered which is excreted. Thus:

$$\text{CR}_X = C_X/C_{\text{IN}} \cdot 100\%$$

It follows that the clearance ratio + fractional reabsorption = 1.0, since

$$\begin{aligned} \text{CR}_X + \text{FR}_X &= C_X/C_{\text{IN}} + (C_{\text{IN}} - C_X)/C_{\text{IN}} \\ &= (C_X + C_{\text{IN}} - C_X)/C_{\text{IN}} \\ &= C_{\text{IN}}/C_{\text{IN}} = 1.0 \end{aligned}$$

Thus the clearance ratio (CR) is the fraction of X filtered that is ultimately excreted in the urine and complements the fractional reabsorption (FR), which is that fraction of X that is not excreted but reabsorbed along the length of the tubule.

The relative osmolar clearance ($C_{\text{OSM}}/C_{\text{IN}}$) is that fraction of filtered osmolytes that is excreted and reflects the extent to which osmolytes are absorbed in their passage along the renal tubule.

The relative free water clearance ($C_{\text{H}_2\text{O}}/C_{\text{IN}}$) is almost always negative in mammals, because their urine is characteristically hyperosmotic, but may vary from 0 to 1 in lower vertebrates. If $C_{\text{H}_2\text{O}}/C_{\text{IN}}$ is 0, then the urine is isosmotic relative to the plasma and contains no added free water. If the $C_{\text{H}_2\text{O}}/C_{\text{IN}}$ were 1.0, the urine would be equivalent to distilled water in composition and contain no dissolved osmolytes. In reptiles this free water is "created" by the reabsorption of osmolytes in excess of water in the posterior (diluting) segment of the nephron and involves the reclaiming of an hyperosmotic reabsorbate. This contrasts with water reabsorption in the proximal tubule which is clearly isosmotic as the urine is not diluted by the process. Water is thus abstracted from the urine in the latter parts of the nephric tubule by the process known as solute-linked water flow and the tubule must be moderately impermeable to the passage of water for this process to occur. This must be so because, if tubular permeability were very high, the reabsorbate would become isosmotic and this would not have the observed effect of diluting the urine. The effect of arginine vasotocin (AVT) in reptiles is usually antidiuretic (i.e. decreased rate of urine production) and this invariably involves a reduction in GFR brought about by an increase in the vascular resistance of the efferent arteriole (glomerular effect). In some species, however, the fractional

reabsorption of filtrate (FR_{H_2O}) also increases and this is usually associated with a fall in both relative osmolar and free water clearances. The decrease in relative osmolar clearance indicates that AVT stimulates solute reabsorption in the tubule and the fall in free water clearance is usually interpreted as an associated increase in tubular permeability. If tubular permeability remained unchanged after the addition of AVT then the increased solute reabsorption would be associated with an increase rather than a decrease in relative free water clearance as the free water in the nephron is created by solute reabsorption. The tubule must therefore have increased permeability as a result of the action of AVT and this accounts for the overall increase in FR_{H_2O} . For this reason the relative free water clearance is often taken as a measure of tubular permeability to water in reptiles, with a decrease in C_{H_2O}/C_{IN} signalling an increase in tubular water permeability.

2.3.3

The Cloacal-Colonic Complex in Reptiles

An urinary bladder is considered to be a "typical" feature in reptiles (Fox 1976), and its absence in crocodilians, snakes and many lizards may represent a derived condition. The tetrapod urinary bladder develops as an evagination of the posterior part of the gut and, in common with the colon, displays some ability to transport both water and solutes. The bladder of chelonians and the Tuatara is permeable to water in vitro and capable of transporting salts (Bentley 1962; Brodsky and Schilb 1960, 1965; Dantzler and Schmidt-Nielsen 1966; Gonzalez et al. 1967; Schmidt-Nielsen and Schmidt 1973) but the bladder of lizards is poorly vascularised with relatively undifferentiated cells in the transitional epithelium. There seems little doubt that desert tortoises use their bladder to store water, which they may reclaim when needed, but the details of this process and its control are not well understood (Minnich 1967, 1977).

Where a bladder is lacking, as is usually the case in lizards, its reabsorptive role appears to be assumed by the colon and or cloaca. The cloaca in reptiles may be complex, as in the lizard *Uromastix hardwickii*, with a coprodaeum, urodaeum and proctodaeum as in birds (Seshadri 1957), or relatively simple as in *Ctenophorus* (*Amphibolurus*) lizards (Bentley and Bradshaw 1972). In this latter case fluid flows retrograde from the ureters into the colon which becomes quite distended with clear fluid and may hold as much as 0.4 ml in a 20 g individual (i.e. 2% of the body mass). Some idea of the osmotic work performed by postrenal structures such as the colon in reptiles can be gauged by comparing the mean relative osmolar clearance (C_{OSM}/C_{IN}) of $23.9 \pm 3.1\%$, measured with ureteral urine in 13 species of reptile, with the figure of less than 1% obtained with voided urine in the case of *C. ornatus* (Bradshaw 1975). This comparison makes it clear that ureteral urine is extensively modified in postrenal sites prior to being voided and a study of the activity of such sites is essential for an appreciation of the overall osmoregulatory responses of the

animal. Transport of water from the reptilian colon may be linked to solute reabsorption, as in birds (Bindslev and Skadhauge 1971), or may occur even in the absence of an overall osmotic gradient due to differences in colloid osmotic pressure between the cloacal fluid and blood (Murrish and Schmidt-Nielsen 1970).

2.3.4

The Cephalic Salt-Secreting Glands

Nasal salt-secreting glands were first identified in marine reptiles by Schmidt-Nielsen and Fänge (1958) and described in terrestrial species not long thereafter. There now exists an impressive literature on their comparative anatomy and physiology but details of their control are still obscure (Bradshaw 1986b; Dantzler and Holmes 1974; Dunson 1969a, 1976, 1979; Lemire 1983; Minnich 1979; Peaker and Linzell 1975). These glands are of some interest because, in contrast to those found in marine birds, they do not all have the same embryological origin and are formed from lachrymal glands in chelonians, external nasal glands in lizards, posterior lingual glands in hydrophid and achrochordid sea snakes and premaxillary glands in homalopsid file snakes. Interestingly, crocodiles were long thought to be the only group of reptiles lacking salt glands until their discovery by Taplin and Grigg (1981) in the tongue of the Australian salt-water crocodile *Crocodylus porosus*. Cephalic salt-secreting glands have even been tentatively identified in the fossil remains of dinosaurs (Osmolska 1979; Whybron 1981).

Despite their embryological disparity, histologically, the salt glands of reptiles are all composed for the most part of "principal cells" (cellules striées of Gabe and Saint Girons 1976) which are known for their ability to transport ionic species in other epithelia. These cells have large numbers of mitochondria and enormous extensions of the lateral cellular membranes creating complex intercellular spaces. The cells are joined laterally by tight junctions and occasional desmosomes close to the apical membrane (Saint Girons et al. 1981). Unlike birds, the basal membrane in the reptilian salt gland undergoes no infolding and mitochondria do not extend into the lateral processes but are localised in the cytoplasm proper (Abel and Ellis 1966; Ellis and Abel 1964). In some species both "light" and "dark" principal cells can be distinguished from the appearance of their cytoplasm although these may result from fixation artefacts (van Lennep and Komnick 1970) or represent transformational states of the one cell (Lemire 1983). The enzyme thought to be responsible for active salt transport in these glands, Na^+/K^+ -activated ATPase, has been localised in the lateral cell membranes of the nasal salt gland of the desert lizard *Dipsosaurus dorsalis* and the lachrymal gland of the marine turtle *Chelonia mydas* (Ellis and Goertemiller 1974; Minnich 1979). Although Na^+/K^+ -activated ATPase is absent from the luminal membrane of the principal cells it has been found in the luminal villi of "tuft cells" located in the peripheral tubules of the lizard nasal gland which are composed primarily of mucus-secreting cells.

It is not always easy to tell from the cytology of a gland whether it is capable of secreting an hyperosmotic salt solution and the Australian skink *Tiliqua rugosa* is a good case in point. Its failure to respond to injections of carbachol (a parasympathomimetic drug which stimulates secretion of the bird nasal gland) led to early perceptions that the large gland in the nasal cavity of this lizard was not capable of salt secretion, despite an early claim to the contrary by Braysher (1971). The gland had not been shown in this particular study, however, to be capable of secreting an hyperosmotic solution, and Saint Girons et al. (1977) subsequently described its unusual cytology, pointing out that it was composed almost equally of cellules striées, known for their ability to secrete concentrated salt solutions, and muco-serous cells, which are devoid of any such ability. It was not until Bradshaw et al. (1984b) cannulated the duct from the gland and collected its secretion that it was clear the gland does indeed function as a salt gland, elaborating a fluid that is about four times more concentrated than the plasma.

The salt-secreting glands of reptiles also differ from those of birds in the diversity of their responses to salt loading. Bird nasal glands are only capable of elaborating an hyperosmotic solution of NaCl (Peaker and Linzell 1975), whereas lizard nasal glands have been shown to secrete both NaCl and KCl with the latter being the more important in herbivorous species. In addition Shoemaker et al. (1972) have shown experimentally that the nasal salt gland of the desert iguana, a *Dipsosaurus dorsalis*, is nothing short of miraculous in being capable of secreting three different cations (including rubidium) and two anions! The fact that the gland is also not stimulated by osmotic loads, as in birds, suggests that control mechanisms are quite different.

2.4

Osmoregulation in Crocodiles, Alligators and Chelonians

2.4.1

Extent of Environmental Exchange

Although crocodiles are restricted to aquatic habitats, they are an ancient group of morphologically conservative archosaurs and their osmoregulation presents some interesting aspects, particularly in those estuarine species that occasionally venture into sea water. Chelonians are for the most part aquatic but a number of species is totally terrestrial and some of these, such as *Gopherus agassizii*, live in very arid habitats in the deserts of North America. Both groups thus provide a good starting point for a comparison with desert-inhabiting reptiles.

There appears to be some net cutaneous water exchange via the integument in crocodiles and turtles, with a gain in fresh water and a loss in sea water as would be expected from the osmotic gradient (Bentley and Schmidt-Nielsen 1965, 1970). Nagy and Peterson (1988) have calculated water flux rates from published data on rates of dilution of the hydrogen isotope tritium, and these

are quite high in both turtles and crocodiles maintained in seawater (Dunson 1985; Robinson and Dunson 1976). The extent to which these net water exchanges represent transcutaneous fluxes is not clear, however, and some drinking of the external medium would appear to be involved (Diefenbach 1973; Bentley 1976). Balment and Loveridge (1993) have recently shown that the peptide hormone angiotensin II is dipsogenic in the Nile crocodile when held in fresh water.

The estuarine crocodile *Crocodylus porosus* has been the best studied and appears capable of quite extraordinarily precise osmoregulation, with plasma osmolality varying less than 25% over a salinity range of 0–64‰ (280–340 mOsm kg⁻¹, plasma sodium concentration 130–159 mmol l⁻¹) (Grigg 1981; Grigg et al. 1986b; Taplin 1988). To some extent this impressive osmoregulatory capacity must be related to the size of this species, which can attain lengths of 7 m and a mass of several tonnes. The surface area to volume ratio is thus quite small in adults and this must reduce considerably the potential rate of exchange of water and electrolytes across external membranes. Taplin (1988) has derived allometric equations describing variation in total body water content and the exchangeable sodium pool with body length in both *C. porosus* and *C. johnstoni* and the variation with body size is quite considerable.

There is also no evidence that estuarine crocodiles accumulate urea in the body fluids on exposure to sea water, as has been documented in the estuarine terrapin *Malaclemys terrapin* (Gilles-Baillien 1970; Cowan 1985) in which plasma osmolality increases by some 40–50% and may reduce overall osmotic water loss (see Table 1.1).

2.4.2

Kidney and Cloaca

There seems to be general agreement in the literature that the kidneys of crocodiles possess only a limited ability to regulate the composition of ureteral urine and that any homeostatic responses are located in the cloacal-colonic complex. This is based essentially on the work of Schmidt-Nielsen and Skadhauge (1967) and Schmidt-Nielsen and Davis (1968) with *C. acutus* and *C. porosus*. These investigators found that urine to plasma ratios (U/P_{OSM}) were high (0.67–0.82) and little affected by either salt loading or dehydration. The U/P_{OSM} of cloacal fluid collected from crocodiles varies from 0.53 to 0.99, however, indicating an enhanced capacity for modifying the osmolality of the urine ultimately voided, and concentrations of sodium are typically low (Coulson and Hernandez 1964, 1970). This is not a general characteristic shared by aquatic reptiles, however, as water and salt reabsorption from the distal tubule of both the turtle *Pseudemys scripta* and the water snake *Nerodia sipedon* is highly responsive to changes in salt and water balance status (Dantzler 1976, 1980).

The only data on osmoregulatory responses of alligatorids (as opposed to crocodilians) to hyperosmotic media come from a laboratory study of Lauren

(1985) on juvenile *Alligator mississippiensis*. After 4 weeks of exposure to 20‰ seawater, plasma sodium concentration increased from 147 to 183 mmol l⁻¹ and the U/P_{OSM} of cloacal fluid from 0.11 to 0.82. Plasma corticosterone levels were also significantly elevated in these animals, which lost some 27% of their initial weight, and it would appear that they were quite stressed by the exposure as mortality was significant.

2.4.3

Salt-Excreting Glands

Taplin (1988) speculates that the inferior osmoregulatory capacity of the alligators compared with that of the crocodiles results from their lack of functional lingual salt glands. These glands were first described in the nineteenth century (Owen 1866) but thought to be mucus-secreting glands of the tongue. They have now been found in all the Crocodylinae examined to date and are capable of secreting hyperosmotic NaCl solutions, often at quite high rates (up to 45 μ mol 100 g^{-0.7} per hour of sodium) (Taplin et al. 1982). According to Taplin (1985), these salt-secreting glands may account for over 90% of the sodium excreted by unfed animals. Their ultrastructure is very similar to that of salt glands of other reptiles with complex folding and interdigitation of the lateral cell membranes, expanded intercellular spaces, abundant mitochondria and an extensive blood supply. At this stage, however, nothing is known of their control other than that they are stimulated by metacholine (Taplin et al. 1985).

2.4.4

Desert Tortoises

2.4.4.1

Ecophysiology

The large (ca. 0.5–5 kg) terrestrial tortoise *Gopherus (Xerobates) agassizii* was once widespread in the deserts of southwestern North America but is now restricted to a small number of reserves in southern Nevada, California, Arizona and northwestern Mexico (Berry 1984; van Devender et al. 1976). Osmoregulation and energetics of a small number of immature individuals in a 9 hectare enclosure in Nevada was studied by Nagy and Medica (1986) over the period March 1976 to April 1978 and a population of smaller individuals was studied by Minnich (1977) and Minnich and Ziegler (1976) near Barstow in California.

The tortoises hibernate in the desert over winter and emerge in the spring to feed on succulent annual plants. These provide excess water and potassium ions that are stored in the urinary bladder, but energy intake, measured with doubly labelled water, was found to be less than required to meet energy expenditure via respiration. Thus, although the animals gained in body mass,

this was essentially due to water while body solids actually declined over spring. As the water content declined in the food plants in late spring the tortoises eventually achieved positive energy balance whilst eating grasses, but they were then in negative water balance and their body mass accordingly declined.

Plasma osmolality increased from 293 to 355 mOsm kg⁻¹, with plasma sodium increasing from 136 to 174 mmol l⁻¹ by July, and the osmolality of the urine increased to become isosmotic by mid-summer. Plasma potassium concentrations were extraordinarily elevated in July with a mean of 15.5 ± 1.8 mmol l⁻¹ and this is one of the highest values recorded for any vertebrate.

As summer progressed the tortoises reduced their activity, spending much of their time in aestivation, but they emerged to drink when there were infrequent thunderstorms and constructed small depressions in which the rain collects (Medica et al. 1980). The effect of drinking was marked in that both plasma and bladder urine osmolality fell to early spring levels. Urine with a high osmotic pressure was first voided and then the bladder filled with dilute urine, essentially storing water by this mechanism which is later used to dilute accumulating dietary salts. These changes are shown in Fig. 2.2.

The restoration of the animals' normal water and electrolyte balance coincided with a resumption of feeding and the tortoises gained energy by this means, although still losing water due to the dry nature of the plant food. Plasma and urine osmolality thus again increased, only to be alleviated by further rain showers in early September. The tortoises continued to accumulate energy reserves until they began feeding on the succulent sprouts of annual plants that germinated in late September, which provoked a return to the spring-like physiological situation through mid-November until hibernation began.

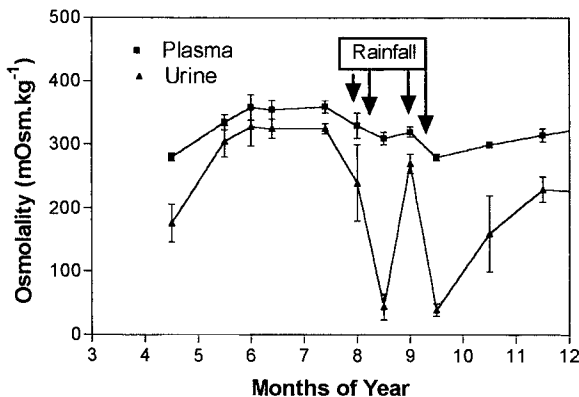


Fig. 2.2. Seasonal changes in plasma and urinary osmolality in the desert tortoise *Gopherus (Xerobates) agassizii* over a 9-month period in Nevada, USA; the effect of rainfall is shown. (Adapted from Nagy and Medica 1986)

Nagy and Medica (1986) speculate that desert tortoises relinquish maintenance of internal homeostasis on a daily basis during most of the year and tolerate large imbalances in their water, energy and salt budgets. This strategy apparently allows them to exploit resources that are only available periodically, whilst balancing their water and salt budgets on an annual basis and showing an overall energetic profit. Peterson (1993) has coined the term "anhomeostasis" to refer to this tendency of the desert tortoises to osmoregulate opportunistically and tolerate significant deviations of the milieu intérieur during late spring and summer. By this means they are able to lay eggs each year, even during droughts (Turner et al. 1986).

But is this really a strategy or instead merely a consequence forced upon the animal by the exigencies of the environment it now occupies? van Devender et al. (1976) provide evidence that the desert tortoise was once more widespread and occupied more mesic habitats in the Pleistocene in North America and the present populations may only be relics that are barely surviving under the more rigorous conditions that prevail today (C.C. Peterson, pers. comm.). Our tendency is to interpret everything in adaptationist terms but, as Gould and Lewontin (1979) have emphasised, the excesses of the "adaptationist programme" have occasionally led to "panglossian" conclusions, particularly in the case of desert reptiles (Bradshaw 1988).

Desert tortoises lack a functional nasal salt gland (Dantzler and Schmidt-Nielsen 1966) and eating their normal diet is apparently osmotically stressful because of the high level of ingested osmolytes. Both Minnich (1977) and Nagy and Medica (1986) agree that it is the inability of the tortoises to cope with dietary potassium that leads to the reduction and eventual cessation of feeding as drought progresses. In many respects this pattern of enforced osmolyte storage in the body fluids is very reminiscent of the Australian agamid lizard *Ctenophorus (Amphibolurus) ornatus*, in which the problem is due to excess dietary sodium rather than potassium (Bradshaw and Shoemaker 1967). Although regulatory responses in summer due to hormones have yet to be measured in free-living desert tortoises, they would appear to be prime candidates for stress, as defined above, with a quite markedly perturbed milieu intérieur during extended periods of the year (Nagy 1988).

2.4.4.2

Kidney Function

An early paper by Dantzler and Schmidt-Nielsen (1966) compared renal function in the desert tortoise *Gopherus agassizii* with that in the freshwater turtle *Pseudemys scripta*. Data from this paper on GFR and associated renal parameters are presented in Table 2.2 and give some idea of the response of the two species to externally imposed variations in water and electrolyte status. These data, of course, were gathered using ureteral urine and thus reflect only the contribution made by the kidneys to any overall homeostatic response.

Table 2.2. Comparison of renal response to water and salt loading in desert and fresh-water chelonians. (Modified from Dantzler and Schmidt-Nielsen 1966)

Condition	GFR ($\text{ml kg}^{-1} \text{h}^{-1}$)	V ($\text{ml kg}^{-1} \text{h}^{-1}$)	$\text{FR}_{\text{H}_2\text{O}}$ (%)	U/P_{OSM}	$\text{C}_{\text{OSM}}/\text{C}_{\text{IN}}$ (%)	$\text{C}_{\text{H}_2\text{O}}/\text{C}_{\text{IN}}$ (%)
<i>Gopherus agassizii</i>						
Normal	4.74	1.9	59.9	0.36	14.4	25.6
Water load	15.12	8.3	45.1	0.61	33.5	21.5
Salt load	2.94			0.57		
<i>Pseudemys scripta</i>						
Normal	4.73	1.5	68.3	0.62	19.7	12.1
Water load	10.27	3.6	64.9	0.60	20.7	7.5
Salt load	2.77			0.84		

From this comparison it is difficult to conclude that the renal physiology of the desert species (*G. agassizii*) is greatly different from that of the aquatic species (*P. scripta*). Both have about the same GFR under normal conditions and a slightly greater fraction of this fluid is reabsorbed in the renal tubules in the aquatic species before being passed to the bladder and cloaca (68.3 versus 59.9%). GFR increases with a water load in both species and declines with a salt load, as would be expected. The desert species has a much higher relative free water clearance ($\text{C}_{\text{H}_2\text{O}}/\text{C}_{\text{IN}}$) under a water load, however (21.5 versus 7.5%), which is the opposite of what one might expect a priori. The relative osmolar clearance ($\text{C}_{\text{OSM}}/\text{C}_{\text{IN}}$) of the desert species is also higher, reflecting perhaps a reduced ability to reclaim filtered solutes under these high flow conditions. Interestingly, the only measurements of GFR in the marine green sea turtle *Chelonia mydas* are almost three times higher, at $14.3 \text{ ml kg}^{-1} \text{h}^{-1}$, than the GFR in either of these two species (Schmidt-Nielsen and Davis 1968).

Perhaps the most significant point to emerge from this study was the reaction of the two species to salt loading and subsequent increases in plasma osmolality. An increase of only 20 mOsm in plasma osmolality was associated with anuria in the freshwater turtle, whereas anuria was only provoked by increases of closer to 100 mOsm in the desert tortoise. This suggests that the desert species is more tolerant of variations in the osmolality of the body fluids and continues to filter blood for longer when salt loaded. The change in U/P_{OSM} following salt loading in *G. agassizii* is not impressive, however, and less than that of the aquatic species. Thus, one is left with the distinct impression that we only have part of the story. The ecophysiological study of Nagy and Medica (1986) shows that desert tortoises use their bladder to both store and reclaim water and electrolytes under different circumstances and a proper comparison needs information on the activity of this and other postrenal sites of water and solute exchange. Dantzler (1970) mentions that the bladder of the desert tortoise is highly permeable to water but notes that neurohypophysial hormones have not yet been found to stimulate water transport in the reptilian bladder (Brodsky and Schilb 1960).

The renal response to infusions of the neurohypophysial peptide AVT has not been studied in either the desert tortoise or this aquatic turtle, but its classic effects in reducing GFR, enhancing tubular water reabsorption and reducing relative free water clearance have been recorded in the aquatic western painted turtle *Chrysemys picta belli* by Butler (1972) and there is no reason to imagine that they would be grossly different.

2.5

Osmoregulation in Lizards

Lizards and snakes are by far the most numerous of the reptiles, with some 3300 and 2300 species respectively (Rage 1992), and their diversity and ease of capture has led to lizards, especially, becoming the favourite subjects of herpetologists and comparative physiologists alike. Much of what we know of osmoregulation in reptiles thus is based on lizards, and then to a great extent on species from arid habitats. This inherent bias in the literature makes it difficult to compare the performance of desert with nondesert species and, as we shall see, relevant information on snakes is extremely limited. In the following I will concentrate on species that have been studied both in the laboratory and in the field and for which we have a more complete set of data than is often the case.

2.5.1

Hypernatraemia and Hyperkalaemia in Lizards

We have seen from the data compiled in Table 1.2 and Fig. 1.3 that lizards appear to have a larger extracellular fluid volume (ECFV) than other reptiles and a correspondingly reduced intracellular fluid volume (ICFV). This expansion of the ECFV is also associated with higher plasma sodium concentrations, although these are not significantly different from those recorded in snakes.

Bentley (1959) appears to have been one of the first to appreciate the need for a detailed study of the water and electrolyte balance of reptiles and his paper on the large scincid lizard *Tiliqua rugosa* was a benchmark in the

Table 2.3. Seasonal variation in plasma electrolyte concentrations in the scincid lizard *Tiliqua* (*Trachydosaurus*) *rugosa* recorded in the region of Perth, Western Australia. (Modified from Bentley 1959)

Season	Number	Sodium conc (mmol l ⁻¹ ± SE)	Potassium conc (mmol l ⁻¹ ± SE)
Winter	10	151.9 ± 1.6	3.5 ± 0.1
Summer	12	195.9 ± 7.1	4.6 ± 0.1
<i>Statistical significance</i>		<i>P</i> < 0.001	<i>P</i> < 0.001

field because it included both observations on wild animals and laboratory investigations. He found that plasma electrolyte concentrations in field-caught animals varied significantly between summer and winter, as shown in Table 2.3:

This appears to be the first record of significant hypernatraemia in a reptile. Note also that the increase in plasma potassium concentration, although apparently of smaller magnitude, is in fact greater (31.4% versus 28.9% for sodium) and equally statistically significant.

Bentley (1959) found that the renal response of *Tiliqua* to the administration of salt solutions was reminiscent of that of newborn mammals. He ascribed this to their very limited glomerular population and hence filtering surface in the kidney, which he calculated was about seven times smaller than that of a similar-sized mammal. He also found that plasma sodium concentrations could rise to levels as high as 230 mmol l^{-1} in the laboratory without apparent ill effect and concluded that these lizards were extraordinarily tolerant to hypernatraemia and may

"conserve body water at the expense of abandoning maintenance of the constancy of body fluid composition"

(my emphasis) during periods of water stress. An interesting paper published at much the same time by a group of Dutch clinicians (Borst et al. 1960) reaches similar conclusions and describes clinical cases in which significant hypernatraemia is tolerated in situations where body fluids are threatened.

These studies serve to bring into focus one of the central questions of this book: whether episodes such as periodic hypernatraemia in desert and other reptiles result from an inherently limited ability to regulate the composition of the body fluids, or whether such excursions should be viewed as adaptive responses to an exigent environment that markedly enhance the individual's chances of survival, albeit at the cost of maintaining the constancy of the milieu intérieur.

2.5.2

Studies of the Agamid Genus *Amphibolurus* (*Ctenophorus* and *Pogona*) in Australia

This widespread genus has been extensively studied since the late 1960s (Bradshaw 1981, 1986a) and serves as a convenient base for comparing the osmoregulatory responses of other lizards. This large and obviously polymorphic genus was analysed in a brief paper by Storr (1982) and the proposed generic groupings of the species have been followed here, although they await confirmation from cognate molecular and genetic studies.

2.5.2.1

The Ornate Dragon Lizard (Ctenophorus ornatus) at Bakers Hill

Seasonal changes in water and electrolyte balance of the 20 g agamid lizard *C. ornatus* were first reported by Bradshaw and Shoemaker (1967), who measured

Table 2.4. Fluid distribution and plasma electrolyte concentrations in a field population of *Ctenophorus ornatus* lizards in semi-arid Western Australia. (Modified from Bradshaw and Shoemaker 1967)

Season	Body fluid compartments (ml 100 g ⁻¹ ± SE)					Plasma electrolytes (mmol l ⁻¹ ± SE)	
	TBW	ECFV	BV	PV	ICFV	Na ⁺	K ⁺
Early summer (November)	73.6 ± 1.0	25.7 ± 0.8	7.6 ± 0.2	5.4 ± 0.1	47.9 ± 0.8	155 ± 2.4	5.5 ± 0.6
Statistical significance	NS	<i>P</i> < 0.01	<i>P</i> < 0.01	<i>P</i> < 0.01	<i>P</i> < 0.01	<i>P</i> < 0.01	NS
Mid-summer (December)	73.8 ± 1.6	33.0 ± 1.3	9.3 ± 0.4	7.1 ± 0.4	41.2 ± 1.6	172 ± 1.5	5.7 ± 0.2
Late-summer (post-rain)	73.2 ± 0.7	25.4 ± 1.1	6.7 ± 0.2	4.8 ± 0.3	47.9 ± 1.5	149 ± 3.9	5.0 ± 0.4
Fully hydrated in laboratory	73.5 ± 0.3	25.5 ± 0.4	7.3 ± 0.1	5.1 ± 0.1	48.0 ± 0.5	150 ± 1.3	5.0 ± 0.2

No statistically significant differences exist between any of the means for November, Late-summer (February) and those from fully hydrated animals in the laboratory. TBW = total body water content; ECFV = extracellular fluid volume; BV = blood volume; PV = plasma volume; ICFV = extracellular fluid volume; NS = not significant with *P* > 0.05.

both the distribution of water within the body and plasma electrolyte concentrations in a free-ranging population at Bakers Hill, some 100 km east of Perth in Western Australia. Data from this study are given in Table 2.4 and show a summer pattern of mild hypernatraemia associated with an expansion of the extracellular fluid volume (ECFV) at the expense of cell water.

The above data make it clear that the lizards were not dehydrated in mid-summer, as their (total body water) TBW had not changed, and that the redistribution of water within the body had been brought about by the addition of sodium ions to the body fluids, rather than due to the loss of ion-free water.

These lizards subsist almost exclusively on a diet of sodium-rich ants of the genus *Iridomyrmex*. During the summer months, when free water is unavailable, sodium ions are retained in the body fluids due to a progressive inhibition of renal function. This sodium is sequestered preferentially in the extracellular fluid by the operation of the Na⁺/K⁺ cellular membrane pump and the ECFV, as a consequence, is expanded in volume by an isosmotic movement of water from the intracellular compartment to maintain osmotic equilibrium. This movement of water from cells to the extracellular fluid is quite obvious from the data, which also includes the independently measured blood and plasma volumes that form part of the ECFV.

This change is a relatively temporary state of affairs, however, induced by the combination of an excess of sodium in relation to preformed water in the diet, and the animals achieve relief from this with the advent of periodic

summer thunderstorms. As with desert tortoises in the North American deserts, *C. ornatus* drink avidly when rain falls and restore their normal water and electrolyte balance within a matter of hours. The data in Table 2.4 for late-summer, for example, were collected a mere 10h after rain fell on the granite rock where the animals occur. Prior to the rain the lizards were anuric but, after drinking, they excreted copious amounts of sodium-rich urine (mean sodium concentration 65 mmol l^{-1}) thus excreting the electrolyte load stored previously in their extracellular fluid. Interestingly, none of the Australian desert agamids has the capacity to recognise standing water and they will readily dehydrate in the laboratory if water supplied to them does not simulate falling rain.

The pattern shown in Table 2.4, with a temporary electrolyte imbalance engendering an isosmotic reorganisation of body water distribution, can be reproduced readily in the laboratory by injections solely of sodium chloride, and it is easy to demonstrate that plasma sodium concentrations can rise to much higher levels, as Bentley (1959) found with *Tiliqua rugosa*. This is also the case in the field and Bradshaw (1970) reported much more significant changes in water and electrolyte balance in the same population of *C. ornatus* after a prolonged drought at Bakers Hill where rain was not recorded for a period of over 3 months.

Plasma, tissue and urinary electrolyte concentrations are given in Table 2.5 and the animals were sampled again, 10h after a summer thunderstorm which terminated the drought.

The mean value for plasma sodium of 243 mmol l^{-1} is extremely high and some individuals had levels up to 300 mmol l^{-1} . Plasma potassium concentra-

Table 2.5. Plasma and tissue electrolyte concentrations in the agamid lizard *Ctenophorus ornatus* after a prolonged drought (pre-rain) and immediately following its termination by rain. (Modified from Bradshaw 1970)

Variable	Pre-rain	Statistical significance	Post-rain	Statistical significance	Fully hydrated
Plasma Na^+	243.0 ± 9.9	$P < 0.001$	166.0 ± 2.7	$P < 0.01$	150.0 ± 1.3
Plasma K^+	12.2 ± 0.6	$P < 0.001$	5.6 ± 0.9	NS	5.0 ± 0.2
Tissue Na^+					
mmol l^{-1} tissue water	75.5 ± 8.3	NS	71.2 ± 10.0	$P < 0.01$	28.5 ± 3.2
mmol kg^{-1} dry mass	216.8 ± 20.5	NS	259.8 ± 41.3	$P < 0.01$	98.2 ± 10.3
Tissue K^+					
mmol l^{-1} tissue water	147.0 ± 3.7	$P < 0.01$	128.2 ± 4.7	NS	123.8 ± 4.9
mmol kg^{-1} dry mass	426.2 ± 16.5	NS	461.2 ± 12.4	$P = 0.05$	406.0 ± 16.2
Tissue water $\text{ml } 100 \text{ g}^{-1}$	74.3 ± 0.6	$P < 0.01$	78.3 ± 0.4	$P < 0.01$	76.8 ± 0.2
Urine $\text{Na}^+ \text{ mmol l}^{-1}$	103.0 ± 9.5	$P < 0.02$	65.3 ± 6.7		
Urine $\text{K}^+ \text{ mmol l}^{-1}$	38.2 ± 10.4	NS	27.1 ± 1.9		

All values are means \pm SE. NS = not significant with $P > 0.05$.

tions were also over twice normal levels at 12.2 mmol l^{-1} and these concentrations, which would be lethal for a mammal, are almost as high as those recorded by Nagy and Medica (1986) in the desert tortoise.

Table 2.5 also shows that intracellular concentrations of sodium and potassium were elevated in these drought animals, in contrast to the situation that one sees each year with mild summers. Not surprisingly, therefore, fluid volumes in these animals were not significantly different from the pattern seen in fully hydrated animals and the mild-summer pattern of an expanded ECFV disappears as the animals are less and less able to maintain all the extra sodium ions exclusively in the extracellular compartment. Cellular rehydration thus proceeds apace with sodium penetration of the intracellular compartment. Rather than being a sign of a restoration of the normal water balance, this indicates the progressive breakdown of membrane pumps which normally restrict the great majority of sodium ions to the extracellular compartment.

The handling of potassium ions in these drought-affected animals appears to be quite different from that of sodium, and tissue concentrations are only slightly elevated prior to rain and kept below 150 mmol l^{-1} of tissue water. This suggests that, although significant hyperkalaemia occurs, tissue levels continue to be regulated, probably by persistent tubular secretion in the kidney which can still continue in non-filtering kidneys through the agency of the renal-portal system (O'Shea et al. 1993).

Some individuals do lose body water and dehydrate quite extensively under such drought conditions, however, and as has been shown by Bradshaw (1971) and Baverstock and Bradshaw (1975), these are the more rapidly growing members of the population. Despite weight losses that may approach 45% of the initial body mass and involve significant mortality within the population, such individuals do not evidence a complete breakdown in regulatory mechanisms and the circulating fluid volume appears to be protected preferentially against such inevitable losses of body water.

This very interesting response is shown in Fig. 2.3 where fluid volumes have been graphed against the estimated weight loss for each individual. These are all pre-rain drought animals from Bakers Hill and the data indicate the considerable degree of individual variation that exists in this 'species' water and electrolyte physiology at this particular time.

In this figure, fluid volumes have been expressed as $\text{ml } 100 \text{ g}^{-1}$ of the animal's original body mass, otherwise the changes shown would be obscured. This is because drought-affected animals lose both body water and solids and the fraction of the body that is water thus changes less (and may even remain the same if water and solids are lost at the same rate). It is thus essential to express the measured fluid volume as a fraction of the original and not the actual, dehydrated, mass if changes are to be correctly interpreted.

When this is done it is clear that the circulating fluid volume (blood and plasma volumes) in dramatically dehydrated individuals is little different from that of fully hydrated lizards and this is confirmed by the fact that blood

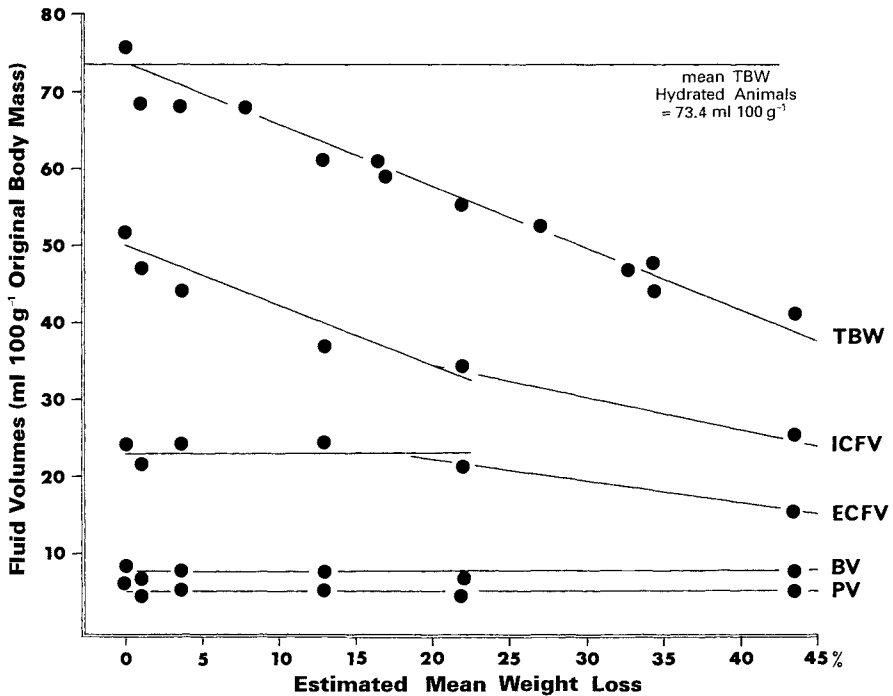


Fig. 2.3. Changes in fluid volumes with progressive dehydration in a sample of fast-growing *Ctenophorus (Amphibolurus) ornatus* at Bakers Hill in Western Australia. TBW Total body water content in ml 100 g⁻¹; ICFV intracellular fluid volume; ECFV extracellular fluid volume; PV plasma volume; BV blood volume. (Adapted from Bradshaw 1986a)

haematocrit also does not change (Bradshaw 1970). The ECFV also appears to remain quite constant until a body mass loss of approximately 25%, after which it too appears to decline. The data are unfortunately very limited but, given the very linear decline in TBW content, it appears clear that the first fluid compartment to suffer is not the ECFV, which one might expect a priori, but the ICFV, even though one might imagine that the intracellular fluid compartment is the more important of the two. Even when the ECFV does begin to decline (>25% weight loss), this loss is borne by the interstitial compartment (ISFV) such that both the volume and viscosity of the circulating fluid in the body is maintained right up until the point of death.

This is indeed an impressive response to dehydration and reminiscent of the situation described in a number of desert mammals such as the camel (Macfarlane et al. 1963; Schmidt-Nielsen 1979), the Mongolian gerbil (Kutcher 1967) and the desert spiny mouse (Horowitz and Borut 1970, 1975) in which plasma volume is maintained, apparently through an increase in the colloid osmotic pressure of the plasma and a reduction in the permeability of capillaries to serum albumin (Borut et al. 1972; Horowitz and Borut 1973).

2.5.2.2

The Western Netted Dragon (Ctenophorus nuchalis) at Shark Bay

This medium-sized (30–50 g) agamid has been the subject of a long-term ecophysiological study at Shark Bay, some 900 km north of Perth, in Western Australia and details may be found in Bradshaw (1981, 1986a) and Bradshaw and De'ath (1991). Despite its size, *C. nuchalis* is an annual species and the young of this oviparous species emerge in mid-summer, in February, and grow rapidly until the onset of the cooler winter season from July till August. Growth resumes in September at an exceptionally high rate, and mating occurs in the austral spring with egg laying in late spring and early summer. Females may lay up to three clutches and the reproductive potential (R_0) of the species is very high, estimated by Bradshaw (1986a) at 2.02.

Adults die progressively after breeding over the summer period (December–March) and by late autumn (April) the population is usually composed almost entirely of newly emerged juveniles. From a total of over 1000 marked individuals, Bradshaw (1981) recorded only 11 that survived into their second year. One of the aims of the long-term study of this species has been to identify the causes of mortality and to measure its incidence, and there now appears little doubt that adults die from the combined effects of chronic dehydration and reduced food intake.

Nagy and Bradshaw (1995) have recently published a conservative analysis of seasonal changes in field metabolic rate (FMR), estimated food intake and water metabolism of *C. nuchalis* over a 4-year period at Shark Bay. Table 2.6 summarises some of these data from adult individuals.

Animals captured in autumn have a significantly lower condition index (Bradshaw and De'ath 1991) and lose weight at a significantly greater rate than animals collected in spring. Their rate of water influx is lower, as is their dry matter intake, and they are in negative water balance (i.e. water efflux > water influx) and with a reduced TBW content. The FMR, measured as rate of CO_2 production, is also significantly reduced from 0.512 ± 0.07 to 0.271 ± 0.03 ml

Table 2.6. Seasonal variation in body composition, rate of water turnover and estimated food intake in *Ctenophorus nuchalis* from Shark Bay. (From Nagy and Bradshaw 1995)

Season	Body mass (g)	Condition index (%)	Change in mass (% d ⁻¹)	TBW (ml 100 g ⁻¹)	Water influx (ml kg ^{-0.82} d ⁻¹)	Water efflux (ml kg ^{-0.82} d ⁻¹)	Dry matter intake (g kg ⁻¹ d ⁻¹)
Spring	37.3 ± 1.9 (49)	112.7 ± 2.6 (49)	-0.1 ± 0.2 (18)	85.1 ± 0.7 (16)	23.7 ± 2.8 (16)	24.3 ± 2.1 ^a (16)	14.5 ± 1.7 (14)
Autumn	28.1 ± 0.9 (122)	94.6 ± 0.9 (122)	-0.8 ± 0.1 (52)	68.7 ± 1.1 (52)	13.8 ± 1.0 (52)	17.3 ± 0.9 ^b (52)	7.1 ± 0.7 (41)
Statistical significance	$P < 0.001$	$P < 0.001$	$P = 0.001$	$P < 0.001$	$P < 0.001$	$P = 0.001$	$P < 0.001$

^a Water efflux not significantly different from influx.

^b Water efflux significantly greater than influx with $P = 0.01$.

$\text{g}^{-1}\text{h}^{-1}$ ($P < 0.01$) and the reasons for their eventual demise are obvious. Nagy and Bradshaw (1995) showed, however, that *C. nuchalis* has the lowest water economy index (WEI-water influx/FMR; see Nagy and Peterson 1988) of any reptile measured to date and this in part explains its impressive survival capacity during the summer months.

Despite this, changes in plasma osmolytes are nowhere near as great as we have seen with *C. ornatus* and there is no evidence of the hypernatraemia that one might expect with such chronic dehydration and water imbalance. Further data are compared for the two seasons in Table 2.7.

Plasma potassium concentration is the only electrolyte to change significantly in these dying animals (a decrease) but plasma osmolality increases significantly by about 7.5%, indicating that other unmeasured osmolytes have increased in the plasma. Plasma levels of circulating corticosteroids (primarily corticosterone in lizards) also decrease significantly rather than increase as one might expect in animals that could be considered to be stressed by their loss of body condition and chronic dehydration.

Bradshaw (1978a) showed by incubating the adrenal glands of animals in the field at different times of the year that the rate of secretion of corticosteroids by the adrenal of *C. nuchalis* is not compromised in late summer and in vitro rates of production were significantly enhanced and positively correlated with those levels circulating in the blood at the time of capture. There was some indication that circulating levels of corticosterone increase gradually throughout summer (although not seen in the above data set) but what was most noticeable was the response of the adrenals to exogenous administration of ACTH or handling stress.

In spring, previously hypophysectomised animals respond with a highly significant increase in plasma corticosterone levels and the response is quite normal in a statistical sense (i.e. it has a gaussian distribution; see Bradshaw 1975, 1986a). In late summer, the response to both ACTH injections and the stress of being held for a number of hours in a sac is quite abnormal, with many

Table 2.7. Seasonal variation in plasma osmolytes in *Ctenophorus nuchalis* from Shark Bay (means \pm SE with number in parentheses)

Season	Plasma Na^+ (mmol l^{-1})	Plasma K^+ (mmol l^{-1})	Plasma Cl^+ (mmol l^{-1})	Plasma osmolality (mOsm kg^{-1})	Plasma glucose (mmol l^{-1})	Plasma steroids (nmol l^{-1})
Spring	153.4 ± 1.1 (49)	5.9 ± 0.1 (49)	117.3 ± 2.2 (48)	294.0 ± 1.7 (48)	17.8 ± 0.5 (48)	83.7 ± 12.6 (48)
Autumn	156.3 ± 1.8 (90)	4.8 ± 0.1 (90)	117.2 ± 1.7 (89)	315.6 ± 3.9 (90)	14.0 ± 0.3 (122)	47.9 ± 3.9 (90)
Statistical significance	NS	$P < 0.001$	NS	$P = 0.0001$	$P < 0.001$	$P = 0.001$

NS = not significant with $P > 0.05$.

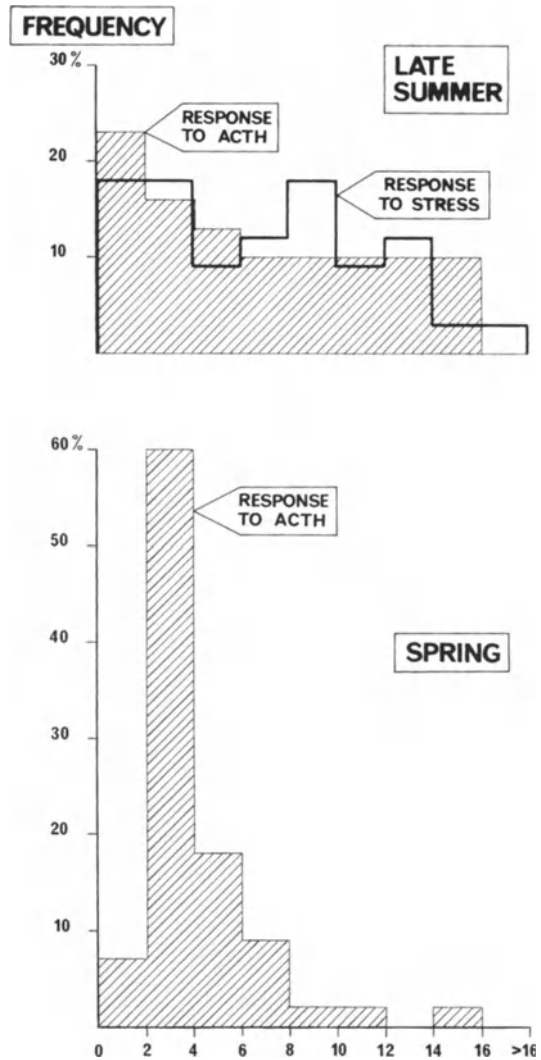


Fig. 2.4. Frequency distribution of plasma corticosteroid concentrations in *Ctenophorus* (*Amphibolurus*) *nuchalis* lizards injected with ACTH after dexamethasone blockade in spring and late summer at Shark Bay in Western Australia. The adrenal response of animals to the stress induced by confinement in late summer is also shown for comparison. (Adapted from Bradshaw 1986a)

CORTICOSTERONE PRODUCTION RATE IN VITRO

ng(mg.hr)⁻¹

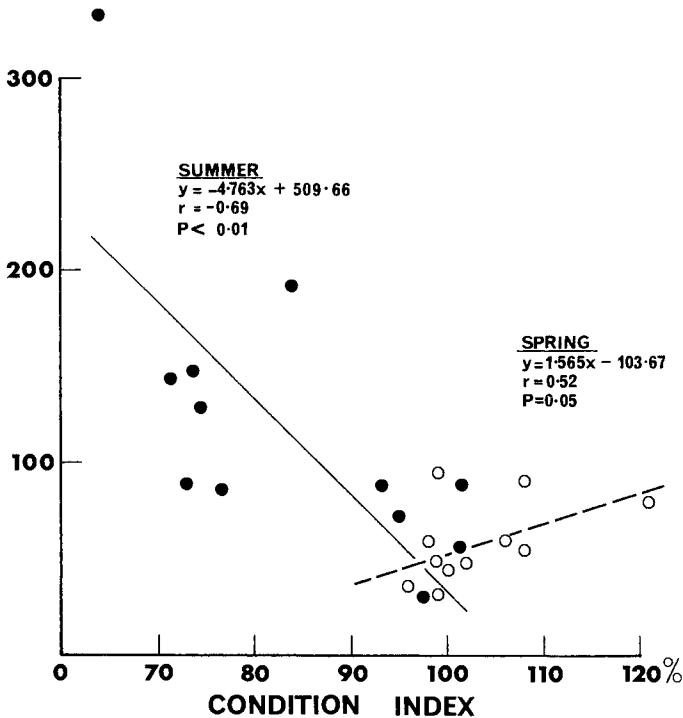


Fig. 2.5. Seasonal variations in rate of adrenal corticosteroidogenesis in vitro in the lizard *Ctenophorus (Amphibolurus) nuchalis* at Shark Bay as a function of body mass condition index. Enhanced rates of corticosterone production are evident in individuals in poor condition in summer. (Adapted from Bradshaw 1986a)

animals failing to respond and others recording very large increases in plasma corticosterone, as shown in Fig. 2.4. The precise significance of this qualitative change in the reaction of the adrenal glands is not clear, but what is obvious is that the gland has not lost its capacity to respond to stressful stimuli by secreting corticosteroid hormones.

Thus whilst an attractive hypothesis might be that *C. nuchalis* die each summer at Shark Bay as a result of exhaustion of the pituitary-adrenal axis (the classic Christian/Selye hypothesis of population stress; see Lee and McDonald 1985) the data clearly do not bear this out. As seen in Fig. 2.5 (Bradshaw 1986a), rates of corticosteroidogenesis in the field are enhanced in late summer and negatively correlated with body condition, i.e. the poorer the condition of the animal, the greater its rate of production of corticosterone in vitro.

This set of field-based experiments was difficult to perform and has not been repeated for any other desert reptile, but the data show clearly that even

in an annual species which routinely dies postreproductively, there is little evidence of an abandonment of all normal regulatory and homeostatic processes. There is evidence that the response becomes "anormal" in that fewer animals respond like the norm in spring, but this presumably reflects the fact that individuals are in the process of dying and that one is no longer dealing with a normal population in the statistical sense.

To some, the above may simply highlight the hazards of attempting to carry out detailed physiological and endocrinological investigations in the field, but this study is the only one to date in which one may glimpse the complexity of the interactions in a changing population of desert animals. To conclude that these animals are dying from a breakdown of homeostatic regulatory processes would be far too premature in the light of the data gathered thus far.

2.5.2.3

Ctenophorus nuchalis and *C. caudicinctus* at Port Hedland

The distribution of these two desert species in Western Australia is shown in Fig. 2.6 with both Shark Bay and Port Hedland, in the arid northwestern Pilbara region of the state indicated (Bradshaw et al. 1991a). The ecology of the ringtail dragon, *C. caudicinctus*, is intimately associated with granite rocks and boulders and its distribution in the southwestern part of the state is replaced by that of *C. ornatus*.

Shark Bay is quite typical of the sandy habitat occupied by *C. nuchalis* in arid Australia (Heatwole 1970) but the climate of Port Hedland, further north, is quite different. As shown in Fig. 2.7 (Bradshaw et al. 1991a), Shark Bay has a regular winter rainfall whereas at Port Hedland (Mallina Station) rain falls primarily during the summer months between January and April as a result of severe tropical cyclones. Despite this, Port Hedland still receives substantial amounts of rain during the winter months of May till August.

Bradshaw et al. (1991a) studied the ecophysiology of these two species over a 7-year period at Mallina Station in an effort to interpret their vastly different patterns of reproduction. *C. nuchalis* is a typical vernal breeder at Shark Bay (Bradshaw 1981) but early collecting work by Storr (1967) suggested that its breeding is restricted to autumn, following the cyclonic rains. As both species occur sympatrically in the region of Port Hedland, it was of interest to see whether *C. nuchalis* accommodated its pattern of breeding to the prevailing rainfall régime.

In fact what happens is that *C. nuchalis* breeds in spring at Port Hedland in those years when winter rainfall is adequate, but defers breeding until autumn, after the cyclones, in those years when winter rainfall is very low or absent (Bradshaw et al. 1991a). We thus have an intriguing situation from the point of view of osmoregulation. At Shark Bay *C. nuchalis* commence dying in early summer, after they have bred, but at Port Hedland the entire population may

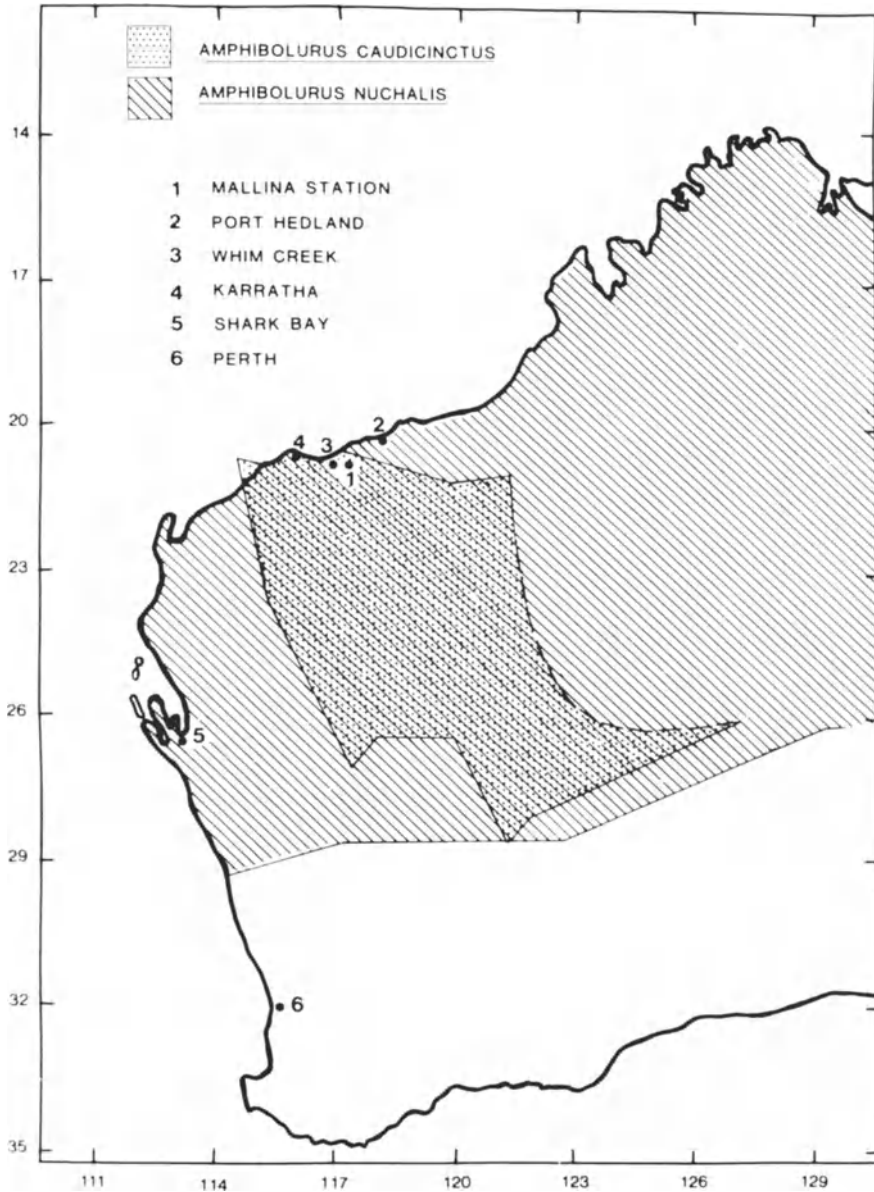


Fig. 2.6. Geographic distribution of the dragon lizards *Ctenophorus* (*Amphibolurus*) *nuchalis* and *C. caudicinctus* in Western Australia. (Adapted from Bradshaw et al. 1991a)

survive through the very hot summer months and only die after breeding in April.

Table 2.8 gives information on the osmoregulatory status of *C. nuchalis* at Port Hedland, classified according to whether the animals bred in spring,

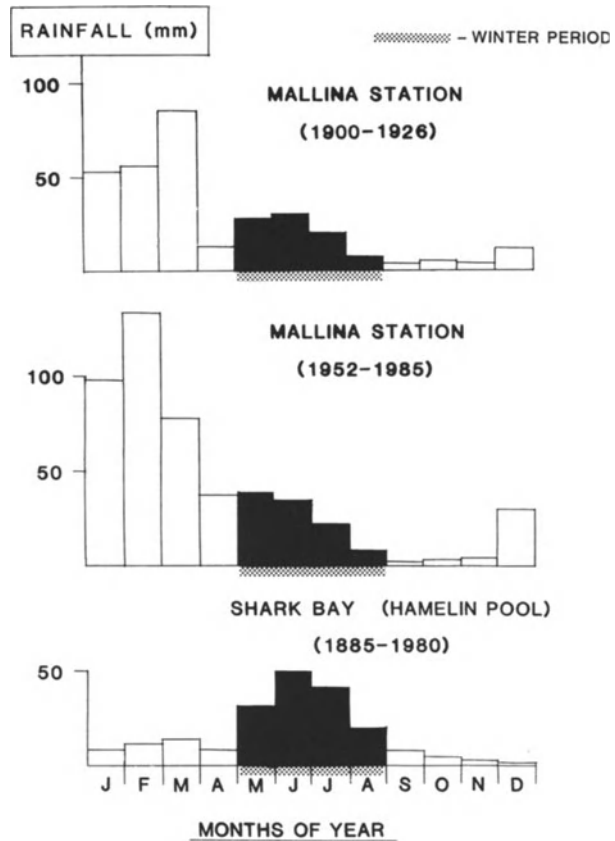


Fig. 2.7. Average monthly rainfall for Mallina Station in the Pilbara region of Western Australia and for Shark Bay, with winter rainfall in black. (Adapted from Bradshaw et al. 1991a)

following adequate winter rains, or in autumn following summer cyclones. These two breeding states are compared with the status of animals collected in spring in those years when breeding was deferred due to lack of adequate resources.

What is clear from the above is that *C. nuchalis* are capable of surviving the summer months, and in a region of the state considerably hotter than Shark Bay. They have a water and electrolyte status in autumn that is little different from that of animals in peak condition in spring, with only plasma sodium concentrations being marginally higher. The autumn-breeding animals at Port Hedland had a high condition index, were not dehydrated, and were in water balance (i.e. influx = efflux) at a time of the year when at Shark Bay they would all be dying or long since dead.

The critical factor here, of course, is that the sequelæ observed at Shark Bay all occur postreproductively and this is also true at Port Hedland where *C.*

Table 2.8. Variation in body condition and osmoregulatory status of *Ctenophorus nuchalis* at Port Hedland with reproductive condition and season. (Modified from Bradshaw et al. 1991)

Season	Reproductive status	Condition index (%)	Total body water (ml 100 g ⁻¹)	Plasma Na ⁺ (mmol l ⁻¹)	Plasma K ⁺ (mmol l ⁻¹)	Water influx (ml 100 g ⁻¹ d ⁻¹)	Water efflux (ml 100 g ⁻¹ d ⁻¹)
Spring	Not breeding	99.0 ± 3.0	80.0 ± 0.84	162.3 ± 1.7	5.40 ± 0.3	2.8 ± 0.6	3.4 ± 0.6
<i>Significance</i>		<i>P</i> < 0.001	NS	<i>P</i> = 0.02	<i>P</i> = 0.05	<i>P</i> = 0.018	<i>P</i> = 0.004
Spring	Breeding	119 ± 4.0	82.2 ± 2.2	157.1 ± 1.1	4.60 ± 0.2	5.7 ± 0.5	7.4 ± 0.9
<i>Significance</i>		<i>P</i> = 0.002	NS	<i>P</i> = 0.01	NS	NS	NS
Autumn	Deferred breeding	102 ± 3.0	82.6 ± 0.9	166.4 ± 2.7	4.16 ± 0.40	8.6 ± 1.1	9.32 ± 1.3

Means ± SE; NS, not significant with *P* > 0.05.

Table 2.9. Variation in body condition and osmoregulatory status of *Ctenophorus caudicinctus* at Port Hedland in the arid Pilbara region of WA. (From Bradshaw et al. 1991)

Season	Reproductive status	Condition index (%)	Total body water (ml 100 g ⁻¹)	Plasma Na ⁺ (mmol l ⁻¹)	Plasma K ⁺ (mmol l ⁻¹)	Water influx (ml 100 g ⁻¹ d ⁻¹)	Water efflux (ml 100 g ⁻¹ d ⁻¹)
Spring	Not breeding	100.5 ± 1.7	76.9 ± 0.9	170.6 ± 2.6	4.4 ± 0.4	2.5 ± 0.3	3.6 ± 0.3 ^a
<i>Significance</i>		NS	<i>P</i> < 0.001	NS	NS	<i>P</i> < 0.001	<i>P</i> < 0.001
Autumn	Breeding	101.6 ± 1.7	82.3 ± 0.8	162.6 ± 4.4	4.3 ± 0.3	8.1 ± 0.5	8.6 ± 0.5

^aEfflux significantly greater than influx with *P* < 0.01.

nuchalis also ultimately die after breeding. The difference is that this may occur in early summer, as it does at Shark Bay, when winter rainfall is high, but is deferred until autumn in those years where the lizards depend on summer cyclonic rains to assure their breeding.

Comparable data are also available for *C. caudicinctus* at Port Hedland (Table 2.9). From the point of view of condition, there is little difference between the animals in late spring and autumn, and plasma electrolyte concentrations are also similar. The major difference is in the water metabolism of the lizards in autumn which is greatly elevated when compared with the lizards captured in the dry part of the year. The total body water content, as well as the rate of water turnover, is elevated in *C. caudicinctus* in late autumn and this reflects the much greater availability of water at this time of year following the summer cyclones. It is also noticeable that, although the spring animals appear in good condition, they appear in slight negative water balance with efflux just exceeding influx.

2.5.3

The Desert Iguana (*Dipsosaurus dorsalis*) in North America

The desert iguana is an herbivorous lizard of some 50–75 g in body mass found in the hotter sandy deserts of southwestern United States. Studies on its water

and electrolyte balance in the field have been conducted in California by Minnich (1970a); Minnich and Shoemaker (1970) and in the laboratory by Minnich (1970b, 1971). The fact that this species is an herbivore rather than insectivore suggests immediately that its dietary intake of electrolytes would be quite different from that of, say, *C. ornatus*. Plants are typically high in potassium, but low in sodium ions, which is the reverse of what one usually finds in insects.

Plasma and tissue electrolyte concentrations from field populations of *D. dorsalis* in different seasons are compared in Table 2.10. The only statistically significant differences in these concentrations concern the much lower plasma sodium and chloride levels recorded in animals sampled in winter ($F_{3,50} = 9.3$, $P < 0.0001$ and $F_{3,50} = 7.6$, $P = 0.0003$ respectively). Otherwise electrolyte levels remained very constant in this field population, suggesting that it is an efficient regulator.

Using data on rates of water turnover of free-ranging animals it is possible to estimate the daily water and electrolyte budget of *D. dorsalis* and this has been done a number of times (Bentley 1976; Minnich 1979). Unfortunately, Bentley (1976) miscalculated potassium loss and overestimated (by a factor of 10, see his Table XV where percent loss of K^+ by the salt gland should be 2.45 and not 24.5%) the importance of the nasal salt gland in potassium excretion in this species. Similarly, the electrolyte balance presented by Minnich (1979) is misleading in that it attributes to the nasal gland that fraction that is unaccounted for in the overall balance.

A quantitative balance is give in Table 2.11, which shows that the excretory role played by the nasal salt gland is quite small. As may be seen, these animals were close to being in water balance, but only excreting about 50% of the electrolytes that they were ingesting. There is thus no evidence that the nasal gland accounts for 43% and 49% of excreted potassium and sodium ions respectively in this lizard as proposed by Minnich (1979; see his Table IV). Instead, the faeces would seem a much more important avenue of electrolyte loss than the nasal gland, especially for potassium in the form of urate salts (Minnich 1972; Minnich and Piehl 1972). Templeton et al. (1972a), in studying the osmoregulatory responses of this lizard in the laboratory also found that

Table 2.10. Seasonal variation in plasma and tissue electrolyte concentrations in the desert iguana, *Dipsosaurus dorsalis* in California. (Modified from Minnich 1970)

Source	Ion (mmol $l^{-1} \pm$ SE)	Spring	Summer (palm desert)	Summer thousand springs)	Winter
Plasma	Sodium	168 \pm 1.9	163 \pm 2.6	165 \pm 2.7	131 \pm 18.2
	Potassium	3.4 \pm 0.40	3.4 \pm 0.2	2.6 \pm 0.4	3.4 \pm 0.1
	Chloride	120 \pm 1.6	120 \pm 2.8	112 \pm 2.2	91.5 \pm 15.8
Muscle	Sodium	44.9 \pm 2.7	40.5 \pm 1.9	40.3 \pm 0.9	42.4 \pm 2.9
	Potassium	122 \pm 3.9	126 \pm 2.5	122 \pm 3.0	117 \pm 4.5
	Chloride	30.0 \pm 1.3	25.9 \pm 1.2	26.4 \pm 1.3	29.9 \pm 1.4

the nasal salt gland contributed significantly to potassium excretion during rehydration, but very little to sodium.

If the nasal salt gland is not the major avenue of electrolyte excretion that it was first thought to be in this species, how then does one account for the remarkably constant plasma electrolyte concentrations in this desert species, especially after a 6 month drought? In fact these appear to be simply a consequence of its diet, which is rich in potassium but very poor in sodium ions. The water and electrolyte composition of the plant diet of *D. dorsalis* is compared with that of the ants habitually consumed by *C. ornatus* in Table 2.12 and the difference is quite appreciable. The average sodium/potassium ratio of the diet of *D. dorsalis* is 0.13, which compares with a figure of 2.75 for *C. ornatus* and reflects the enormous difference in normal sodium intake of the two species.

Table 2.11. Water and electrolyte budget of the desert iguana *Dipsosaurus dorsalis* under field conditions in southern California. (Modified from Bradshaw 1986a)

	Water (%)	Na ⁺ (%)	K ⁺ (%)
Gain			
Dietary	26.4	916	9744
Metabolic	3.6	—	—
Total	30.0	916	9744
Loss			
Urinary	0.78 (2.8)	188 (39.8)	3835 (67.7)
Faecal	18.6 (66.5)	281 (59.5)	1691 (29.9)
Salt gland	?	3 (0.7)	139 (2.4)
Evaporation	8.6 (30.7)	—	—
Total	27.98	472	5665

Water in ml kg⁻¹ per day; electrolytes in $\mu\text{mol kg}^{-1}$ per day.

Table 2.12. Water and electrolyte composition of representative diets of *Dipsosaurus dorsalis* (herbivore) and *Ctenophorus ornatus* (insectivore). (From Minnich 1970; Bradshaw and Shoemaker 1967)

Species	Locality	Water content (%)	Electrolyte concentration (mmol l ⁻¹)		
			Sodium	Potassium	Na ⁺ /K ⁺ ratio
<i>Dipsosaurus dorsalis</i>	Palm desert	55.6	39.1	360	0.11
Spring					
Summer	Palm desert	51.0	34.3	364	0.09
Summer	Thousand Palms	40.1	84.7	481	0.18
<i>Ctenophorus ornatus</i>	Bakers Hill	77.0	200.8	102	1.97
Winter					
Summer	Bakers Hill	74.8	290.0	82.4	3.54

These comparisons serve to highlight the difficulty of assessing the osmoregulatory or homeostatic capacities of any species based on field data alone. Homeostatic capacities can only properly be assessed in the laboratory, where water and electrolyte intake can be controlled, preferably by injection, and both renal and extrarenal rates of excretion measured precisely. As we shall see later in Chapter 3, when such experiments are conducted *C. ornatus* turns out surprisingly to be the better regulator of the two species and one can predict that *D. dorsalis* would experience even greater perturbations of its milieu intérieur if it were ever exposed to sodium intakes such as those experienced by the Australian agamid at Bakers Hill.

2.5.4

The Chuckwallas (*Sauromalus obesus* and *S. hispidus*)

This North American desert lizard is also an herbivore but much larger in size than the desert iguana (300–600 g) and it occupies rocky hillsides in regions where rainfall is erratic and the only source of free water is from the vegetation on which they subsist. Norris and Dawson (1964) first described an active salt-secreting nasal gland in this species and they also identified accessory abdominal lymph sacs which they thought may function to expand the extracellular fluid and store extra body fluid. Smits (1986) has shown that the electrolyte composition of the fluid in these sacs is very similar to that of plasma, but the protein content is only half that of serum. These analyses show that the fluid in the lymph sacs is an extravascular form of extracellular fluid and similar in composition to true lymph. The volume ECFV, measured as thiocyanate space, is 38.9 ml 100 g⁻¹ in *S. hispidus* and 35 ml 100 g⁻¹ in *S. obesus* (Nagy 1972), which is much higher than that found in other lizards (see Table 1.2) and supports the suggestion that the sacs serve to expand the ECFV.

Nagy (1972, 1973) studied a marked population of chuckwallas on Black Mountain in the Mojave desert between 1970 and 1971 and described changes in water and electrolyte balance of free-ranging individuals during the summer period. In spring, chuckwallas emerged from their winter hibernation and commenced feeding on rapidly growing annual herbs which contained abundant levels of digestible energy and nitrogen (Nagy 1988; Nagy and Shoemaker 1975) but also very high levels of potassium and water. The excess water was excreted in the form of copious urine, and potassium ions were presumably eliminated both via the urine and the nasal gland (Nagy 1973). Although the lizards continued feeding on the drier vegetation available to them in late spring and early summer, and were able to maintain energy balance, they nonetheless lost body mass, and by October of 1970, reached a mean of 63.4% of their initial mass in early April. During this period they avoided eating annuals and consumed only perennial plants which were still moist at the time. Their diet thus contained less water, higher electrolyte concentrations (especially potassium) and lower amounts of digestible nitrogen than their early spring diet. Despite this weight loss the chuckwallas were able to maintain

relatively constant plasma electrolyte concentrations, plasma sodium only increasing by about 6% from 178 to 188 mmol l^{-1} and plasma potassium levels showed no change.

During the summer months the chuckwallas ceased eating entirely and aestivated in rocky crevices, emerging for only an hour or so at sunset every third day on average (Nagy 1973). They continued to lose body mass slowly over this period and, as shown in Fig. 2.8, the specific activity of injected tritium in their body fluids showed almost no change over a 10 month period of drought. The half-life ($t_{1/2}$) of injected tritiated water (HTO) increased from 14.5–28.4 days in spring to 475–887 days over summer, autumn and winter. As the lizards were aphagic over this long period, the only water influx was that from metabolic water production which was clearly almost negligible.

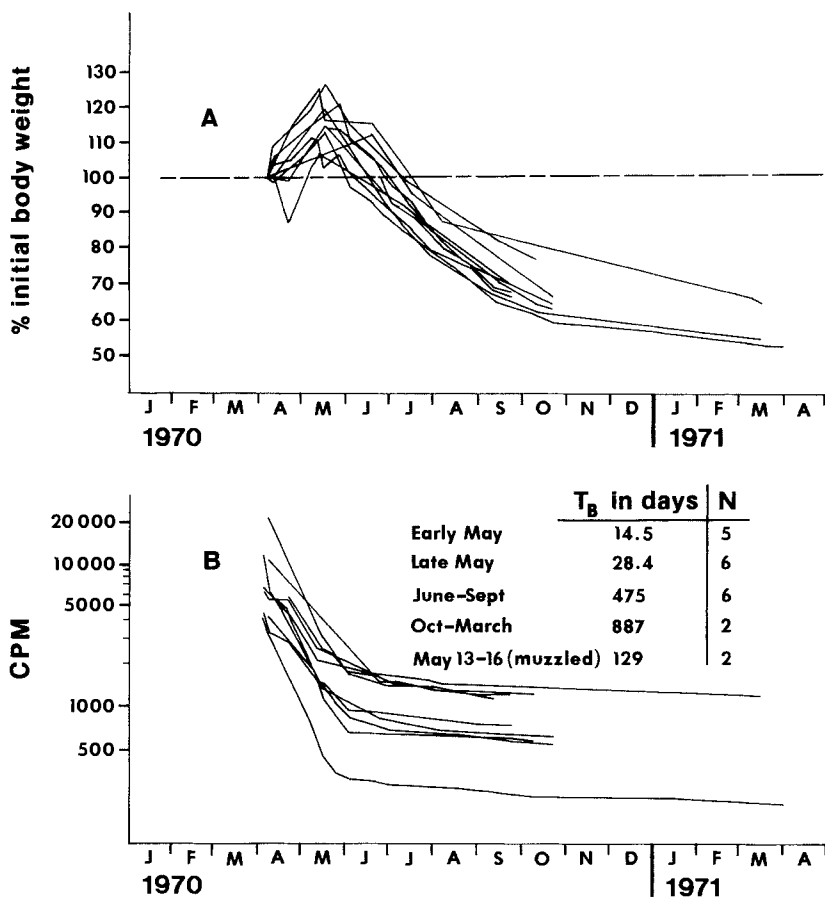


Fig. 2.8A,B. Seasonal changes in A body mass and B tritium disappearance from the plasma of free-living chuckwallas (*Sauromalus obesus*) in the Mojave desert. Counts per minute (CPM) are from 10 μ l plasma samples and have been corrected for radioactive decay and adjusted to account for the curve shifts due to reinjection of tritiated water. T_B is the mean biological half-life. (Modified after Nagy 1972 and Bradshaw 1986a)

Nagy (1972) measured the distribution of fluid in the various compartments in both spring and autumn-dehydrated animals and the data are shown in Table 2.13.

These data show an interesting difference when compared with the response of *C. ornatus* to chronic dehydration. In this species we have seen how ECFV and circulating fluid volumes are actively protected at the expense of the ICFV which declines preferentially with progressive loss of body mass and water. By contrast, in *S. obesus* water and body solids are lost together and at similar rates so that the proportion of fluid to mass does not change appreciably in dehydrated individuals. By expressing fluid volumes as a fraction of the initial body mass rather than the actual dehydrated body mass, however (as with *C. ornatus* in Fig. 2.3), it is possible to show clearly that the fluid loss is shared equally between all fluid compartments in this species.

This is what Smits (1985, 1986) also found in the closely-related chuckwalla, *S. hispidus* which occurs on the arid Isla La Ventana in the Gulf of California, Mexico. The ECFV in hydrated individuals is very large (38.9 ml 100 g⁻¹, thiocyanate space) and the volume of fluid in the lateral lymph sacs varies between 0.5 and 2 ml 100 g⁻¹. With dehydration and isosmotic fluid loading, fluid is either withdrawn from or added to these sacs, but the changes parallel very closely those in the ECFV. More significantly, in the case of dehydration, fluid losses were shared equally between the ECFV and the ICFV.

Interestingly, plasma sodium concentrations in field animals were much lower in this species (150–171 mmol l⁻¹) and potassium levels were higher (5.3–6.9 mmol l⁻¹) than recorded by Nagy (1972) for *S. obesus* (see also Table 1.2). Templeton (1964) also recorded a mean plasma sodium concentration of

Table 2.13. Seasonal change in fluid compartments and plasma electrolyte concentrations in chuckwallas (*Sauromalus obesus*) in the mojave desert

Season	Body fluid compartments (ml 100 g ⁻¹)						Plasma electrolytes (mmol l ⁻¹)	
	Body mass (%)	TBW	ECFV	PV	BV	ICFV	Na ⁺	K ⁺
Spring	100.0	76.3	35.1	7.0	9.8	36.3	178	4.6
Autumn (expressed as ml 100 g ⁻¹ <i>actual</i> mass)	55.0	73.0	32.9	6.1	8.6	40.0	188	3.9
Autumn (expressed as ml 100 g ⁻¹ <i>initial</i> mass)		40.2	18.1	3.4	4.7	22.0		
Relative change (%)	-47.4	-48.4	-51.4	-52.0	-39.4			

Volumes expressed both as a proportion of actual and initial body mass – calculated from Nagy, 1972.

169 mmol l⁻¹ from a laboratory study with *S. obesus*. Thus, although in each study the animals apparently showed a capacity for precise osmoregulation so far as electrolyte concentrations were concerned, there appear to be significant differences between the actual levels maintained and the question merits further investigation.

One may only speculate on the major physiological difference between the chuckwallas and the Australian agamids in their response to inevitable fluid deprivation, but it may well be a consequence of the very much larger ECFV in chuckwallas which, at close to 36% of the body mass is well above the 25% usually found in all other lizards (see Table 1.2). Smits (1986) also found that the ECFV of *S. hispidus* was expanded in response to KCl loading and suggested that this may result from enhanced secretion of aldosterone retaining sodium, and hence water, in this compartment (Bradshaw and Grenot 1976; and see Bradshaw 1978b). Smits (1985) commented that the diet of *S. hispidus* contains the highest concentrations of potassium recorded for any reptilian herbivore (2500 $\mu\text{mol K}^+ \text{g}^{-1}$) and we have already seen that high K⁺ levels in the diet appear to inhibit feeding in the desert tortoise. All three species also have relatively high plasma K⁺ levels when compared with other reptiles (see Table 1.2) and this may well represent a case of hyperkalaemia tolerated in order to better manage water and energy budgets.

2.5.5

Two Saharan Lizards: Le Fouette-Queue (*Uromastix acanthinurus*) and the Varanid *Varanus griseus*

Uromastix acanthinurus is a large (300–770 g) agamid herbivore that may be found in some of the most arid parts of the North African Sahara and has been studied in some detail in the region of Béni-Abbès in Algeria by Grenot (1976) and by Lemire et al. (1979, 1982). Over 60 plant species have been identified in its diet (Dubuis et al. 1971) and a large and relatively stable population was followed for a number of years in the region of the oasis of Béni-Abbès which occurs at the confluence of the four major Saharan biotopes: djebel (mountains), reg (rocky plains), erg (mobile dunes) and oued (water courses). Typical densities are of the order of 0.1–0.2 individuals per hectare, but may reach three to six per hectare in very favourable habitats, such as the Monts d'Ougarta (Grenot and Vernet 1973).

Details of the osmoregulatory capacities of this species will be discussed, then compared with those lizards already described as well as the carnivorous varanid lizard *V. griseus*, which also occurs in the same arid regions of North Africa.

Preliminary results from *U. acanthinurus* suggested that it might prove to be an excellent regulator, experiencing little seasonal variation in plasma electrolyte concentrations (Bentley 1971; Grenot 1976) but Lemire et al. (1982), in a careful study in which data from different populations were not combined, showed clearly that this species experiences substantial changes in the compo-

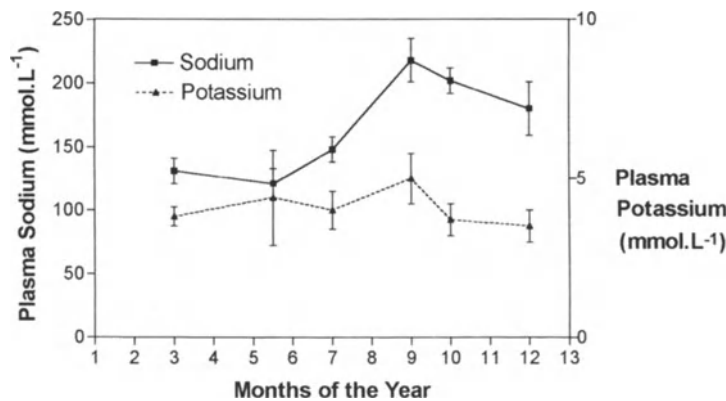


Fig. 2.9. Seasonal variation in plasma sodium and potassium concentrations in the large Saharan agamid lizard *Uromastix acanthinurus* captured in the Monts d'Ougarta in Algeria. (Modified after Lemire et al. 1982)

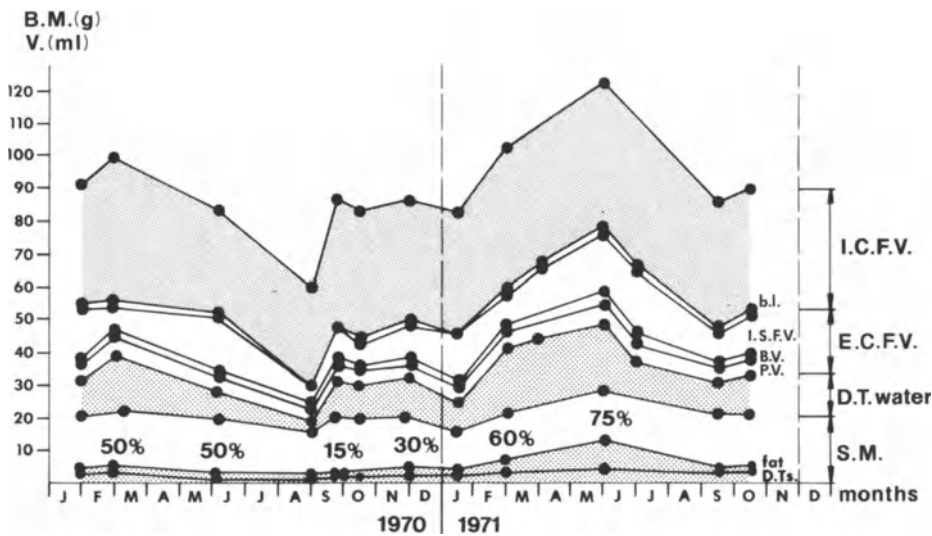


Fig. 2.10. Seasonal changes in body composition of the Saharan agamid lizard *Uromastix acanthinurus* adjusted for an individual weighing 100 g (snout-vent length: 13.6 cm) from the Monts d'Ougarta in Algeria during 1970 and 1971. BM Body mass in g; ICFV intracellular fluid volume; ECFV extracellular fluid volume; bladder fluid (b.l.) + interstitial fluid volume (ISFV) + blood volume (BV) + plasma volume (PV); DT water contained within the digestive tract; solid matter (SM) comprises fat and dry digestive tube content (DTs); % percentage of individuals captured with abdominal fat reserves. (Modified after Lemire et al. 1982; Bradshaw 1986a)

sition of its body fluids throughout the year. Plasma sodium concentrations in a population from the mountains of Ougarta, for example, ranged from an average of 122 to 218 mmol l⁻¹ (78%) and potassium varied between a mean of 3.1 and 5.0 mmol l⁻¹ (61%) over a period of 12 months between 1970 and 1971,

as shown in Fig. 2.9. Changes in fluid volumes over the same period were also reported by Lemire et al. (1982) and are shown normalised for an hypothetical 100 g animal in Fig. 2.10. The late summer-autumn period (August-September) is obviously the most difficult for the animals and maximum mass loss coincided with the elevated electrolyte concentrations shown in Fig. 2.9.

By the end of the summer of 1970 the lizards had fallen to approximately 60% of their initial body mass with maximal losses being recorded in the water content of the digestive tract (DT), the ECFV and ISFV, and the fat bodies. The ECFV was reduced from 29 to 15 ml 100 g⁻¹ over the 1970 summer and from 33 to 20 ml 100 g⁻¹ in the succeeding summer. These changes in body composition follow changes in water content of the plants on which *Uromastix* feed and, as shown in Fig. 2.11, this declines markedly during the summer months in some of the primary food sources.

Lemire et al. (1982) also found evidence of significant individual variation in the response of *U. acanthinurus* to conditions of prolonged drought, with some animals maintaining a favourable water and electrolyte balance whilst others were clearly severely affected (Table 2.14).

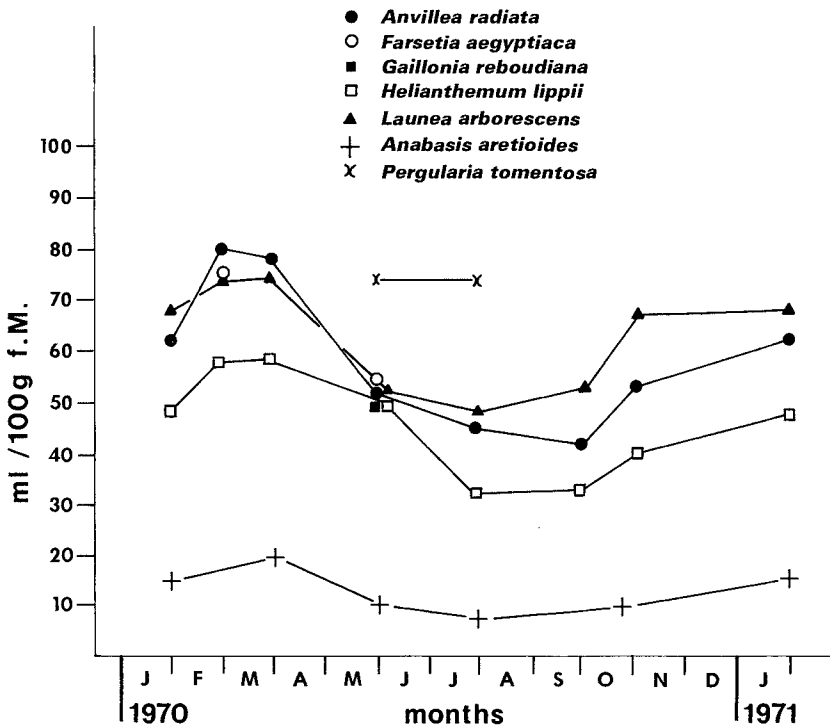


Fig. 2.11. Seasonal changes in the water content (ml 100 g⁻¹ fresh mass) of leafy and fleshy tips of flowers and plants consumed by the Saharan agamid lizard *Uromastix acanthinurus* studied in Algeria. Each point represents the average value from ten samples collected at various sites. (Adapted from Lemire et al. 1982; Bradshaw 1986a)

Table 2.14. Water and electrolyte balance of *Uromastix acanthinurus* from Monts d'Ougarta during the summer of June, 1970. (From Lemire et al. 1982)

Parameter	Hydrated animals (n = 8)	Statistical significance	Dehydrated animals (n = 6)
Condition index (mass %)	90.1 ± 9.0	$P < 0.01$	72.8 ± 11.4
Condition index (water %)	90.1 ± 9.0	$P < 0.005$	64.8 ± 11.8
Condition index (solids %)	94.9 ± 9.8	NS	87.6 ± 16.6
Plasma sodium (mmol l ⁻¹)	159.3 ± 5.6	$P < 0.005$	207.9 ± 13.2
Plasma potassium (mmol l ⁻¹)	3.2 ± 0.5	NS	3.4 ± 0.8
Total body water (ml 100 g ⁻¹)	75.3 ± 0.9	$P < 0.005$	70.3 ± 0.5

Data presented as means ± SE. NS = not significant.

This degree of individual variation in osmoregulatory response to the stress of chronic dehydration is very reminiscent of that seen in fast and slow-growing *C. ornatus* in Australia, in which the variation can be traced to differences in pituitary-adrenal function which have a profound impact on the renal response of different individuals to electrolyte loading (see Baverstock and Bradshaw 1975; Bradshaw 1971). Whether such variations in rate of growth exist in *U. acanthinurus* is not known, however, nor whether the above variation in physiological responses has any genetic basis, as it does in *C. ornatus* (Bradshaw 1986a).

Plasma potassium concentrations, in contrast to sodium, are well regulated in field populations of *U. acanthinurus* and this appears to reflect the activity of the nasal salt gland of this species. A well-developed salt gland was described by Grenot (1968) and this has been studied extensively in the laboratory (Lemire 1983; Lemire et al. 1970, 1972, 1979, 1980, 1982; Lemire and Vernet 1982, 1983) where it has been shown to be much more effective at excreting potassium than sodium ions. Relatively large amounts of potassium are also excreted in the form of insoluble urate salts (Lemire 1983).

Unfortunately, a complete ecophysiological study has never been carried out on this interesting animal, primarily because of the difficulties involved in working in the remote areas of the Sahara where it is found; but some data are available on rates of water turnover in field animals (Lemire et al. 1979). There are problems with some of these data, however, especially those involving animals held in seminatural enclosures and fed a mixture of lucerne and native plants. Water turnover of these individuals was typically high and they were in negative water balance.

Data from a small number of free-ranging animals were reported by Lemire (1983) and these are summarised in Table 2.15. There is a dramatic difference between the water balance of the animals in the two seasons with a vast imbalance in September 1977 and very high rates of water turnover. As the animals were losing, on average, over 5% of their body water per day they could hardly sustain this for long. In fact the lizards appeared to be disturbed by the experimental procedure as they all vacated their habitual burrows and

Table 2.15. Rates of water turnover measured in free-ranging *Uromastix acanthinurus* at Igli (Hamada De Guire) in Algeria in September 1977 and May 1978. (Modified from Lemire et al. 1979; Lemire 1983)

Season	Initial body mass (g)	Final body mass (g)	Δ BM (% d ⁻¹)	Initial body water (ml 100 g ⁻¹)	Final body water (ml 100 g ⁻¹)	Δ BW (% d ⁻¹)	Water influx (ml 100 g ⁻¹ d ⁻¹)	Water efflux (ml 100 g ⁻¹ d ⁻¹)
September 1977 (n = 5)	413.2 ± 235	389.5 ± 232	-1.0 ± 0.43	78.3 ^a ± 2.2	54.2 ^a ± 2.0	-4.39	75.1 ^b ± 2.0	101.3 ^b ± 2.0
May 1978 (n = 12)	297.0 ± 170	279.7 ± 160	-0.38 ± 0.09	80.7 ± 3.2	79.5 ± 4.5	-0.09	11.4 ± 2.4	12.8 ± 5.6

Differences between values paired by superscripts within the same row (a-a, b-b) are highly statistically significant with $P < 0.005$.

dug new burrows further afield. This was obviously a very costly exercise in terms of water and more than accounts for the aberrant data.

In May 1978, however, the lizards had rates of water turnover that were almost eight times lower than in the previous September and they were maintaining water balance. I would suggest that these data are much more representative for *U. acanthinurus* in its natural environment and attest to its appreciable water economy in the field. Allometric predictions (Withers and Bradshaw 1995) give a daily water influx of 8.6 ml for a 300 g desert lizard, which is very close to that measured by Lemire (1983). A diagrammatic summary of these water balance studies is shown in Fig. 2.12 and one should note that *U. acanthinurus* is able to balance water losses by metabolic water production alone when aestivating in its burrow.

U. acanthinurus thus presents some broad similarities when compared with the North American chuckwalla *S. obesus*. They both experience high potassium intakes from their herbivorous diet which they cope with more-or-less well via their nasal salt glands and the excretion of urate salts (Lemire 1983), but an inadequate water intake from their plant diet in summer appears to be their major problem. They are thus forced to endure chronic dehydration but, as with *C. nuchalis*, plasma and blood volumes are not affected by this enforced dehydration which is thus borne entirely by the interstitial fluid. The change in ICFV is also of lesser magnitude and *U. acanthinurus* thus presents a third type of response to chronic dehydration which may be classified as shown in Table 2.16 for the three reptilian species studied to date.

In the two agamids, the circulating fluid volume (PV and BV) is protected at all times. The only difference is that the Australian lizard preferentially takes water from the intracellular rather than the extracellular compartment. The North American lizard evidences no preferential protection of any fluid compartment, all of which appear to be depleted equally in dehydration.

The desert monitor *V. griseus*, which extends from North Africa to the west of Pakistan, has been studied in the same region of Béni-Abbès in the Algerian Sahara by Vernet (1977) and Vernet et al. (1988a) and compared with *U.*

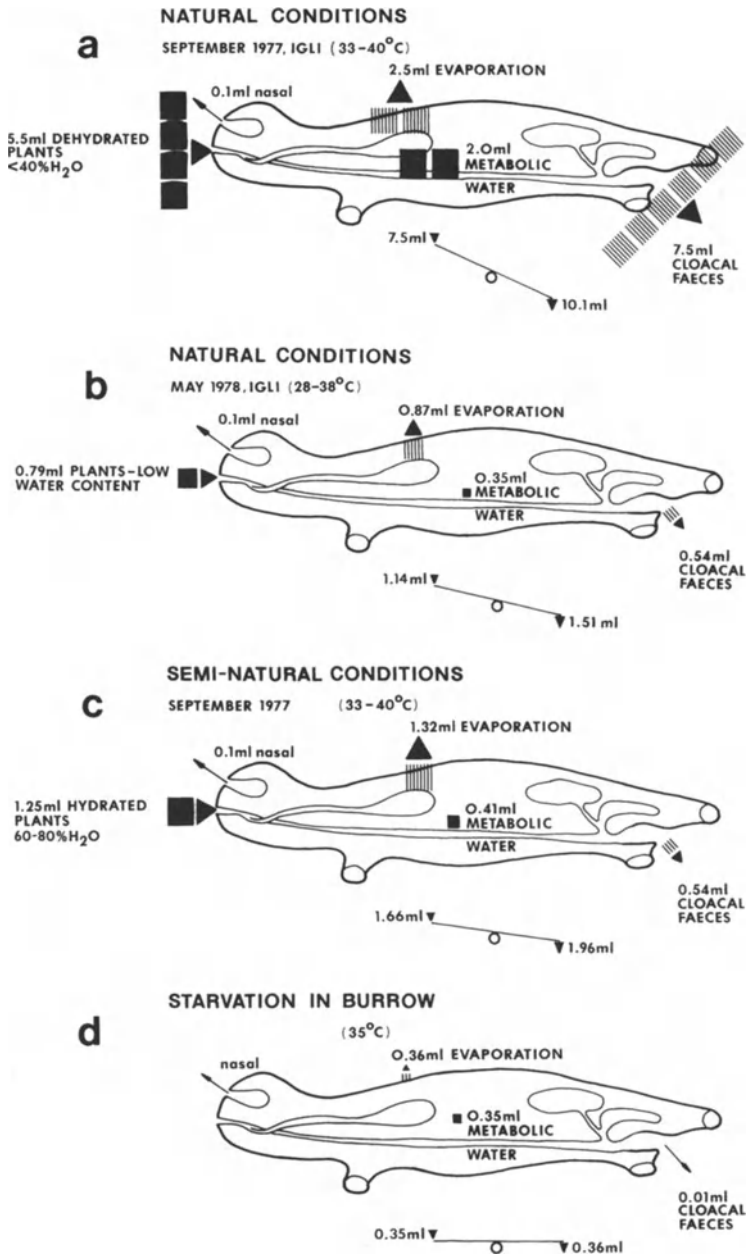


Fig. 2.12. The hydric balance of the Saharan agamid lizard *Uromastix acanthinurus* under natural and simulated conditions in the field in North Africa. (Adapted from Lemire 1983; Bradshaw 1986a)

Table 2.16. Apparent fluid hierarchy in three species of desert lizards as evidenced by their response to chronic dehydration

Species	Level of fluid protection
<i>Ctenophorus ornatus</i>	PV and BV > ISFV = ECFV > ICFV
<i>Uromastix acanthinurus</i>	PV and BV > ICFV > ISFV = ECFV
<i>Sauromalus obesus</i>	PV and BV = ISFV = ECFV = ICFV

acanthinurus by Vernet et al. (1988b). *V. griseus* is slightly larger than *Uromastix* and is an opportunistic predator with a very large home range of 100–400 hectare, although population densities are very low at two to six animals per square km. Annual activity in the sandy habitats where it is found is limited to only 5 months of the year as the lizard hibernates during winter and aestivates during the hottest months of summer in the Sahara.

Rates of water turnover in free-ranging individuals were reported by Vernet et al. (1988a) for the period May–June 1980 from hamada habitat at Guir and wadi habitat in the region of Saoura. These were, on average, lower than those recorded for *U. acanthinurus* in May 1978, with a mean influx of 4.5 ± 3.1 and a mean efflux of 3.0 ± 0.5 ml 100 g⁻¹ per day. Although these animals appear to be in water balance, there was great variation in the measured water influx of the different individuals, some of which were resting in burrows whilst others covered distances of up to 7.5 km. When the data are inspected individually, six of the eight lizards were in fact in negative water balance over the period of measurement.

Data from animals studied in a semicaptive situation and fed a diet of lizards and small mammals are a little more informative, and rates of water influx varied from 4.0–4.5 ml 100 g⁻¹ per day, with the animals showing a weight gain of 1.3–2.4% of the body mass per day and exhibiting a significantly positive water balance. Vernet et al. (1988a) estimate a figure of 2.83 ml 100 g⁻¹ per day for the maintenance of water balance in *V. griseus*. This rate is similar to the mean reported in free-ranging Australian *V. gouldii* (*rosenbergi*) by Green (1972b) (2.2 ml 100 g⁻¹ per day) and later, more extensive work with this species by Green et al. (1991a), has shown that rates of water turnover may vary seasonally by as much as 300%. In fact high levels of individual variation seem to have been encountered and commented upon in almost all studies of varanids to date (Dryden et al. 1990; Green et al. 1986, 1991b) and behaviour appears to be a more important determinant of water flux rates than body mass in this group of lizards. As seen in Fig. 2.13, the exponent in the power curve describing variation in mean water influx as a function of body mass is 1.196, indicating that water turnover rate per unit mass does not vary significantly between varanid species regardless of size.

Some data on fluid and electrolyte balance of *V. griseus* in the Sahara are given in Vernet et al. (1988b) and, as with *U. acanthinurus*, body mass and body water increase soon after the animals emerge from hibernation and then

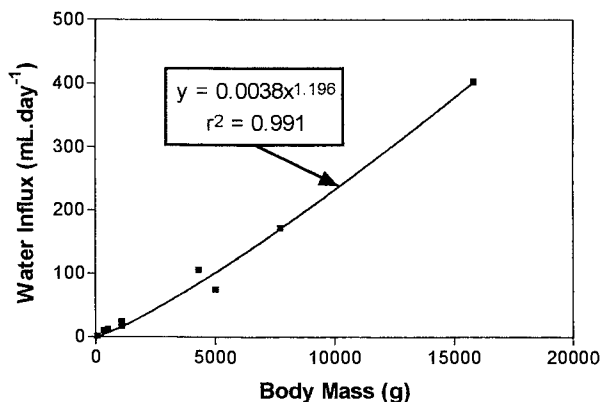


Fig. 2.13. Allometric relationship between rate of water influx, measured with tritiated water, and body mass in free-ranging varanid lizards

decline again during late summer and autumn. Plasma sodium concentrations varied from a mean of 140 mmol l^{-1} in June 1971 to 202 mmol l^{-1} in March 1973 (44.3%) which is less than recorded for *U. acanthinurus* over the same period ($122\text{--}212 \text{ mmol l}^{-1}$, 73.8%).

Vernet et al. (1988b) note that plasma potassium concentrations “varied little” (p. 194), but an inspection of the data presented there shows a range of $3.1\text{--}5.0 \text{ mmol l}^{-1}$, representing an overall variation of 61.2%, which is in fact greater than for sodium. One of the common pitfalls in interpreting data is that when the absolute value is small, as in the case of plasma potassium versus sodium concentrations, there is an understandable tendency to overlook variations that may be small in absolute terms, but that are nonetheless relatively quite large.

What is clear, however, is that the nasal salt gland of *V. griseus* is more efficient than that of *U. acanthinurus* at eliminating sodium ions, and ratios of $\text{K}^+ / (\text{K}^+ + \text{Na}^+)$ fall to about 0.2 after NaCl loading, compared with a minimum of 0.5 for *Uromastix*. Bradshaw et al. (1984a) and Vernet et al. (1988b) were able to reduce the Na^+ / K^+ ratio of nasal salt of *U. acanthinurus* from 81.0 to 2.5 with repetitive injections of NaCl, but the gland always excretes more potassium than sodium under all circumstances. The salt gland of *V. griseus*, by contrast, characteristically eliminates more sodium than potassium, even after KCl loading, and this proclivity for sodium excretion, rather than potassium, seems a general feature of the nasal salt glands of varanids (Dunson 1974; Minnich 1979; Saint Girons et al. 1981).

2.5.6

The Mountain or Thorny Devil (*Moloch horridus*)

No survey of desert lizards would be complete without mention of this small bizarre agamid from the sandy regions of Australia (see cover photograph).

Best known for its “water-absorbing” capacities, this lizard is able to extract water from moist sand and convey it to its mouth via fine microscopic channels between epidermal scales that transport the water by strong capillary forces (Bentley and Blumer 1962; Gans et al. 1982; Withers 1993). Other desert lizards are also known to “harvest” rain, including *U. acanthinurus* (Seshadri 1957) and the ecologically similar North American lizard *Phrynosoma cornutum* (Sherbrooke 1990), but the role of the skin has been best studied in *M. horridus*, including in the field (Sherbrooke 1993).

Withers and Bradshaw (1995) have recently studied the water and energy balance of free-ranging *M. horridus* at Bungalbin, some 1000 km northeast of Perth in Western Australia. A number of field trips were made in summer over a 3 year period and conditions varied from cool, very wet, and extremely hot to what might be considered typical for the area (i.e. no rain and daily air temperatures in the vicinity of 38–40 °C). Body composition and turnover data from this study are presented in Table 2.17.

M. horridus is entirely myrmecophagous and has a slow, unsteady gait rather reminiscent of that of a chameleon and it typically finds an ant trail on which it will feed slowly for periods of up to an hour. Withers and Dickman (1995) have timed feeding bouts and estimate that the lizards may consume up to 1500 ants per day. One of the aims of the study was to determine whether the unusual behaviour and highly specialised diet of this species is associated with enhanced water and energy economy in the arid and semi-arid regions where it occurs. Indeed, the data in Table 2.17 show that the average rate of water turnover of some 0.7–1.0 ml 100 g⁻¹ per day was substantially lower and only 31% of that predicted from standard allometric relations for desert lizards (Nagy 1982a). The FMR, measured with oxygen-18 during the trips when rain did not fall, was also only 60% of that predicted for a similar-sized iguanid lizard by Nagy (1982b). Data for *M. horridus* are plotted against allometric predictions in Fig. 2.14 with FMR shown as ■ and water turnover rate as ●.

Table 2.17. Body composition, water turnover and field metabolic rate of free-ranging *Moloch horridus* in Western Australia. (From Withers and Bradshaw 1995)

Season	Body mass (g)	ΔBM (% d ⁻¹)	Body water content (ml 100 g ⁻¹)	Water influx (ml 100 g ⁻¹ d ⁻¹)	Water efflux (ml 100 g ⁻¹ d ⁻¹)	FMR (mlCO ₂ g ⁻¹ h ⁻¹)	Na ⁺ (mmol l ⁻¹)
April 1989 (cool, n = 8)	32.7 ± 2.9	0.6 ± 0.21	74.9 ± 2.0	1.6 ± 0.2	1.1 ± 0.2	0.098 ± 0.02	—
Feb 1990 (wet, n = 8)	43.1 ± 5.3	-0.9 ± 0.60	82.3 ± 1.5	2.9 ± 0.8	3.7 ± 0.8	—	161.6 ± 2.2
Feb 1991 (hot, n = 4)	51.5 ± 5.5	-0.3 ± 0.15	—	0.7 ± 0.3	0.9 ± 0.3	0.145 ± 0.03	—
March 1993 (n = 10)	30.6 ± 1.9	-0.7 ± 0.08	76.2 ± 1.6	0.7 ± 0.1	1.2 ± 0.1	0.158 ± 0.03	192.2 ± 5.7

Data as means ± SE; FMR, Field metabolic rate.

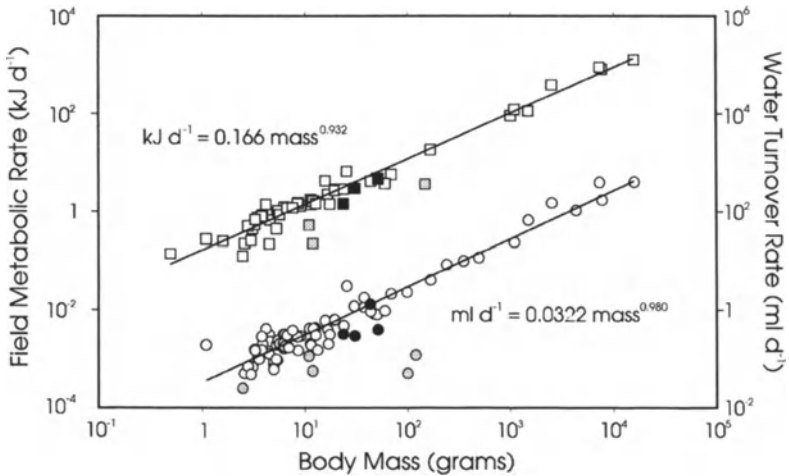


Fig. 2.14. Allometric relationships between field metabolic rate (FMR) in kJ day^{-1} (■) (measured with oxygen-18) and water influx (in ml day^{-1} , measured with tritiated water) (●) in the free-ranging Australian agamid lizard *Moloch horridus*. (Adapted from Withers and Bradshaw 1995)

Rates of food intake were also estimated using sodium-22 and did not differ significantly between trips, averaging 2.2 mmol kg^{-1} per day for influx and 2.6 mmol kg^{-1} per day for sodium efflux, and appear quite high for lizards (Bradshaw et al. 1987, 1991b; Nagy and Bradshaw 1995). Rates of sodium intake, calculated from estimates of the numbers of ants eaten and their sodium content (Withers and Dickman 1995), were considerably lower, however, than indicated by turnover of sodium-22 and suggest either that some sodium is being sequestered in the body fluids or that the *Moloch* may have been ingesting sodium from an additional source other than ants.

2.6

Osmoregulation in Snakes

Information on the osmoregulatory strategies of snakes is very limited, and virtually nonexistent for desert species. The dearth of studies on this aspect of the biology of snakes is understandable, given the difficulties of collecting blood from animals with no readily accessible veins for routine phlebotomy, and any work that has been done has necessitated cardiac punctures or caudal vein bleeding. One suspects, however, that snakes as a group differ fundamentally from lizards in their response to the challenges of high temperatures and lack of free water that characterise desert environments in that their behaviour is much more labile. Desert agamids and iguanids, for example, are rigorously diurnal, regardless of season, but there are numerous reports in the literature of snakes adopting a nocturnal habit during the hottest months of the year (Saint Girons 1980; Cloudsley-Thompson 1988). Such a behavioural response

would have a profound effect on the water and electrolyte physiology of any desert-living reptile and appreciably extend its capacities to regulate and maintain the milieu intérieur within tolerable limits.

The royal snake *Spalerosophis cliffordii* is a 300 g desert snake found in the Middle East. It was studied in the laboratory by Dmi'el and Borut (1972) and Dmi'el and Zilber (1971), who measured water balance of nonforaging individuals. The major source of water loss was evaporative via the skin and, when kept at 30 °C and fed mice, they were able to maintain water balance without access to free water. This is a nocturnal species of desert snake and, although its ecophysiology has not been studied, the above results suggest an ability to survive in areas where there is no surface water.

Overall water loss of a desert viper, the asp *Cerastes cerastes*, is even lower than that of *S. cliffordii* and this is due to a reduced rate of cutaneous loss, a lower metabolic rate and an enhanced level of extraction of oxygen from the inspired air (Dmi'el 1972).

A very interesting case of an extremely low rate of evaporative water loss in a snake is that of the Montpellier couleuvre *Malpolon monspessulanus*, which is widely distributed in the mediterranean, including North Africa, but which is not normally classified as a desert species (Grenot 1988). The rate of water loss of this snake, at 4.4 ml kg^{-1} per day, is three times lower than that of the desert snake *S. diadema*, studied by Dmi'el (1972) (13.2 ml kg^{-1} per day). Dunson et al. (1978) speculate that the mixture of fatty acids and proteins that are also secreted by the nasal gland of this species have a water-proofing function when spread over the skin. De Haan (C.J. Grenot, pers. comm.) does not agree, however, maintaining that these secretions are used only for territory marking; the question obviously needs further study.

Although there have been no field studies published on osmoregulation in snakes, kidney function has been studied in the laboratory in four species from different habitats. These experiments give some insight into the ways in which snakes economise water and respond to excesses of solute. The four snakes are the arid-living bull snake *Pituophis melanoleucus*, studied by Komadina and Solomon (1970); the freshwater snakes *Natrix sipedon* and *N. cyclopion*, studied by Dantzler (1967, 1968); Elizondo and LeBrie (1969); LeBrie and Elizondo (1969); and the olive sea snake *Aipysurus laevis* that has recently been studied by Yokota et al. (1985) and by Benyajati et al. (1985).

Comparative data from these studies are presented in Table 2.18 and the response of the different species to both water loading and salt loading are compared. Data from the original publications have been recalculated so that an overall picture of the renal response of each species to salt loading is clear. These data are most interesting because they suggest, in contrast to what one usually observes in terrestrial vertebrates, that the GFR increases, rather than decreases, with salt loading. *N. sipedon* shows essentially no change in GFR with salt loading, but the other three species, including the desert snake, record significant elevations of GFR.

Table 2.18. Comparative renal function in three species of snakes from terrestrial, freshwater and marine habitats. (Modified from Dantzler 1967, 1968; Komadina and Solomon, 1970; Yokota et al. 1985; Elizondo and LeBrie 1969; LeBrie and Elizondo 1969; Benyajati et al. 1985)

	Treatment	GFR (ml kg ⁻¹ h ⁻¹)	V (ml kg ⁻¹ h ⁻¹)	Relative clearances			
				R _{H₂O} (%)	C _{H₂O} /C _{IN} (%)	C _{OSM} /C _{IN} (%)	FR _{Na} (%)
<i>Natrix</i>	Hydrated	28.4	17.5	38.4	49	12.6	92.8
<i>sipedon</i>	Salt load	26.5	18.5	30.0	44	25.7	82
% Change		-6.7	+5.7	-21.9	-10.2	+103.9	-11.6
<i>Natrix</i>	Hydrated	9.8	6.5	34.0	49	17	91.1
<i>cyclopion</i>	Salt load	11.4	9.8	14.0	54	32	70
% Change		+16.3	+50.8	-58.8	+10.2	+88.2	-23.2
<i>Pituophis</i>	Hydrated	10.9	2.5	77.4	13	9.5	97.9
<i>melanoleucus</i>	Salt load	16.1	6.1	62.2	22	15.8	85.4
% Change		+47.7	+144.0	-19.6	+69.2	+66.3	-12.8
<i>Aipysurus</i>	Hydrated	0.8	0.11	86.3	0	15.1	95.0
<i>laevis</i>	(control)						
	Salt load	2.2	0.68	69.1	6.4	23.9	79.0
% Change		+175.0	+518.2	-19.9	+++	+58.3	-16.8
Mean % change	Effect of Salt load	+58 ± 40	+180 ± 116	-30 ± 9	+23.1 ^a ± 23.8	+79 ± 10	-16 ± 3

Date expressed as mean ± SE.

^a Excluding data from *Aipysurus laevis* for this variable.

Changes in urine flow rate (V) are consistent within all species and salt loading provokes a saline diuresis which involves a decrease in the fractional reabsorption of filtrate (R_{H₂O}), an increase in relative free water and osmolar clearances (C_{H₂O}/C_{IN} and C_{OSM}/C_{IN}), and a marked decrease in fractional reabsorption of sodium ions (FR_{Na}).

What these data thus suggest is that the snakes all respond homeostatically to the increased salt levels in their bodies by very effectively increasing the rate of sodium excretion via the kidneys. This is most evident from the increase in relative osmolar clearance and the mechanism of the response is clearly a fall in the rate of sodium reabsorption within the kidney. What is most interesting about this response is that, as we shall see in the next chapter, it differs from that usually seen with lizards when challenged with a salt load, where the response is invariably antidiuretic and involves the release of the hormone AVT. What one might predict from the above data is that salt loading does not stimulate the release of AVT in snakes.

Terrestrial lizards respond by decreasing GFR and rate of urine production, and this is usually associated with a decrease in both relative free water clearance and osmolar clearance – virtually the opposite of what we see above

(see Table 2.2). It would thus appear that the response of the snakes is designed to eliminate the extra sodium in a copious urine, whereas that of the lizards is concerned with conserving water, whilst at the same time eliminating the extra sodium. This might be thought to be a most appropriate response for water snakes such as *Natrix* and *Nerodia*, but what of the desert-living bull snake and the sea snake which lives in sea water where free water is also at a premium?

2.7

Conclusions

Although most reviewers are at pains to emphasise the variability of the responses of different reptiles to similar osmoregulatory challenges (e.g. Dantzler and Holmes 1974; Shoemaker and Nagy 1977; Dantzler 1980), I believe that one may discern a number of common features which deserve comment.

The kidneys of crocodiles evidence little ability to effect major changes in the composition of the body fluids and the cloacal-colonic complex and lingual salt glands appear to be much more important osmoregulatory organs in this group, especially in estuarine species which occasionally venture into salt water.

The renal function of desert and non-desert tortoises seems little different when studied in the laboratory, and the major difference appears to be the ability of the desert species to continue producing urine, despite significant elevation of the plasma osmolality. This response is clear evidence of their greater tolerance to variations in the milieu intérieur than the aquatic species, but it could also be seen as being rather nonadaptive, because a prompt anuric response to hypernatraemia would conserve water. Again, we see the difficulty of rigorously classifying osmoregulatory responses in desert reptiles and a fertile mind can readily marshal arguments to support almost any response as being "adaptive".

Minnich (1979) argues (e.g. p. 455) that hyperkalaemia is not tolerated in reptiles, and yet plasma potassium concentrations as high as $12\text{--}16\text{ mmol l}^{-1}$ have been recorded in field studies of both desert lizards and tortoises. As mentioned above when discussing the data from *V. griseus*, large variations in plasma potassium concentration are often overlooked, simply because the absolute values are very small when compared with plasma concentrations of ions such as sodium.

What does seem clear is that the absence of a cephalic salt-secreting gland in the desert tortoise *G. agassizii* does not assist its osmoregulation, and high potassium intake from its exclusively plant diet appears to be a factor in down-regulating feeding during early summer and autumn. Potentially harmful excess electrolytes appear to be stored in the bladder (which must therefore be impermeable to them at this stage) and excreted and replaced by water whenever summer rain falls. Interestingly, Yokota et al. (1985), in their study of the

renal responses of the sea snake, provided the first evidence suggesting that plasma levels of potassium may be important in regulating the GFR in reptiles.

Peterson (1993) argues eloquently that the desert tortoise utilises a tactic of “anhomeostasis” to allow it to survive in the desert regions where it is now found, but he sees this more as a last effort on the part of the species to survive, rather than as being a cogent physiological strategy that has evolved to fit this species to its desert environment. The question of stress will be considered in Chapter 3, as the definition proposed above necessitates that one also has information on levels of regulatory hormones as well as on the state of the milieu intérieur. Reptiles such as the desert tortoise and the Australian agamids of the genus *Ctenophorus* (*Amphibolurus*), which lack salt glands, obviously experience particular difficulties in maintaining water and electrolyte balance in their natural habitats.

Hypernatraemia in lizards is not a peculiarity of antipodean species, but occurs in all species that are exposed to a high sodium intake via their diet. As we shall see in more detail in Chapter 3, however, “good” and “poor” physiological regulators cannot be distinguished on the basis of field data alone, and information is also needed from the laboratory where the response of different species to controlled osmoregulatory challenges can be assessed.

Genuine species differences emerge, however, in the manner in which unavoidable water losses are partitioned within the body. The intracellular fluid, which a priori one might expect to be the most precious fluid in the body, is the first to be sacrificed in dehydrating *C. ornatus*. Absolute blood and plasma volumes are protected intact up until the point of death in both *C. ornatus* and *U. acanthinurus*, but *S. obesus* appears to make no distinction between any of the fluid volumes and all are depleted equally in chronically dehydrated animals. Whether this is because they benefit initially from an expanded ECFV, compared with the other two species, is not clear at this stage.

What is clear from the above is that desert species of reptiles do not appear to abandon regulatory responses when faced with the challenges of high diurnal temperatures and a lack of free water. The nature of their responses appears limited both by phylogeny (whether for example they possess salt glands) and the nature of their particular ecological constraints (e.g. the electrolyte content of their habitual diet). Within this context, however, they show a remarkable ability to survive modifications of the milieu intérieur that would be lethal for birds and mammals, and there is no doubt that reptiles, as a group, show much greater tolerance limits.

The little that is known about osmoregulation in snakes, and it is indeed very little, suggests that they may differ fundamentally in their osmoregulatory responses from terrestrial lizards and it is to be hoped that the coming years will see the publication of more studies on these fascinating reptiles.

Activity and Hormonal Control of Excretory Organs

3.1

Avant Propos

Information has accumulated in recent years on the extent to which pituitary and adrenal hormones modulate the activity of those organs primarily responsible for controlling rates of water and electrolyte excretion in reptiles: the kidneys, cloacal-colon complex and the cephalic salt-secreting glands. The topic has been reviewed periodically over the years (Bradshaw 1972, 1975, 1986a; Dantzler and Holmes 1974; Minnich 1979; Dantzler and Braun 1980; Braun and Dantzler 1987; Dantzler 1989a,b) but the data are still very fragmentary and garnered from only a very small number of species.

As mentioned in the previous chapter, many of the earlier studies also need to be viewed with some caution, either because the temperature conditions were almost certainly not ideal for the revelation of osmoregulatory responses in high temperature reptiles or because the time span employed was of very short duration. For example, Schmidt-Nielsen and Skadhauge (1967) carried out a careful study on the freshwater crocodile and found that the animals showed little evidence of homeostatic responses to variations in water and electrolyte status; however, it was not clear whether this was an inherent property of the reptile being studied, which may excrete electrolytes by preference via their lingual salt glands (as suggested recently by Dantzler 1989a), or was instead the result of an inadvertent choice of experimental conditions. As with any case of negative results in science, the findings need to be interpreted with caution.

Attempts to demonstrate the existence of homeostatic renal responses to salt loading and deprivation in the small agamid lizard *Ctenophorus ornatus*, for example, were only successful after the animals were maintained at a constant temperature of 37 °C for a period of over a week and renal parameters deduced from the collection of voided rather than ureteral urine (Bradshaw 1972). Subsequent studies with this and other species of reptile show that they can respond to exogenous injections of adrenocorticotrophic hormone (ACTH) by increasing the rate of secretion of adrenal steroids within 30 min (Bradshaw 1978b; Bradshaw and Grenot 1976; Licht and Bradshaw 1969); thus it is not at all clear why they should take days, rather than hours, to effect homeostatic changes in renal function. Hormonal receptors may be down-

regulated in animals kept in captivity for long periods of time, but there is certainly ample evidence to show that intravenous injections of arginine vasotocin (AVT) can be immediately effective in modifying renal parameters in some species, and the problem obviously merits further attention.

Another difficulty with studies involving captive animals is that, frequently with reptiles, a large proportion of individuals dies within weeks or months of being transported from the field to the laboratory (Bradshaw 1986a). Any experimental work is thus forcibly carried out with a subset of survivors which almost certainly does not reflect with fidelity the original genetic constitution and perhaps the full range of physiological characteristics of the natural population. An example is provided by studies of renal function in the Australian zebra finch (*Taeniopygia costanotis*) in which the ability of this species to tolerate saline drinking solutions up to 800 mmol, originally reported by Oksche et al. (1963), could not be confirmed subsequently by other workers in Europe and North America using aviary-bred animals. Collecting animals directly from the field, and from the same locality, confirmed that this ability is indeed present in wild populations but is lost within a matter of generations in captive-bred birds (Bentley 1971; Skadhauge and Bradshaw 1973, 1974).

3.2

The Kidney

3.2.1

Renal Clearances and the Handling of Water and Solutes

Comparative aspects of renal function in reptiles are restricted essentially to classical clearance studies in which the response of different species to water and salt loads, and occasionally dehydration, have been compared (Dantzler 1976). Results from micropuncture studies have only been reported to date in a single species of lizard (*Sceloporus cyanogenys*) (Stolte et al. 1977) and data from the perfusion of isolated renal tubules are available from only one snake (*Thamnophis sirtalis*) (Beyenbach 1984; Beyenbach et al. 1980; Dantzler 1978; Dantzler and Bentley 1978a,b). Circulating levels of AVT have been measured in three species of reptile to date, only one of which, *Varanus gouldii*, however, has been the subject of renal studies (Bradshaw and Rice 1981; Rice 1982).

Details of kidney function in tortoises and snakes have already been presented (see Tables 2.2 and 2.18) and I shall concentrate here on comparable data from terrestrial lizards, the group that has received the most attention to date. Renal responses of the various species to water and salt loading and, in some cases, dehydration are presented in Table 3.1. There are a number of features that emerge on inspection of these data. All species appear to respond to a water load with a marked increase in the glomerular filtration rate (GFR), except for the *Tuatara* in which individual variation is too great for statistical significance. U/P_{OSM} does decline from 0.99 with dehydration to 0.68 with water loading, however, indicating a significant modification of renal function in this

Table 3.1. Comparative kidney function in terrestrial lizards and the tuatara

Species and habitat	Treatment	GFR (ml kg ⁻¹ h ⁻¹)	V (ml kg ⁻¹ h ⁻¹)	U/P _{OSM}	R _{H₂O}	Relative clearances (%)		
						C _{H₂O} /C _{IN}	C _{OSM} /C _{IN}	FR _{Na}
<i>Sphenodon punctatus</i> Mesic ¹	Normal	3.8 ± 0.4		0.89 ± 0.03				
	Water load	4.8 ± 1.3		0.68 ± 0.04				
	Dehydrated	3.4 ± 1.3		0.99 ± 0.03				
<i>Tiliqua scincoides</i> Mesic-semi arid ²	Normal	15.9 ± 1.0		0.5 ± 0.07				
	Water load	24.5 ± 2.0		0.43 ± 0.04				
	Salt load	14.5 ± 0.5		0.66 ± 0.03				
	Dehydrated	0.69		0.79				
<i>Tiliqua rugosa</i> Mesic-semi arid ²	Normal	1?	0.24 ± 0.05		76			
	Water load	3?	11.3 ± 0.09					
	Salt load	?	0					
	Dehydrated	?	0					
<i>Hemidactylus</i> sp. Mesic ⁴	Normal	10.4 ± 0.8	2.6 ± 0.2	0.64 ± 0.02	74.2 ± 2.0	8.8 ^a	16.2 ± 0.4	84.2 ^a
	Water load	24.3 ± 1.7	12.1 ± 1.3	0.74 ± 0.02	51.7 ± 2.9	13 ^a	33.6 ± 2.9	63.8 ^a
	Salt load	11.0 ± 2.2	2.4 ± 0.5	0.80 ± 0.02	82.2 ± 0.3	4.3 ^a	17.8 ± 0.3	82.7 ^a
	Dehydrated	3.3 ± 0.4	1.3 ± 0.1	0.74 ± 0.02	60.1 ± 1.8	10.2 ^a	29.7 ± 2.3	69 ^a
<i>Phrynosoma cornutum</i> Desert ⁴	Normal	3.5 ± 0.3	2.0 ± 0.2	0.93 ± 0.04	42.3 ± 2.4	3.9 ^a	53.0 ± 1.0	54.9 ^a
	Water load	5.5 ± 0.5	1.8 ± 0.1	0.90 ± 0.04	64.5 ± 2.6	3.2 ^a	32.3 ± 2.6	74.8 ^a
	Salt load	1.7 ± 0.4	0.6 ± 0.1	1.00 ± 0.01	60.5 ± 3.2	0 ^a	39.7 ± 3.5	65.2 ^a
	Dehydrated	2.1 ± 0.2	0.8 ± 0.1	0.97 ± 0.02	60.6 ± 2.7	1.2 ^a	38.5 ± 2.8	61.9 ^a
<i>Tropidurus</i> sp. Desert ⁴	Normal	3.6 ± 0.4	1.9 ± 0.2	0.96 ± 0.02	47.1 ± 2.7	2.1 ^a	50.0 ± 2.6	53.2 ^a
	Water load	4.5	2.0	0.99	56.5	0.4 ^a	43.1	63.0 ^a
	Salt load	2.4	1.2	1.01	50.0	0 ^a	51.7	52.4 ^a
	Dehydrated	1.2 ± 0.2	0.5 ± 0.3	0.97 ± 0.02	50.3 ± 4.3	1.1 ^a	48.2 ± 4.0	64.9 ^a

Table 3.1 (Contd.)

Species and habitat	Treatment	GFR (ml kg ⁻¹ h ⁻¹)	V (ml kg ⁻¹ h ⁻¹)	U/P _{OSM}	R _{H₂O}	Relative clearances (%)		
						C _{H₂O} /C _{IN}	C _{OSM} /C _{IN}	FR _{Na}
<i>Varanus gouldii</i> Desert ⁵	Normal	6.8 ± 1.3		0.45 ± 0.04				
	Water load	12.8 ± 1.7		0.39 ± 0.03				
	Salt load	8.4 ± 0.8		0.71 ± 0.02				
<i>Varanus gouldii</i> ^b	Water load	15.9 ± 1.4	7.4 ± 0.6	0.40 ± 0.06	52.4 ± 4.7	27.3 ± 6.2	20.3 ± 2.1	95.8 ± 0.7
	Salt load	5.6 ± 1.1	0.9 ± 0.2	0.98 ± 0.01	82.3 ± 2.3	1.6 ± 0.3	16.1 ± 2.4	89.9 ± 2.7
	Dehydrated	11.0 ± 0.9	1.9 ± 0.2	0.72 ± 0.06	82.8 ± 1.8	5.8 ± 1.3	11.9 ± 1.4	95.8 ± 0.9
<i>Ctenophorus ornatus</i> Semi-arid ⁷	Water load ^b	51.4 ± 4.3	3.7 ± 0.5	0.23 ± 0.06	93.0 ± 0.5	6.0 ± 0.5	1.0 ± 0.5	99.9 ± 0.06
	Salt load ^b	19.2 ± 4.6	2.0 ± 0.4	0.96 ± 0.02	87.8 ± 3.3	5.6 ± 0.4	11.6 ± 1.3	88.4 ± 2.0
<i>Ctenophorus ornatus</i> ⁸	Water load	51.3 ± 2.4	33.2 ± 1.1	0.45 ± 0.05	35.2 ± 3.1	35.3 ± 2.6	29.2 ± 3.4	78.4 ± 2.3
	Salt load	12.3 ± 3.8	1.0 ± 0.3					
<i>Dipsosaurus dorsalis</i> Desert ⁹	Water load ^b	10.3			19			98.9
	Salt load ^b	10.6			7.6			95.5
<i>Sceloporus cyanogenys</i> Desert ¹⁰	Water load	21.0 ± 3.7		0.46 ± 0.03		19?	9?	92.6?
	Dehydrated	11.0 ± 3.7		0.67 ± 0.02		26?	18?	88?

¹ Schmidt-Nielsen and Schmidt (1973); ² Schmidt-Nielsen and Davis (1968); ³ Shoemaker et al. (1966); Bentley (1959); ⁴ Roberts and Schmidt-Nielsen (1966);⁵ Green (1972a); ⁶ Bradshaw and Rice (1981); ⁷ Bradshaw (1972); ⁸ Bradshaw (1978a); ⁹ Bradshaw et al. (1972); ¹⁰ Stolte et al. (1977); Davis et al. (1976).^a Calculated from mean values presented in paper. ^b Clearances estimated from voided urine.

species. A number of species shows little or no decline in GFR with salt loading when compared with "normal" values (*Tiliqua*, *Hemidactylus* sp., *Dipsosaurus dorsalis* and perhaps *V. gouldii*). All of the other species, however, respond to salt loading with a significant decrease in GFR and rate of urine production, i.e. the treatment induces an antidiuresis.

The response to dehydration is more uniform and all species, with the exception again of the *Tuatara*, evidence a marked antidiuresis that involves a reduction in GFR. This glomerular antidiuresis may also be accompanied by changes in tubular function which enhance its effectiveness, as in the case of *V. gouldii*. Dehydration in this species also involves a significant increase in the fractional reabsorption of filtrate (FR_{H_2O}) a decrease in both relative free water (C_{H_2O}/C_{IN}) and relative osmolar clearance (C_{OSM}/C_{IN}). There is thus both a reduction in the rate at which fluid is presented to the nephric tubule by the glomerulus and an increase in the rate at which fluid and solutes are extracted from the fluid as it passes to the ureter.

These data suggest that regulation of water excretion by the kidney is a common feature in all these reptiles and the major mechanism is through an increase or a decrease in the rate at which water is filtered from the blood. The way in which the different species deal with the other osmoregulatory problem of an excess of solutes clearly varies, however, and may, or may not, involve a change in GFR. Where GFR does not decline, there may be associated changes in tubular reabsorption of solutes which have the effect of increasing rates of sodium excretion; urine to plasma ratios (U/P_{OSM}) increases significantly, for example, compared with normal values following salt loading in *Hemidactylus* sp. ($F_{3,30} = 8.77$, $P = 0.0003$).

Most puzzling amongst the data in Table 3.1, however, and this has intrigued reviewers for more than two decades, is the response of the two desert species studied by Roberts and Schmidt-Nielsen (1966) in which the lizards invariably produced isosmotic urine no matter what the experimental treatment (i.e. U/P_{OSM} close to 1.0). They thus appear to lack the ability to dilute the urine and the authors linked this to the absence in these species of mitochondria-rich cells in the distal tubule with the ultrastructure of salt-transporting cells, characterised by extensive infoldings of the basement membrane. As Dantzler (1970) observes in one of his reviews

"The possible advantage of a failure of the distal tubule of the desert-dwelling lizards to dilute the urine is obscure."

and in a later paper he suggests that dilution of the urine in these species may occur in postrenal structures, such as the cloaca and colon (Dantzler 1980). What is clear, is that if these two species were to void to the exterior urine similar in composition to that collected from their ureters, they would not survive for long, as relative osmolar clearances vary from 32 to 52% and that rate of solute loss from the body would be disastrous.

Another possible interpretation of these data is suggested by the small study of Shoemaker et al. (1966) in which the effects of body temperature on kidney

function were investigated in the large Australian skink *Tiliqua rugosa*. Renal clearances and rates of reabsorption of sodium were studied as a function of body temperature in this species and it was found that sodium reabsorption was virtually inhibited at low temperatures (below the preferred), i.e. the animals voided isosmotic urine. This species has a preferred body temperature for activity of approximately 34°C, which is some 4°C lower than that of *Phrynosoma cornutum* (Heath 1965), and probably that of the Galapagos lava lizard (*Tropidurus* sp.). Unfortunately, the thermal requirements of the gecko studied by Roberts and Schmidt-Nielsen (1966) are not known, as the lizard is not identified to species level in the paper and described only as *Hemidactylus* sp., a tropical gecko from Puerto Rico. Two species in this genus occur on Puerto Rico, *H. brooki* and *H. mabouia*: neither thermoregulates to any extent (Avery 1982) and both are likely to have a thermal preferendum situated between 24 and 28°C (R.A. Avery, pers. comm.).

This may help explain the divergent responses of the species studied by Roberts and Schmidt-Nielsen (1966). The authors state that the animals were maintained in terraria kept at 80–85°F (27–29°C) but actual laboratory experiments are very likely to have been carried out at standard room temperature, which is closer to 20–22°C in the United States. If this were the case, then the tropical gecko, with a much lower temperature preferendum than that of the two desert iguanids, is more likely to have responded appropriately to the experimental treatments – and thus varied the osmolality of its urine more than the other two species. The two arid-living lizards, however, may well have been in a similar situation to *T. rugosa*, studied by Shoemaker et al. (1966), where a temperature some 10°C below the preferendum was sufficient to inhibit tubular sodium reabsorption. Even if the experiments were carried out at 27–29°C, this would have been an ideal temperature for the gecko, but still some 8–10°C below the preferendum for the desert species.

Stoner (1985) has also drawn attention to an inconsistency in the anatomical argument because, although both *Phrynosoma* and *Tropidurus* lack cells in the distal tubule with extensive infoldings of the basal membrane, so too does the snake *T. sirtalis*, and yet this produces a dilute urine under all circumstances (Beyenbach et al. 1980; Bishop 1959; Peek and McMillan 1979a). It is to be hoped that further studies on these particular species of lizards may help to resolve this apparent paradox.

Even though the tropical gecko *Hemidactylus* sp. showed significant changes in tubular function with treatment in the study of Roberts and Schmidt-Nielsen (1966), these often appear to be inappropriate and the fractional reabsorption of solute (FR_{H_2O}), for example, was significantly lower in dehydrated animals than in normal individuals. The U/P_{OSM} of the urine also increased significantly over that of controls in all experimental treatments ($F_{3,30} = 8.77$, $P = 0.0003$), including water loading, in which the relative osmolar clearance (C_{OSM}/C_{IN}) at 33.6% was the highest recorded in the study. The animal's reaction to the challenge of salt depletion is thus quite inappropriate and unlikely to enhance its homeostasis.

If we attempt to classify the renal responses of the lizards in Table 3.1 in any way, it is clear that all respond to variations in the availability of water with appropriate changes in both GFR and urine production. Some also respond to salt loading with a glomerular antidiuresis (*T. rugosa*, *P. cornutum*, *Tropidurus* sp., *V. gouldii* and *C. ornatus*), which in a number of species (*V. gouldii*, *C. ornatus*, *D. dorsalis* and *S. cyanogenys*) also involves a significant reduction in the fractional reabsorption of sodium in the tubules (FR_{Na}).

What is obvious, however, when examining the above data is that they are for the most part incomplete for any one species and the classical paradigm describing renal function in reptiles has thus been cobbled together from a number of eclectic sources. This paradigm states, essentially, that all reptiles evidence an antidiuresis when deprived of water and that this invariably involves a reduction in GFR due probably to a decrease in both the number of glomeruli filtering and the single nephron filtration rate (SNGFR). In some, but not all species, the antidiuresis may also be assisted by associated changes in tubular function which further reduce the rate of urine production. These are an increase in fractional reabsorption of filtrate and a decrease in relative free water clearance, indicative of an increase in water permeability of the nephron which thus allows water to be reclaimed by the body. These concerted modifications in renal function are clearly homeostatic in design and suggest the action of both pituitary and adrenal hormones which are known to have major effects on the handling of water and solutes by the mammalian kidney.

Due to the ability of the hormone AVT to mimic all of the above effects when injected in species such as the water snake *Natrix (Nerodia) sipedon* (Dantzler 1967) and the freshwater tortoises *Pseudemys scripta* and *Chrysemys picta belli* (Butler 1972; Dantzler and Schmidt-Nielsen 1966), it is generally believed to operate so physiologically. Rarely, however, have all the effects been demonstrated in a single species and only in the case of *V. gouldii* have these been correlated with changes in circulating levels of AVT (Bradshaw and Rice 1981).

3.2.2

Neurohypophyseal Hormones

It has been appreciated for some time that the reptilian kidney is sensitive to pituitary extracts containing the neuropeptide AVT, which characteristically brings about a glomerular antidiuresis and may also, in some species, provoke changes in tubular handling of water and electrolytes (Sawyer and Pang 1979; Sawyer and Sawyer 1952). Other peptides of molecular weight close to 1000 have also been isolated from the reptilian pars nervosa including the neural peptides oxytocin (OT) and 8-isoleucine oxytocin, or mesotocin (MT) (Munsick 1966; Sawyer and Pang 1979), but little is known of their function. AVT influences kidney function in reptiles and also has a strong vasoconstrictor effect on the oviduct and "uterus" of viviparous species (Fergusson and Bradshaw 1991, 1992; Guillette 1979). Thus, osmoregulatory and reproductive

effects are not separated as they are in mammals. Both mesotocin and oxytocin also constrict the reptilian oviduct, but at much higher doses than with AVT (La Pointe 1969, 1977).

Both oxytocin and mesotocin provoke a glomerular antidiuresis in the water snake *N. sipedon* (Dantzler 1967), but only at doses which are probably pharmacological ($20\text{--}40\text{ mU kg}^{-1}$) and the effect seems to be secondary to a depression of the systemic arterial blood pressure. Sawyer and Sawyer (1952) reported that oxytocin produces a glomerular antidiuresis in the alligator *Alligator mississippiensis* at somewhat lower dosages (10 mU kg^{-1}), and the same effect was reported in the scincid lizard *T. rugosa* by Bentley (1959), but it seems still likely that these renal effects are the result of a fall in renal perfusion pressure (Woolley 1959). Recent developments in isolation and characterisation techniques for polypeptides have led to questioning of the early evidence suggesting that oxytocin is indeed present in the reptilian pituitary gland, but the recent confirmation of the presence of oxytocin in the ratfish *Hydrologus* (Gilles et al. 1993) suggests that it may indeed be real. Oxytocin has also been reported as occurring in another lower vertebrate, the frog *Rana pipiens*, and Galli-Gallardo et al. (1979) and Pang and Sawyer (1978) have more recently reported that mesotocin induces diuresis in some amphibians. As yet, however, renal effects of this peptide at "physiological" doses have not been described in reptiles.

The effects of exogenous administration of AVT on renal function have been studied in a number of species of reptile. The hormone decreases GFR without changing systemic arterial pressure at doses as low as 0.7 mU (3.1 ng kg^{-1}) in the water snake *N. sipedon* during water diuresis (Dantzler 1967) and the freshwater turtle (Dantzler and Schmidt-Nielsen 1966). Relative free-water clearance ($C_{\text{H}_2\text{O}}/C_{\text{IN}}$) is also reduced at the same time suggesting that AVT also has the effect of enhancing tubular reabsorption of fluid by increasing the water permeability of the nephron. Very similar responses to slightly higher doses of AVT ($2.25\text{ mU} = 10\text{ ng kg}^{-1}$) were recorded in the freshwater turtle *C. picta belli* by Butler (1972), the only difference here being that AVT had the effect of increasing relative osmolar clearance rather than reducing it, as is more usually the case.

A decrease in overall GFR has been observed in crocodilians following the administration of 5 mU of the mammalian hormone-equivalent vasopressin, but no studies have yet been reported with AVT (Burgess et al. 1933; Coulson and Hernandez 1964; Sawyer and Sawyer 1952).

In lizards, AVT, at a higher dosage of 50 ng kg^{-1} , reduced the GFR in *V. gouldii* (Green 1972a), although this effect may have also provoked changes in systemic blood pressure. AVT also reduced GFR in *S. cyanogenys* and the effect was wholly glomerular as relative free water clearance ($C_{\text{H}_2\text{O}}/C_{\text{IN}}$) was unaffected (Stolte et al. 1977). These authors were unable to demonstrate any effect of AVT on distal tubular permeability of this species in micropuncture studies and the only direct observation indicating an effect of AVT on the water permeability of the tubular epithelium of a lower vertebrate has not been made in a reptile, but in the urodele amphibian *Necturus maculosus*, in which the

U/P_{OSM} increased from 0.2 to 0.9 under the influence of the hormone (Garland et al. 1975). Even this observation has been challenged, however, by Pang et al. (1982), who found that AVT was only effective if perfused via the arterial and not the renal-portal blood system: Moreover, the effect was eliminated by the use of an AVT analogue (KBIV-24) which inhibits the vascular, but not the tubular actions of AVT. Stoner (1977) was also unable to detect any effect of AVT on the osmotic water permeability of isolated, perfused late distal and collecting tubules from the urodele *Ambystoma tigrinum*.

These various experimental studies have led to the general acceptance of the idea that AVT does function as a physiological antidiuretic hormone in reptiles, reducing GFR and enhancing tubular permeability to water, but, as highlighted in a review by Dantzler and Holmes (1974) some two decades ago – "... this has never been completely documented by the production of hormone deficiencies by ablation of the hypothalamic neurosecretory cells and correction of the defect by hormone replacement."

Preliminary results from such a study with the agamid lizard *Ctenophorus (Amphibolurus) ornatus* were published by Bradshaw (1975, 1976) and full details given in Bradshaw (1978a). Electrolytic lesions were placed in the base of the hypothalamus in order to interrupt the hypothalamo-hypophyseal tract and these were found to inhibit completely the normal antidiuretic response of this species to salt loads, as shown in Fig. 3.1.

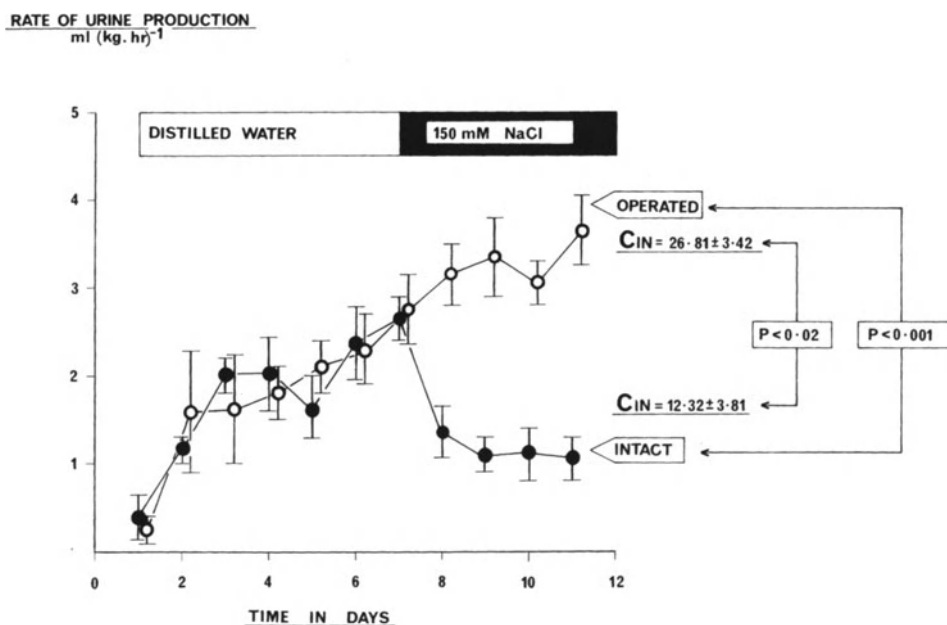


Fig. 3.1. Rate of urine production with chronic water and saline diuresis in intact and hypothalamic-lesioned (Operated) *Ctenophorus (Amphibolurus) ornatus* lizards. All fluid loads are 10 ml 100 g⁻¹ day⁻¹; data are presented as mean \pm SE. (Adapted from Bradshaw 1986a)

The effect of AVT injections in these tract-lesioned animals was also investigated and the renal response to a high dosage of 47.2 ng kg^{-1} of AVT is shown in Fig. 3.2. A typical glomerular and tubular antidiuresis is observed with a pronounced fall in both relative free water clearance ($C_{\text{H}_2\text{O}}/C_{\text{IN}}$) and relative osmolar clearance ($C_{\text{OSM}}/C_{\text{IN}}$) which was sustained for a period of approximately 2 h after the injection.

Hypothalamic lesioning was also found to have an effect on the rate of reabsorption of sodium ions by the tubules of *C. ornatus*, as seen from the data presented in Table 3.2. These data show that the lesioned animals were slightly anti-diuretic when compared with controls and that this was due to a lower relative osmolar clearance that could be attributed to a significantly elevated rate of sodium reabsorption in the tubules. As AVT is also known to increase solute reabsorption in the tubule (see Fig. 3.2 above) it seems unlikely that this effect of the lesions was due to the absence of circulating AVT in the lesioned animals and the lesions may have affected the secretion of other hormones, such as prolactin from the pars distalis. Brewer and Ensor (1980) found that prolactin administration stimulated GFR in the freshwater turtle *Chrysemys picta*, and the location of the hypothalamic lesions in *C. ornatus*, close to the region of the median eminence, may have impacted on portal blood flow and influenced the secretory functioning of the pars distalis.

A direct approach to the question of whether AVT functions as a physiological antidiuretic hormone in reptiles was taken by Rice (1982), who developed a sensitive radioimmunoassay to measure changes in circulating levels of this hormone in the large varanid lizard *V. gouldii*. A highly sensitive radioimmunoassay for AVT was first described by Rosenbloom and Fisher (1974) and preliminary data on circulating levels reported in frogs (Sawyer and Pang 1975) and chickens (Koike et al. 1977). The assay was optimised (Rice 1982) and then was used to explore changes in renal function with: (1) chronic water loading, (2) salt loading and (3) dehydration by Bradshaw and Rice (1981), who also measured concurrent changes in the levels of the adrenal steroid hormones aldosterone and corticosterone using the methods developed by Bradshaw and Grenot (1976). Subsequent to this study, plasma AVT levels

Table 3.2. The effect of hypothalamic lesions on the handling of water and electrolytes in the agamid lizard *Ctenophorus ornatus* undergoing water diuresis. (Modified from Bradshaw 1978b)

Treatment	GFR	V	Relative clearances (%)		Fractional reabsorption (%)		
			$C_{\text{H}_2\text{O}}/C_{\text{IN}}$	$C_{\text{OSM}}/C_{\text{IN}}$	Water	Na^+	K^+
Intact	51.3 ± 2.4	33.2 ± 1.1	35.3 ± 2.6	29.2 ± 3.4	35.2 ± 3.1	78.4 ± 2.3	-17.4 ± 23.6
Tract-operated	47.1 ± 4.9	24.1 ± 1.1	36.5 ± 4.0	18.4 ± 2.7	45.2 ± 4.2	88.6 ± 2.3	58.6 ± 16.2
Statistical significance	NS	$P < 0.001$	NS	$P < 0.05$	NS	$P < 0.02$	NS

Data presented as mean \pm SE. GFR and V in $\text{ml kg}^{-1} \text{ h}^{-1}$. Ureteral urine.

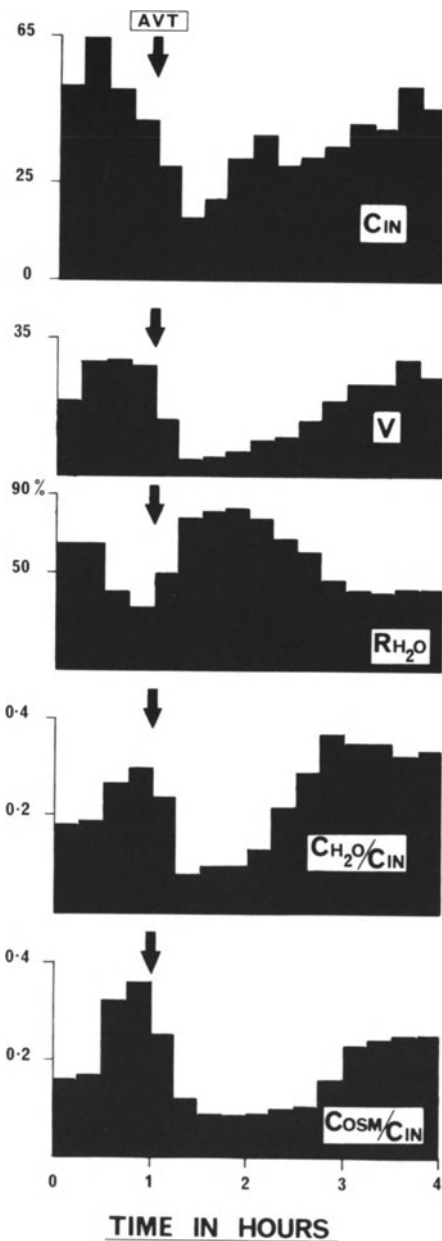


Fig. 3.2. Renal response of hypothalamic-lesioned *Ctenophorus* (*Amphibolurus*) *ornatus* to an intravascular injection of 472 ng kg^{-1} of the neurohypophysial peptide arginine vasotocin (AVT). Clearance of inulin (C_{IN}) and rate of urine production (V) expressed in $\text{ml kg}^{-1} \text{ h}^{-1}$. The lizard was maintained on a constant water load by stomach gavage and ureteral urine was collected via a cloacal cannula similar to that employed by Roberts and Schmidt-Nielsen (1966). (Bradshaw 1986a)

have been reported in green sea turtles (*Chelonia mydas*) during oviposition (Figler et al. 1989), and in the viviparous lizard *T. rugosa* throughout the gestation period (Fergusson and Bradshaw 1991); AVT has also been detected by HPLC in the snake *Bothrops jaraca* (Silveira et al. 1992). No other study to date, however, has investigated AVT levels in relation to kidney function. Data from Bradshaw and Rice (1981) are presented in Table 3.3 and show that circulating levels of AVT do indeed increase in this species with both dehydration and salt loading.

Essential changes in GFR and rate of urine flow (V) as well as circulating levels of AVT with the three treatments are shown graphically in Fig. 3.3, with statistically significant differences between dehydrated and salt-loaded animals, compared with controls indicated by an asterisk ($P < 0.05$). As may be seen, the overall response to dehydration is both qualitatively and quantitatively different from that to salt loading in *V. gouldii*. The GFR does not change with dehydration, but urine volume declines by over 50% as a result of an increase in fractional reabsorption of filtrate from 53 to 83%. We thus see a purely tubular response provoked by the doubling of circulating AVT levels from 1.3 to 3.9 pg ml^{-1} , acting to increase tubular reabsorption of water, which is confirmed by the very large decrease in relative free water clearance ($C_{\text{H}_2\text{O}}/C_{\text{IN}}$) from 27 to 5.8%. This response of *V. gouldii* is very reminiscent of that of the water snake *N. sipedon*, studied by Dantzler (1967), who found that the tubules of this species are much more sensitive to AVT than the glomeruli.

Salt loading involves a further increase in circulating AVT levels from 3.9 to 7.1 pg ml^{-1} which now provoke a very significant glomerular antidiuresis, with a fall in GFR from 20.6 to 4.1 $\text{ml kg}^{-1} \text{h}^{-1}$. Urine volume is also further reduced,

Table 3.3. Plasma hormone concentrations of AVT, aldosterone and corticosterone and changes in renal function in *Varanus gouldii* with prolonged water diuresis, saline diuresis and dehydration. (Modified from Bradshaw and Rice 1981; Bradshaw 1986a)

Plasma hormone concentration	Hydrated		Dehydrated		Salt loaded
AVT (pg ml^{-1})	1.6 \pm 0.4	$P < 0.01$	3.9 \pm 0.3	$P < 0.001$	7.1 \pm 1.5
Aldosterone (ng dl^{-1})	45.9 \pm 4.6	NS	42.0 \pm 7.0	$P < 0.01$	18.3 \pm 6.0
Corticosterone ($\mu\text{g dl}^{-1}$)	9.1 \pm 2.1	NS	9.3 \pm 1.7	$P < 0.01$	19.2 \pm 2.6
Renal parameters					
V ($\text{ml kg}^{-1} \text{h}^{-1}$)	7.8 \pm 0.7	$P < 0.01$	3.3 \pm 0.4	$P < 0.01$	1.2 \pm 0.1
C_{IN} ($\text{ml kg}^{-1} \text{h}^{-1}$)	20.8 \pm 2.5	NS	20.6 \pm 2.1	$P < 0.01$	5.8 \pm 0.8
$\text{FR}_{\text{H}_2\text{O}}$ (%)	53.0 \pm 4.7	$P < 0.01$	82.6 \pm 1.3	$P < 0.01$	73.4 \pm 2.7
$C_{\text{H}_2\text{O}}/C_{\text{IN}}$ (%)	27.0 \pm 4.1	$P < 0.01$	5.8 \pm 0.9	NS	4.1 \pm 0.6
$C_{\text{OSM}}/C_{\text{IN}}$ (%)	20.0 \pm 1.5	$P < 0.01$	11.6 \pm 0.7	$P < 0.01$	22.5 \pm 2.5
FR_{Na} (%)	95.2 \pm 1.2	NS	95.6 \pm 0.6	$P < 0.01$	88.9 \pm 1.5
FR_{K} (%)	29.5 \pm 8.6	NS	11.4 \pm 10.9	$P < 0.01$	-70.1 \pm 30.2
FR_{Cl} (%)	84.4 \pm 2.6	NS	89.0 \pm 0.7	$P < 0.01$	76.7 \pm 2.8

All data presented as mean \pm SE. Ureteral urine.

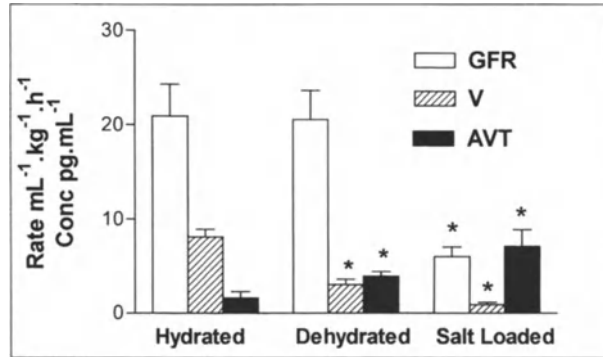


Fig. 3.3. Renal function and circulating levels of arginine vasotocin (AVT) in the varanid lizard *Varanus gouldii* with water loading, dehydration and salt loading régimes. Glomerular filtration rate (GFR), measured as the clearance of inulin, and rate of urine production (V) both expressed in $\text{mL kg}^{-1} \text{h}^{-1}$. AVT concentration in pg mL^{-1} . (Modified after Bradshaw and Rice 1981)

but relative free water clearance would appear to be at a minimum at 4.1% and the urine produced at this stage is close to isosmotic.

We see from this study, in which changes in AVT levels were measured for the first time, that the tendency in the literature to categorise given species as either “glomerular” or “tubular”, according to the nature of the antidiuresis provoked by dehydration or salt loading, is far too simplistic and the response may be either one or the other or both depending upon the level of AVT in the circulation. Dehydration, which does not involve a maximal increase in AVT levels in *V. gouldii*, is associated with a purely tubular antidiuresis but salt loading, which appears to provoke maximal rates of AVT secretion, invokes a much greater antidiuresis involving both glomeruli and tubules and one would predict a similar response in *N. sipedon*.

Changes in solute excretion with the three treatments in *V. gouldii* are more complex and need interpretation. Hydrated animals undergoing prolonged water diuresis have a great need to conserve solutes; thus, fractional reabsorption of sodium ions (FR_{Na}) is very high (95.2%) and the relative osmolar clearance ($C_{\text{OSM}}/C_{\text{IN}}$) is also relatively low (20%; i.e. 80% of all filtered solutes are being reabsorbed along the tubule). With dehydration, and increased levels of AVT, we see the classic fall in relative free water clearance, mentioned above, and a significant decrease in relative osmolar clearance to 11.6%, which is also associated with the action of AVT as seen in Fig. 3.2 above. By stimulating dilution of the urine through enhanced salt reabsorption, AVT is then able to increase the rate of water reabsorption in reptiles through segments of the tubule made permeable by the action of AVT. AVT thus has two separate effects in the reptilian tubule, on salt transport and on the movement of water along an osmotic gradient created between the tubular lumen and the interstitial fluid by that salt transport.

In salt-loaded animals, however, the animal needs to eliminate excess solutes from the body, and AVT on its own would impede this process via its action on salt reabsorption. The decrease in C_{OSM}/C_{IN} is thus overridden in these animals by the action of adrenal steroids and fractional reabsorption of sodium falls significantly to 88.8% (Fig. 3.4). As we shall see in the next section, the action of more than a single hormone needs to be considered when attempting to interpret complex changes in renal parameters of animals responding to various experimental régimes involving variations in water and electrolyte status.

The results presented by Rice (1982) and by Bradshaw and Rice (1981) with *V. gouldii* provide strong evidence supporting the contention that AVT functions as a physiological antidiuretic hormone, and this is strengthened by the effects of hypothalamic lesions in abolishing the antidiuretic response to salt loading in *C. ornatus*. Unfortunately, as is all too often the case with data on kidney function in reptiles, both experiments have not been done on the same animal. AVT has yet to be measured in *C. ornatus* because sufficient blood cannot be collected from these 20 g lizards for the assay (0.5–1.0 ml of plasma is needed), and the effect of electrolytic lesions placed in the hypothalamus to block AVT secretion has yet to be investigated in *V. gouldii*.

Plasma levels of arginine vasopressin (AVP) are known to vary in a very regular manner with changes in plasma osmolality in mammals, however, (Schmidt-Nielsen 1979) and Rice (1982) found a similar relationship for AVT in *V. gouldii*, as shown in Fig. 3.5.

Further evidence that this hormone functions as a physiological antidiuretic hormone in *V. gouldii* is provided by the integrated response of this species to intravenous injections of AVT at a dosage of 25 ng kg^{-1} and to follow-up injections of the drug probenecid, which inhibits transport of organic acids in the kidney and has been shown to be a powerful diuretic and competitive inhibitor of AVT in amphibians and reptiles (Dantzler et al. 1970).

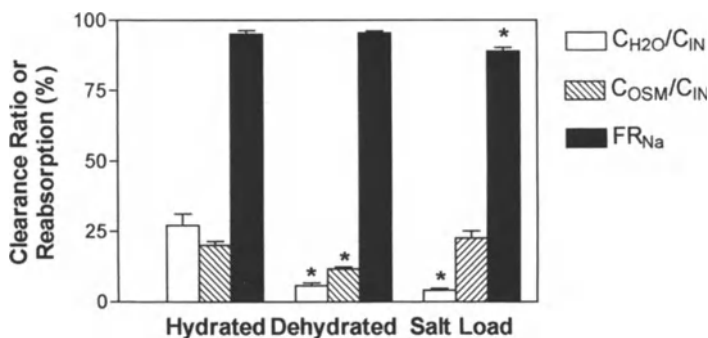


Fig. 3.4. Changes in relative free-water clearance (C_{H_2O}/C_{IN}) and relative osmolar clearance (C_{OSM}/C_{IN}) plus fractional reabsorption of sodium (FR_{Na}) in water-loaded, dehydrated and salt-loaded *Varanus gouldii*. (Modified after Bradshaw and Rice 1982)

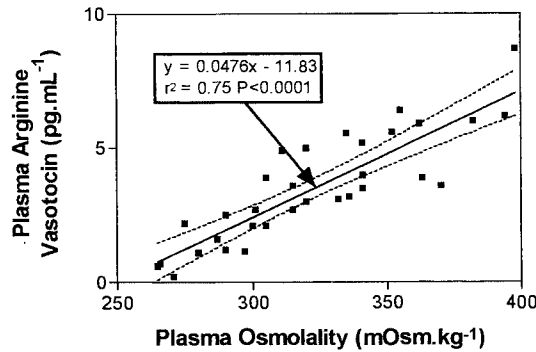


Fig. 3.5. Correlation between plasma osmolality and circulating levels of arginine vasotocin (AVT) in the varanid lizard *Varanus gouldii*. (Modified after Rice 1982)

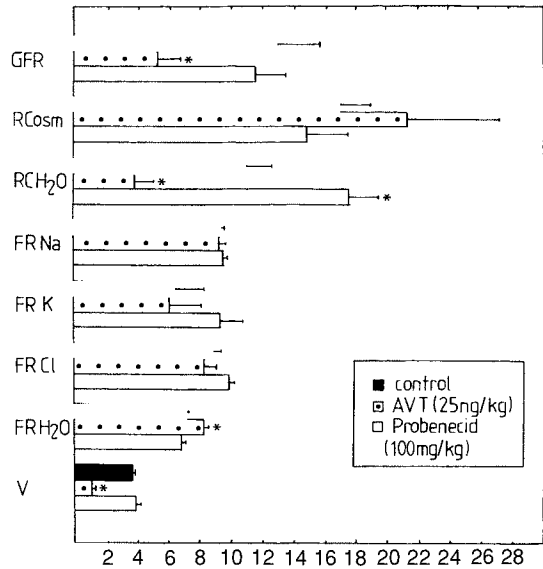


Fig. 3.6. Changes in glomerular filtration rate (GFR, ml.kg⁻¹.h⁻¹), relative osmolar (RCosm, %), and free-water clearance (RCH₂O, %), fractional sodium (FRNa, %/10), potassium (FRK, %/10), chloride (FRCl, %/10) and water reabsorption (FRH₂O, %/10) and ureteral urine flow (V, ml.kg⁻¹.h⁻¹) following an intravascular injection of 25 ng.kg⁻¹ of arginine vasotocin (AVT), followed 2.5 h later by 100 mg.kg⁻¹ of probenecid. Statistical comparisons relate to control values with *P < 0.05. Mean \pm SE is reported with $n = 6$. (Adapted from Bradshaw and Rice 1981)

The data from Bradshaw and Rice (1981) are presented in Fig. 3.6. A marked antidiuresis was provoked by the relatively high dosage of AVT and GFR was reduced to about 50% of the control value. The fractional reabsorption of water also increased significantly, indicating a tubular component to the

antidiuresis, and this is confirmed by the significant depression of the relative free water clearance. The relative osmolar clearance was in fact higher in AVT-injected animals than in controls, although the difference was not statistically significant; but *V. gouldii* may be similar to the freshwater turtle *Chrysemys picta belli*, studied by Butler (1972), in this regard in showing enhanced excretion of osmolytes with exogenous AVT. The effect of probenecid, injected 2.5 h after the AVT, in abolishing the specific effects of AVT was dramatic and both the GFR and rate of urine production (V) were restored to their control values. The effect of probenecid on relative free water clearance was most pronounced and this increased to levels higher than seen in controls.

Taken together, these data from the Australian varanid lizard *V. gouldii* provide a strong circumstantial case for AVT being a genuine antidiuretic hormone in this species. It is to be hoped that similar studies on renal function will be conducted with other species of reptile, now that an AVT assay is available; such studies are essential before one can generalise on the role of AVT and other neurohypophysial peptides as essential moderators of kidney function in reptiles.

3.2.3

Adrenocortical Hormones

Aldosterone and corticosterone (compound B) appear to be the major secretory products of the reptilian adrenal (Sandor 1972; Vinson et al. 1979) although other steroids such as 18-OH-corticosterone (18-OH-B) and deoxycorticosterone (DOC) have been reported in the literature, along with cortisol (compound F). As is the case with most lower vertebrates, however, the nature of the action of these hormones on the kidney is not well understood. Partly, this is because of the difficulties experienced by most workers in demonstrating any effect of exogenous aldosterone injections on renal function in lizards (Bradshaw 1972; Bradshaw et al. 1972; LeBrie 1972; Templeton et al. 1972a), and the failure of all experiments using spironolactone, which is a potent aldosterone antagonist in mammals (Bradshaw et al. 1972; Butler and Knox 1970; Elizondo and LeBrie 1969).

Studies involving adrenalectomy, the classical way in which the impact of adrenal hormones has been codified in mammals, have also been singularly uninformative (see Callard and Callard 1978 for a review), primarily because of the technical difficulties associated with this operation in reptiles where the adrenals, particularly on the right, are closely adhered to the vena cava.

LeBrie and Elizondo (1969) approached this problem in an original fashion and induced adrenal insufficiency in the water snake *N. cyclopion* by vascular occlusion, rather than attempting the far more difficult operation of surgical adrenalectomy. They found that their "operated" animals displayed an increased rate of renal loss of sodium and chloride ions when compared with intact controls. They were able to reduce this loss with injections of aldosterone, which increased reabsorption of both sodium and water by approximately

24%, primarily they thought, through an action on the proximal rather than the distal segment of the nephric tubule.

The effects of hypophysectomy and dexamethasone blockade on renal function were investigated in the lizards *C. ornatus* and *D. dorsalis* by Bradshaw (1972); Bradshaw et al. (1972) and Chan et al. (1970), and these procedures were associated with an increase, rather than a decrease, in sodium reabsorption, which is inconsistent with aldosterone's common action as a mineralocorticoid. Depressing adrenal function either by hypophysectomy or dexamethasone blockade also reduces the rate of secretion of other steroids, such as corticosterone, to negligible levels and replacement studies in *C. ornatus* with both corticosterone and ACTH suggested that this steroid is natriuretic or salt-excreting in this species. Circulating levels of corticosterone also increase with chronic saline diuresis in both *C. ornatus* and *D. dorsalis* which is consistent with this interpretation (Bradshaw 1972; Bradshaw et al. 1972). Chan et al. (1970) found that the accumulation of salt and water that they observed in hypophysectomised *D. dorsalis* could be rectified with injections of corticosterone plus prolactin, but not by prolactin alone, lending further support to the notion that corticosterone functions as a natriuretic hormone in these lizards (Bradshaw 1975).

The effects of both hypophysectomy and dexamethasone injection on renal function in *C. ornatus* undergoing prolonged saline diuresis are shown in Fig. 3.7, with significant differences between treatments and control animals indicated (* $P < 0.05$).

The corresponding response of hypophysectomised and dexamethasone-blockaded animals to injections of 585 mU 100 g⁻¹ per day of mammalian ACTH and 20 µg⁻¹ per day of corticosterone is shown in Fig. 3.8.

Circulating levels of aldosterone were first measured in a reptile by Bradshaw and Grenot (1976), who found a significant negative correlation with change in plasma sodium concentrations in the lizards *Uromastix*

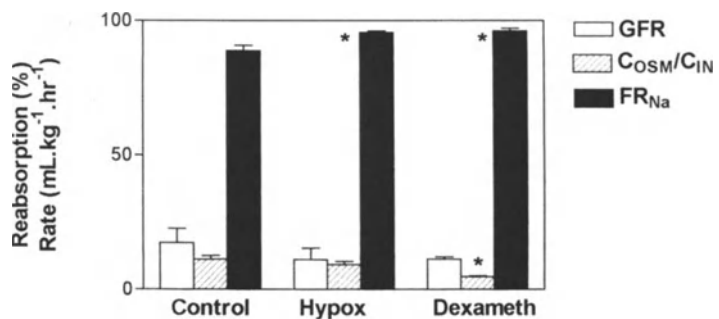


Fig. 3.7. The effects of hypophysectomy and dexamethasone injection on renal function in the agamid lizard *Ctenophorus* (*Amphibolurus*) *ornatus*. GFR, glomerular filtration rate in mL.kg⁻¹.hr⁻¹; C_{OSM}/C_{IN} relative osmolar clearance (%); FR_{Na} fractional reabsorption of sodium (%). (Modified after Bradshaw 1972)

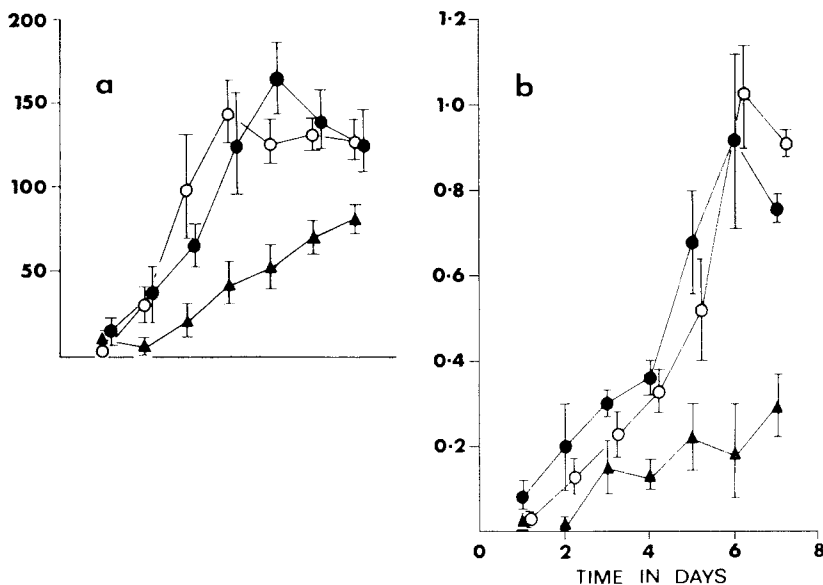


Fig. 3.8a,b. Effects of injection of corticosterone and mammalian ACTH on the mean sodium concentration of the voided urine and the total daily sodium excretion of the agamid lizard *Ctenophorus (Amphibolurus) ornatus* undergoing saline diuresis produced by daily injections of 10 ml 100 g⁻¹ per day of 150 mmol NaCl. ACTH dosage: 585 mU 100 g⁻¹ per day; corticosterone: 20 µg 100 g⁻¹ per day. a Mean sodium concentration of urine in mmol l⁻¹. b Mean sodium excretion in mmol 100 g⁻¹ per day. Closed triangles Control; open circles corticosterone; closed circles ACTH. (Adapted from Bradshaw 1972)

acanthinurus and *T. rugosa*, although the slope of the regression was much lower and barely significant in the latter, non-desert, species. A similar negative correlation for aldosterone was found in *V. gouldii* by Bradshaw and Rice (1981) and this contrasts with a strong positive correlation between plasma levels of corticosterone and sodium. The response of *V. gouldii* to sodium loading is thus the same as that of *C. ornatus* and *D. dorsalis*, i.e. an increase in the rate of secretion of corticosterone. The nature of these two opposite correlations with variation in sodium status for *V. gouldii* is shown in Figs. 3.9 and 3.10. It is interesting to speculate how a nonzoned adrenal gland, such as that of *V. gouldii*, is capable of responding differentially to a common electrolyte stimulus.

If we now try to interpret the changes in renal function observed with change in sodium status in *V. gouldii* (summarised in Table 3.3 and Fig. 3.3), it is evident that there are in fact two possible explanations: either that aldosterone is a classic mineralocorticoid, or that corticosterone is natriuretic in this and other species of lizards. As the concentrations of the two hormones vary in opposite directions with salt loading (corticosterone up and aldosterone down) and there is separate, circumstantial, evidence that corticosterone stimulates salt excretion via the kidney, the fall in fractional reabsorption of

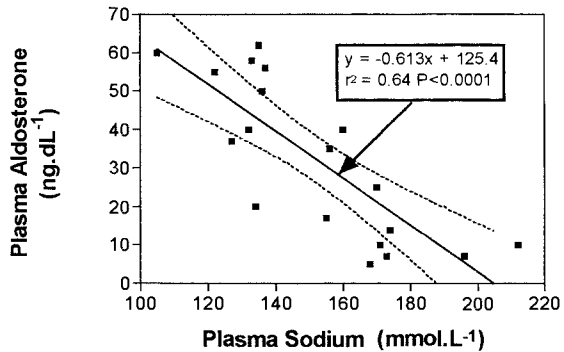


Fig. 3.9. Variation in plasma aldosterone concentration with change in plasma sodium concentration in the varanid lizard *Varanus gouldii*. (Modified after Bradshaw and Rice 1981)

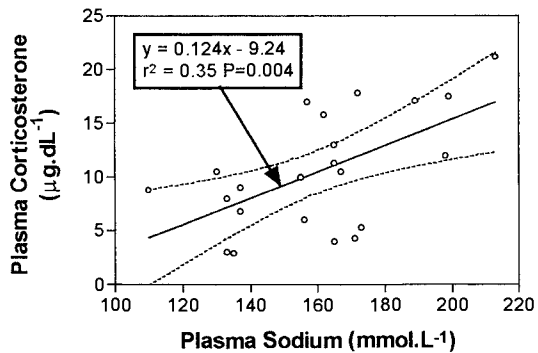


Fig. 3.10. Variation in plasma corticosterone concentration with change in plasma sodium concentration in the varanid lizard *Varanus gouldii*. (Modified from Bradshaw and Rice 1981)

sodium (FR_{Na}) observed could equally be due to the high levels of corticosterone as to the fall in aldosterone.

Essentially, this is a logical problem that can only be solved by observing the effects of removing both hormones from the circulation, and then replacing them one by one. The theoretical possibilities are shown in Table 3.4 as follows: If we make the basic assumption that hormones are needed when their concentration in the blood is high, then we can predict that adrenalectomised *V. gouldii* would have difficulties retaining sodium under conditions of water loading, if aldosterone acts as a natriferic (i.e. sodium-saving) mineralocorticoid. Equally, if rates of sodium excretion under conditions of salt loading are stimulated by high circulating levels of corticosterone, then we would predict that adrenalectomised individuals would experience difficulties in excreting the extra salt.

The logic of the above table necessitates experiments with bilaterally adrenalectomised animals and, despite the difficulty of this operation in rep-

Table 3.4. Nature of changes in circulating levels of aldosterone and corticosterone with water and saline diuresis in reptiles and their possible actions at the level of the kidney

Treatment	Aldosterone	Corticosterone
Water loading	High ^a	Low
Salt loading	Low	High ^a
Action of hormone	Natriferic	Natriuretic

^a Situation where the hormone would be expected to act.

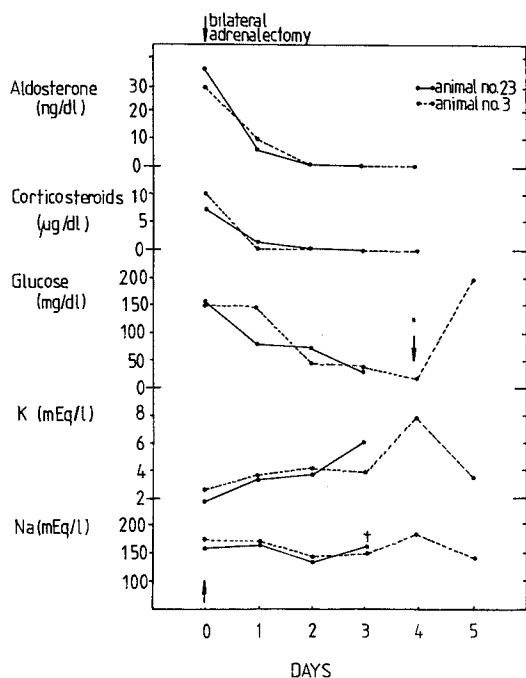


Fig. 3.11. The effect of bilateral adrenalectomy on circulating levels of adrenal steroids, and plasma glucose and electrolyte concentrations in two individual *Varanus gouldii*. (Adapted from Rice et al. 1982; Bradshaw 1986a)

tiles, Rice et al. (1982) were able to remove successfully the adrenals from a number of *V. gouldii*. The animals were maintained in good health with an appropriate replacement régime of daily injections of both the synthetic glucocorticoid dexamethasone and glucagon. The rapid fall in plasma levels of both aldosterone and corticosterone, as well as glucose, following adrenalectomy in two individuals is shown in Fig. 3.11.

Data on renal function of adrenalectomised and intact animals with both salt and water loading, from the study of Rice et al. (1982), are shown diagrammatically in Fig. 3.12. It is clear that, despite their lack of adrenal glands and

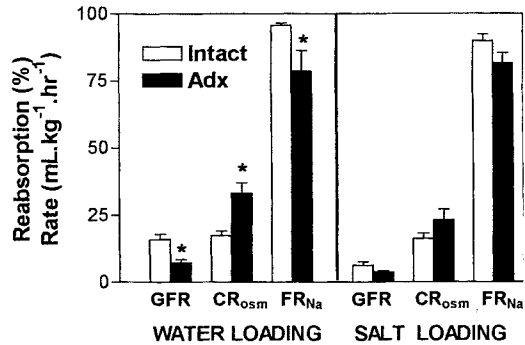


Fig. 3.12. Renal response to water and salt loading of intact and previously adrenalectomised (Adx) *Varanus gouldii* lizards. GFR Glomerular filtration rate in $\text{mL kg}^{-1} \text{h}^{-1}$; CR_{osc} relative osmolar clearance (%); FR_{Na} fractional reabsorption of sodium ions (%). Data expressed as mean \pm SE. (Adapted from Rice et al. 1982)

attendant hormones, the renal response of adrenalectomised animals to salt loading was quite normal. As we may see from the data in this figure, adrenalectomised animals subjected to water loading have a significantly lower GFR, higher relative osmolar clearance ($\text{C}_{\text{OSM}}/\text{C}_{\text{IN}}$) and lower rate of fractional reabsorption of sodium ions (FR_{Na}). Their ability to respond homeostatically to the challenge of the water load is thus seriously impaired and they have difficulty both in excreting the extra water and in retaining sodium ions. Given that, under these circumstances, aldosterone levels are high in intact animals, we may conclude that the impairment in adrenalectomised individuals is the result of the absence of this hormone from the circulation. As we would predict from this, renal function was unchanged following adrenalectomy in salt-loaded individuals, in which aldosterone levels are normally minimal, and the fact that they lacked corticosterone did not impair their ability to excrete effectively the extra sodium ions.

To complete this study, one needs to carry out replacement therapy with both aldosterone and corticosterone in order to confirm that aldosterone does indeed enhance the rate of tubular reabsorption of sodium. Results from Rice et al. (1982) are given in Fig. 3.13. As anticipated, aldosterone significantly increased fractional sodium reabsorption in *V. gouldii* in adrenalectomised salt-loaded individuals from $81.6 \pm 3.8\%$ to $92.1 \pm 0.8\%$ and also significantly stimulated potassium secretion by the kidney. Aldosterone thus has in *V. gouldii* the same effects renally as observed in mammals – sodium reabsorption and potassium excretion – and thus functions in this species as a classic mineralocorticoid.

Interestingly, corticosterone at the same dosage of $100 \mu\text{g kg}^{-1}$ was almost as effective as aldosterone in increasing the FR_{Na} and it also had a smaller, though still significant, effect on potassium excretion. These data from *V. gouldii* thus support the contention of Nishimura (1985), that the so-called glucocorticoids demonstrate significant mineralocorticoid actions in nonmammalian verte-

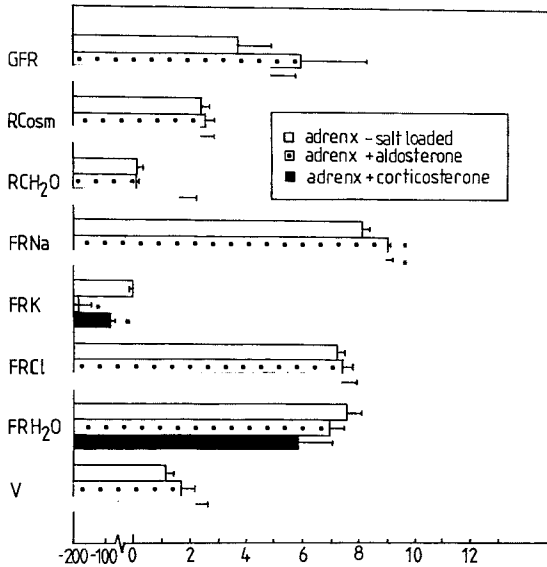


Fig. 3.13. Renal response of salt-loaded, bilaterally adrenalectomised (adrenx) *Varanus gouldii* lizards to intravenous injections of either aldosterone or corticosterone at a dosage of $100 \mu\text{g kg}^{-1}$. Columns represent mean values \pm SE with $*P < 0.05$. Scales as for Fig. 3.6. (Adapted from Rice et al. 1982; Bradshaw 1986a)

brates and provide convincing evidence of a renal tubular action of the mineralocorticoids in enhancing sodium reabsorption.

What is clearly required is further work with species such as *C. ornatus* and *D. dorsalis* to clarify the renal effects of corticosterone, which would appear to be the opposite of those observed in *V. gouldii*. One of the difficulties, however, is getting enough blood to measure circulating aldosterone levels (0.5–1.0 ml of plasma is needed, as for AVT). There is also the technically difficult surgical requirement of adrenalectomy, without which it is doubtful one would have been able to disentangle the hormonal relationships in *V. gouldii*.

It would be unwise too to assume that all reptiles, or even all lizards for that matter, share a common system of hormonal control of their renal function and agamids and iguanids may well differ radically from lizards such as varanids. Levels of aldosterone reported by Duggan and Lofts (1978, 1979) in the sea snake *Hydrophis cyanocinctus* are many times higher than those reported by Bradshaw and Grenot (1976) and Bradshaw and Rice (1981) for lizards. Aldosterone levels measured by Uva et al. (1982) and Hadj-Bekkouché et al. (1993) in the tortoises *Testudo hermanni* and *T. mauritanica* are also much lower, and the actions of this hormone at the level of the kidney may be totally different in such species.

It is also now possible to interpret the effects of the other treatment explored by Bradshaw and Rice (1981) with *V. gouldii* – dehydration. Circulating levels

of aldosterone at $45.9 \pm 4.6 \text{ ng dl}^{-1}$ were as high in dehydrated as in water-loaded individuals and there was also no significant difference in the fractional reabsorption of sodium ions. Dehydration involves hypovolaemic stimuli and these may have led to high levels of aldosterone via the secretion of angiotensin II, as shown by Bradshaw (1978b), and the tactic of the animal is to attempt to minimise water loss by saving sodium. Under such circumstances the inherent natriferic effect of AVT is also beneficial to the animal and both aldosterone and AVT assist the animal in regaining homeostasis.

Under conditions of salt loading, however, any inherent natriferic effect of the higher AVT levels is obviously overridden by the very large concomitant fall in aldosterone levels in the plasma, which provokes a significant decrease in sodium reabsorption by the kidney. The net effect is one of an increase in the rate of solute excretion along with conservation of water under the action of AVT.

3.2.4

Localisation of Action of Arginine Vasotocin in Kidney Tubules

The physiological results outlined above make it clear that AVT may act both at the level of the glomerulus and the nephric tubule in provoking an antidiuresis in reptiles. The glomerular effect is clearly a vascular one of vasoconstriction acting, it is thought, on the afferent arteriole to reduce the GFR (Dantzler 1989a,b) or on the mesangial tissue of the glomerulus (Braun and Dantzler 1987; Dworkin et al. 1983; Ichikawa and Brenner 1977). Such vascular effects of neurohypophysial hormones have been shown to act in mammals via V_1 receptors which activate Ca^{2+} ions as a secondary messenger (Jard 1983; Imbert-Teboul et al. 1993).

The other, tubular, effects of AVT on water and salt reabsorption are thought to depend on the presence of V_2 -like receptors located in the basolateral membranes of the epithelial cells which release cyclic AMP (cAMP) as a secondary messenger (Morel and Doucet 1986). AVT is well known, for example, for its action in promoting sodium and chloride transport in frog skin and bladder (Bentley 1971; Jard and Morel 1963) as well as in the thick-ascending limb (TAL) of the loop of Henle in the mammalian kidney (Greger 1985; Morel 1983; Rocha and Kokko 1977). AVT also facilitates water transport across such membranes by increasing their permeability – a process again which has been shown to be cAMP-dependent and involves the insertion of water channels in the luminal membrane (Grantham and Burg 1966; Hays 1990; Valenti et al. 1987).

Dousa (1974) was unable to demonstrate any effect of AVT on tissue levels of cAMP in the kidneys of crocodiles, but François Morel, at the Collège de France in Paris, working with a small group of colleagues, has been responsible for the development of an extremely sensitive micromethod capable of detecting the presence of V_2 receptors in discrete segments of the mammalian nephron (Imbert et al. 1975; Morel 1983; Morel et al. 1978, 1981). The kidney is

perfused rapidly with collagenase and then tubular segments are identified visually and separated by microdissection. They are then incubated with ^{32}P -ATP, which is converted to cAMP by the action of the enzyme adenylate cyclase. Radioactively labelled cAMP is separated chromatographically from its precursor and the rate of production of cAMP by the tissue thus measured (Morel et al. 1978). In the presence of a hormone, this rate is increased 10- or 20-fold, if the appropriate hormone receptor is present in the membrane. With suitable modification, the method may also be used to measure the hormonal sensitivity of the salt-transporting enzyme Na^+/K^+ -ATPase in the kidney tubules and thus investigate the renal effects of steroid hormones such as aldosterone (Doucet 1988; Doucet et al. 1979; Katz et al. 1979).

The method represents a major breakthrough in studies of renal physiology in that it permits localisation, at the cellular level, of sections of the kidney nephron that are sensitive to neurohypophysial hormones such as AVP and AVT. This method has only been applied to date in kidneys from white rats, mice and rabbits, but it has already provided a wealth of detail on the sensitivity of the mammalian nephron to the action of both peptides and steroid hormones (de Rouffignac 1990; Morel and Doucet 1986).

This method has been developed over the past few years in my laboratory and applied to the kidney of *C. ornatus* which is, as we have seen, one of the best-studied lizards from the point of view of hormonal control of kidney function. Major difficulties were encountered initially in mastering the very different renal architecture of the reptilian kidney, particularly that of *C. ornatus*, which is unlike that of any other reptile yet described (O'Shea et al. 1993). The tubules in the kidney are extremely difficult to identify and to isolate in sufficient lengths for hormonal study, but some data are now available on the distribution of AVT-sensitive sites in the nephron of this lizard (Bradshaw and Bradshaw 1996) as shown in Fig. 3.14. The response of the glomeruli is not shown here but, as would be expected, they showed no effect of added AVT on rates of production of cAMP, confirming that the action of AVT on this segment is other than by a cAMP-dependent V_2 -like receptor. Statistically significant responses to the addition of AVT were found, in contrast, in the thin intermediate segment (IS) and all segments of the collecting-duct. Most significantly, there was no evidence for AVT receptors in the distal convoluted tubule (DCT).

The lack of AVT sensitivity in the DCT is at first sight surprising, as this segment in both amphibian and reptilian nephrons has generally been considered to be the major site for both NaCl and water reabsorption (Dantzler 1982; Nishimura 1985; Stoner 1985). There is some difficulty, however, and considerable confusion in the literature over the nomenclature of the distal tubule, especially in nonmammalian vertebrates (Hentschel and Elger 1989).

The straight, unbranched, terminal portion of the distal convoluted tubule seen in *C. ornatus* corresponds precisely to the "late distal tubule" (LDT) as defined by Stoner (1985), but this would be termed a "connecting segment" by many other workers and not considered part of the DCT proper (Dantzler

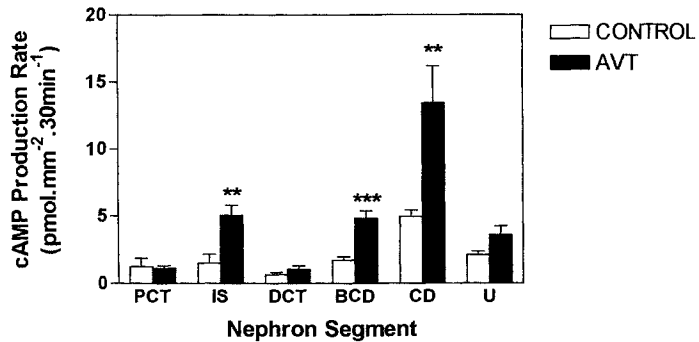


Fig. 3.14. Localisation of arginine vasotocin (AVT)-sensitive adenylate cyclase activity along the nephron of the arid agamid lizard *Ctenophorus ornatus*. Data are expressed per mm² of the outer membrane of the tubule. PCT Proximal convoluted tubule; IS thin-intermediate segment; DCT distal convoluted tubule; BCD branched collecting duct; CD collecting duct; U ureter; G glomerulus; LDT late distal tubule. The statistical significance of differences in mean values is shown with ** $P = 0.01$ and *** $P = 0.001$. (Adapted from Bradshaw and Bradshaw 1996)

1989b; Davis et al. 1976; Hentschel and Elger 1987; Uchiyama 1994). We have considered this segment to be part of the collecting-duct system, because microscopically it is clearly quite distinct from the preceding convoluted section of the tubule, and the rate of cAMP production after incubation with AVT was no different from that in confluent, branched-collecting ducts (BCDs). Hentschel and Elger (1989), on evolutionary grounds, also include this unbranched end-portion of the distal tubule in the collecting system and describe it as

“not belonging to the nephron proper”

but rather as a

“connecting tubule for the nephron with the aborescent system of the collecting ducts”.

We thus agree with Hentschel and Elger (1989) and differ from Stoner (1985) in the nomenclature of this segment.

Hentschel and Elger (1989) consider that the early distal tubule (“diluting segment”) commences at the end of the thin IS and that, in mammals, it is equivalent to the thick-ascending limb of the loop of Henle (TAL). Stoner (1985), however, specifically excludes the TAL as forming part of the distal nephron, on functional grounds, and divides the rest of the DCT into three sections: early, connecting and late. Clearly, with such divergent opinions, it is often difficult to know precisely which section of the tubule is being referred to by a particular author.

In *C. ornatus* and the garter snake *Thamnophis sirtalis*, the ciliated IS extends from the end of the proximal convoluted tubule (PCT) to the glomerulus in a relatively straight section and appears little different in diameter from the

DCT at this point (O'Shea et al. 1993). The early part of what we would call the DCT proper in reptiles – commencing immediately posterior to the point of contact with the glomerulus – appears never to have been investigated physiologically in either lizards or snakes and all in vitro studies to date have been carried out with more distal sections of the DCT.

Sections of distal tubules from *T. sirtalis* were microperfused by Beyenbach and Dantzler (1978) and Beyenbach et al. (1980), who detected an amiloride-sensitive NaCl transport system. The associated transluminal potential difference was lumen negative, however, and unresponsive to AVT (Beyenbach 1984). In the collecting tubules of the mammal, a lumen-negative voltage of –20 to –30 mV is present as a result of this method of Na⁺ transport across the apical membrane which lacks chloride channels (O'Neil and Sansom 1984). Na⁺ enters the cell via amiloride-sensitive channels and is then extruded actively across the basolateral membrane by a Na⁺/K⁺-ATPase pump which is aldosterone-sensitive (Morel and Doucet 1986). AVP is thought to increase water permeability of the collecting ducts in a similar manner to AVT acting on the amphibian bladder. Binding is to a V₂ receptor and an activated protein kinase stimulates a rearrangement of cytoskeletal elements resulting in the insertion of water channels in the apical membrane (Hays 1990).

In mammalian studies, a positive luminal voltage of +3 to +7 mV across the apical membrane of epithelial tissues is invariably associated with the ability of these cells to reabsorb both Na⁺ and Cl[–] against a concentration gradient via a furosemide-sensitive 1K⁺/1Na⁺/2Cl[–] cotransport system (Greger 1985; Greger et al. 1983; Hebert and Andreoli 1984). The effect of ADH on these cells is to stimulate active Cl[–] transport which takes place through the Cl[–] conductance channels in the basolateral membrane (Greger 1985). Hall and Varney (1980) suggest that ADH acts primarily by activating the chloride channels which lower intracellular Cl[–] and thus, secondarily, increase the activity of the cotransport system. This system is restricted to the water-impermeable epithelia of the thin- and thick-ascending limbs of the mammalian loop of Henle, a region that Morel (1983) has shown is stimulated by AVP binding to the V₂ receptor.

In a preliminary study in *T. sirtalis*, Yakota and Dantzler (unpublished, cited in Dantzler 1989a) measured a positive luminal membrane voltage in the thin IS suggesting that this may be a possible site of Na⁺ transport and dilution of the urine in this reptile. Hentschel and Elger (1989), in a major review of the anatomy of the vertebrate nephron, suggest that

“It is conceivable that the thin portion of the loop of Henle is a region homologous to the intermediate segment of lower vertebrates.”

and the expanding straight section of the IS which runs directly to the glomerulus in the reptile may also well be the antecedent of the mammalian TAL.

If this is indeed the case, then it is not surprising that we have detected sensitivity to AVT in this thin IS, as the TAL in mammals is the major site of furosemide-sensitive active salt transport from lumen to interstitium. We thus

suggest that the IS is the primary site of dilution in the kidney of *C. ornatus* with the reabsorption of an hyperosmotic reabsorbate across an epithelium having relatively low permeability to water.

The micropuncture study of Stolte et al. (1977) on the lizard *S. cyanogenys* is difficult to reconcile with this hypothesis as the U/P_{OSM} in the tubules of normal animals fell progressively throughout the collecting duct system, and into the ureter, and was unresponsive to added AVT. The fact, however, that the U/P_{OSM} also fell progressively, from 0.79 to 0.56, when it would have been expected to increase, indicates that these animals were not responding appropriately to the salt load and it is thus difficult to gauge the significance of these negative data.

As the reptilian kidney normally appears to reabsorb water from an urine that has already been diluted (see Sect. 2.3.2), we would anticipate that the primary site of water reabsorption be further caudad in the tubule, in the collecting duct system, and not throughout, as implied by the micropuncture data from *S. cyanogenys* (Stolte et al. 1977). The extensively branched collecting duct system is indeed the site of major AVT sensitivity in *C. ornatus* and all sections that were microdissected (BCT, CD) evidence high levels of reactivity to AVT. Reactivity, and therefore AVT receptor concentration, is of equal intensity in BCT and CD (measured relative to control values for each segment) and equalled two to three times control values.

Rates of cAMP production are usually expressed per mm length of tubule isolated but, in this case, because of the substantial size of the collecting ducts, rates have been expressed per mm^2 , with the area calculated as that of the surface of a cylinder having the same diameter and length as the tubule. A diagrammatic representation of the nephron of *C. ornatus* is given in Fig. 3.15.

The data on the possible presence of AVT receptors in the ureter are suggestive, but the variation is too high for statistical significance. It may prove however that the ureter in reptiles is more than just a simple conduit for urine to the exterior and, given what we know of the essential activity of postrenal sites in reptiles in completing and extending the osmotic work of the kidney, we would anticipate that AVT receptors may be found in the cloaca and colon which are major sites of water reabsorption in *C. ornatus* and other reptiles.

3.3

The Cloacal-Colonic Complex

It has been appreciated for many years by workers in the field that postrenal reabsorptive sites such as the cloaca and the bladder are of considerable importance for the water and electrolyte economy of reptiles (Bentley and Schmidt-Nielsen 1965; Junqueira et al. 1966; Schmidt-Nielsen and Skadhauge 1967; Skadhauge 1977) but their precise study and quantification has been difficult until relatively recently. In vitro measurements with isolated tissues have served to establish that both water and salt are transported by these tissues, but the actual rates measured are about one-twentieth of those

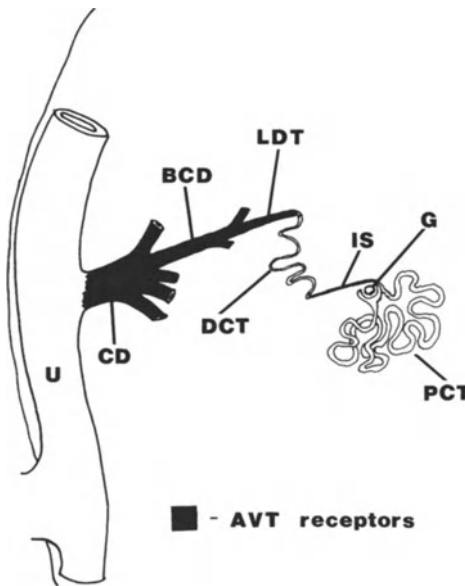


Fig. 3.15. The nephron of the agamid lizard *Ctenophorus* (*Amphibolurus*) *ornatus* showing those segments of the nephron in black that have been found to possess arginine vasotocin (AVT) receptors. Abbreviations as for Fig. 3.14. (Adapted from Bradshaw and Bradshaw 1996)

Table 3.5. Estimated absolute and fractional rates of reabsorption of water and electrolytes from post-renal sites in reptiles. (Modified from Minnich 1979; Bradshaw 1975; Skadhauge and Duvdevani 1977)

Species	Treatment	Sodium $\mu\text{mol kg}^{-1} \text{h}^{-1}$	Potassium $\mu\text{mol kg}^{-1} \text{h}^{-1}$	Free water $\text{ml kg}^{-1} \text{h}^{-1}$	Fluid $\text{ml kg}^{-1} \text{h}^{-1}$
<i>Ctenophorus ornatus</i>	Hydrated	1013.8 (98.8)	231.2 (92.9)	18.8 (86.9)	27.1 (88.1)
	Salt loaded	501.4 ^a (63.4) ^a	25.7 ^a (35.5) ^a	4.4 ^a (97.6)	8.7 ^a (88.8)
<i>Crocodylus acutus</i>	Hydrated				0.75 (21)
	Dehydrated	42 (75)	5.7 (6.8)		0.14 (17)
	Salt loaded	7.1 (30)	9.7 (64)		0.11 (21)
<i>Sceloporus cyanogenys</i>	Normal	144 (75)	54 (82)	(99)	2.8 (96)
	Hydrated	-108 (33)	0.7 (1.2)	(86)	3.2 (79)
	Hydrated + 12.5 ng kg ⁻¹ AVT	-125 (38)	-73 (44)	(89)	2.1 (65)
<i>Sphenodon punctatum</i>	Hydrated	60 (43)	-3.2 (15)		0.22 (11)

Data presented as means, with a - sign indicating net secretion. Fractional rates of reabsorption are given as percentages in parentheses.

^a Statistically significant difference compared with hydrated value with $P = 0.01$.

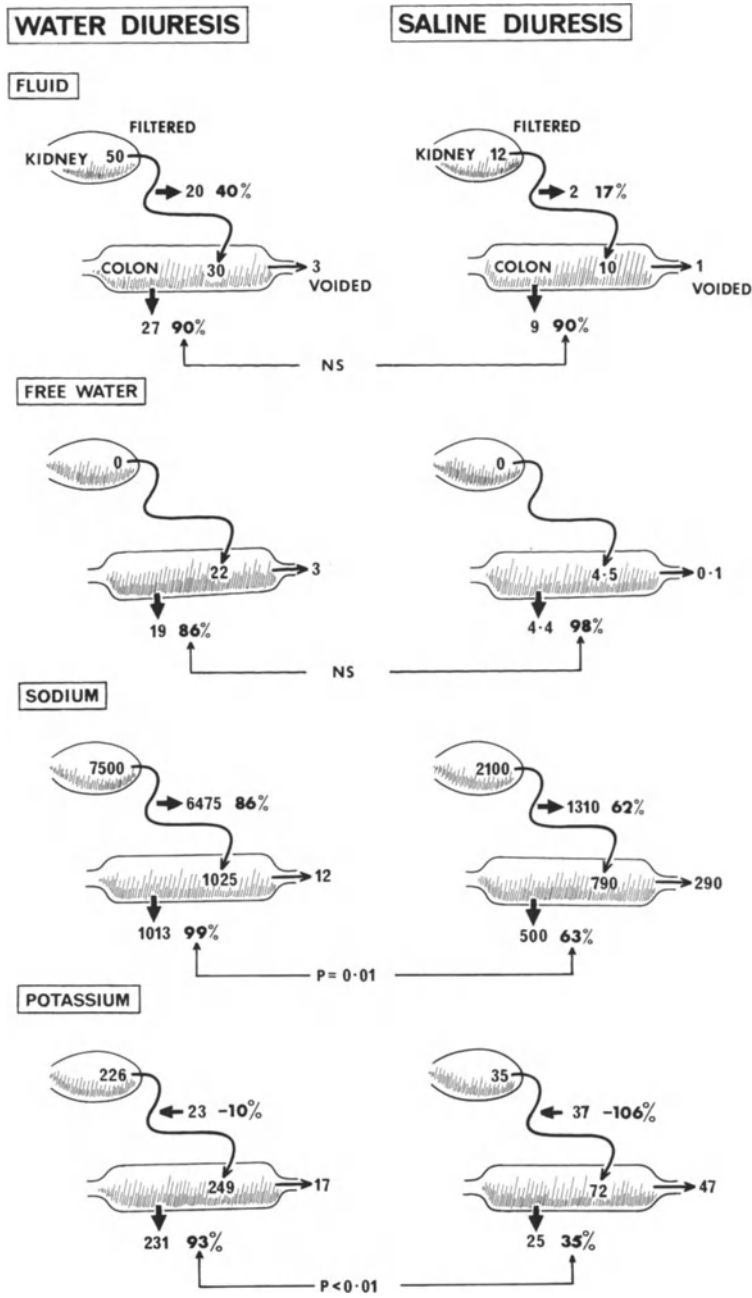


Fig. 3.16. The parameters of colon function in the Australian agamid lizard *Ctenophorus (Amphibolurus) ornatus* during prolonged water and saline diuresis. The lizards were maintained with chronic injections of 10 ml 100 g⁻¹ per day of either distilled water or 150 mmol NaCl for a period of 10 days. Transport parameters are expressed in ml kg⁻¹ per hour for volumes and $\mu\text{mol kg}^{-1} \text{h}^{-1}$ for sodium and potassium. Filtered loads for sodium and potassium are also expressed in $\mu\text{mol kg}^{-1} \text{h}^{-1}$. (Adapted from Bradshaw 1986a)

estimated *in vivo* (Bentley and Bradshaw 1972; Dantzler and Schmidt-Nielsen 1966), due doubtless to the absence of vascularisation and adequate mixing.

Estimates of transmural fluxes of water and electrolytes across the cloaca of the agamid lizard *C. ornatus* were calculated by use of the difference technique by Bradshaw (1975) and are shown in Table 3.5, along with data from other reptiles, and summarised diagrammatically in Fig. 3.16. This technique is based on a direct comparison of renal parameters derived from the collection of both ureteral and bladder or voided urine in the one species, and under the same conditions of water and electrolyte availability. As we have already seen (Sect. 2.3.3), the relative osmolar clearance ($C_{\text{OSM}}/C_{\text{IN}}$) of some 13 species of reptiles, based on the collection of ureteral urine, is of the order of 24%, but falls to approximately 1% when calculated with spontaneously voided urine. This gives some idea of the activity of postrenal sites in conserving body electrolytes.

An examination of these data shows that rates of fluid reabsorption may vary from 11% from the bladder in *Sphenodon punctatum* to as high as 96% from the cloaca of *S. cyanogenys*. The rate of sodium reabsorption from the cloaca appears to fall in *Crocodylus acutus* with salt loading, but the rate of fluid reabsorption remained unchanged. Fractional reabsorption of fluid fell with water loading in *S. cyanogenys*, but the sodium response appears inappropriate, with a change from net reabsorption to net secretion. The addition of 12.5 ng kg^{-1} of AVT to hydrated animals also had no appreciable impact on postrenal function.

The data from *C. ornatus* are simpler to interpret, with approximately 90% of the fluid presented to the cloacal-colonic complex being reabsorbed under all circumstances, but there is a significant decrease in the postrenal reabsorption of both sodium and potassium ions following salt loading. Estimated rates of electrolyte reabsorption are also much higher in this semi-arid lizard than in the other reptiles studied.

The difference technique is open to many criticisms, some of which also apply to static studies in which fluid of known composition is instilled into the cloaca or bladder and left there for a period of time, following which transport parameters are estimated from its subsequent change in composition (Braysher and Green 1970; Brodsky and Schilb 1960). Our understanding of the cloacal-colonic complex and its control, however, has been considerably enhanced by more recent studies in which the segment has been perfused *in situ* in conscious animals at known rates with solutions of predetermined composition. This perfusion technique was first developed by Skadhauge (1967) to study the colon of the chicken and has now been modified and applied to two lizard species, *Agama stellio* (Skadhauge and Duvdevani 1977) and *V. gouldii* (Bradshaw and Rice 1981).

Data from these two studies are summarised in Tables 3.6 and 3.7 and show that both water and electrolytes are reabsorbed from the cloaca of *A. stellio*, with potassium being secreted under all circumstances. Water reclamation was

Table 3.6. Rates of water and solute reabsorption from the perfused cloaca of the desert lizard *Agama stellio*. (Modified from Skadhauge and Duvdevani 1977^a)

Treatment	Fluid (ml kg ⁻¹ h ⁻¹)	Sodium	Potassium (μmol kg ⁻¹ h ⁻¹)	Chloride	Reabsorbate (mmol l ⁻¹)
Normal	2.39	203	-45	131	121
Hydrated	1.83	246	-31	204	229
Dehydrated	3.34	167	-42	125	75
Salt load	2.04	139	-38	83	90

^a Note that the units in their Table IV should be μmol kg⁻¹ h⁻¹ and not meq kg⁻¹ h⁻¹ as stated.

Table 3.7. Transmural water and electrolyte fluxes across the colon and cloaca of the lizard *Varanus gouldii* measured during *in vivo* perfusion. (Modified from Bradshaw and Rice 1981)

Parameter	Hydrated	Significance	Salt loaded	Significance	Dehydrated
Perfusion rate (ml kg ⁻¹ h ⁻¹)	6.8		2.4		3.8
Reabsorbate (ml kg ⁻¹ h ⁻¹)	1.38 ± 0.07	<i>P</i> < 0.01	0.97 ± 0.08	<i>P</i> < 0.01	1.55 ± 0.17
Electrolyte reabsorption (μmol kg ⁻¹ h ⁻¹)					
Sodium	157 ± 10.3	<i>P</i> < 0.01	47 ± 7.5	NS	50 ± 7.3
Potassium	-13 ± 1.4	<i>P</i> < 0.01	-3.1 ± 0.5	<i>P</i> < 0.01	-7.3 ± 0.8
Chloride	77 ± 7.7	<i>P</i> < 0.01	29 ± 3.5	<i>P</i> < 0.01	57 ± 6.3
Fractional reabsorption (%)					
FR _{Na}	39.9 ± 1.3	<i>P</i> < 0.01	32.1 ± 3.5	NS	26.3 ± 3.2
FR _{Cl}	21.8 ± 1.9	NS	25.1 ± 3.3	NS	31.0 ± 3.5
FR _{H₂O}	22.1 ± 1.6	<i>P</i> < 0.01	40.8 ± 1.6	NS	40.4 ± 2.5
Concentration of reabsorbate (mmol l ⁻¹ NaCl)					
	140.3		63.4		61.5

Data presented as mean ± SE. All fractional data subjected to arcsine transformation.

lowest with water hydration, and the reabsorbate was hyperosmotic. Neither salt loading nor dehydration increased the rate of water reabsorption significantly, however, although the rate of reabsorption of sodium and chloride fell after salt loading. The finding of an hyperosmotic reabsorbate with water loading suggests the presence of some solute-linked water flow, as has been shown to occur in the cloaca of the crocodile (Schmidt-Nielsen and Skadhauge 1967), the intestine of the eel (Skadhauge 1969) and the human rectum (Edmonds and Pilcher 1969).

In the study of Rice and Bradshaw (1981) with the large varanid lizard *V. gouldii*, rates of perfusion were adjusted with each treatment to approximate the rates of urine flow measured in prior studies of kidney function and thus replicate presentation rates of fluid and solutes to the colonic epithelium. From Table 3.7 it is clear that saline loading is associated with a significant reduction in the absolute rates of reabsorption of sodium, chloride and water

from the colon; potassium secretion is also reduced. When the data are expressed fractionally, that is, relative to the presentation rate for each component – which is a function of the rate of perfusion – it may be seen that water reabsorption increases significantly from 22.1 to 40.8% with salt loading, and sodium reabsorption falls from 39.9 to 32.1%. Fractional reabsorption of chloride is unchanged and, as already noted, potassium secretion is reduced.

These changes are thus homeostatic in nature and further aid the animal to conserve water and lose salt and thus complement and extend the changes in kidney function that are associated with salt loading. One might be tempted to conclude from these data, because AVT levels rise and those of aldosterone fall with salt loading (see Table 3.3), that the observed increased rate of water reabsorption from the colon is due to AVT and the decrease in excretion of sodium is a direct result of the change in aldosterone concentration. Unfortunately, a close examination of the data from dehydrated individuals is sufficient to dispel this rather convenient conclusion.

As seen from Table 3.7, colon function in chronically dehydrated *V. gouldii* is essentially identical with that of saline-loaded individuals, with a high rate of reabsorption of water and a decreased fractional reabsorption of sodium ions. Levels of AVT increase from a mean of 3.9 ± 0.3 in dehydrated animals to $7.1 \pm 1.5 \text{ pg ml}^{-1}$ with salt loading, but there is no concomitant increase in the rate of water reabsorption from the colon. Equally, any possible natriferic (i.e. sodium reabsorbing) effect of AVT is negated by the data, as rates of reabsorption of sodium decrease rather than increase with the rise in blood levels of AVT.

The rate of sodium reabsorption from the colon also seems to be independent of circulating levels of aldosterone as it is low and equal in both salt-loaded and dehydrated individuals, despite the fact that aldosterone levels are maximally elevated at $42.0 \pm 7.0 \text{ ng dl}^{-1}$ in dehydrated animals and fall to a minimum of $18.3 \pm 2.6 \text{ ng dl}^{-1}$ with salt loading.

Braysher and Green (1970) presented data to suggest that AVT at a dosage of 100 ng kg^{-1} enhanced both sodium and water reabsorption from the cloaca of *V. gouldii*, but this involved a static procedure with a cannulated cloaca and, in the light of the dynamic perfusion data from the same species, these early conclusions need to be treated with some caution. It is true that the increased rate of water reabsorption from the cloaca of salt-loaded and dehydrated *V. gouldii* occurs in the face of a decreasing osmotic gradient (the U/P_{OSM} increases from 0.40 with hydration to 0.98 with salt loading) and this suggests the involvement of hormonal mechanisms. There is, however, no overwhelming evidence from either study to implicate neurohypophysial hormones in the control of postrenal water and electrolyte transfer in *V. gouldii* and Murrish and Schmidt-Nielsen (1970) have argued that at least water reabsorption from the cloaca is passive in lizards (but see Skadhauge 1978b for a critique of this suggestion).

There is also little information available on the possible physiological effects of hormones on bladder function in reptiles, although aldosterone has been

shown to affect sodium transport in *Testudo graeca* (Bentley 1962) and *Chrysemys picta* (Le Fevre 1973). Despite the well-known response of the amphibian bladder to AVT (Bakker and Bradshaw 1977), that of reptiles seems generally unresponsive to neurohypophysial hormones (Bentley 1962; Brodsky and Schilb 1960) and Gilles-Baillien (1969) failed to observe any effect of AVT on water permeability of the bladder of *T. hermanni*. It would be most interesting, however, to investigate the hormonal responsiveness of the bladder of the desert tortoise *Gopherus agassizii*, as the ecophysiological study of Peterson (1995) shows clearly that this species depends upon its bladder to both store and reclaim water. A fascinating paper by Beuchat et al. (1986) also shows how the bladder in neonatal, but not adult, *Sceloporus jarrovi* lizards may function as an extrarenal osmoregulatory organ that can buffer water compartments against osmotic perturbation.

Recent in vitro electrophysiological studies by Badia et al. (1987) on the colon of the lizard *Gallotia galloti* from the Canary Islands have shown that this tissue exhibits the classical properties of a "leaky" epithelium – i.e. low potential difference and short-circuit current, high tissue conductance and relatively high unidirectional sodium and chloride fluxes compared with net movements (Schultz 1977). The predominant sodium transport mechanism in the colon of this lizard appears to be an electroneutral mechanism, mediated by the presence of an amiloride-sensitive, Na^+/H^+ exchange process coupled to a $\text{Cl}^-/\text{HCO}_3^-$ antiport in the apical membrane of colonocytes.

Diaz and Lorenzo (1989, 1991) have recently reported that acute or chronic administration of aldosterone brings about a substantial increase in transmural potential difference, short-circuit current and net sodium transport by the colon of this species, showing that this hormone can also act on leaky as well as tight epithelia (Grubb and Bentley 1987; Will et al. 1985). Some of the results from the later study with *G. galloti* are shown in Table 3.8.

All the effects of aldosterone on the colon were blocked by administration of amiloride, which also abolished the net flux in control tissues but did not affect the short-circuit current, confirming the electrically silent nature of sodium absorption under basal conditions. Diaz and Lorenzo (1991) point out that chronic treatment with aldosterone was necessary to achieve maximal effect

Table 3.8. Effect of acute or chronic administration of aldosterone on electrical potential difference (PD), short-circuit current (SCC) and net reabsorptive sodium transport by the colon of the lizard *Gallotia galloti*. (Modified from Diaz et al. 1991)

Treatment	PD (mV)	SCC ($\mu\text{mol cm}^{-2} \text{h}^{-1}$)	Na flux _{NET} ($\mu\text{mol cm}^{-2} \text{h}^{-1}$)
Control	1.58 ± 0.37	0.56 ± 0.14	0.79 ± 0.33
Aldosterone (100 $\mu\text{g kg}^{-1}$) acute	4.75 ± 0.63**	1.50 ± 0.12**	3.22 ± 0.21***
Aldosterone chronic	4.81 ± 1.05**	1.60 ± 0.25**	3.71 ± 0.61***

Data expressed as mean ± SE. ** $P < 0.01$, *** $P < 0.005$.

and suggest that the hormone promotes a morphological transformation or differentiation of new cells in the colonic epithelium containing amiloride-sensitive sodium channels.

These results are complemented by those of Diaz et al. (1994) with the same lizard, in which aldosterone decreased both potential difference and short circuit current of short-circuited colonic tissue in vitro and had no effect on net sodium transport, but significantly increased the rate of reabsorption of chloride ions. The residual flux, being the difference between the short-circuit current and the net sodium and chloride fluxes, was increased very significantly by aldosterone treatment, and in a dose-dependent manner. The everted colon reabsorbed fluid at a rate of 0.46 ml cm^{-2} per hour under control conditions, but this was converted to net secretion with the addition of aldosterone at a dosage of $100 \mu\text{g } 100 \text{ g}^{-1}$. These results, with the colon short-circuited, are consistent with an increase in apical permeability to sodium ions and clearly suggest that the primary action of aldosterone may be to stimulate potassium secretion.

As mentioned above, efforts to show any clear effect of AVT on rates of water reabsorption from the colon of reptiles have been unsuccessful to date, and Bentley (1962) found this hormone did not change water permeability of the colon of the tortoise *T. graeca*, nor did it have any effect on the colon of two species of *Amphibolurus* (*Ctenophorus*) lizards (Bentley and Bradshaw 1972). The placement of electrolytic lesions in the hypothalamus of *C. ornatus*, however, resulting in the loss of the ability of this lizard to respond antidiuretically to salt loads (see Fig. 3.1), also had an effect on rates of sodium and potassium reabsorption from the colon (Table 3.9).

Changes in the rate of fluid reabsorption from the colon of the tract-operated *C. ornatus* are not statistically significant, but those for both sodium and potassium are, and the effect of the lesions is thus to reduce the rate of electrolyte reclamation from the urine. This effect is exactly the reverse of the same lesions, in the same individuals, at the level of the nephron (see Table 3.2) and we may see why the hypothalamic lesions have no overall impact on salt excretion in this lizard: They increase the fractional reabsorption of sodium

Table 3.9. Estimated absolute and fractional rates of water and electrolyte reabsorption from the colon of tract-operated and intact *Ctenophorus ornatus* during chronic saline diuresis. (Modified from Bradshaw 1978b)

Group	Fluid $\text{ml kg}^{-1} \text{ h}^{-1}$	Free water $\text{ml kg}^{-1} \text{ h}^{-1}$	Sodium $\mu\text{mol kg}^{-1} \text{ h}^{-1}$	Potassium $\mu\text{mol kg}^{-1} \text{ h}^{-1}$
Intact	9.0 ± 1.2 (91.6)	4.2 ± 0.6 (93.4)	871.9 ± 33.4 (88.8)	62.9 ± 13.3 (68.3)
Tract-operated	13.1 ± 1.3 (78.2)	9.4 ± 2.7 (87.4)	969.3 ± 59.3 (73.2)*	$20.3 \pm 4.3^{***}$ (33.7)**

Data presented as mean \pm SE. Fractional rates of reabsorption are expressed as percentages and given in parentheses. * $P < 0.05$, ** $P < 0.02$, *** $P = 0.001$ when compared with corresponding value for intact animals.

ions by the kidney, but decrease their rate of reabsorption in the colon. The two effects thus cancel one another, and the lesions have no net effect on rates of sodium excretion.

Changes such as these after lesioning the hypothalamic region are very suggestive of the operation of hormones, but it is difficult to identify what they may be at this stage. The effects on sodium reabsorption are inconsistent with the known actions of AVT which, if anything, is natriferic at the level of the nephron and its loss from the circulation should logically lead to decreased rates of fractional reabsorption of sodium. Equally, the data do not clearly implicate adrenal steroids such as aldosterone, as the effects on the kidney tubule and the colon are opposite, and one would expect aldosterone to increase rates of sodium reabsorption at both sites.

Aldosterone is known to stimulate solute reabsorption from the colon and coprodaeum of domestic fowl (Thomas and Skadhauge 1979; Thomas et al. 1979) and from the human large intestine (Edmonds and Pilcher 1969), and a similar basic effect of this hormone on the colon of the reptile would not be surprising, as suggested by the work of Diaz and Lorenzo (1991). AVT receptors need to be looked for in the colon and cloaca of reptiles and it would be premature to conclude at this juncture that the reabsorptive activity of such postrenal sites in reptiles is not influenced by pituitary and adrenal hormones (Skadhauge 1978b and see Lorenzo et al. 1990 for an effect of vasopressin on lizard colon).

3.4

Cephalic Salt-Secreting Glands

Marine birds and a number of reptiles are unique amongst vertebrates in possessing specialised cephalic glands capable of secreting strongly hyperosmotic salt solutions which are voided to the exterior, thereby facilitating osmoregulation of the animal. Nasal salt-secreting glands were first discovered in marine birds and shown also to occur in marine reptiles soon thereafter (Schmidt-Nielsen and Fänge 1958). There now exists an extensive literature on their comparative anatomy and physiology, although still almost nothing is known of the basic mechanism by which they elaborate an hyperosmotic fluid (for reviews see Bradshaw 1985, 1986a; Dantzler and Holmes 1974; Dunson 1969a, 1976, 1979; Peaker and Linzell 1975; Templeton 1972).

The salt gland in birds is located supra-orbitally and develops embryologically from the nasal gland (Schmidt-Nielsen and Fänge 1958). In reptiles, selection for the development of a functional salt gland appears to have been intense, because glands of varying embryological origin have been pressed into service in different taxonomic groups. In chelonians, the gland is a modified lachrymal gland (Cowan 1974, 1985); in lizards it is invariably the external nasal gland (Gabe and Saint Girons 1976), whereas in sea snakes (Hydrophiidae) and marine file snakes (Achrochordidae), the salt gland is located sublingually (Dunson and Dunson 1973; Dunson and Taub 1967).

Dunson and Dunson (1979) identified a small premaxillary gland as a salt gland in the marine homalopsid snake *Cerberus rhynchops*, and an unusual lateral nasal gland has also been described in the Montpellier snake *Malpolon monspessulanus* (Dunson et al. 1978).

Crocodylians were thought for many years to be the only reptilian group to lack salt-secreting glands (Dunson 1969), but their unexpected discovery in the tongue of *Crocodylus porosus*, by Taplin and Grigg (1981), has completed the picture of a group lacking a renal-concentrating mechanism but nonetheless one in which many species possess a powerful extrarenal mechanism for the elimination of salt.

Basically, reptilian salt glands differ from the analogous salt glands of marine birds in three fundamental ways: (1) embryologically, their origins are far more diverse, as shown above; (2) structurally, the basement membrane of the principal cells is never infolded and (3) functionally, they display a much greater versatility in their pattern of electrolyte secretion. From what little one may glean of their mechanism of action and control, there would also appear to be some important differences between the salt glands of birds and reptiles.

In marine birds the enzyme Na^+/K^+ -ATPase is localised both in the extensively folded and interdigitated lateral and basal membranes of the principal cells (Ernst 1972), whereas it occurs only in the lateral cell membranes of reptiles (Ellis and Goertemiller 1974) and the basal membrane is quite flat, despite some erroneous claims to the contrary (Crowe et al. 1970).

The ultrastructure of a "typical" external nasal salt gland of a lizard (*V. gouldii*) is shown in Plate 3.1 (Saint Girons et al. 1981) and compared in Plate 3.2 with that of the scincid lizard *T. rugosa* (Saint Girons et al. 1977), in which the gland is composed half of principal cells and half of mucus-secreting cells.

Broad comparative data on reptilian salt glands are brought together in Table 3.10, classified according to embryological origin, diet and habitat, and the electrolyte composition of the secretion. An inspection of the data in this table reveals a close correlation between the habitat and the diet of each reptile, and the electrolytic composition of the nasal gland secretion. All the aquatic Chelonia are primarily sodium secretors ($\text{K}^+/\text{Na}^+ < 1.0$), regardless of diet, and I would predict that the secretion of the terrestrial *Geochelone*, when its composition is described completely, will be low in sodium because of its herbivorous diet.

With lizards, we see the complete spectrum from almost pure sodium secretors, such as the marine iguana *Amblyrhynchus*, to pure potassium secretors ($\text{K}^+/\text{Na}^+ > 1.0$), such as the large North African agamid *Uromastix*. All the terrestrial herbivores (with the exception of *Conolophus*) are essentially potassium secretors, with some, such as *Uromastix* and *Sauromalus*, being unable to reduce the K^+/Na^+ ratio of the secretion below 1.0, even with chronic sodium chloride loading (Bradshaw et al. 1984a). The one varanid from which the nasal secretion has been collected (*Varanus semiramax*) is a littoral species, feeding on mangrove crabs (Dunson 1974), and it is an almost pure sodium secretor.

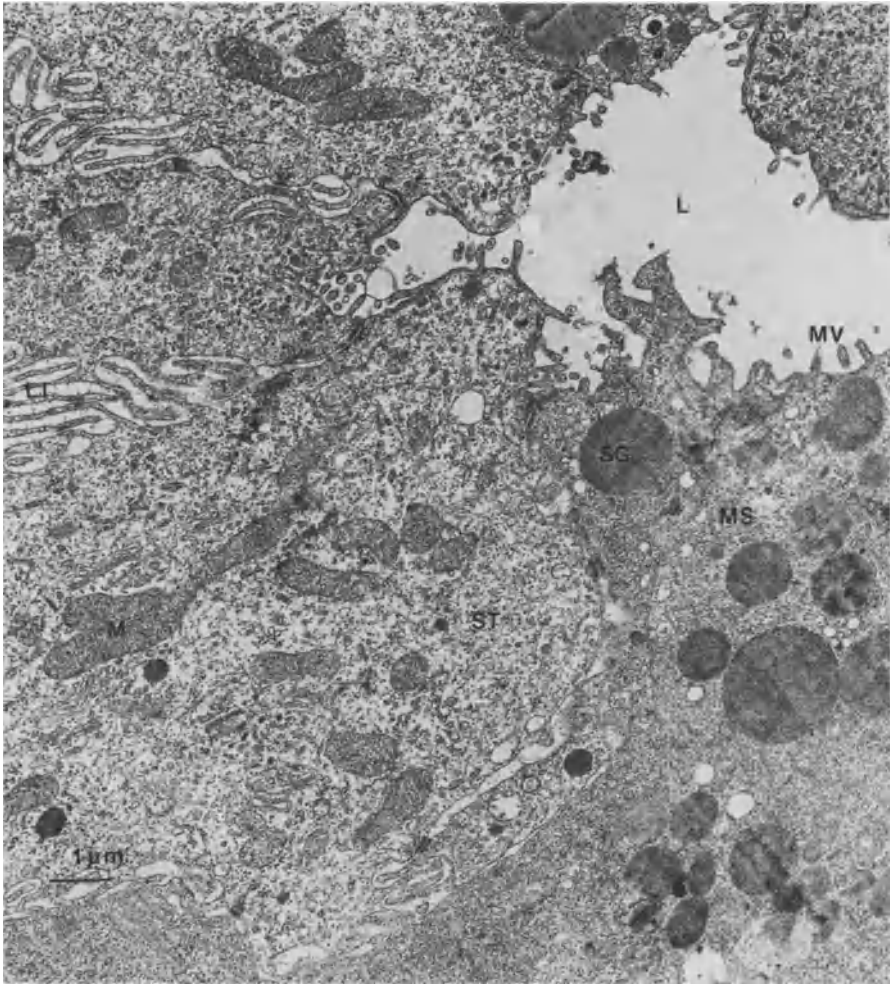


Plate 3.1. Electron microscope transverse section of a secretory tubule of the external nasal gland of the varanid lizard *Varanus gouldii* showing the extensive development and folding of the lateral cell membranes. Apical segments of both striated segments (cellules striées) (ST) and muco-serous cells (MS) are indicated. L Lumen; LI lateral interdigitations; M mitochondria; MV microvilli; SG secretory granules. (Adapted from Saint Girons et al. 1981)

All of the marine snakes are virtually pure sodium secretors, as would be expected from their habitat and carnivorous diet, based on fish, and the same is also true for the crocodiles. Where the glands exist in reptiles, their function thus appears to co-vary strongly with the osmoregulatory constraints characteristic of the habitat of each species and this suggests their evolution through the agency of natural selection. Perhaps the most puzzling thing about these glands is why they are not even more widespread amongst reptiles,

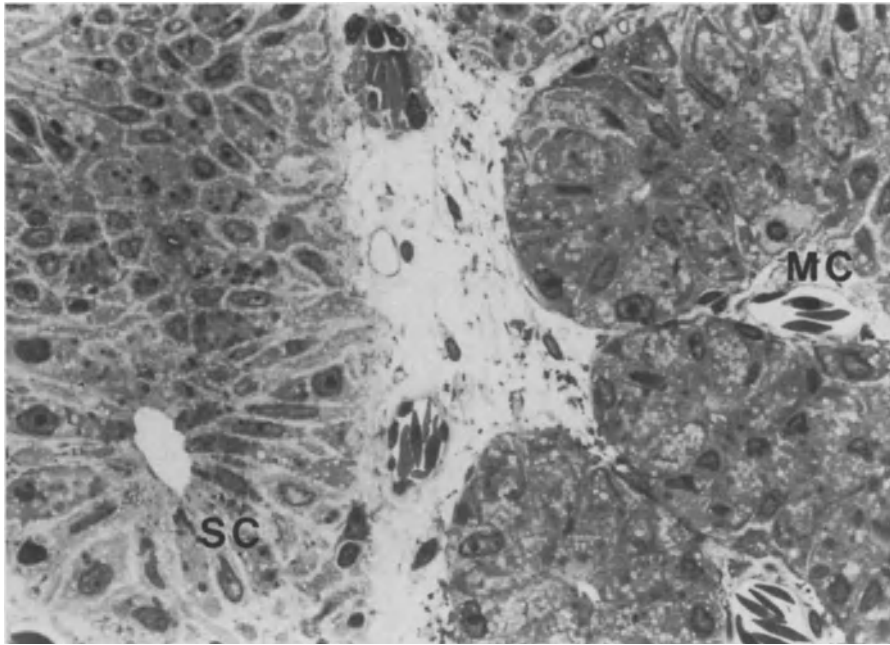


Plate 3.2. Light microscope section of the external nasal gland of the scincid lizard *Tiliqua rugosa* showing how the gland is composed roughly equally of both classic muco-serous secretory cells (MC) and mitochondria-rich striated segments (cellules striées) (SC) normally associated with salt transport. (Adapted from Saint Girons et al. 1977)

particularly in species such as *C. ornatus* that manifestly have need of them. Minnich (1979) gives a table of reptiles that have been shown to lack functional salt glands.

Very little is known of the control, hormonal or otherwise, of reptilian salt glands (Sandor and Mehdi 1980), although the fact that some respond to injections of parasympathomimetic drugs such as mecholyl (methacholine) and are inhibited by atropine (Dunson 1970; Norris and Dawson 1964; Schmidt-Nielsen and Fänge 1958) suggests that nervous innervation may be of importance, as in birds (Norris and Dawson 1964; Peaker and Linzell 1975). In lizards the cholinergic nerve which initiates salt secretion appears to be the lateral ethmoidal nerve, the fibres of which form plexuses around the tubules in the salt gland (Oelrich 1956; Templeton 1972) but do not penetrate the tubules in either turtles or lizards (Abel and Ellis 1966; Barnitt 1972).

A major difference between the salt glands of birds and reptiles could reside in their response to increasing osmotic pressure of the plasma. In birds, increasing plasma osmolality triggers glandular secretion; thus, sucrose and mannitol are as effective as salt solutions in triggering the gland to secrete (Peakier and Linzell 1975). Shoemaker et al. (1972) found, however, that osmotic stimuli were not sufficient to stimulate the nasal salt gland of the iguanid

Table 3.10. Comparative data on cephalic salt-secreting glands in reptiles, ranked according to the measured K^+/Na^+ ratio of the secretion

Taxon	Embryological origin	Genus	Habitat ^a and diet ^b	Electrolyte concentration (mmol l ⁻¹)		
				Na ⁺	K ⁺	K ⁺ /Na ⁺
Chelonia	Lachrymal					
Cheloniidae		<i>Caretta</i> ¹	M, C	732–878	18–31	0.03
		<i>Chelonia</i> ²	M, H	685	21	0.03
		<i>Lepidochelys</i> ³	M, C	713	29	0.04
Emyridae		<i>Malaclemys</i> ⁴	F, E, C	682	32	0.05
Testudinae		<i>Geochelone</i> ⁵	T, H	?	233–260	?
Lacertilia	External nasal					
Iguanidae		<i>Amblyrhynchus</i> ⁶	M, H	1434	235	0.16
		<i>Conolophus</i> ³	T, H	692	214	0.31
		<i>Iguana</i> ⁷	T, H	232–728	290–616	2.7–0.4
		<i>Ctenosaura</i> ⁸	T, H	67–475	220–537	8.0–0.5
		<i>Dipsosaurus</i> ^{7,9}	T, H	494–1032	640–1387	2.8–0.3
		<i>Sauromalus</i> ^{8,10}	T, H	82–150	378–1102	7.4–3.1
Varanidae		<i>Varanus</i> ¹¹	T, C	654	54	0.08
Scincidae		<i>Tiliqua</i> ¹²	T, O	167–434	226–433	2.6–0.5
Agamidae		<i>Uromastix</i> ^{7,13}	T, H	639	1398	87–2.2
Ophidia						
Hydrophiidae	Posterior lingual	<i>Lapemis</i> ¹⁴	M, C	676	23	0.03
		<i>Aipysurus</i> ¹⁴	M, C	798	28	0.04
		<i>Hydrophis</i> ¹⁴	M, C	509	20	0.04
		<i>Pelamis</i> ¹⁵	M, C	620	28	0.05
		<i>Laticauda</i> ¹⁶	M, C	686	57	0.08
Achrochordidae		<i>Achrochordis</i> ¹⁷	M, C	483	15	0.03
Homalopsidae	Premaxillary	<i>Cerberus</i> ¹⁸	M, C	414	55	0.13
Crocodylia	Lingual	<i>Crocodylus</i> spp. ¹⁹	E, F, C	386–740	10–16	0.03
		<i>Osteolaemus</i> ¹⁹	F, C	545	15	0.03

¹Schmidt-Nielsen and Fänge (1958); ²Holmes and McBean (1964); ³Dunson (1969a); ⁴Dunson (1970); ⁵Peaker (1978); ⁶Dunson (1969b); ⁷Schmidt-Nielsen et al. (1963); ⁸Templeton (1964); ⁹Shoemaker et al. (1972); ¹⁰Nagy (1972); ¹¹Dunson (1974); ¹²Bradshaw et al. (1984); ¹³Bradshaw et al. (1984); ¹⁴Dunson and Dunson (1974); ¹⁵Dunson (1968); ¹⁶Dunson and Taub (1967); ¹⁷Dunson and Dunson (1973); ¹⁸Dunson and Dunson (1979); ¹⁹Taplin (1988).

^aHabitat: M = marine, E = estuarine, F = freshwater, T = terrestrial.

^bDiet: C = carnivore, O = omnivore, H = herbivore.

lizard *D. dorsalis* and speculated that actual ionic concentrations of alkali metals must increase before the gland will respond. The nasal salt gland of *D. dorsalis* is also quite remarkable in also being able to respond to salt loading with potassium acetate, succinate and bicarbonate as well as rubidium chloride (RbCl).

The sensitivity of reptilian salt glands to adrenocortical hormones such as corticosterone was first noted by Holmes and McBean (1964) and aldosterone was reported to inhibit sodium loss from the nasal salt gland of the adrenalectomised iguanid lizard *D. dorsalis* by Templeton et al. (1968) in a short abstract. Bilateral adrenalectomy in this species was followed by a marked increase in the rate of excretion of sodium ions from the nasal gland

and injections of aldosterone were able to correct this loss, the full details being reported in Templeton et al. (1972a,b).

The response of the nasal gland of intact specimens of this same species to injections of a variety of adrenal steroids was investigated by Shoemaker et al. (1972), who maintained the lizards in small metabolism cages, in a dry atmosphere, and collected the nasal salt formed daily. This species normally responds within 24 h to salt loading by excreting a concentrated salt solution composed of a mixture of both NaCl and KCl, regardless of the nature of the salt injected, as shown in Fig. 3.17.

The "fidelity" of the salt secretion (i.e. its resemblance to the salt injected) improves with repetitive injections, however, and the K^+/Na^+ ratio may vary from about 3.0 to 0.3. Daily intraperitoneal injections of 15 μ g of aldosterone had the effect of virtually abolishing sodium excretion by the gland whilst leaving that of potassium intact (see Fig. 3.17b) suggesting that this hormone may have the same basic effect as already seen with the kidney and colon, i.e. natriferic and kaliuretic. The effects of other hormones such as corticosterone, cortisol, ACTH and the synthetic steroid dexamethasone on the nasal secretions of *D. dorsalis* were all similar to that of aldosterone, although only dexamethasone was as potent.

The large north-African agamid lizard *Uromastix acanthinurus*, known as the Fouette-Queue or Dob, possesses a well-developed nasal salt gland that was described by Grenot (1968) and has since been studied extensively, both anatomically and physiologically, by Lemire et al. (1970, 1972, 1980) and by Lemire (1983) and Lemire and Vernet (1982). Studies on the hormonal control of this nasal gland were reported by Bradshaw et al. (1984a), who measured circulating levels of aldosterone and corticosterone in salt-injected animals and assessed the effects of exogenous injections of aldosterone and dexamethasone.

The response of this gland to two injections of 1 mmol KCl, spaced several days apart, is shown in Fig. 3.18 and, as may be seen, the gland differs from that of *D. dorsalis* in secreting an almost pure solution of KCl. Injections of 1 mmol NaCl, rather than KCl, have a small stimulatory effect on the rate of salt excretion by the nasal gland of *U. acanthinurus*, and the K^+/Na^+ of the secretion falls from over 80 to 2.5, but still remains more KCl than NaCl, as seen in Fig. 3.19. The gland is thus incapable of elaborating a pure NaCl solution and is clearly adapted for the unique elimination of KCl. Plasma levels of corticosterone were essentially unchanged following injections of either NaCl or KCl (see Bradshaw et al. (1984a) but those of aldosterone changed significantly, increasing with KCl, and decreasing with NaCl, as seen in Fig. 3.20. The statistical significance of changes in circulating levels of aldosterone in *U. acanthinurus* with salt loading (either KCl or NaCl) is shown in Fig. 3.20 with $*P < 0.05$ and $**P < 0.01$.

These data suggest an active role for aldosterone in modulating both the rate and the nature of the secretion from the salt gland through a primary action on the secretion of potassium ions and an associated inhibition of

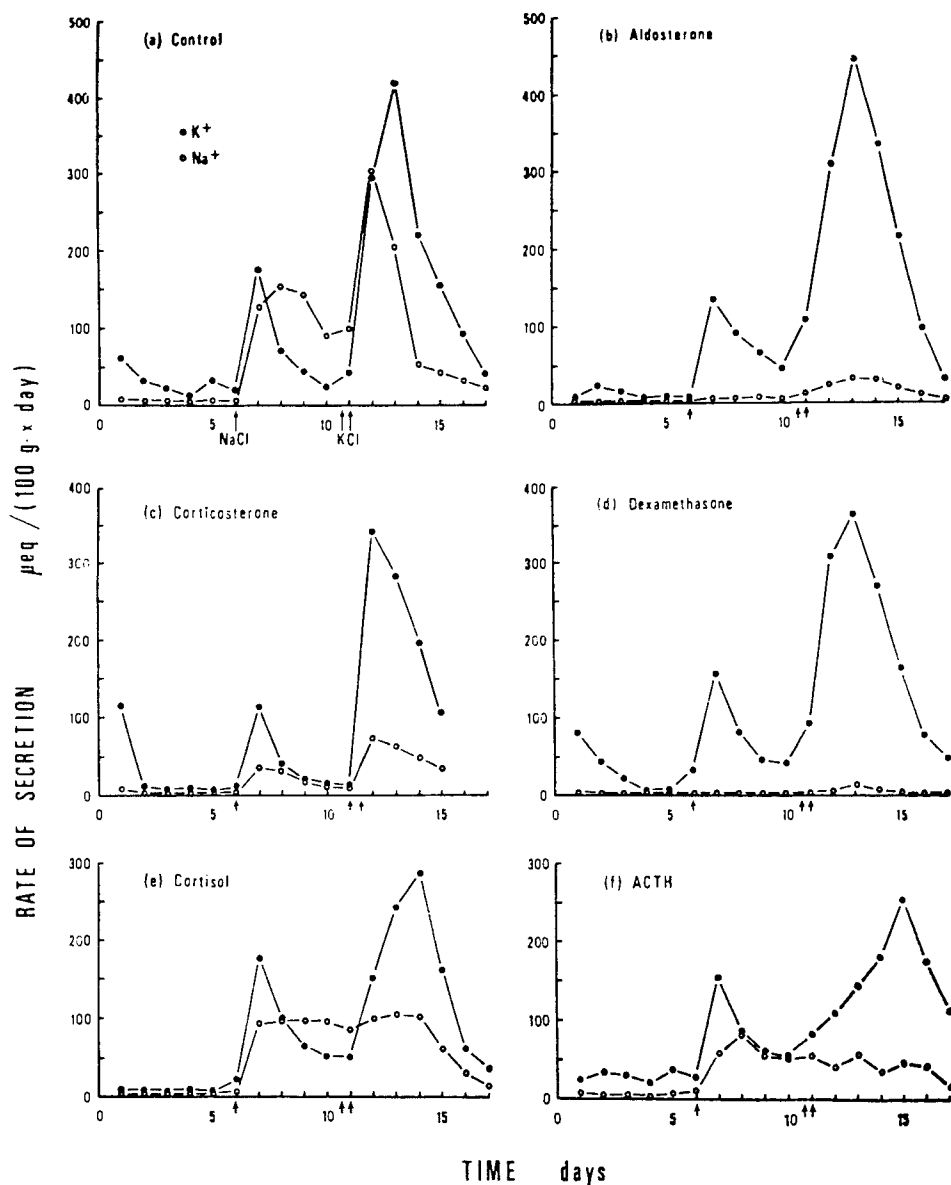


Fig. 3.17a-f. Rates of secretion of potassium (closed circles) and sodium (open circles) from the nasal salt gland of the desert iguanid lizard *Dipsosaurus dorsalis*. Intraperitoneal injections of 2 mmol NaCl and KCl per 100g were given on days 6 and 11 respectively and the lizards received daily injections of vehicle (a) or various hormones (b-f) commencing on day 0. Points represent the amount of salt collected over the previous 24 h. (Modified after Shoemaker et al. 1972; Bradshaw 1986a)

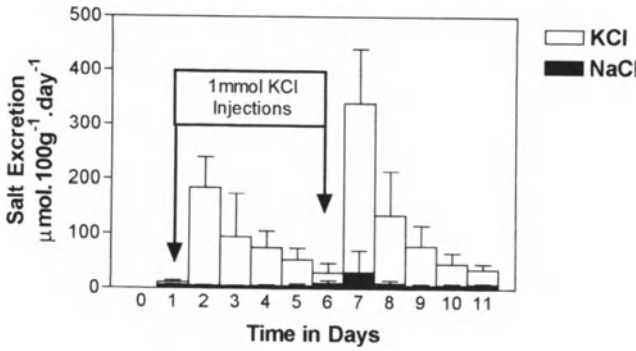


Fig. 3.18. Daily salt excretion by the nasal salt gland of the agamid herbivorous lizard *Uromastix acanthinurus* following two intraperitoneal injections of 1 mmol KCl on days 1 and 6 of an 11-day experiment. (Adapted from Bradshaw et al. 1984a)

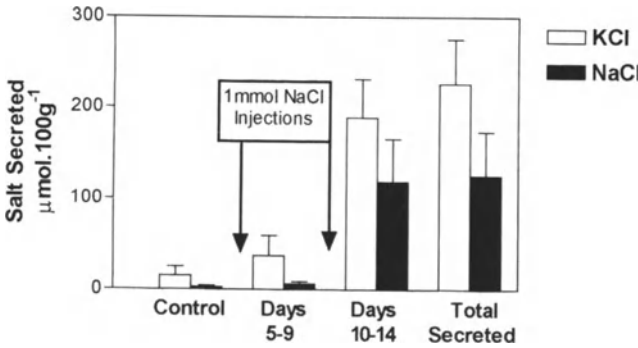


Fig. 3.19. Excretion of KCl and NaCl by the nasal salt gland of the agamid lizard *Uromastix acanthinurus* following two intraperitoneal injections of 1 mmol NaCl spaced a few days apart. (Adapted from Bradshaw et al. 1984a)

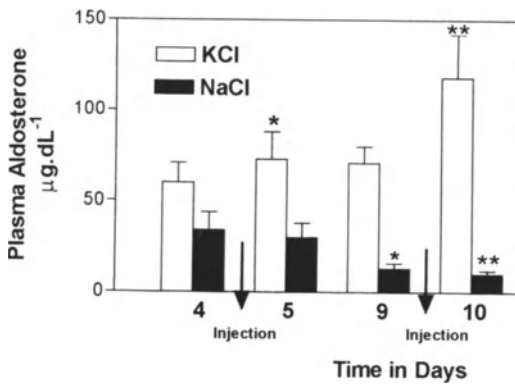


Fig. 3.20. Changes in mean plasma levels of aldosterone in the agamid lizard *Uromastix acanthinurus* following two intraperitoneal injections of either KCl or NaCl spaced a few days apart. * $P < 0.05$; ** $P < 0.01$. (Adapted from Bradshaw et al. 1984a)

sodium secretion. Experimental data to support this contention are few, but Bradshaw et al. (1984a) regressed plasma aldosterone concentrations against the total amounts of both potassium and sodium ions excreted with chronic salt loading and obtained the suggestive relationships shown in Fig. 3.21.

A very significant positive correlation is evident between the mean plasma aldosterone concentration over the time-course of the experiment, and the total amount of potassium ions excreted, with $y = 9.19x + 34.7$ ($r^2 = 0.79$, $P < 0.001$) where y is the total $\mu\text{mol } 100\text{g}^{-1}$ of KCl excreted and x is the mean aldosterone concentration in ng dL^{-1} . The correlation with NaCl excretion, however, is negative, and the slope is not significantly different from zero ($r^2 = 0.34$, $P = 0.09$).

These data on changes in aldosterone levels in the plasma provide a clue as to why none of the hormone treatments used by Shoemaker et al. (1972) actually stimulated salt secretion by the nasal gland of *D. dorsalis*. Injections of KCl lead, within a few days, to maximal plasma concentrations of aldosterone in *U. acanthinurus* and, if this hormone is indeed controlling the secretory activity of the gland, injections of exogenous aldosterone are unlikely to have any further effect on a gland already secreting to capacity. The only effect likely to be observed is an inhibitory one on sodium excretion, and this is exactly what is seen with both *D. dorsalis* and *U. acanthinurus*. Dexamethasone, again, was as potent as aldosterone in inhibiting sodium excretion in *U. acanthinurus*, and spironolactone, which acts as an aldosterone antagonist in mammals (Parvez et al. 1979), was without effect (Bradshaw et al. 1984a).

Mention was made in Section 2.3.4 of the difficulty sometimes experienced in deciding, on histological criteria alone, whether a particular nasal gland is capable of elaborating an hyperosmotic salt solution, and the large Australian skink *T. rugosa*, whose unusual external nasal gland is shown in Plate 3.2, was a case in point. Bradshaw et al. (1984b) cannulated the duct from the gland and, as seen in Table 3.11, injections of both NaCl and KCl provoke

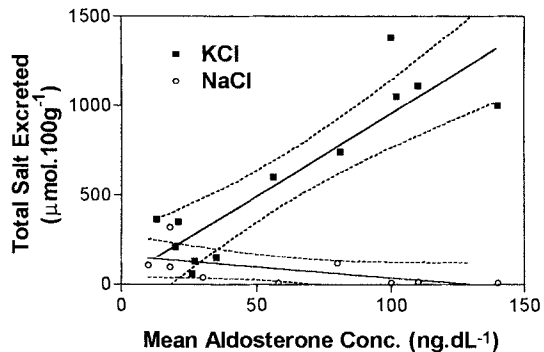


Fig. 3.21. Correlation between total salt excreted (potassium plus sodium) by the nasal salt gland of the agamid lizard *Uromastix acanthinurus* and the mean circulating plasma level of the hormone aldosterone following salt loading with either KCL or NaCl. (Modified after Bradshaw et al. 1984a)

Table 3.11. Nasal gland secretions of *Tiliqua rugosa* with two salt-loading régimes. (From Bradshaw et al. 1984)

Régime	Rate of secretion ($\mu\text{l } 100 \text{ g h}^{-1}$)	Concentration (mmol l^{-1})			Osmolality (mOsm kg^{-1})	F/P _{OSM}	Rate ($\mu\text{mol } 100 \text{ g h}^{-1}$)	
		Na ⁺	K ⁺	K ⁺ /Na ⁺			Na ⁺	K ⁺
NaCl	13.3 \pm 3.3	434 \pm 15	226 \pm 21	0.52 \pm 0.16	1025 \pm 34	3.6 \pm 0.1	5.9 \pm 1.5	3.0 \pm 0.7
	NS	$P < 0.05$	$P < 0.05$	$P < 0.05$	NS	NS	NS	$P < 0.05$
KCl	19.5 \pm 1.3	167 \pm 26	433 \pm 71	2.6 \pm 0.1	1124 \pm 112	3.6 \pm 0.4	3.3 \pm 0.7	8.3 \pm 0.8

the secretion of a fluid with a fluid to plasma osmolar ratio (F/P_{OSM}) of about 3.5.

Rates of electrolyte excretion by the nasal gland of *T. rugosa* are actually quite high when compared with those of other terrestrial lizards (see Table XXI in Minnich 1979) and the gland is capable of significantly modifying the electrolytic composition of its secretion when the animal is injected with either NaCl or KCl. Rates of secretion of K⁺ with KCl loading are significantly greater than those of Na⁺ with NaCl loading, however, indicating that the gland is more efficient at excreting potassium ions, as would be anticipated from its omnivorous diet.

The hormonal control of this salt gland may differ from that of *D. dorsalis* and *U. acanthinurus* (and probably also that of *V. gouldii*), as Bradshaw et al. (1984b) found that plasma aldosterone levels in *T. rugosa* showed little significant variation with change in plasma sodium concentration, as shown in Fig. 3.22.

Plasma aldosterone levels fall very significantly in *U. acanthinurus* with increasing plasma sodium concentrations ($y = -1.84x + 308.4$, $r^2 = 0.61$, $P = 0.001$) but the relationship is much flatter with *T. rugosa*, although the regression is still just statistically significant ($y = -0.34x + 58.2$, $r^2 = 0.40$, $P = 0.001$). From this one might predict that aldosterone is much less likely to be a hormone controlling the secretory activity of the nasal salt gland in *T. rugosa*, in contrast to what one might expect with *U. acanthinurus*.

Bradshaw et al. (1984b) approached this question by searching for high-affinity binding of adrenal steroids in cytosolic preparations from the nasal gland of *T. rugosa* and receptors for both corticosterone and aldosterone were detected, as shown in the Scatchard plot (Scatchard 1949) reproduced in Fig. 3.23. As may be seen, the cytosolic receptors from the nasal gland display a significantly higher binding affinity for corticosterone than for aldosterone ($K_d = 5.2 \times 10^{-9} \text{ M}$ versus $12.9 \times 10^{-9} \text{ M}$) and also a higher receptor concentration in the cytosol (0.147 versus 0.039 pmol mg⁻¹ protein). These data would thus suggest that, if the secretory activity of the nasal salt gland of *T. rugosa* is controlled by a steroid hormone, then this is more likely to be corticosterone than aldosterone. Plasma levels of corticosterone have also been shown to increase significantly with sodium loading by Bradshaw et al. (1984b) in this species.

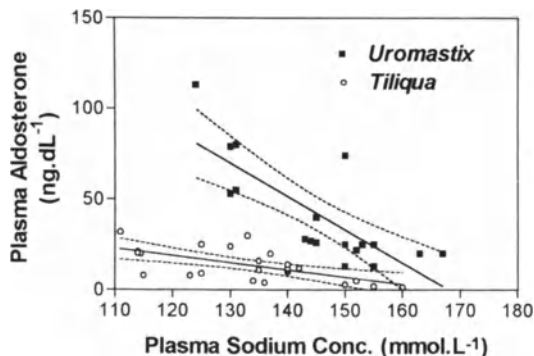


Fig. 3.22. Variation in plasma aldosterone levels with change in plasma sodium concentration in the Saharan agamid lizard *Uromastix acanthinurus* and the Australian skink *Tiliqua rugosa*. (Adapted from Bradshaw and Grenot 1976; Bradshaw et al. 1984b)

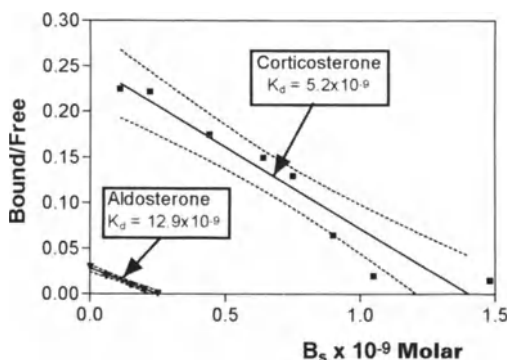


Fig. 3.23. Scatchard plot of high affinity binding of both aldosterone and corticosterone to cytosol prepared from the nasal salt gland of the skink *Tiliqua rugosa*. (Adapted from Bradshaw et al. 1984b)

Another unusual feature to emerge from the receptor study of the nasal gland of *T. rugosa* is that there appears to be significant seasonal variation in the level of high-affinity binding of corticosterone, which reaches a maximum during the short spring breeding season of this species from late September till mid-November. Levels of both nonspecific and specific binding of corticosterone to cytosolic receptors throughout a 12-month period are shown in Fig. 3.24. These data suggest that the gland may well have a dual function, as suggested indeed by its unusual histology.

If corticosterone does function to stimulate salt secretion from the principal cells, then the steroid-binding data show that this could only occur effectively during the breeding season. During other periods of the year the gland may well cease to elaborate an hyperosmotic fluid and operate as a simple mucus-secreting gland in the nasal cavity, and laboratory experiments would suggest that this change in function may be associated with alterations in the diet. Salt-

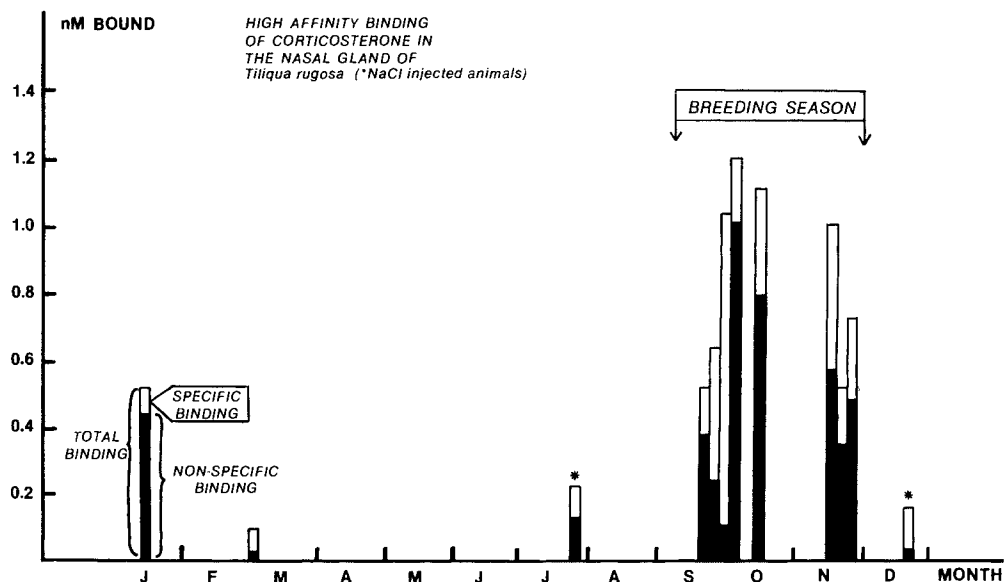


Fig. 3.24. Seasonal variation in high-affinity binding of corticosterone by cytosol extracted from the external nasal gland of the scincid lizard *Tiliqua rugosa*. The breeding season for this species, which appears to coincide with maximum binding (both specific and nonspecific) is indicated. (Adapted from Bradshaw et al. 1984b; Bradshaw 1986a)

loading, either with NaCl or KCl, is sufficient to activate the secretory activity of the gland and it would be of great interest to know whether the salt intake of *T. rugosa* increases significantly throughout the spring breeding period.

To date there have been no studies published of the underlying secretory mechanism in reptilian salt glands but, by analogy, this is generally assumed to be similar to that of the avian salt gland (Holmes and Phillips 1985; Nicholson and Lutz 1989). In spite of a considerable number of investigations (see Peaker and Linzell 1975; van Lennep and Komnick 1970; van Lennep and Young 1979) the manner in which an hyperosmotic solution is elaborated is poorly understood and there are currently three theories en vogue:

1. Active transport of Na^+ across the apical membrane of the principal cells of the tubule with transcellular water flow (Peaker 1971)
2. Active transport of sodium into the intercellular spaces of the principal cells and the resulting paracellular flow of an hyperosmotic fluid into the lumen (Ernst and Mills 1977; Lowy et al. 1989)
3. Isosmotic fluid secretion by the peripheral cells at the blind end of the tubule and reabsorption of water by the principal cells to produce an hyperosmotic secretion (Ellis et al. 1977)

All these theories have suffered from a dearth of information concerning actual intracellular and luminal concentrations of ions (see Peaker 1971). An innovative approach to this problem was taken by Marshall et al. (1985), who

used a windowless, energy dispersive X-ray detector, attached to a scanning electron microscope, to estimate intracellular concentrations in freeze-fractured specimens (Marshall 1984). Much to everyone's surprise this study with ducklings has shown that the fluid in all sections of the secretory tubules is isosmotic and only becomes hyperosmotic in the collecting duct system running from the gland to the external nares, as shown in Fig. 3.25.

As usual, antecedents can be found for almost any discovery in science and, long before it was appreciated that avian nasal glands were salt-secreting organs, Marples (1932) had described the presence of columnar cells in the collecting ducts of birds with functional glands, compared with only squamous cells in those without. Both Kirschner (1977) and van Lennep and Young (1979) also speculated on the possible role of the collecting ducts in the bird salt gland, drawing attention to the pivotal part played by the collecting ducts in the mammalian kidney in reabsorbing water from the urine. Marshall et al. (1985) note that the area occupied by the collecting-duct system in the salt gland of the duckling is large and that the ducts are well vascularised.

These results are at variance with all three theories outlined above accounting for an hyperosmotic secretion by the gland and do not support the contention of Hanwell et al. (1971), that the mitochondria-rich principal cells secrete an hyperosmotic fluid. They are, however, consistent with current theories of ductal modification of a primary secretion, as found in the kidney and in a number of other exocrine secretory systems (Thaysen 1979). Marshall et al. (1985) speculate that active chloride transport may be the driving force for the secretion, coupled with a high requirement for inwards pumping of K^+ ions which are completely extracted from the blood. Sodium ions may then follow a paracellular route, as suggested by Ernst and Mills (1977) and by Greger and Schlatter (1984) for the shark rectal salt gland.

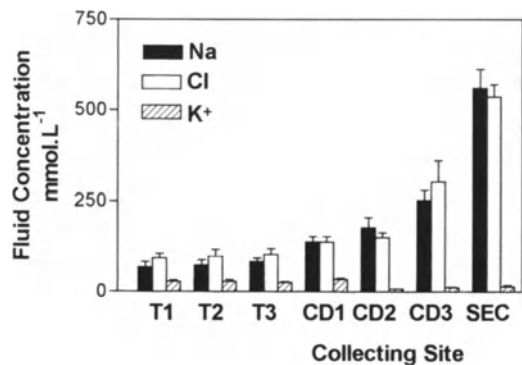


Fig. 3.25. Concentrations of sodium, potassium and chloride in various tubular segments of the nasal salt gland of the duck, measured by windowless, energy dispersive, X-ray detector. *T1* Blind end of secretory tubule; *T2* at level of principal cells; *T3* open end of tubule; *CD1* central canal; *CD2* secondary collecting duct; *CD3* main collecting duct; *SEC* secretion. (Adapted from Marshall et al. 1985)

A promising recent innovation was reported by Shuttleworth et al. (1987), who developed a technique for perfusing the isolated head of the desert lizard *Sauromalus obesus* and measuring potassium secretion rates by the nasal salt gland. Rates of potassium secretion at $50 \mu\text{mol } 100 \text{ g}^{-1} \text{ h}^{-1}$ are amongst the highest reported for any vertebrate salt gland and the study demonstrated that the salt gland of this species has the remarkable capacity to clear the entire potassium content of the blood every hour.

Clearly, the application of X-ray microanalysis techniques to the bird nasal gland has had a major impact on thinking about the underlying mechanism of action of the gland and it is to be hoped that this method will soon be applied to reptilian nasal glands. The fact that the collecting-duct system has come to occupy such a prominent position in the bird salt gland as a possible site for water reabsorption is also very suggestive of hormonal interactions. The discovery of receptors for arginine vasotocin in the collecting duct of the kidney of the reptile, described above, suggests that this hormone could also be implicated in the control of secretion by the nasal salt gland.

3.5

Conclusion

The growth in our understanding of the physiological activity and hormonal control of excretory organs in reptiles has been nothing short of impressive over the last three decades, especially when one realises that in the late 1960s it was considered debatable whether reptiles even possessed homeostatic osmoregulatory capacities. The information reviewed in this chapter makes it clear that, in common with other vertebrates, reptiles actively regulate the milieu intérieur through the agency of familiar pituitary and adrenal hormones that act both at the level of the kidney and at a variety of post- and extrarenal sites of water and electrolyte exchange.

Kidney function is the area that has been most studied in reptiles and there are a number of generalities that can be made based on the existing database:

1. The rate at which blood is filtered by the kidneys (GFR) varies markedly with the hydration state of the animal and all species evidence the ability to reduce the GFR, and hence provoke an antidiuresis, when deprived of adequate supplies of water. This response appears to be mediated by the neurohypophysial peptide hormone AVT acting on the glomerular vasculature to reduce blood flow and hence the rate of ultrafiltration of the plasma. This response is also evident to some extent in the only surviving member of the Order Rhynchocephalia, the New Zealand tuatara *Sphenodon punctata*, and thus must represent a plesiomorphic reptilian character.
2. In some, but not all species, AVT has an additional effect on the urinary tubule of the kidney, enhancing both solute and water reabsorption. Recent work has localised receptors for AVT to the thin-intermediate segment of

- the nephron (which may be the homologue of the TAL of the loop of Henle in mammals) as well as to the entire collecting-duct system.
3. The response to an excess of solute in the body varies markedly between the different reptilian groups. In most snakes, salt loading appears to provoke an increase in the GFR, whereas it has either the opposite or no effect on the GFR in lizards. Salt loading is thus associated with a saline diuresis in snakes, rather than an antidiuresis as in lizards, and this would appear to reflect the lower priority placed on water conservation by snakes than by terrestrial lizards.
 4. Where the GFR in lizards does not change with salt loading, excess solutes are eliminated via homeostatic changes in the renal handling of sodium ions, which appear to be mediated via the adrenal steroid hormone aldosterone. This appears to act on the kidney tubules exactly as a classic mineralocorticoid in mammals, being both natriferic (i.e. sodium-saving) and kaliuretic (i.e. potassium-excreting).
 5. It would be premature to conclude, however, that a single mechanism is common to all species. The adrenal response to salt loading is not identical in all species, and hormonal changes in those lizards that have been studied to date are summarised in Table 3.12.
 6. Corticosterone may thus be natriuretic in some species (e.g. *C. ornatus* and *D. dorsalis*), as suggested by their physiological responses, and natriferic in others, such as *V. gouldii*.
 7. Some progress has been made in our understanding of the functioning of post- and extrarenal sites of water and electrolyte exchange, such as the bladder, the cloacal-colonic complex, and the various cephalic salt-secreting glands found in reptiles. Postrenal modification of both the volume and composition of the urine flowing from the kidneys is obligatory in all reptiles if they are to survive, and these unique structures both extend and complete the osmotic work of the kidney.
 8. At this stage, there is no overwhelming evidence implicating pituitary and adrenal hormones in the control of rates of water and electrolyte reabsorption from the cloaca and colon, although this has always been suspected, and there are data in the literature suggestive of a role for both

Table 3.12. Adrenal response to salt loading in lizards

Species	Response to salt loading	
	Aldosterone	Corticosterone
<i>Varanus gouldii</i>	Decrease	Increase
<i>Uromastix acanthinurus</i>	Decrease	No change
<i>Ctenophorus ornatus</i>	?	Increase
<i>Dipsosaurus dorsalis</i>	?	Increase
<i>Tiliqua rugosa</i>	No change	Increase

AVT and aldosterone. Further work to identify the presence or absence of hormonal receptors in these tissues is needed to clarify this question.

9. There is good evidence, however, that the nasal salt glands are target organs for steroid hormones, and both aldosterone and corticosterone have been implicated in different species, with cytosolic receptors for the latter being described in the skink *T. rugosa*. Nothing is known of the mechanism, or mechanisms, by which these embryologically diverse glands elaborate an hyperosmotic salt solution, however, and it is to be hoped that X-ray micro-beam analysis techniques, which have proved so fruitful in the case of the avian nasal gland, will soon be applied to those of reptiles.

Thermal Homeostasis

4.1

Generalities

It is now well appreciated that, with one or two notable exceptions (e.g. Hutchinson et al. 1966), reptiles do not possess the physiological capacities needed to elevate their body temperature above that of their surroundings, due to their low rates of metabolism coupled with a very high thermal conductance compared with that of birds and mammals (Bartholomew 1982; Fraser and Grigg 1984; Stevenson 1985). Early reviews of reptilian thermoregulation emphasised the high precision of temperature control by nonphysiological means displayed by lizards inhabiting desert regions (e.g. Schmidt-Nielsen and Dawson 1964; Templeton 1970), but this inherent bias towards desert species in the literature has been tempered by more recent studies. Many tropical and nocturnal species of lizards have been found to thermoregulate poorly or not at all (Huey 1982), suggesting the existence of a wider range of thermoregulatory capacities in reptile than first thought. Behavioural thermoregulation has become nonetheless the most important of organising paradigms in reptilian ecophysiology and a voluminous literature attests to its continuing influence in structuring the thinking of workers in the field.

One of the first challenges to the then prevalent view that precise thermoregulation was a *sine qua non* of the reptilian way of life was that of Huey and Slatkin (1976), who estimated the costs and benefits of maintaining a high and constant body temperature. They concluded that lizards should thermoregulate carefully only in environments where the associated costs of doing so are low. Deserts are typically such places, as heat is never in short supply; thus raising the body temperature is relatively easy, and the well-developed high temperature avoidance strategies of lizards ensure they do not overheat during the hottest periods of the day (Bradshaw 1986a). There is thus little doubt that desert lizards maintain excellent thermal homeostasis, but what needs to be established is whether this is a direct product of evolutionary adaptation or merely a consequence of the habitat in which these species are found.

4.2

The Interpretation of Field Studies

The vast literature on reptilian thermal relations in the field has been reviewed by Brattstrom (1965) and, more recently, by Avery (1982). One of the difficulties in interpreting these results is the great variability in the way in which many of the data have been collected. The famous “beer-can” experiment of Heath (1964b) showed the extent to which many early workers over-interpreted their data, assuming that any temperature differential between the animal and its environment was evidence of thermoregulatory capacities. Clearly one may only conclude that a particular behaviour is thermoregulatory if, in the absence of that behaviour, the animal’s body temperature is significantly different. Few studies have ever applied this test and, in many cases with animals in the field, it is difficult to see how one could. Thermoregulatory abilities are thus most often adduced from the data without any supporting experimental proof.

The complexity of thermal relations even in a highly thermophilic desert lizard such as the desert iguana *D. dorsalis* is highlighted by the study of Withers and Campbell (1985) using operant conditioning techniques. They found that mean and maximal body temperatures and high and low set points varied significantly with the environmentally determined cost for thermoregulation. Surprisingly, the lizards would not expend more than $0.025\text{--}0.30\text{ ml O}_2\text{ g}^{-1}\text{ h}^{-1}$ to maintain a high body temperature, but would let it fall, even though this represents only 2–6% of their resting metabolic rate. A closely related study by Campbell (1985) on the supposedly eurythermic alligator lizard *Gerrhonotus coeruleus* revealed that this lizard is quite capable of precise thermoregulation when the environmental cost of doing so is constant and this conclusion has also been confirmed by the recent study of Kingsbury (1994) with another species of alligator lizard, *Elgaria multicarinata*. The suggestion from this work is that these species are not thermoconformers as previously thought, but rather “facultative thermoregulators” which may also vary their preferred body temperature in relation to the prevailing thermal régime. This is a sobering conclusion and, if found to be more widespread, will force a major revision of our current understanding of behavioural thermoregulation in reptiles. The generally accepted belief amongst herpetologists, that preferred body temperatures of reptiles are taxonomically very conservative, except perhaps in the genus *Anolis*, may need rethinking.

A promising new approach to this problem has been detailed in a recent paper by Hertz et al. (1993), who developed a protocol for comparing body temperatures of an animal in the field with the operant temperatures available in its immediate environment. As they point out, a satisfactory protocol for estimating the extent and effectiveness of temperature regulation in any reptile, or ectotherm for that matter, does not exist. Their protocol depends upon showing that the body temperatures of an animal differ significantly from those of a null model – i.e. an hypothetical thermoconforming or

nonregulating “control”. The expected null distribution of body temperatures for thermoconforming controls is obtained by randomly mapping the thermal environment – usually with the aid of physical models designed to measure the available “operative temperatures”. The limitations of the method revolve around the problem of adequately sampling these operative temperatures. Thermal environments in the field can be extremely complex and may require an inordinate amount of time and effort to map them adequately. Add to this spatial variation the problem of temporal variation – extending to seasons – and some idea of the complexity of the problem becomes apparent. The method also assumes a single thermal “set-point” temperature to which the animal adheres and, as we have seen, this may be overly simplistic. Nonetheless, at the moment, it represents the most promising approach of those available and complements the work of biophysical modelers attempting to describe the thermal environment of small animals (Bakken 1989, 1992; O’Connor and Spotila 1992; Porter and Tracy 1983; Tracy 1982).

Some data from Hertz et al.’s study, illustrating the utility of the method, are shown in Table 4.1, in which d_b is defined as the mean deviation of the body temperature (T_b) from a set-point determined in the laboratory and this parameter effectively measures the precision of thermoregulation for a given species. d_e is similarly the average deviation of the environmental operative temperatures (T_e) from that same set-point and is thus an index of the average thermal quality of a habitat from the organism’s point of view. The “effectiveness” (E) of temperature regulation is calculated as $E = 1 - (d_b/d_e)$ and ranges from 0 to 1, with 0 indicating an absence of effective thermoregulation.

These data illustrate very neatly the fact that *Anolis cooki* is an effective thermoregulator in its desert environment (E ranging from 0.38 to 0.67) and that, even though body temperature variability is as low in *Anolis gundlachi*, this is not evidence of a high thermoregulatory ability in this species (E ranging from 0.00 to 0.14), but reflects instead a coincidence between the animal’s set-point and the mean of the operative temperatures available in its environment.

Table 4.1. Effectiveness of thermoregulation in three species of *Anolis* lizards. (Modified from Hertz et al. 1993)

Species and season	Habitat	T_b	T_e	d_b	d_e	E
<i>Anolis cooki</i>	Desert	30.8 ± 0.3	29.9 ± 0.1	0.8 ± 0.1	2.4 ± 0.1	0.67
Winter						
Summer		32.1 ± 0.2	32.8 ± 0.1	1.3 ± 0.1	2.1 ± 0.1	0.38
<i>Anolis cristatellus</i>	Mesic 1150 m	23.5 ± 0.4	19.0 ± 0.1	5.0 ± 0.4	9.2 ± 0.1	0.46
Winter						
Summer		27.2 ± 0.3	23.4 ± 0.3	2.5 ± 0.2	5.0 ± 0.1	0.50
<i>Anolis gundlachi</i>	Mesic 210 m	23.9 ± 0.2	23.9 ± 0.1	0.9 ± 0.1	0.9 ± 0.1	0.00
Winter						
Summer		25.7 ± 0.1	25.1 ± 0.1	0.6 ± 0.1	0.7 ± 0.1	0.14

T_b , T_e . See text for definition.

4.3

Physiological Mechanisms

4.3.1

Metabolic Characteristics of Ectotherms

Two fundamental physiological characteristics distinguish reptiles from birds and mammals – ectothermy and the use of anaerobic metabolism to generate energy for high or sustained activity. Reptiles thus typically have low rates of energy utilisation but it is less often appreciated that their efficiencies of biomass conversion are much greater than those of endotherms. Pough (1983) reported that 16 species of small birds and mammals converted only 1.4% of the energy they assimilated into biomass, compared with an average conversion efficiency of 46.3% for eight species of amphibians and reptiles. Thus, despite their low rates of energy flow and the small proportion of primary productivity they consume, reptiles (and amphibians) are of great importance in terrestrial ecosystems because of their high conversion efficiencies and the energy they make available to other organisms. In a forest ecosystem in New Hampshire, for example, Burton and Likens (1975) calculated that the population of red-backed salamanders (*Plethodon cinereus*) produced $4922 \text{ kcal ha}^{-1}$ per year which was approximately five times greater than that of the entire avian community of the forest and about the same as that of the small rodents.

This greater conversion efficiency than that of endothermic animals is a direct result of the reliance of reptiles on external sources of heat for thermoregulation rather than depending upon heat produced by the oxidative metabolism of foodstuffs (Pough 1980). Recent years have seen an upsurge of interest in the very different metabolic relations of reptiles, particularly in relation to the still unsolved problem of the evolution of endothermy (Else and Hulbert 1987; Hulbert 1988).

4.3.2

Sources of Heat Production in Reptiles

It is well understood that the rate of oxygen consumption, and hence heat production, of any reptile is many orders of magnitude less than that of a similar-sized mammal, when measured at the same body temperature. This difference is reflected in the standard allometric equations relating resting oxygen consumption (V in ml h^{-1}) to body mass (in g) where $V = 0.424 \text{ g}^{0.82}$ for lizards at 37°C compared with $V = 3.9 \text{ g}^{0.75}$ for mammals (Bennett and Dawson 1976; Kleiber 1961). Less well understood is the biochemical basis for this large difference.

Else and Hulbert (1985) measured the number and density of mitochondria in various tissues from mammals and reptiles and found that total mitochondrial surface area increased allometrically in both groups with body mass; but although the curves are roughly parallel, the intercepts for the respective

equations are significantly higher in mammals than in reptiles. In liver, kidney, heart and brain, the total mitochondrial membrane surface area is on average fourfold greater than in similar-sized ectotherms. Half this difference can be attributed to the greater absolute size of these organs in endotherms than in ectotherms, the rest being the result of increased mitochondrial densities in these tissues. Total mitochondrial area in skeletal muscle from mammals was only twice as large as that of reptiles but the cytochrome oxidase activity of these mitochondria per mg of mitochondrial protein was found to be roughly double that of mitochondria isolated from reptilian muscle (Hulbert and Else 1989).

Table 4.2 presents some of these allometric data on tissue metabolic capacities from mammals and reptiles.

The enhanced metabolic activity of mammalian tissues is thus primarily a consequence of mammals having larger tissues with a greater proportion of their volume occupied by mitochondria plus, in the case of some tissues such as skeletal muscle and lung, an enhanced enzymatic activity of the mitochondria themselves.

As much of the energy of cells is expended in maintaining differential electrochemical gradients across the cell membrane, attention has focused on the membrane-bound Na^+/K^+ -ATPase pump in both endotherms and ectotherms. Hulbert and Else (1990) argue that the cells of endotherms are much "leakier" than those of ectotherms and cite as evidence much higher rates of flux of ^{42}K and ^{22}Na when these radioactive isotopes are added to cultured cell layers in vitro. The sodium-dependent (i.e. ouabain-inhibitable) fraction of the total tissue oxygen consumption is also greater in liver and kidney from endotherms than from ectotherms, and it has been deduced from this that mammalian cells require a greater amount of energy to maintain the same transmembrane ion gradients as do reptiles and produce more heat as a result.

The overall composition of the tissues also varies between ectotherms and endotherms with the latter having approximately 50% more protein and phospholipid per unit mass than the corresponding reptilian tissue. The fatty acid composition of the phospholipids of mammalian tissues also differs from that

Table 4.2. Allometric equations for summated tissue weights and mitochondrial membrane surface areas in reptiles and mammals. (Modified from Else and Hulbert 1985)

Summated organs	Reptiles		Mammals	
	Total tissue mass (g)	Surface area of mitochondria (m^2)	Total tissue mass (g)	Surface area of mitochondria (m^2)
Liver, kidney, brain, heart, lung, skeletal muscle	$0.24W^{1.07}$ (± 0.34) ^a $r = 0.98$	$0.30W^{1.11}$ (± 0.36) $r = 0.97$	$0.54W^{1.00}$ (± 0.31) $r = 0.96$	$6.85W^{0.76}$ (± 0.73) $r = 0.77$

^a95% Confidence limits of the exponent given in parentheses, followed by the correlation coefficient (r) for the regression; W body mass of animals.

found in reptiles with significant increases in the long-chain polyunsaturated fatty acid content of membranes, including those of mitochondria (Hulbert and Else 1989). Membrane fatty acid composition is known to be influenced by thyroid hormones and thyroidectomy (Hulbert 1978; Withers and Hulbert 1987) which also have an impact on rates of metabolism and thermoregulation.

The leakier membranes of endothermic mammals may explain their sensitivity to hypoxia and anoxia, as at low temperatures and low oxygen tensions ion gradients essential for cellular activity are degraded rapidly, presumably as a result of the high permeability of the cell membranes. Guppy et al. (1987) suggested that reptiles are able to sustain regularly daily variations in body temperature of some 25 °C because of tight junctional complexes in their membranes which ensure that membrane ion gradients are not disrupted.

Geiser (1990, 1991) has presented evidence to show that changing the ratio of saturated to unsaturated lipids in the diet of mammals can have profound effects on membrane composition and body temperature in hibernating mammals. Unsaturated dietary fatty acids enhance daily torpor and hibernation in mammals, including marsupials (Geiser and Kenagy 1987; Geiser et al. 1992b), and feeding a diet high in polyunsaturated fatty acids to the lizard *T. rugosa* had the effect of lowering its preferred body temperature by some 3–5 °C (Geiser et al. 1992a), as seen in Fig. 4.1.

The discovery that reptiles rely to a very large extent on anaerobic rather than aerobic pathways for the generation of energy needed to sustain high levels of activity is usually attributed to the late Walt Moberly (Moberly 1968), who worked with the common iguana *Iguana iguana*. Bennett and Licht (1972) estimated that the 64% of the total energy utilised by *I. iguana* during 5 min of activity was derived from anaerobiosis. On the basis of measurements of total lactate production and estimates of aerobic scope, these authors went on to calculate that 80–90% of the total energy expended by a number of lizards

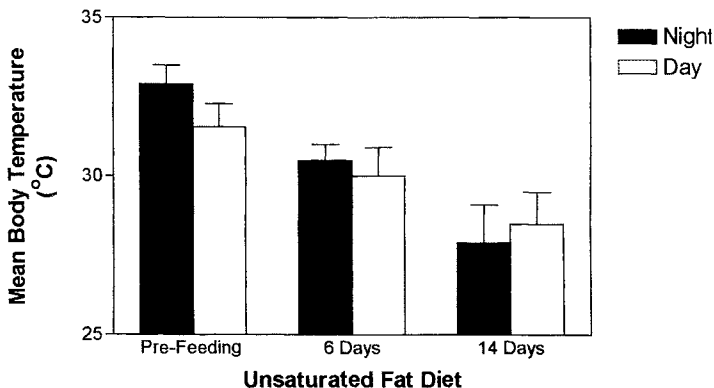


Fig. 4.1. Mean selected body temperature of the skink *Tiliqua rugosa* at night and during the day in a photothermal gradient prior to and 6 and 14 days after being fed a diet high in unsaturated fats. (Adapted from Geiser et al. 1992a)

during the first 30 s of activity is associated with lactate formation. Whereas aerobic scope in reptiles is very limited, and temperature-dependent, anaerobic scope (i.e. the maximal rate of lactate production) and anaerobic capacity (i.e. the maximal amount of lactate produced) are not markedly temperature-dependent (Bennett 1982; Bennett and Dawson 1976). As a result, most ectotherms have the potential to use maximal anaerobic response at the lower end of the range of body temperatures experienced whilst active in nature (Gatten 1985; Hertz et al. 1988; Pough 1980). Guppy and Davison (1982) point out, however, that some tissues, such as cardiac muscle, may have levels of key aerobic enzymes such as citrate synthetase and β -hydroxybutaryl CoA dehydrogenase in lizards that are indicative of mammalian level metabolic capacities.

Data from an early study by Bennett and Dawson (1972) with the desert iguana *D. dorsalis* separating aerobic and anaerobic components of ATP production are shown in Fig. 4.2.

Anaerobic metabolism through glycolysis involves the degradation of glycogen or glucose to lactic acid with the production of three molecules of ATP for every molecule of carbohydrate transformed, compared with 37–39 ATP molecules via aerobic pathways. There is also a report of green sea turtles (*Chelonia mydas*) forming succinate and alanine through amino acid catabolism during the anaerobiosis associated with diving (Hochachka 1973) and pyruvate has been detected in some lizards (Bennett 1982), but the contribution of these other substrates to ATP production is thought to be minimal. Although excessive lactate build-up is inimical for mammals because of the resulting disruption of their blood equilibrium, reptiles – with their limited capacities for oxygen transport – appear extremely reliant upon and tolerant of ATP generation by lactate production with reports in the literature of blood levels exceeding 100 mg%.

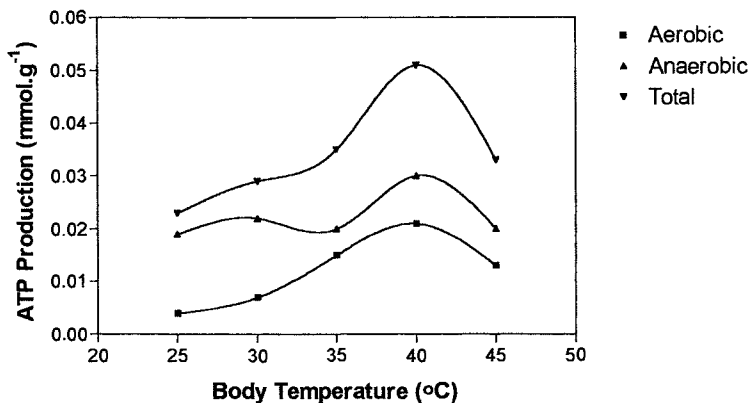


Fig. 4.2. Estimated weight-specific production of ATP (in mmol g^{-1} body mass) by the desert iguana *Dipsosaurus dorsalis* during maximum activity, partitioned into aerobic and anaerobic components. (Modified after Bennett and Dawson 1972)

The startling ability of the Indian python *Python molurus* to raise its body temperature some 5°C above ambient air temperature for many days when brooding eggs was first revealed in a paper by Hutchinson et al. (1966). This pattern of endothermy is only found in females that are brooding eggs or prepared to oviposit and results from spasmodic contractions of the body musculature (van Mierop and Barnard 1976, 1978). As Bartholomew (1982) points out, this is

“the most striking and incontrovertible instance of physiological temperature control available for any member of the Class Reptilia”

and the metabolic response to temperature of brooding female pythons is very similar to that of endotherms, even showing a small thermoneutral zone extending from 26°C to 32°C. Whether this should be equated with shivering thermogenesis in mammals is debatable, however, as this implies the existence of hypothalamic regulatory centres controlling heat production events that have not been identified in pythons to date.

More recent studies of thermoregulation in brooding Australian diamond pythons (*Python spilotes spilotes*), by Harlow and Grigg (1984) and Slip and Shine (1988), show that brooding females are able to maintain a temperature differential of as much as 9°C, and occasionally 13°C, above the ambient environment and maintain a constant body temperature close to 31°C for periods of up to 2 months in the field. Interestingly, the much smaller ball python, *Python regius*, with a mass of approximately 2 kg, shows the same behavioural repertoire as the larger pythons, coiling around and apparently incubating its eggs for a 5 month period, but without any thermal advantage. Although the rate of oxygen consumption of brooding females is significantly higher than that of nongravid females at all temperatures, the body temperature is only elevated by a few tenths of a degree above ambient – presumably because of the very high heat transfer coefficients of these smaller pythons (Ellis and Chappell 1987). It would thus appear that this striking example of maternal behaviour in pythons may not necessarily always have a basis in thermogenesis (Shine 1988).

4.3.3

Thermal Hysteresis and Changes in Dermal Vascularity

The first evidence of thermal stratification within the bodies of reptiles came with the discovery of significant head-body temperature differences in some lizards (Heath 1964a; Webb et al. 1972), although the physiological significance of these is still unclear (Heatwole 1976). Many species have steep head-body temperature gradients with head temperatures in some cases differing by as much as 6°C from the cloaca in fresh-water turtles (Webb and Johnson 1972). This reinforces again the conclusion that cloacal temperatures may be misleading when attempting to interpret thermally linked behaviour patterns in reptiles.

Head-body temperature differences are most pronounced during the heating phase in reptiles and become less evident when the body temperature achieves stability close to the preferred level (Johnson 1972, 1974). This suggests that they reflect preferential shunting of incoming heat to the brain and head region and this is consistent with the lack of significant thermal stratification within the body during cooling.

Rates of heating and cooling have been studied in a number of reptiles since the pioneer observations of Bartholomew and Tucker (1963, 1964) with Australian lizards. In most cases the two rates are not identical and show clear evidence of hysteresis, very small lizards with large surface area to volume ratios being sometimes an exception (Grigg et al. 1979; Fraser and Grigg 1984; Turner 1987). Dead lizards heat and cool at the same rate, confirming that the observed thermal hysteresis is a clear example of physiological regulation of body temperature in reptiles (Bartholomew 1982).

In lizards, as in other reptiles, the physiological and ecological significance of such control over rates of heating and cooling is presumably the increase in amount of time that the body temperature of the animal remains close to levels that are favourable for activity and they can thus be regarded as homeostatic mechanisms. The primary physiological processes which underlie thermal hysteresis in reptiles are changes in cardiac function plus variations in dermal vascularity. In some species changes in albedo or reflectance of the integument and evaporative cooling by panting may also play a role. The heart rate typically accelerates during the heating phase in lizards, compared with the cooling phase, and is associated with an increase in cardiac output, coupled with a fall in the arterio-venous difference for oxygen (Baker and White 1970). The mechanism for this is thought to be a right-to-left cardiac shunt allowing venous blood to bypass the pulmonary circuit and enter the left systemic arch (White 1976).

Table 4.3 (from Bartholomew 1982) summarises the physiological bases for temperature control in endotherms and reptiles and shows clearly that reptiles are not as devoid of physiological control mechanisms for the regulation of body temperature as is sometimes supposed.

Bartholomew (1982) pointed out that the "factorial metabolic scope" (the maximum divided by the resting metabolic rate) of lizards with preferred body temperatures between 35 and 40 °C is such that some species may briefly attain rates of heat production that approximate the basal rates of similar-sized birds and mammals. The thermal conductance of, particularly, small reptiles is so high, however, that such additional heat would be lost from the body almost as rapidly as it is produced and only in large reptiles, with a very high thermal inertia, could such heat production be of significance for thermoregulation. In larger lizards such as *Tiliqua scincoides*, *Amblyrhynchus cristatus* and varanids, there is some evidence that endogenous heat production may contribute to observed differences in rates of heating and cooling.

Cowles (1958), in an early important paper, first produced experimental evidence to suggest that reptiles may exert control over rates of blood flow

Table 4.3. A comparison between physiological components of thermoregulation in endotherms and reptiles. (From Bartholomew 1982)

Physiological process	Birds	Mammals	Crocodiles	Turtles	Lizards	Snakes	<i>Sphenodon</i>
<i>Endogenous heat</i>							
<i>Production</i>							
High BMR	+	+	-	-	-	-	-
Shivering thermogenesis	+	+	-	-	-	?	-
Locomotor thermogenesis	+	+	+	+	+	+	+
Chemical thermogenesis	+?	+	-	-	-	-	-
<i>Integumentary control</i>							
Pilomotor or filomotor	+	+	-	-	-	-	-
Albedo changes	-	-	-	-	+	?	?
<i>Evaporative cooling</i>							
Panting, gaping	+	+	+	+	+	+	?
Saliva spreading	-	+	-	+	-	-	-
Urinating on body	+	-	-	+	+	-	-
Sweating	-	+	-	-	-	-	-
<i>Regional heterothermy</i>							
Vascular shunting	+	+	+	+	+	+	+
Cardiac shunting	-	-	+	+	+	+	+

through the peripheral tissues. He introduced small volumes of heated saline under the skin of *D. dorsalis* and measured the time taken for these to dissipate under different experimental régimes, concluding that some control was exerted over dermal vascularity. This was confirmed in two species of lizards, *A. cristatus* and *I. iguana*, by Morgareidge and White (1969) using radioactively labelled xenon (^{133}Xe). Xenon is highly soluble in saline and plasma but converts to a gas again on passage through the lungs and is lost rapidly from the body in this way. The ^{133}Xe was injected subcutaneously in a saline solution and then the rate of washout of the label from the lizard measured with a gamma counter positioned close to the site of injection. Local heating of the skin was found to induce vasodilatation (i.e. increased rate of washout of the label) and local cooling produced vasoconstriction. These changes were unrelated to changes in either heart rate, core temperature, or any portion of the skin other than that undergoing heat flux.

Weathers (1971) suggested that local changes in subcutaneous blood flow in the desert iguana *D. dorsalis* were a direct consequence of heat on the vascular smooth muscle and Baker et al. (1972) concluded that overall control of heat

transfer in lizards depends upon a selective redistribution of blood between the shell and the core. It is generally assumed that such control over the distribution of heat within the body is adaptive and facilitates effective thermal homeostasis under field conditions. Direct evidence of this is lacking at the moment and, as Bartholomew (1982) has pointed out, there does not appear to be any obvious correlation between the capacity to control rate of change in body temperature and either habitat or the preferred body temperature.

A similar approach to the ^{133}Xe washout technique but using radioactively labelled krypton (^{85}Kr) was used by Rice and Bradshaw (1980) to extend these studies on dermal vascular control and analyse the impact of changes in integumental colour and albedo which occur simultaneously during heating and cooling in many reptiles. Ever since the work of Atsatt (1939) on desert lizards from southern California it has been assumed that obvious and regular alterations in skin coloration and reflectivity, consequent upon changes in body temperature, assist in thermoregulation. Typically, animals with low body temperatures are dark and they pale or "blanch" progressively as the body temperature reaches, and then exceeds, the preferred level (but this is not always the case in desert lizards – e.g. *Agama agama*; Harris 1964). Simple physical principles would argue that dark bodies should heat faster than pale ones but it has long been appreciated that the thermoregulatory significance of changes in colour may be confounded by the potentially competing and confounding requirements of crypsis (Crisp et al. 1979; Norris 1967).

Temperature-dependent changes in integumental reflectance of the agamid lizard *Ctenophorus (Amphibolurus) nuchalis* are shown in Fig. 4.3, along with variation in dermal vascularity expressed as the half-time ($t_{1/2}$) for the removal of subcutaneously injected ^{85}Kr .

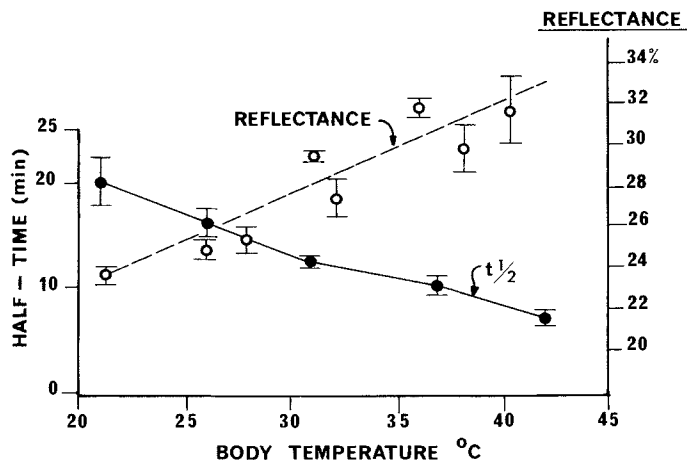


Fig. 4.3. Temperature-dependent changes in reflectance and dermal vascularity (measured as the half-time for removal of subcutaneously injected ^{85}Kr) of the Australian desert agamid lizard *Ctenophorus (Amphibolurus) nuchalis*. (Adapted from Rice and Bradshaw 1980; Bradshaw 1986a)

Dermal reflectance in this lizard increased in a linear fashion in a similar manner to the lizard *Liolaemus multiformis* studied by Pearson (1977), from approximately 24% at a body temperature of 20 °C to almost 32% at 40 °C – a relative increase of some 33%. This change in reflectance is considerably greater than the 15% recently reported for the African chameleon *Chamaeleo dilepis* which is found in open savannah habitat in Kenya (Walton and Bennett 1993). Dermal vascularity also increased as a function of body temperature in *C. nuchalis* as shown by the decreasing half-life for injected ^{85}Kr , which fell from approximately 20 min to less than 7 min over the same temperature range. Local heating of the skin was also found to increase the clearance rate of ^{85}Kr , even though heart rate and deep body temperature were unaffected, indicating a capacity for autoregulation of blood vessels, as also found in the common iguana *I. iguana* (Baker et al. 1972).

Rice and Bradshaw (1980) also used injections of synthetic melanocyte-stimulating hormone (α -MSH) to darken *C. nuchalis* and hypophysectomy to lighten them and then studied their thermal heating and cooling profiles. As seen in Fig. 4.4, α -MSH-injected animals always heated more rapidly and reached higher equilibrium temperatures with the same radiant input than controls. Surgical hypophysectomy, which resulted in permanent pallor, had no effect on ^{85}Kr clearance rates, but rates of heating in these individuals were significantly lower than controls and they reached lower equilibrium body temperatures.

These differences in rate of heating result uniquely from differences in reflectivity and provide a clear demonstration of the potential significance of physiological changes in reflectance and albedo for thermoregulation in small lizards. As would be predicted, rates of cooling in α -MSH-injected and hypophysectomised individuals did not differ from controls, as the primary modes of heat transfer during cooling are by long-wave radiation and convection which are not affected by changes in integumental wavelength in the visible range.

Instantaneous rates of temperature change are also given in Table 4.4, measured in both live and dead individuals rendered permanently dark or pale. This gives a measure of the extent to which physiological control (vascular) and physical (reflectivity) changes operate in concert.

The instantaneous rate of temperature change (IRT) varied by 69.7% in living animals compared with only 29.5% in dead animals. This reflects the extent to which vascular changes may augment the effect of variations in integumental reflectance on rates of heating. In the living animal, the effects are additive and synergistic, as local heating of peripheral vessels leads to their dilatation with increased peripheral flow and an enhanced transfer of heat to the core. This effect is most clearly evident when ^{85}Kr washout rates are measured during heating and cooling.

^{85}Kr washout rates were faster during heating than cooling in control animals ($t_{1/2} = 8.03$ versus 12.98 min) but were reduced in hypophysectomised (permanently pale individuals) and did not differ significantly during heating

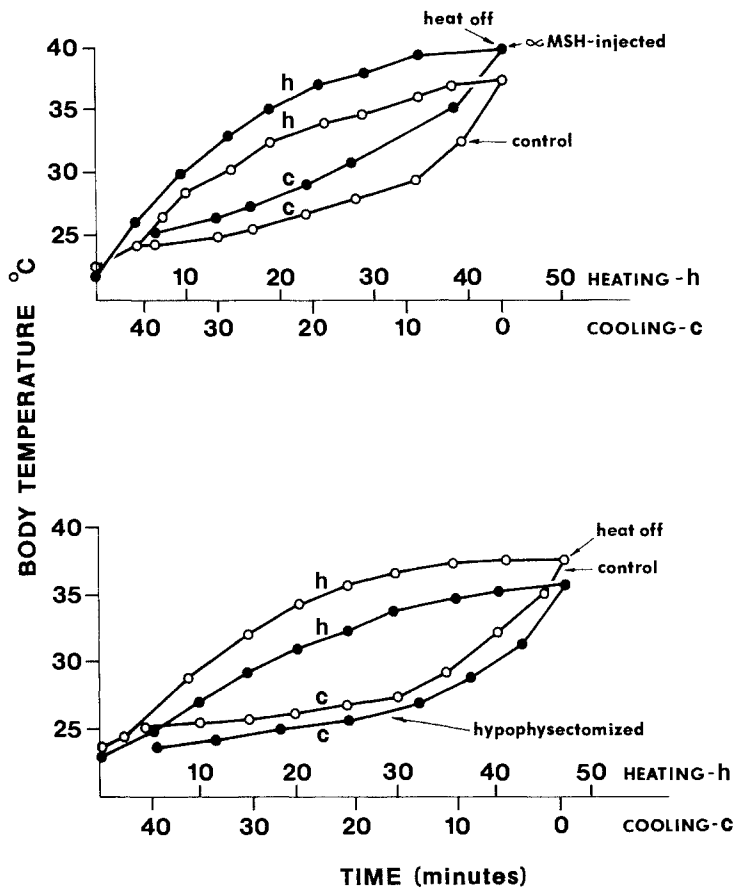


Fig. 4.4. Heating and cooling curves of intact, α -MSH injected and hypophysectomised *Ctenophorus* (*Amphibolurus*) *nuchalis*, showing both thermal hysteresis and the effect of permanent changes in dermal reflectance. (Modified after Rice and Bradshaw 1980; Bradshaw 1986a)

Table 4.4. Instantaneous rate of temperature change (in $^{\circ}\text{C min}^{-1}$) during heating and cooling of live and dead *Ctenophorus nuchalis*. (From Rice and Bradshaw 1980)

	α -MSH injected		Control		Hypophysectomised
Heating					
Live	1.09 ± 0.09 $P < 0.001$	$P < 0.001$	0.66 ± 0.08	$P < 0.001$	0.35 ± 0.03 NS
Dead	0.61 ± 0.04		$P < 0.02$		0.43 ± 0.06
Cooling					
Live	0.69 ± 0.16 $P < 0.001$	NS	0.69 ± 0.07	NS	0.87 ± 0.14 $P < 0.02$
Dead	0.31 ± 0.01		NS		0.23 ± 0.08

and cooling ($t_{1/2} = 13.65$ and 11.47 min respectively). Injections of α -MSH into hypophysectomised animals darkened them and dramatically accelerated the clearance of ^{85}Kr , reducing the half-time to the levels seen in control animals. Thus, despite the fact that vascular mechanisms were intact in hypophysectomised individuals (as shown by their normal rates of clearance of ^{85}Kr at stable body temperatures) these are not activated in the dynamic heating situation in the absence of α -MSH which darkens the skin. Reduced reflectivity at low body temperatures thus appears to be critical in the desert agamid *C. nuchalis* for the initiation of vascular responses which result from local heating of the skin and subsequent autoregulation of dermal blood vessels.

Surprisingly, a study in which the reflectivity of the skink *Egernia cunninghami* was changed, by painting them with a black water-soluble chalk solution, found that this retarded rather than accelerated the rate of heating (Fraser 1985) and the author speculates that the use of a chalk-based solution may have had the effect of insulating the animals from the radiant heat. This emphasises the need to employ more physiological means of varying the reflectivity of the integument when designing such experiments. Turner (1987) has also pointed out that reporting only a time constant to describe temperature changes in reptiles implies that the transient temperatures of reptiles behave as first-order systems. He presents evidence to suggest that they may behave more like overdamped second-order systems and recommends the use of second-order linear differential equations as better descriptors of thermal hysteresis.

A recent field study by Tosini et al. (1991) compared rates of heating in melanistic and pale forms of lizards of the genus *Podarcis* but found that differences in energy input due to differences in coloration were only of the order of 2% and too small to affect overall rates of body heating.

4.3.4

Panting and Evaporative Heat Loss

The astute observations at the beginning of this century by Langlois (1902) documented that many species of reptiles gape when heat stressed, followed by obvious panting with even greater heat stress, and he assumed this to be of thermoregulatory significance, as in mammals and birds. Panting has been most exhaustively studied in the North American desert lizard *S. obesus* by Crawford and Barber (1974) and Crawford and Kampe (1971). Gaping occurs at body temperatures above 40°C , tidal volume increases by two thirds, breathing rate increases fivefold and evaporative water loss increases sharply. Panting in this species has a greater cooling effect on the brain than the rest of the body (Crawford 1972) but it is still able to maintain its body temperature some 4°C below ambient when exposed to air temperatures of 47°C (Case 1972). Other lizards in which panting has been shown to reduce significantly the body temperature include *D. dorsalis* (Templeton 1960), *Crotaphytus collaris*

(Dawson and Templeton 1963) *Pogona* (*Amphibolurus*) *barbatus*, *T. rugosa* (Warburg 1965) and *U. acanthinurus* (C.J. Grenot, pers. comm.), with limited control in *Elgaria* (*Gerrhonotus*) *multicarinata* (Dawson and Templeton 1966).

Panting can be initiated by selectively heating the brain of chuckwallas but, when spontaneous panting is inhibited by cooling the brain, slight increases in skin temperature will reinitiate panting (Crawford and Barber 1974). This indicates that both central and peripheral stimuli are involved in the normal initiation of panting in reptiles. Dupré and Crawford (1985b) found skin temperature at the onset of panting to be independent of heat load in the desert iguana *D. dorsalis*, suggesting that the peripheral (skin) temperature is the body temperature used by the central thermoregulatory centre to cue thermal panting. Panting threshold is reduced by parietectomy in the agamid lizard *Amphibolurus miricatus* (Firth and Heatwole 1976), but only if radiant heat loads are employed.

Panting thresholds differ markedly between species and Fig. 4.5 suggests a significant relation with the critical thermal maximum (CTM). Thus, although various studies have shown that the CTM and panting threshold for a given species may be influenced by a wide range of environmental factors, including photoperiod, thermal acclimation, season, rate and mode of heating, time of day and dehydration (see Heatwole 1976 and Huey 1982), they appear to be linked together and change in concert.

Dupré and Crawford (1985a) have studied the effect of dehydration and changes in plasma osmolality on the panting threshold in the desert iguana *D. dorsalis*. The effects of some of their experimental treatments are shown in Fig. 4.6. Dehydration results in a progressive elevation of the panting threshold from 42 to 43.5°C and rehydration with hypo-osmotic saline reduced the panting threshold to below that of control individuals. Loading with hyperosmotic, but not isosmotic, saline also had the effect of substantially

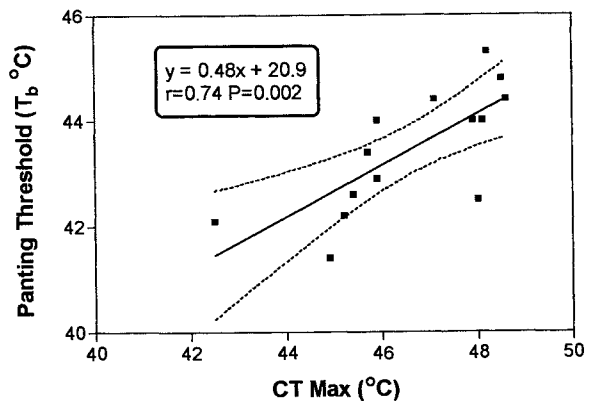


Fig. 4.5. Correlation between the body temperature at which panting is initiated and the critical thermal maximum (CTMax) of 14 species of North American lizards. (Adapted from Whitfield and Livezey 1973; Bradshaw 1986a)

elevating the panting threshold to almost 46°C, suggesting that the effect of dehydration is through its elevation of the osmotic pressure of the body fluids.

This was confirmed in a later study by Dupré and Crawford (1986) with *D. dorsalis* and, as seen in Fig. 4.7, there is a significant positive relationship between panting threshold and plasma osmotic pressure in this species which was elevated by injections of either hyperosmotic NaCl (3 mol) or sucrose (3 mol).

These data show very clearly that plasma osmolality is a key factor in setting the skin temperature at which panting is initiated in this desert lizard and the nature of the relationship suggests an homeostatic function. Dupré and Crawford (1986) also showed that reduction in body fluid volumes, brought

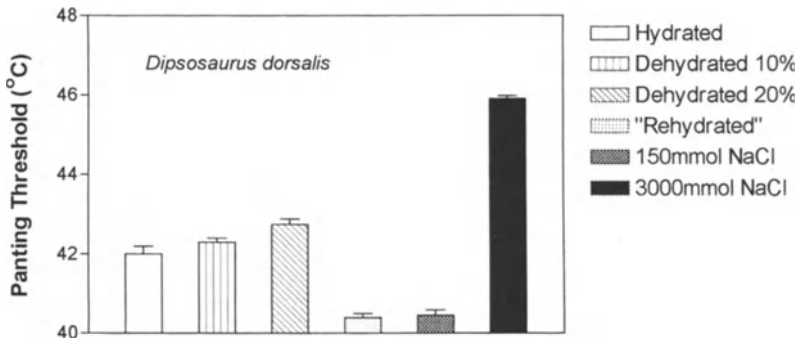


Fig. 4.6. Skin temperature at the onset of panting in the desert iguana *Dipsosaurus dorsalis* during dehydration, "rehydration" with 10mmol NaCl and 1% body mass injections of 150 and 3000mmol NaCl. (Adapted from Dupré and Crawford 1985b)

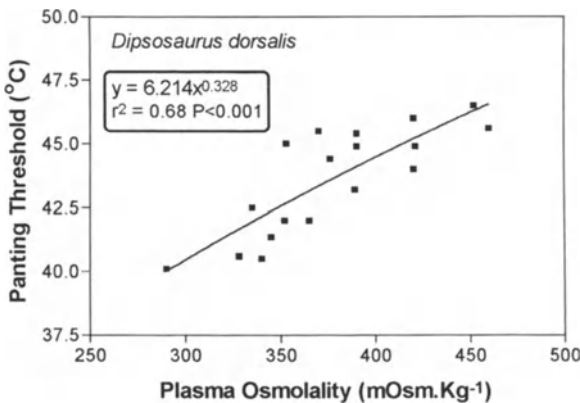


Fig. 4.7. Variation in panting threshold (skin temperature) of the desert iguana *Dipsosaurus dorsalis* with change in plasma osmolality provoked by intraperitoneal injections of 3 mol NaCl. (Modified after Dupré and Crawford 1986)

about by exsanguination of 1 ml of whole blood per 100 g of body mass also had a similar effect to salt loading, with a mean increase of the panting threshold of 0.7 ± 0.2 °C. Taken together, these data suggest that fluid loss and consequent hypernatraemia lead to an elevation of the panting threshold which would operate homeostatically to conserve body water. As these same stimuli are known to be potent releasers of the neurohypophyseal peptide arginine vasotocin (AVT) in reptiles (see Chap. 3.2.2), the end effect may well be through this hormone rather than a direct effect of plasma osmolality. As we shall see in Section 4.3.6, data from other lizards suggest that this peptide hormone is involved in modulating thermoregulatory responses to changes in fluid and electrolyte régimes.

4.3.5

The Pineal Eye and Photoperiod

The impact of photoperiod on physiological processes, be they thermoregulatory or reproductive, has always been more difficult to demonstrate in reptiles than in mammals, giving rise to the general perception that temperature far outweighs photoperiod in importance as an environmental organiser of essential physiological events in this group of vertebrates (Licht 1984). The question of the functional significance of the pineal or parietal eye in lizards has proven even more intransigent of resolution. Observations in the literature can again be traced back to Langlois (1902) who found that the panting threshold in the North African lizards *U. acanthinurus* and *Varanus arenarius* (*griseus*) depended on light falling directly on the parietal eye and could be inhibited by interposing an opaque screen.

The pineal organ in lizards is a saccular structure, the epithelium of which is composed of both photoreceptive and secretory cells (Quay 1979), and appears to function as a neuroendocrine transducer of daily photoperiod (Firth and Turner 1982; Oksche 1984). Some lizards also possess a parietal eye in the roof of the skull which is equipped with a cornea, lens and photosensitive retina and is connected to the pineal organ by the pineal nerve. Chelonians and snakes lack a parietal eye but possess pineal organs which are probably secretory. Crocodilians lack both a pineal organ and a parietal eye.

Levels of the hormone melatonin (n-acetyl-5-methoxytryptamine) and the enzyme which catalyses the terminal step in its biosynthesis, hydroxyindole-O-methyl transferase (HIOMT) cycle diurnally in the lizard pineal organ and pinealectomy or melatonin administration disrupt circadian activity rhythms in a number of species (reviewed by Engbretson 1992 and Underwood 1984).

Glaser (1958) and Stebbins and Eakin (1958) first suggested that the parapineal organ and parietal eye function together as a radiation dosimeter in lizards after observing increased exposure to the sun and bright lights of parietalectomised animals (Stebbins and Eakin 1958). In support of this hypothesis, removal or masking of the photoreceptive parietal eye has been

shown to result in the selection of higher body temperatures by *Anolis carolinensis*, *Sceloporus magister* and *Varanus monitor* in laboratory thermoclines (Hutchinson and Kosh 1974; Engbretson and Hutchinson 1976; Roth and Ralph 1976; Kulshreshtha and Khan 1988). Interestingly, removal of the intracranial pineal organs appears to have the opposite effect and Stebbins (1960) reported that operated individuals of *Sceloporus occidentalis* in a field population had lower active body temperatures than controls. A similar effect of pinealectomy has been reported in *C. collaris* under semi-natural conditions (Firth et al. 1988) and in laboratory thermal gradients (Firth et al. 1980).

Firth et al. (1989b) extended this work with *C. collaris* in the laboratory by showing that the effect of pinealectomy in reducing selected body temperatures is much more pronounced during the scotophase than the photophase, which is consistent with observations that the pineal organ is most active at night (Meissl and Dodt 1981). The overall impact on temperature selection in this lizard is shown in Fig. 4.8.

Pinealectomy in another species, the desert chuckwalla *S. obesus*, surprisingly had no effect on its thermoregulation, however, and the authors of this study speculated that this may have been due to seasonal effects, citing the fact that a cyclic thermal environment in spring enhances the rhythm of plasma and pineal levels of melatonin in the Australian skink *T. rugosa* (Firth and Kennaway 1987; Firth et al. 1989b).

The Italian ruins lizard *Podarcis sicula* has a characteristic unimodal activity pattern in spring which becomes bimodal in summer, returning to unimodality in autumn (Foà et al. 1994). Pinealectomy has the effect of lengthening the free-running period of locomotor rhythms and abolishing completely the bimodal activity pattern (Innocenti et al. 1994), an effect thought to be due to the absence of melatonin secretion which is abolished by pinealectomy in this species (Foà et al. 1992).

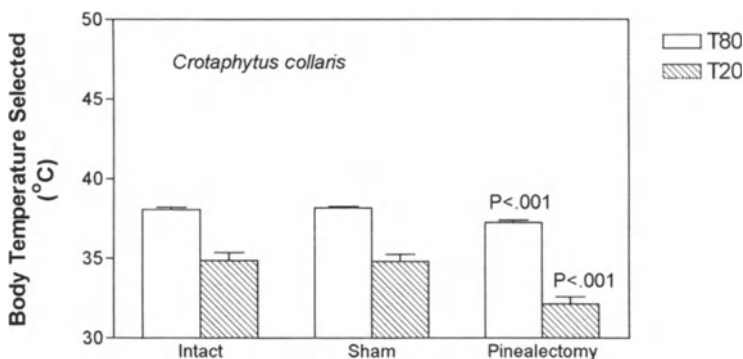


Fig. 4.8. Mean body temperatures selected by intact, sham-operated and pinealectomised *Crotaphytus collaris* lizards in a photothermal gradient. T80 and T20 are the 80th and 20th percentiles respectively and approximate the upper and lower set temperatures for shuttling behaviour. (Adapted from Firth et al. 1989b)

Effects of photoperiod on thermoregulation are more subtle and often difficult to detect. The lacertid green lizard *Lacerta viridis*, for example, displays a distinct annual cycle in its day and night time selected body temperatures which appears to be controlled by photoperiod (Rismiller and Heldmaier 1988). Green lizards respond to an artificial long photoperiod (16h light, 8h dark) at all times of the year with modifications in both diel patterns and levels of selected body temperature to summer-like conditions. These results suggest that photoperiod is a more important *Zeitgeber* for seasonal cueing of temperature selection than previously thought, and that seasonal variations in body temperature cycles are not evidence of "imprecise" thermoregulation but reflect instead seasonal acclimatory changes.

Effects of photoperiod on thermoregulation of the collared lizard *C. collaris* were also reported by Sievert and Hutchison (1991), who also found that the position of the light source over the thermal gradient (i.e. positioned at the hot or the cold end) influenced the diel cycle of thermal selection. The position of the light source also significantly affected mean selected body temperatures and these studies serve to underline the ways in which lighting position, heat and photoperiod may all be used as separate cues in behavioural thermoregulation by lizards.

4.3.6

Hormonal Influences on Thermoregulation

There are a number of hormones that have been shown to impact on thermoregulatory responses of reptiles and we have already seen how α -MSH, which darkens the integument of lizards by dispersing melanin in the dermal melanophores, can have a significant impact on rates of heating and equilibrium body temperatures in the lizard *C. nuchalis* (Rice and Bradshaw 1980). Colour change in reptiles can be mediated by nervous as well as humoral changes, however (Bradshaw and Waring 1969), and circulating levels of α -MSH have yet to be measured in any reptile and be associated with thermoregulatory responses. Given that the structure of α -MSH is contained within the parent hormone molecule ACTH, it would not be surprising if this hormone also has an effect on skin colour in reptiles and, perhaps indirectly, influence thermoregulation.

Monoamines such as adrenaline and noradrenaline and other neurotransmitters might be expected to influence thermoregulatory behaviour in reptiles but, although their presence has been detected in the preoptic and hypothalamic regions of turtles and lizards (Parent 1979), nothing is known of their thermoregulatory significance.

By far the greatest attention has been given to the pineal hormone melatonin, which typically shows a diurnal concentration cycle in both the pineal organ and the plasma of lizards (Underwood 1985), with levels being highest during the night. Removal of the parietal eye of the scincid lizard *T. rugosa* abolishes this diurnal rhythm of plasma melatonin titres, but only when the

lizard is exposed to a coincident photothermal cycle (Firth and Kennaway 1980). When the lizard was exposed to a light-dark cycle with no associated thermal rhythm, pinealectomy had no effect on plasma melatonin levels. Firth and Turner (1982) speculate that this may result from differing spectral sensitivities of the parietal eye to visible and infrared radiation; however, this has not been verified to date, although Tosini and Avery (1995) have shown in *Podarcis muralis* that shielding the parietal eye induces a transient shift in thermal set point which is wavelength-dependent and which may involve dermal light receptors (Tosini and Avery 1996).

Injections of melatonin in *Amphibolurus muricatus* lower the panting threshold in this species when heated with an incandescent lamp (as does parietectomy, mentioned above), but the reverse effect (i.e. an elevated panting threshold) was observed when parietectomised individuals were heating

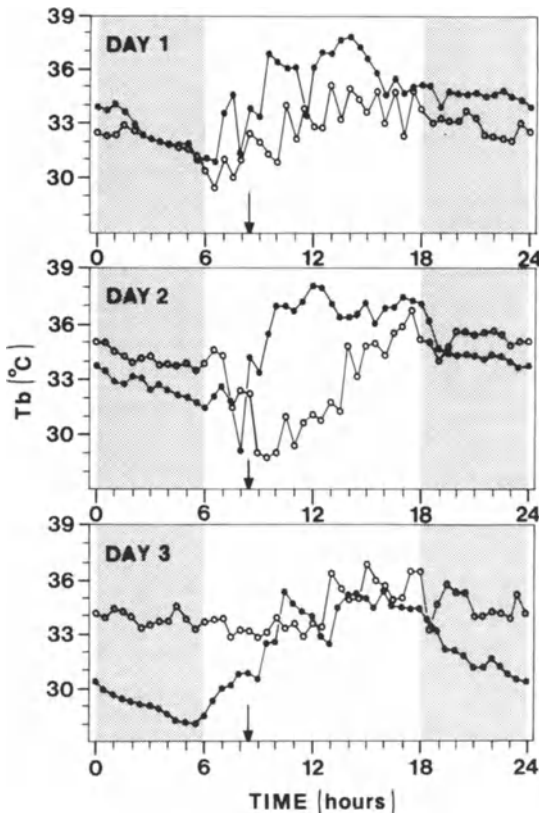


Fig. 4.9. Mean body temperatures (T_b) selected by *Crotaphytus collaris* during 3 days in a photothermal gradient. Closed circles indicate T_b s of individuals injected with melatonin; open circles are controls. Each point is the mean of six individuals; arrow indicates the time of injection; stippling indicates the scotophase. (Adapted from Cothran and Hutchinson 1979; Bradshaw 1986a)

non-radiantly (Firth and Heatwole 1976). Skinner (1991) found that injections of melatonin decreased the preferred body temperature in the South African lizard *Cordylus vittifer*. Nonetheless, some idea of the difficulty of obtaining clear experimental results in this field is given in Fig. 4.9 in which the effects of melatonin injections on mean body temperature in the lizard *C. collaris* are monitored continuously in a thermal gradient over a period of 3 days (Cothran and Hutchinson 1979). A clear effect of the hormone in elevating the selected body temperature during the photophase is evident on days 1 and 2, but the reverse effect is seen on day 3.

Firth et al. (1989a) compared daily rhythms in plasma melatonin levels in the tuatara (*Sphenodon punctata*) and the large Australian skink *T. rugosa* and found that both were keyed to different body temperatures: approximately 15°C in the case of the cool-living tuatara compared with 25°C in the skink which inhabits semi-arid situations in southern Australia. The overall thermoregulatory significance of melatonin in reptiles is, however, far from clear at this stage and much more work needs to be done.

The steroid hormone progesterone has been shown to have a marked effect on behavioural thermoregulation in the viviparous skink *Sceloporus cyanogenys* (Garrick 1974), significantly depressing body temperature levels and temperature thresholds for thermoregulatory behaviour, as shown in Fig. 4.10.

The body temperature selected by both pregnant and progesterone-injected females was significantly lower than that of other groups, suggesting a direct effect of this hormone on behavioural thermoregulation in this viviparous species. This has also been demonstrated in another viviparous lizard of the same genus, *S. jarrovi* (Beuchat 1986) and in *Lacerta vivipara* (Lecomte et al.

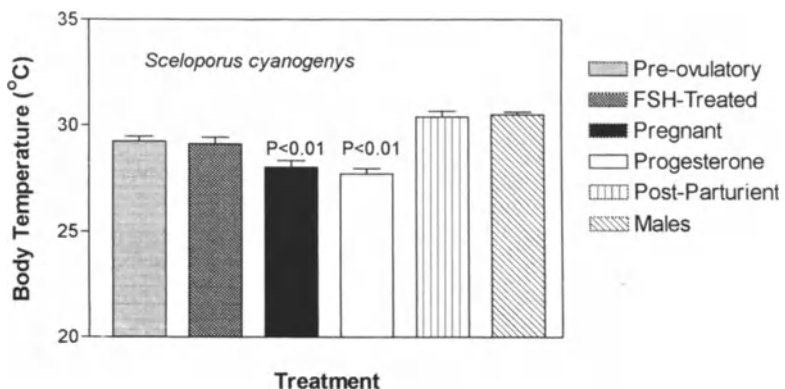


Fig. 4.10. The effect of a number of experimental treatments and the reproductive condition in female and male *Sceloporus cyanogenys*. FSH-injected animals were injected subcutaneously with 10 µg of NIH-FSH-S-9 (ovine) in water every other day for 14 days. Progesterone animals were postparturient females injected subcutaneously with 0.05 ml of an aqueous suspension of progesterone (Scherring's Proluton, 100 mg ml⁻¹) at a dosage of 5 mg twice every 5 days. (Adapted from Garrick 1974)

1993; Patterson and Davies 1978), although the reverse effect, with pregnant females selecting slightly higher body temperatures, has been reported in *Chalcides ocellatus* (Daut and Andrews 1993), *Chalcides bedriagai* (Hailey et al. 1987), *Hoplodactylus maculatus* (Werner 1990; Werner and Whitaker 1978) and a number of snakes (see Sect. 4.5.3).

Beuchat and Ellner (1987) have used *S. jarrovi* to test predictions of life-history theory and they constructed a Leslie matrix life-history model to predict the optimal body temperatures that should be maintained by pregnant females. Central to the model is a trade-off between increased embryonic mortality at high temperatures and reduced growth and increased mortality in females at lower temperatures (Beuchat 1988). The model predicts closely the reduced body temperatures selected by pregnant females in the laboratory and in the field and confirms that this behaviour is a fitness-maximising compromise between divergent thermal optima for embryonic development and for the mother's survival and growth.

A recent paper by Braña (1993), on the wall lizard *P. muralis*, suggests that interactions between selected body temperatures and the physiological condition of reproducing females may be even more complex. This lizard is oviparous, but gravid females were found to select significantly lower body temperatures than either males or nongravid females in the field, but not in a photothermal gradient in the laboratory. The authors interpret this change in behaviour in terms of the added costs associated with a natural environment containing predators. Gravid females in the field reduce their activity, remain close to refugia and effectively convert their predator avoidance tactic from one of flight to crypsis. In the laboratory, in the absence of predators (and presumably the lizards' ability to sense this) their activity is unchanged. The nature of the changes in thermoregulatory behaviour brought about by alterations in physiological and endocrinological condition are thus quite complex and papers such as those just cited perform a great service in helping to unravel the many factors involved.

The involvement of the neurohypophysial peptide AVT in reptilian thermoregulation is suggested by a number of studies showing effects of dehydration and/or salt loading in lizards. The effect of increasing plasma osmolality and fluid loss by exsanguination in raising the panting threshold of the lizard *D. dorsalis* (Dupré and Crawford 1986) has been noted in Section 4.3.4 above. Dupré and Crawford (1985a) showed that hyperosmotic salt loading depressed the upper threshold skin temperature and both the lower threshold skin and core temperatures of this same species. Intraperitoneal injections of 3 mol NaCl increased plasma osmolality from 363 ± 9.9 to 459 ± 13.8 mOsm kg⁻¹ and the lower limit core temperature fell significantly from 39.28 ± 0.10 °C to 37.05 ± 0.25 °C. This was in contrast to dehydration to 80% of initial body mass which was without effect on temperature selection and contrasts with the results of desiccation in *Sceloporus undulatus* (Crowley 1987) in which 16–20% mass loss induced a roughly 2 °C fall in selected body temperature. Hyperkalaemia, in-

duced by intraperitoneal injections of KCl, in the chuckwalla *S. obesus* was also associated with a significant fall in body temperature from $36.6 \pm 0.7^\circ\text{C}$ to $34.8 \pm 0.9^\circ\text{C}$ (Smits et al. 1986).

A similar effect of hypernatraemia on preferred body temperature has been observed in the Australian agamid lizard *Ctenophorus* (*Amphibolurus*) *ornatus*, which inhabits granite tors in the semi-arid regions of Western Australia (see Bradshaw 1986a). Rather than elevate blood sodium concentration with a single massive salt injection of 3 mol NaCl as with the protocol of Dupré and Crawford (1985a), hypernatraemia in *C. ornatus* was induced over a period of 3 days with injections of 2 ml 100 g^{-1} of isosmotic (150 mmol) NaCl into unfed animals. As the lizards constantly lose ion-free water by insensible evaporation from the integument, in the absence of any other input of free water, the injections induce appreciable hypernatraemia, as shown in Table 4.5. Salt loading significantly increased the plasma sodium concentration in both intact individuals and in those in which the hypothalamo-neurohypophyseal tract had been interrupted by the placement of electrolytic lesions, which block the secretion of the hormone AVT (Bradshaw 1975, 1976, 1986a, 1996). Plasma sodium concentrations did not differ, however, between intact and tract-operated individuals prior to the commencement of salt loading, showing that the lesion had no effect on normal water and electrolyte balance.

Data on mean body temperatures selected in a photothermal gradient with these same experimental treatments are presented in Fig. 4.11. An analysis of variance (ANOVAR) of the data shows that neurohypophysectomy had no effect on the preferred body temperature of hydrated individuals, but salt loading significantly depressed the preferred body temperature of intact, but not neurohypophysectomised, individuals – even though their plasma sodium concentration was similarly elevated by the treatment, as seen in Table 4.5.

The addition of AVT has the effect of depressing the preferred body temperature in salt-loaded neurohypophysectomised individuals to the same level as seen in intact salt-loaded individuals, showing that the effect on preferred body temperature is not due to hypernatraemia itself, but to the release of AVT normally provoked in lizards by hypernatraemia.

The tight negative relationship between plasma sodium concentration and preferred body temperature in *C. ornatus* is also shown in Fig. 4.12, and although normal circulating levels of AVT have not been assayed in *C. ornatus*, one may predict a similar relationship with titres of this hormone and selected body temperatures.

As discussed in some detail in Section 3.2.2, AVT is known for its action in controlling osmoregulatory functions of the kidney in reptiles, but the effect of this hormone on thermoregulatory behaviour may also be interpreted in an homeostatic context. Hypernatraemia, due to high dietary intake of sodium, is a common problem facing many desert lizards (see Bradshaw 1986a for a review) and lizards such as *C. ornatus* are obliged to endure marked perturbations of their milieu intérieur until the excess salt can be excreted following

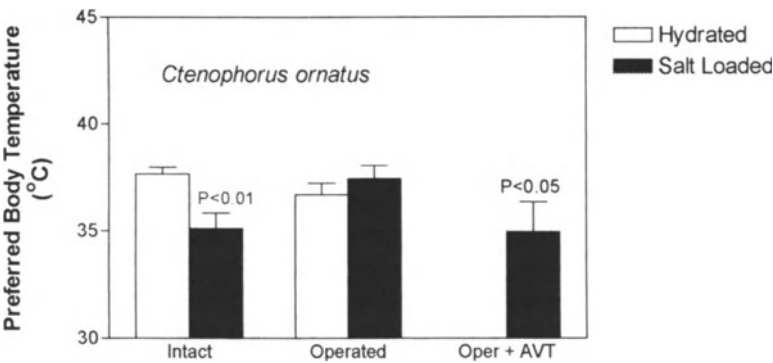


Fig. 4.11. The effect of salt loading on preferred body temperature in intact and neurohypophysectomised *Ctenophorus ornatus*, and the effect of injections of arginine vasotocin (AVT) in salt-loaded, operated individuals. Salt-loaded animals were injected with 2 ml 100 g⁻¹ of 150 mmol NaCl for 3 days and AVT was injected intraperitoneally for 3 days at a dosage of 5 ng 100 g⁻¹. (Adapted from Bradshaw 1996)

Table 4.5. Plasma sodium concentrations in intact and tract-operated *Ctenophorus ornatus* with progressive salt loading. (From Bradshaw 1996)

Treatment	Plasma sodium conc. (mmol l ⁻¹)	
	Intact	Tract-operated
Hydrated	166.7 ± 5.9	171.4 ± 2.9
Salt-loaded	180.1 ± 5.2	185.7 ± 2.1
Salt-loaded + AVT ^a		196.6 ± 3.2

^a AVT injected intraperitoneally at a dosage of 5 ng 100 g⁻¹ for 3 days.

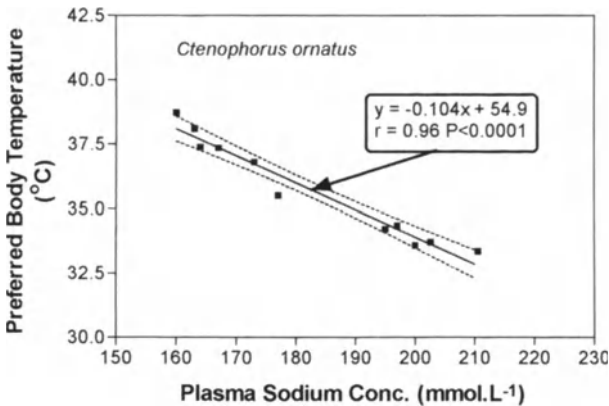


Fig. 4.12. Relationship between preferred body temperature and plasma sodium concentration in the agamid lizard *Ctenophorus ornatus*. (Adapted from Bradshaw 1996)

summer rainstorms. By reducing the body temperature when salt-loaded, animals would reduce their rate of evaporative water loss and thus prolong the period that they are able to survive with increasing levels of hypernatraemia. The effect of AVT on preferred body temperature in prolonging survival is thus very analogous to the effect of melatonin on the panting threshold, as noted above.

These are the first data indicating that the neurohypophysial peptide AVT has an effect on thermoregulatory behaviour in a reptile and, although the site of action of the hormone within the brain is unknown at this stage, Bons (1983) has mapped AVT and mesotocin secretory systems in the brain of four lizard species, *Podarcis (Lacerta) muralis*, *Arcanthurus pardalis*, *A. boskianus* and the gecko *Tarentola mauritanica*.

There are some data available on the effects of thyroxine (T_4) on levels of activity and thermoregulation in lizards but the effects are not clear cut (Lynn 1970) although peak levels of thyroid hormones tend to coincide with seasonal periods of maximum activity (John-Alder 1984; Kar and Chandola-Saklani 1985). Thyroidectomy, as would be expected, reduces activity in lizards (Gerwein and John-Alder 1992), but this is not repaired by injections of T_4 , which do not affect overall rates of energy expenditure (Joos and John-Alder 1990). A recent study by Steinberg et al. (1993) with the teiid lizard *Ameiva undulata* found no effects of thyroid hormone on thermoregulation per se but showed that T_4 injections increased organismal excitability without stimulating either the rate of metabolism of the lizard or its spontaneous patterns of behaviour. Clearly, far more work needs to be done before the full functional significance of thyroid hormones in reptiles becomes apparent.

4.4

Behavioural Mechanisms

The question of whether reptiles regulate their body temperature around a single set-point, as is implied by the early literature on "eccritic" and preferred body temperatures of different species, is of some relevance in the context of homeostatic control systems. The concept of homeostasis implies the maintenance of some optimal state or condition by autoregulatory processes, and this hypothetical endpoint, be it blood pressure, glucose concentration or plasma osmolality, is always assumed to encompass some narrow but finite range of values to which the system always tends. Deviation from this range of normal values is usually taken as evidence of pathology.

4.4.1

The Neuronal Basis for Thermoregulation

There has been considerable discussion on this point in the reptilian literature, with some models postulating a single thermal set-point (McGinnis 1966; de Witt 1967a,b; McGinnis and Dickson 1967; de Witt and Friedman 1979),

whereas Heath (1970) proposed a coupled on-off model that received some experimental support (Berk and Heath 1975a; Cabanac 1979; Garrick 1979). Placing lizards in a shuttle-box situation rather than an uniform thermal gradient readily reveals the existence of two apparent set-points, one low (LBTS) and the other high (HBTS), controlling heat seeking and heat avoidance behaviour respectively as seen in Fig. 4.13. Data such as these from the desert iguana *D. dorsalis* form the basis for the stochastic dual-limit model of behavioural thermoregulation of Barber and Crawford (1977) and electrophysiological studies with lizards provide additional support. Electrophysiological studies with the skink *Tiliqua scincoides*, by Cabanac et al. (1967) and by Myrhe and Hammel (1969), resulted in the identification of two sets of temperature-sensitive neurones in the preoptic region of the brain. Cold-sensitive neurones increased their firing rate with decreasing brain temperature (low Q10 neurones) whilst the warm-sensitive (high Q10 neurones) increased their rate of firing with increasing brain temperatures. Activity curves for these two sets of cold- and warm-sensitive neurones were found not to overlap in the range of body temperatures of active *T. scincoides*, suggesting the presence of an upper and a lower set-point rather than a single preferendum.

Attempts have been made to localise the regions of the brain responsible for controlling thermoregulatory behaviour in the desert iguana *D. dorsalis* and Berk and Heath (1975a) and Kluger et al. (1973) investigated the effects of

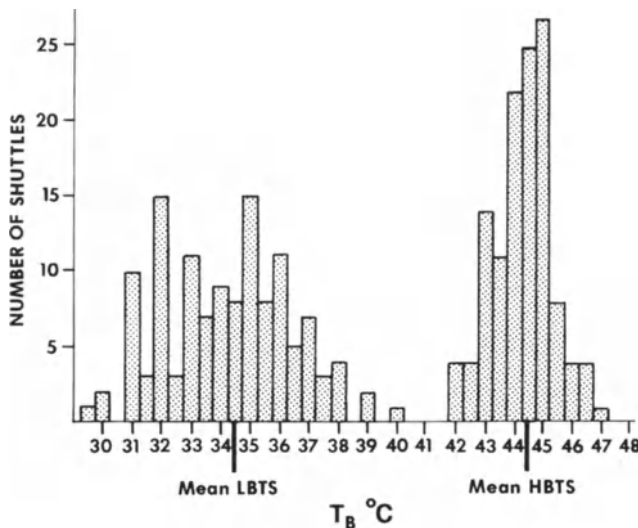


Fig. 4.13. Frequency distribution of body temperatures recorded from a single *Dipsosaurus dorsalis* in a "shuttle box" situation, showing absence of overlap between high and low temperatures. T_b Body temperature; LBTS low body temperature at shuttling; HBTS high body temperature at shuttling. (Modified after Berk and Heath 1975a; Bradshaw 1986a)

lesions in the posterior hypothalamic region. Lesions in the medial preoptic area, suprachiasmatic nuclei, and anterior hypothalamus significantly lowered the lower set-point and frequency of shuttling. Lesions of the mammillary bodies in the posterior hypothalamus also reduced the lower set point as well as the frequency of shuttling, as shown in Table 4.6. These data show both a progressive decrease in shuttling frequency with increasing damage to the mammillary bodies and a significant decrease in the low temperature shuttling set-point with 80% damage. It must be kept in mind, however, that the mammillary bodies are regions in the reptilian brain through which major nerve tracts pass (Pearson and Pearson 1976) and the effects of these lesions thus cannot be ascribed to any identifiable nuclei.

In the last 20 years little work seems to have been done on interpretative neuronal models for reptilian thermoregulation. The "three neurone model", proposed by Berk and Heath (1975a; Fig. 4.14), still seems the most promising and is discussed in some detail by Firth and Turner (1982). As these authors point out, however, these cybernetic models make many assumptions about the type and sensitivity of neurones to thermal and other stimuli, none of which has ever been tested. The models should thus be valued for their heuristic insights into thermoregulation, rather than being viewed as realistic descriptions of neuronal events.

de Witt and Friedman (1979) have suggested that the characteristic negatively skewed temperature distribution of reptiles indicates the regulation not of body temperature per se but of some physiological rate process whose rate itself is an exponential function of temperature. This rate process has yet to be identified in any species and it is of interest to note that the numerical model of Barber and Crawford (1977) can account for negative skewness in body temperatures, if one assumes a lower sensitivity for the lower set-point (LBTS) than the upper set-point (HBTS).

The question of whether reptiles adhere to a single preferred body temperature or instead are behaviourally motivated by separate upper and lower set-points is quite germane to the problem of the maintenance of thermal homeostasis in reptiles. If there is only a single set-point, animals could be considered to be stressed as soon as their body temperature exceeds this (see Bradshaw 1992b). Otherwise one would be forced to conclude, as did de Witt

Table 4.6. Modifications to thermoregulatory behaviour of the lizard *Dipsosaurus dorsalis* following damage to the mammillary bodies. (Modified from Kluger et al. 1973)

Condition	N	Shuttling frequency	HBTS (°C)	LBTS (°C)	Mammillary destruction %
Controls	5	1.49 ± 0.32	41.2 ± 0.39	37.3 ± 0.49	0
Lesioned	3	0.49 ± 0.03 ^a	40.9 ± 1.06	35.5 ± 0.64	25
Lesioned	5	0.08 ± 0.04	39.4 ± 0.72	32.6 ± 1.44 ^a	80

^a $P < 0.05$.

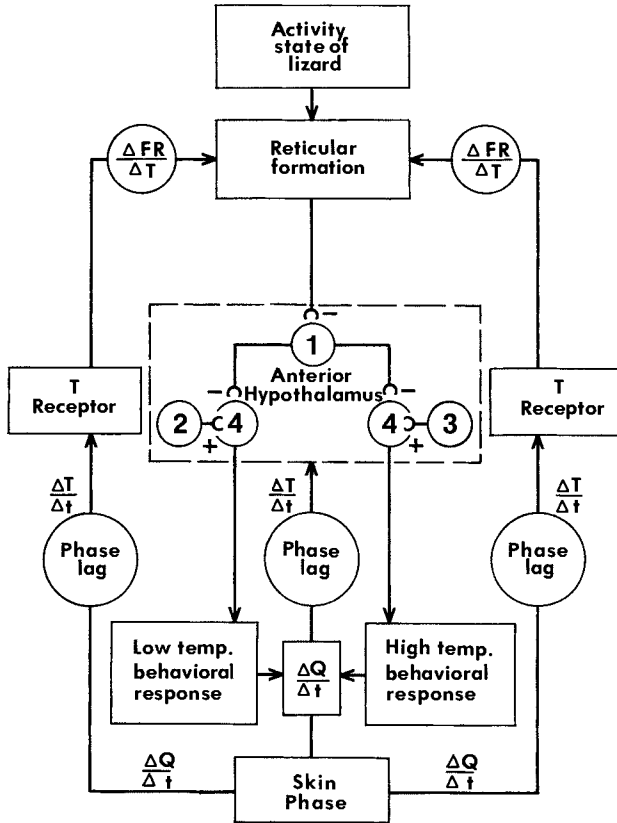


Fig. 4.14. Hypothetical neuronal network to describe thermoregulation in reptiles. 1 Temperature-insensitive neurone; 2 low Q10 cold neurone; 3 high Q10 warm neurone; 4 motoneurone; Q heat content; FR firing rate; T temperature; t time; + excitatory synapse; -- inhibitory synapse; T receptor peripheral thermal receptor located in the skin. (Adapted from Berk and Heath 1975a; Bradshaw 1986a)

(1967b) when studying the desert iguana, that the lizards permit their body temperature to rise above the preferendum when engaged in territorial behaviour and predator defence, but maintain the preferred body temperature during feeding and courtship. With the second two set-point model, such complex explanations are unnecessary and one would only invoke the concept of stress if the body temperature exceeded the HBTS which, for example, in *D. dorsalis* is 41.7°C, some 7°C below the CTMax for this species (Whitfield and Livezey 1973). More recent studies appear to accept the two set-point model of thermoregulation as being the best descriptor of thermal changes in ectotherms (Dreisig 1985).

4.4.2

Maintenance of Thermal Homeostasis in the Field

4.4.2.1

Turtles

Of all the reptiles the Chelonia are perhaps the most divergent, with debate still continuing over their origins (Gaffney et al. 1987; Lee 1993), their decreased rate of karyotypic change since the Mesozoic (Bickham 1981), and the reasons for their enhanced longevity (Gibbons 1987). They are an evolutionarily conservative group that displays wide ecological diversity. In all of the continents, except Australia, the Chelonia are represented by terrestrial species, many displaying gigantism, and most are now classified as rare and endangered and threatened with extinction.

Information on field body temperatures of turtles has been reviewed by Avery (1982) and Meek and Avery (1988) and a considerable amount of this relates to basking behaviour in aquatic species and its possible physiological advantage (Boyer 1965; Crawford et al. 1983; Schwarzkopf and Brooks 1985; Lacher et al. 1986). Interestingly, the very large marine leatherback turtle (*Dermochelys coriacea*) is reported to be able to maintain its body temperature as much as 18°C above ambient sea temperatures (Friar et al. 1972; Goff and Stenson 1988) and Goff and Stenson (1988) report the presence of what they interpret as brown fat in this species.

Of most interest, from the point of view of homeostasis, are the terrestrial species, especially those inhabiting arid and desert regions. Thermoregulation in Hermann's tortoise (*Testudo hermanni*) was studied in Croatia by Meek (1984, 1988), who found that thermoregulation was not precise, with mean body temperatures varying between 24.8 and 30.4°C, depending upon local climatic conditions. Significant seasonal variations were also noted but these were interpreted not as differences in preferred body temperature but as variations imposed by the thermal constraints of an environment where temperatures fluctuate widely. Further south, in Greece, body temperatures up to 35°C were recorded in summer from *T. hermanni* and between 36 and 37°C in *T. marginata* (Willemsen 1991). Activity is typically unimodal in spring changing to bimodal in summer and autumn, as in *P. sicula* (Foà et al. 1994). Clear cases of habitat separation are often seen in *T. hermanni* and *T. graeca* (Watson 1962) but attempts to interpret these in terms of thermoregulatory abilities and constraints have met with little success; instead Wright et al. (1988) advance an evolutionary hypothesis for Aegean populations of tortoises.

Meek and Avery (1988), in discussing thermoregulation of *T. hermanni* in southern France, suggest that the species here is a thermoconformer, due to the reduced opportunities for basking in the heavily wooded habitats where it is still found (Pulford et al. 1984). A recent paper by Huot-Daubremont et al. (1996), using indwelling temperature-sensitive transmitters, shows clearly,

however, that the tortoise does thermoregulate in the Var region (Gonfaron near to St Tropez) maintaining a body temperature of close to 31 °C for several hours during the day.

The subtlety of thermoregulation in *T. hermanni*, and the difficulty that one may have in interpreting field data, is well illustrated by the study of Chelazzi and Calzolari (1986), in which familiarity with the environment was shown to have a marked impact on the efficacy of thermoregulation. Tortoises were introduced into areas and their thermoregulation compared with that of residents in a novel design. Residents (experienced) were found to reach maximum body temperatures on average 2 h earlier than introduced (naive) tortoises and their body temperature showed a greater independence from ambient temperatures. The introduced tortoises, by contrast, behaved essentially as thermoconformers, with body temperatures closely tracking air temperatures. This highlights the significance of an individual's knowledge of the thermal structure of its immediate environment in maintaining thermal homeostasis.

This interesting study immediately makes one question the validity of so many laboratory studies on thermoregulation in reptiles, in which the animals are introduced into an alien environment of which they have no prior experience and then expected to behave as if they were in their natural habitat. Further analysis of the effects of habituation and experience on thermoregulation in reptiles would be most desirable.

Thermoregulation has been studied in ornate box turtles (*Terrapene ornata*) in two widely separated populations in the United States by Ellner and Karasov (1993), and body temperatures of individuals from Wisconsin, measured in a thermal gradient in the laboratory were some 6.3 °C lower than animals from Kansas. Field studies confirmed that this difference was due to active selection of lower temperatures by the Wisconsin individuals and this was interpreted as a strategy increasing potential daily activity time. Such a large difference in apparent preferred body temperature of individuals of the one species is most unusual and, although many acclimatory and seasonal factors are known to condition the preferred body temperature, one would need to confirm that sibling species are not somehow involved in this case. The authors note that the laboratory animals were not acclimated to the same temperature (the Kansas data are from Legler 1960) and the question of genotypic versus phenotypic adaptation remains unresolved.

By far the greatest amount of work on thermoregulation has been done with terrestrial desert tortoises of the genus *Gopherus* and *Xerobates* (Bour and Dubois 1984) in the United States (see Spotila et al. 1994). Gopher tortoises appear to have differentiated from emydine pond tortoises by the early Eocene, but the desert tortoise *G. agassizi* and its relatives may have only differentiated in the middle to late Pleistocene in North America (van Devender et al. 1976; van Devender and Moodie 1977). This underlines again the fact that the deserts and their herpetofauna in the United States are relatively recent phenomena, compared with those in North Africa and Australia

(Bradshaw 1986a). This makes the study of the nature and evolution of homeostatic mechanisms in indigenous species very interesting in a comparative context.

Activity and thermoregulation of the gopher tortoise *G. polyphemus* were studied over an 8 year period in southern Florida by Douglas and Layne (1978), who found that the tortoises were active in every month of the year, peaking in May–August. Body temperatures of active animals averaged 34.7°C and clear signs of thermal stress were noted in summer in animals tethered in full sun. Shade-seeking, frothing at the mouth and rapid breathing occurred at a body temperature of 38°C, suggesting that this species has little ability to tolerate elevated internal temperatures. This study emphasises the importance of the burrow as a thermal refugium for this species and this has been incorporated in recent habitat models for desert tortoises (Schamberger and Turner 1986).

The most comprehensive study of thermoregulation in desert tortoises to date is that reported by Zimmerman et al. (1992, 1994) with *Xerobates (Gopherus) agassizii* in the Mojave desert. Body temperatures of desert tortoises varied widely depending upon time of day, microhabitat selection (primarily use of burrows) and time of the activity season. Comparison with operative temperatures shows that the tortoises regulate their body temperature, however, primarily by retreating to cool burrows during the hottest part of the day when operative temperatures reach 60–70°C in the Mojave desert. Retreat to burrows occurred typically when operative temperatures reached approximately 40°C and body temperatures of the tortoises were typically maintained at about 35°C.

This comprehensive study shows clearly that desert tortoises manifest little of the high precision control over body temperature that is so characteristic of many desert lizards. The authors attributed this to the lack of shuttling behaviour in the desert tortoises which is one of the major mechanisms by which small desert lizards regulate their body temperature between tolerable limits. The eurothermy of the desert tortoises is similar to that shown by crocodiles which depend on their large body size and high thermal inertia to maintain relatively constant body temperatures.

What is also clear is that these desert tortoises are totally dependent upon their burrows to avoid potentially lethal temperatures during the day and they have a very limited behavioural repertoire when compared with even large desert lizards such as the chuckwalla (*S. obesus*) (Nagy 1973), although they may resort to evaporative cooling (McGinnis and Voigt 1971). A study such as the interesting one of Huey and Kingsolver (1993) has yet to be carried out with desert tortoises but the data to hand suggest they have rather limited abilities to contend with the exigencies of their desert environment (Ruby et al. 1994). As we have already seen when considering their water and electrolyte homeostasis (see Sect. 2.4.4.), they spend much of the year out of balance, and Peterson (1993, 1995) has coined the term “anhomeostasis” to characterise their tendency to exploit available resources in a very opportunistic manner. van Devender et al. (1976) go further and suggest that the present desert-living

populations of *X. agassizii* are Pleistocene relics that are only just surviving under present-day conditions of aridity.

4.4.2.2

Lizards

There is little hope or point in this short monograph in summarising the vast amount of literature that now exists on thermal relations of lizards in desert and other environments. What is needed, rather, is a critical analysis of the extent to which desert species maintain thermal homeostasis in the field and whether their abilities evidence any obvious impact of natural selection. Deserts are one of the environments in which one would most expect lizards to be challenged by problems of effective thermoregulation and show evidence of stress if their body temperature exceeds levels that are optimal for activity or conducive to their long-term survival.

Stress was defined by (Selye 1952) as

“a state of non-specific tension in living organisms”,

giving rise to the vexed problem of how best to identify its presence and measure its intensity (Grime 1989). Circulating levels of adrenal corticosteroids are often taken as a direct measure of stress in vertebrates, but in most cases these same hormones initiate homeostatic regulatory processes which also assist the organism in combating the stress. We can, however, define stress as

“the physiological resultant of demands which exceed an organism’s regulatory capacities”

(Bradshaw 1986a, 1992b) and then dissociate potentially harmful changes of state from beneficial regulatory responses.

Using this definition, a stressed animal would thus be expected to display a significant deviation of its milieu intérieur from whatever state is considered optimal and evidence a maximal activation of regulatory responses, which have nonetheless been surpassed or overwhelmed. In the context of thermoregulation, we would look for evidence of stress in a combination of significantly elevated body temperatures, despite full deployment of heat avoidance strategies. This raises, of course, the question of how high should the body temperature be elevated before we bring into play the concept of stress: above the preferred, above the upper temperature for shuttling (HBTS), the panting threshold, CTMax, or even close to the lethal? My hope is that we may resolve this question through an examination of some specific cases from the literature on desert lizards.

Table 4.7 lists the critical temperatures for two species of desert lizards from North America and Australia and illustrates the wide range of temperatures, spanning some 10 °C above the preferred, within which stress could be considered to operate. As may be seen from the data in the last row of the table, the

Table 4.7. Behavioural and physiological correlates of heating above the preferred body temperature (PBT) in lizards. (From Bradshaw 1986a)

Temperature	Definition	<i>Dipsosaurus dorsalis</i> (°C)	<i>Ctenophorus nuchalis</i> (°C)
Preferred body temperature	Mean temperature selected in a thermal gradient	38.5 °C ¹	36.4 °C ²
Maximum voluntary temperature (HBTS)	Body temperature at which lizard shuttles to shade	41.7 ³	?
Panting threshold (PT)	Body temperature at which mouth opens and ventilation rate increases	44.5 ⁴	44.1 ⁵
Critical thermal maximum (CTMax)	Body temperature at which animal loses righting reflexes but from which recovery is possible	48.6 ⁴	48.5 ⁶
Lethal temperature (LT)	Lowest "high" body temperature from which recovery is not possible	50.2 ⁷	49.0 ⁸
Highest body temperature recorded in field (T _b Max)		42.0 ⁹	43.8 ¹⁰

¹ De Witt (1967a); ² Bradshaw and Main (1968); ³ Berk and Heath (1975a); ⁴ Whitfield and Liverzey (1973); ⁵ Heatwole (1970); ⁶ Heatwole (1976); ⁷ McGinnis and Dickson (1967); ⁸ Bradshaw and Main (1968); ⁹ de Witt (1967b); ¹⁰ Bradshaw and Main (1968).

highest body temperature recorded in the field for either species is close to, but below, the panting threshold, suggesting that this may be a good operative temperature for the onset of thermal stress.

One interesting approach to the question of the efficacy of thermoregulation is that taken by Pianka (1986), who contrasted the thermoregulatory responses of desert lizards from three continents. Regressions of body versus air temperatures were plotted for some 82 species of lizards from North America, the Kalahari desert and Australia. A second plot of the slope versus the ordinate for each species is shown in Fig. 4.15 and reveals a surprising linear correlation of high significance. Plotting the constant versus the exponent in power curves which have the general form $y = ax^b$, or the ordinate against the slope in linear regressions where $y = ax + c$ (which can be viewed as the equation of a power curve not passing through the origin where the exponent $b = 1.0$), can be a very revealing way of comparing the adaptive strategies of different species and was also used by Bradshaw (1986a) to compare rates of evaporative water loss of desert lizards. In this case, here, what is being compared is the extent to which different species deviate from an isomorphic plot of body versus air temperature.

In the case of a perfect thermoconformer, body temperature would always be identical with air temperature and the equation of the line would be $y = x$

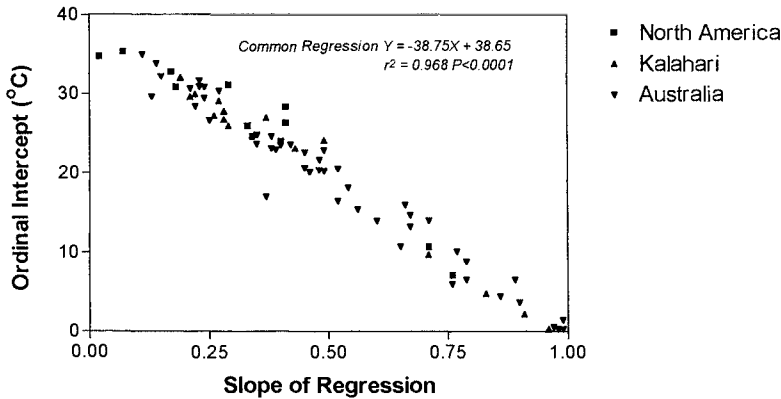


Fig. 4.15. Regression of ordinal intercept (in °C) versus slope of species plots of body versus air temperature for 82 species of desert lizards from North America, the Kalahari desert and Australia. (Modified after Pianka 1986)

with a slope of 1.0 and an ordinal intercept of zero. A perfect regulator, by contrast, would maintain a constant body temperature of, say 38°C regardless of the air temperature, and the line would be parallel to the abscissa, with a slope of zero and an ordinal intercept of 38. The equation of this line would be $y = 0x + 38$, or $y = 38$ for all values of x .

When one plots the slope against the ordinal intercept, as in Fig. 4.15, the species are effectively being arranged on a continuum according to their thermoregulatory capacities – with the best regulators having low slopes, and flat curves, and the poorest having steeper slopes that tend to 1.0 in the extreme case of pure thermoconformity. Pianka (1986) speculates that the ordinal intercept of 38.7°C of this common regression may represent some

“innate design constraint imposed by lizard physiology and metabolism.”

This seems unlikely, however, and would seem only to be the consequence of an inherently rectilinear data set of air and body temperatures which range in both cases between 0° and 40°C.

This approach makes it clear, however, that there is enormous variation, even amongst desert lizards, in the extent to which they apparently thermoregulate. The slope of the body temperature/air temperature regression is 0.71 for *Xantusia vigilis* and 0.76 for *Coleonyx variegata* from North America; 0.96 for *Chondrodactylus angulifer*, 0.91 for *Colopus wahlbergi* and 1.03 for *Pachydactylus rugosus* from the Kalahari desert; 0.89 for *Varanus tristis*, 0.99 for the pygopodid *Pygopus nigriceps* and 0.99 for the gecko *Nephurus vertebralis*, all from Australian desert regions. Do these data from Pianka (1986) really suggest that all these species are thermoconformers, or do they reflect instead the vagaries of field-based measurements of body temperatures in species that are in general either nocturnal or secretive?

Many early workers who studied desert lizards assumed that they are active at body temperatures that are close to their CTMax (Cowles and Bogert 1944; Curry-Lindahl 1957, 1979; Cloudsley-Thompson 1971; Hamilton 1973). This is all the more believable when it has been observed that *Uta stansburiana*, for example, will reach its CTMax in 1 min if tethered on the surface in midday sun in the desert (Tinkle 1967) and that hatchling *Uta* will die before reaching shelter if placed between bushes only seven or eight feet apart at midday. However, as Huey (1982) has pointed out, in his excellent review of reptilian thermal relations, more recent field studies demonstrate that reptiles are rarely active at near-threshold temperatures, except in emergencies.

Huey (1982) has compiled data from different reptilian groups. These are shown in Table 4.8 and make clear that most lizards in fact operate with very wide thermal safety margins. As may be seen from this table, activity temperatures of lizards are, on average, 10–13 °C below the CTMax and the highest temperatures ever recorded in the field for the various species sampled are some 6.5 °C less than their respective CTMax.

Can we conclude from this that desert lizards never experience thermal stress in their natural environment – defined here as a body temperature elevated significantly above vital limits – despite the operation of normal heat avoidance or dissipation strategies? Regretfully, this is not the case, if only because we lack adequate data with which to test such a proposition. An interesting paper by van Berkum et al. (1986) on the tropical lizard *Ameiva festiva* made the point that

“although these lizards are active foragers, their speed and duration of movement in the field fell far below the levels of speed and stamina that they achieved in the lab(oratory) when measured at temperatures they regularly experienced in the field”.

They speculate that the phenotypic capacities of animals may not be shaped by routine activities, but instead by rare events that may be critical for an animal's survival – a point already made by Gans (1979) in developing his concept of “excessive construction”.

Table 4.8. Activity temperatures of reptiles in relation to critical temperatures. (Modified from Huey 1982)

Group	CTMax – T _b	CTMax – T _b Max
<i>Turtles</i>	13.7 ± 1.10	7.4 ± 1.24
<i>Lizards</i>		
Diurnal species	10.4 ± 0.56	6.4 ± 1.03
Nocturnal/fossorial	13.0 ± 1.36	6.5 ± 1.17
<i>Snakes</i>	13.1 ± 0.66	6.8 ± 0.66

See Table 4.7 for definitions

In this sense, although it is clear that desert lizards normally do not experience body temperatures that would induce them to pant and which could be considered stressful, this does not prove that such temperatures do not occur from time to time and could be of real importance in determining fitness. A case in point was that recorded inadvertently by Bradshaw and Main (1968) at Port Hedland, in the arid Pilbara region of Western Australia, close to noon on a day with a shade air temperature of 45.5 °C when, paradoxically, large numbers of small lizards (geckos and agamids) were seen elevated high above the ground in shrubs and bushes. The body temperatures of these lizards ranged from 41.0 to 46.0 °C (mean 44.3 °C) and a temperature profile done at the time confirmed that soil temperatures were well in excess of 60 °C. The shade temperature in small clumps of *Triodia pungens* close to the ground ranged from 47.1 to 51.5 °C and, clearly, the coolest place at the time was as far above the ground as possible.

The panting threshold for one of the species concerned, the agamid *Diporophora bilineata*, is given by Heatwole (1976) as 31.3–40.4 °C, so we may assume that in this particular case there is good reason to believe that these lizards were being exposed to considerable thermal stress. Other cases are almost equally anecdotal. Grenot (1967) mentions observing the large Saharan agamid lizard *U. acanthinurus* panting at the mouth of its burrow at Béni-Abbès in Algeria, although the body temperature at this time was not known.

Perhaps the best test case of desert lizards being exposed to high body temperatures whilst active should be the lizard *Angolosaurus skoogi* that inhabits slip dune faces in the Namib desert (Seely et al. 1988). Hamilton and Coetzee (1969) extended their “maxithermy” hypothesis from desert insects to include these lizards, but, although actual body temperatures were not measured, the study of Pietruszka (1987) failed to confirm the thermal microhabitat predictions inherent in this concept. Nagy et al. (1991) have measured the field metabolic rate (FMR) of free-ranging individuals in situ, which was found to be about half that expected for a lizard of its size, although rates of water flux were similar to those of other desert lizards. Information is now available on water and electrolyte balance of this unusual animal (Clarke and Nicolson 1994) but details of its thermoregulatory behaviour incorporating actual body temperatures are still lacking.

Another iguanid lizard with most unusual thermoregulatory behaviour is *Sceloporus merriami*, which is constrained in its activity by having, at 32.2 °C, the lowest preferred body temperature of any North American desert iguanid (Grant and Dunham 1988). A recent careful study by Grant (1990) has established that average body temperatures of active animals are lower in the morning than the evening (33.3 versus 37.0 °C). By measuring available operative temperatures throughout the day it was shown that these are much broader in the morning (30–60 °C) than in the evening (36–38 °C) and that the lizard is forced to accept higher body temperatures, higher rates of metabolism and water loss, and reduced locomotor performance if it is to be active at all in the afternoon. Actual body temperatures were observed not to exceed 40 °C and

Grant (1990) cites a figure of approximately 41 °C for "lethal thermal stress" in this species.

The chuckwalla *S. obesus* is another case in point. Although excellent data are available on its ecophysiological relationships, there is some confusion in the literature as to its thermoregulatory capacities. McGinnis and Falkenstein (1971) reported a mean body temperature of 35.9 °C for animals maintained in an enclosure. This is similar to the temperature reported in laboratory animals (Muchlinski et al. 1989) but lower than that reported by Zimmerman and Tracy (1989) and some 2.5–2.9 °C lower than found by Muchlinski et al. (1990) in a careful field study with instrumented free-ranging animals. Even more confusing, Case (1976) measured temperatures as high as 43–46 °C from animals wired with thermocouples.

Muchlinski et al. (1990) found that chuckwallas ceased activity once their body temperatures reached approximately 38 °C and then retreated into rock crevices. Temperatures there, however, could rise to quite high levels in late afternoon and the maximum recorded was 42.9 °C, well below the 46 °C recorded by Case (1976) and the CTMax of 46.7 °C for this species given by Cowles and Bogert (1944). I am not aware that the panting threshold has been determined for *S. obesus* but I would expect it to be close to 44 °C.

Nagy (1973) notes that the chuckwalla abandons all diurnal activity, and hence thermoregulation, for long periods in the field when starved and in poor condition. Rates of CO₂ production measured with doubly labelled water typically fall in mid-summer to levels close to or even below 0.05 ml g⁻¹ h⁻¹, which is lower than basal levels for this species of 0.168 ml g⁻¹ h⁻¹ predicted from the equation of Bennett and Dawson (1976) for iguanid lizards. Nagy (1972) documents changes during the drought year of 1970–1971 in the Mojave desert where marked individuals lost some 55% of their initial body mass and the specific activity of injected tritiated water remained constant (indicating no significant input of free water) for a period of 10 months. These individuals thus experienced severe water stress (see Sect. 2.5.4 and Table 2.13) but would appear to have avoided potential thermal stress during this exceptional drought by abandoning any attempt at thermoregulation.

There are other instances of a breakdown in thermoregulatory behaviour as a consequence of detrimental changes in the milieu intérieur of desert lizards. A combination of hypernatraemia and chronic dehydration leads to a loss of normal thermoregulatory behaviour in the field of the Australian agamid lizard *Ctenophorus* (*Amphibolurus*) *ornatus* (Bradshaw 1970), and Henzell (1972), working with several desert species of the genus *Egernia*, noted that dehydration had a detrimental effect on the precision of thermoregulation. Cogger (1974) found that even mild starvation was sufficient to lower the activity temperatures of the desert mallee dragon *Ctenophorus* (*Amphibolurus*) *fordii* in central Australia and Rice and Bradshaw (1980) noted that a loss of condition in *C. nuchalis* was associated with a temporary loss of the ability to alter skin reflectance with change in body temperature (see Section 4.3.3 above). Lee (1980), working with two tropical species of *Anolis*,

found that well-nourished individuals thermoregulated more precisely than poorly nourished ones. This conclusion was disputed by Henle (1992), who argued that a lack of thermally suitable habitat is the cause.

Thermal homeostasis and its maintenance appear to be conditional, at least in desert lizards, on the proper operation of other, more general, homeostatic processes controlling water, electrolyte, energy and probably nitrogen balance of the animal. If the condition of the animal declines, then a breakdown in thermoregulatory behaviour would appear to be one of the first obvious consequences. Parenthetically, this does make one wonder whether some of the puzzling effects of parietectomy and pinealectomy on thermoregulatory behaviour in lizards (see Sect. 4.3.5 above) may not be due to changes in other physiological parameters which are usually not monitored in such experiments. Instances of desert lizards experiencing thermal stress would appear to be rare in the literature, but this does not mean necessarily that they are without significance. Studying animals in the field during periods of climatic extreme (in this case, prolonged hot droughts) may be more revealing in the long run of the impact of natural selection on such populations than any number of studies carried out during so-called normal years.

4.4.2.3

Snakes

In contrast to the wealth of data available on thermoregulation of lizards, snakes have been poorly studied and little detailed information is available on the thermoregulatory behaviour of desert species in the field. A recent paper by Rosen (1990) suggests that

“intrageneric variation in PBT (preferred body temperature) of snakes has yet to be demonstrated unequivocally”,

noting that all records fall between 28 and 30 °C. Snakes are difficult, as well as sometimes dangerous, animals to study and their secretive and frequently nocturnal habit does not make them ideal subjects. Nocturnality appears to be much more common in snakes than in lizards. Huey (1982) provides data on the frequency of nocturnality in reptiles, citing 19.6% of lizard species which contrasts with 53.5% of snakes. Shine (1994), in a recent review of life-history variation of Australian snakes, concludes that body mass is the most important single factor in explaining observed ecological differences, but unfortunately thermoregulatory strategies did not form part of this analysis.

Lillywhite (1987) has recently reviewed much of what is known on thermoregulation in snakes and contests the earlier conclusion that snakes are imprecise regulators (Avery 1982). Instead, more recent field studies were cited, such as that of Peterson (1987) in which instrumented snakes were monitored over a period of days. In this study temperature-sensitive transmitters were surgically implanted in ten *Thamnophis elegans vagrans*. With the

use of models to provide information on available operative temperatures, Peterson (1987) found that for

“most of the time the physical environment prevented the garter snakes from attaining their preferred temperatures”.

In warm conditions it was found that the snakes thermoregulated precisely but selected temperatures lower than those generally chosen by lizards (mean = 29.9°C).

A careful field study of thermoregulation in Australian blacksnakes (*Pseudechis porphyriacus*) by Shine (1987) found that there was very little variation in activity temperature range which fell between 28°C and 32°C, regardless of season, habitat and ambient temperature. Figure 4.16 is taken from this study and shows the extremely effective thermoregulation of this snake, with body temperatures above ambient in spring and below in summer.

A further study of this same species at a later time found that body temperatures of snakes were significantly lower in summer than in spring, and this corresponded with a reduction in the level of activity brought about, it was thought, by prevailing drought conditions and a paucity of prey items (Shine and Lambeck 1990). This highlights the need for caution in concluding, on the basis of a single study over a limited time period, that thermoregulatory behaviour is essentially invariant or, conversely, labile.

Nevertheless, a similar conclusion was reached by Hammerson (1987), working with the racer *Coluber constrictor* in west-central California. This species shows wide geographic variation in scalation, body size and proportions, coloration, dentition, diet and clutch and egg size, but was found to maintain a body temperature of about 32°C, regardless of location. Plummer

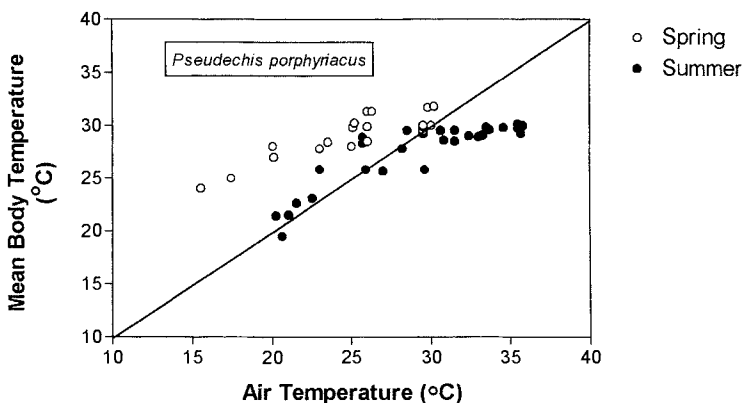


Fig. 4.16. Mean body temperatures of the black snake *Pseudechis porphyriacus*, for each hour of the day, compared with air temperatures during spring and summer in the semi-arid region of New South Wales, Australia. The line represents $y = x$. (Modified after Shine 1987)

(1993) similarly found that the mean activity temperature of arboreal green snakes (*Opheodrys aestivus*) was 29.3 °C, but measurements of operative temperatures with life-size models showed that, contrary to predictions, this species is not heliothermic and closely tracks available shade temperatures. Hopefully, with the wider application of techniques for measuring operative temperatures in field studies of temperature regulation in snakes, a better understanding of their thermoregulatory strategies will emerge.

There appear to be few studies in the literature in which an attempt has been made to assess the reaction of desert species of snakes to excessively high temperatures. Hammerson (1989) studied the snake *Masticophis flagellum* in San Diego County, California, and noted that these snakes retreated to underground burrows at the relatively low body temperature of 30.4 °C. Some individuals were observed, however, to crawl across substrates that exceeded 50 °C, but this apparently had little effect on their body temperature, presumably because they were able to soon enter shade or a cool burrow. Huey et al. (1989) analysed preferences shown by garter snakes (*Thamnophis elegans*) for rocks of varying thickness as thermal retreats. Both very thin (<20 cm) and thick (>40 cm) rocks were avoided and the authors speculated that the intermediate thickness rocks chosen by the snakes enabled them to avoid overheating (thin) but remain in a relatively warm environment conducive to the continuation of physiological processes ("physiologically optimal microhabitats"). The elegant model posits an active "underground life" for snakes which would set them apart from other reptiles, such as lizards.

Although Rosen (1990) has concluded that the evidence for thermal differentiation amongst snakes is poor, the very interesting recent study of Secor and Nagy (1994) with the sidewinder *Crotalus cerastes* and the coachwhip *Masticophis flagellum* shows that active body temperatures may vary significantly at certain times of the year. The sidewinder is a nocturnal "sit-and-wait" predator and the mean body temperature of active animals was 25.3 ± 0.1 °C. The coachwhip is a diurnal widely foraging species and the mean body temperature of active individuals was significantly higher (33.1 ± 0.1 °C) in the summer months. The FMR, measured with doubly labelled water, was also higher in coachwhips than in sidewinders during the active season, as were rates of water flux and estimated feeding rates. Body temperatures of up to 39 °C were recorded from coachwhips before they retreated to rodent burrows, making it one of the most thermophilic of snakes studied to date. Overall energy expenditure of coachwhips was some two to three times higher than sidewinders, and the low-cost form of locomotion of the latter species (Secor et al. 1992) is obviously another factor contributing to its greater economy.

From the above, it is clear that there is still much to be learned about thermoregulatory behaviour in snakes. From the literature, it would appear that they are thermally much more conservative than lizards, but there are so few detailed studies of desert-living species that even this is not certain. Hopefully, the coming years will see greater attention to snakes and the routine

application of operative temperature techniques which have proven so useful in interpreting thermoregulatory behaviour in lizards.

4.5

Conclusion

The study of reptilian thermoregulation and its behavioural and physiological components has progressed enormously since the pioneer study of Cowles and Bogert (1944), showing that snakes and lizards are not just hapless captors of their immediate thermal environment. The initial organising concept of a single preferred or ecritic body temperature maintained by behavioural means is still accepted as a working hypothesis by many workers but has lost ground in recent years. The stochastic dual-limit hypothesis of Barber and Crawford (1977) has received considerable experimental support and a number of studies provide a good electrophysiological grounding for the model (Cabanac et al. 1967; Myrhe and Hammel 1969; Kluger et al. 1973; Cabanac 1979).

Although lip-service is frequently given to the notion that the preferred temperature(s) for a species may vary from time to time, in practice it is usually treated as being almost as invariant as a taxonomic character. The much more sophisticated studies that have been carried out with lizards in recent years, however, have shown that this is a gross oversimplification and that lizards may exert some considerable control over their thermoregulatory preferences. Species such as the Alligator lizard *Gerrhonotus coeruleus*, for example, which was previously classified as a thermal conformer, have been shown by the work of Campbell (1985) to be a precise regulator, when the cost of doing so is constant; such lizards form a group of apparently "facultative regulators". The study of Withers and Campbell (1985) with the desert iguana *D. dorsalis* also makes it very clear that upper and lower set-points for shuttling are quite plastic and vary significantly with the environmentally determined cost of thermoregulating. A recent paper by Tosini et al. (1995) also shows that upper and lower set points in *P. muralis* and *L. vivipara* vary incrementally with increasing infrared irradiance. Thus, although many workers are initially attracted to reptiles as experimental subjects because of their apparent simplicity compared with birds and mammals, a greater familiarity soon reveals this to be an illusion.

One of the most important developments in the field in recent years has been the realisation that finding animals in the field with high and constant body temperatures does not necessarily mean that they are excellent thermoregulators. There is still debate over how best to measure the precision of thermoregulation in reptiles (variance of T_b , slope, or coefficient of determination of T_b versus ambient temperature, T_a , regressions, etc.), but what is very evident is that these measurements must include the environment in some way. Thermoregulation is a homeostatic concept embodying the notion of the animal's temperature being maintained at a different level from that of the

immediate environment. In the past this has simply meant the air temperature somewhere close to the animal, but the advent of operative temperatures has changed all this. Only by comparing a reptile's body temperature with those temperatures available in its immediate environment can we decide whether the animal is thermoregulating effectively, or perhaps instead merely tracking environmental temperatures close to those which it prefers for activity. The recent work of Hertz et al. (1993) serves as an excellent example of how this question can be approached in field studies of more than one species living syntopically.

Thoughtful articles by Pough (1980, 1983) have led to a better understanding of the advantages, rather than the dependent disadvantages, of ectothermy and the much higher rates of energy conversion and productivity of ectotherms than endotherms in terrestrial ecosystems. The fact, too, that their anaerobic scope and anaerobic capacity are not markedly temperature-dependent means that there can be real gains for reptiles remaining active at temperatures that do not coincide with their preferendum.

Changes in physiological condition may have an important impact on thermoregulation in reptiles and feeding, pregnancy, dehydration, starvation and salt-loading are all instanced in the literature. To date, little is known of the mechanisms involved although there is good evidence that steroid hormones, such as progesterone, and the monoamine melatonin are intimately involved in these responses. The recent demonstration that the peptide hormone AVT, which is known for its control of osmoregulatory processes in reptiles, is also responsible for reducing selected body temperatures following salt loading (Bradshaw 1996) makes it clear that osmoregulatory and thermoregulatory responses are integrated in the whole animal. We should perhaps look more carefully for other examples of concerted homeostatic responses to challenging environmental stimuli such as dehydration, hypernatraemia and direct loss of body fluids.

The success of the stochastic dual set-point model in accounting for thermoregulatory behaviour in lizards raises some interesting questions concerning the concept of homeostasis. Although never explicitly stated, homeostasis implies to most physiologists the existence of a single set-point around which lies an area of normality. If physiological parameters fall outside this range then pathology is assumed to be the cause. With an upper and a lower set-point, however, the concept of homeostasis is less clear. Do we imagine that the normal range of temperatures associated with activity is that region between the two set-points, or does each set-point carry with it its own separate "aura of normality"?

These questions have yet to be answered, but they are relevant when one considers the problem of thermal stress in desert reptiles. I have suggested that one can only consider the question of stress if it can be defined and measured precisely, and the working definition I have offered (Bradshaw 1986a, 1992a,b) is a significant deviation of the milieu intérieur, despite full deployment of normal regulatory responses. In the case of temperature regulation, this

amounts to finding an animal in the field with a significantly elevated body temperature associated with high temperature avoidance patterns of behaviour. The problem with this, obviously, is how elevated should the body temperature be before we consider it to be indicative of thermal stress? Further work will be needed to clarify this but the panting threshold appears to represent a good first approximation. There are very few instances in the literature of lizards with body temperatures in the field above this point, which is considerably lower than the CTMax. This suggests that desert lizards are rarely exposed to thermal stress in the routine course of their life. Desert tortoises, by contrast, would appear to be much more susceptible to thermal stress as they are slow moving and entirely dependent on their burrow for protection. Desert snakes have not been studied in sufficient detail for one to say at this stage whether they ever encounter thermally stressful situations.

It is as well to recall, however, that we know little of the actual forces that shape the phenotype of desert reptiles and, as alluded to in the text above, what we think are relatively rare occurrences may well have an important evolutionary impact on the species. Studying animals during periods of extreme weather conditions or over many generations may thus be important in revealing instances of differential mortality which may have important consequences for the genetic composition of the surviving population.

Conclusion

The concept of homeostasis has been one of the most successful and enduring organising paradigms in the field of general and comparative physiology and, as we have seen, may be usefully extended to include primarily behavioural phenomena, such as thermoregulation in reptiles. Although Claude Bernard is generally credited for the concept, the term “homeostasis” was in fact coined by Walter Cannon in 1929 and then fully developed in his influential text *The Wisdom of the Body*. Claude Bernard’s signal contribution was to enunciate in the late nineteenth century the concept of a protected milieu intérieur, or internal environment, the maintenance of which is essential for the proper functioning of the vertebrate animal.

Although the precise composition of this milieu intérieur has only ever been measured in a very small fraction of the living vertebrates, the variation encountered has been significantly small for it to be generally accepted that this is a state to which all vertebrates tend. Osmoconformers such as the cyclostome hagfishes and the chimaeroid fishes are obvious exceptions but are generally regarded as very primitive fish and thus relegated to a separate and unique category.

Studies on lizards in the late 1950s and early 1960s were the first to show that plasma electrolyte concentrations may vary more in individuals studied in the field than in those maintained under constant conditions in the laboratory. There were two reactions to the publication of these data from Australian reptiles: firstly, that reptiles might abandon osmoregulation in the field when it became too costly and, secondly, that Australian reptiles were somehow different from those in other countries and perhaps inferior regulators.

This picture of reptiles representing perhaps some lower level of organisation was reinforced by contemporary laboratory studies on kidney function and adrenal physiology in crocodiles, turtles and lizards. These had failed to find any evidence of homeostatic responses to routine osmotic challenges such as water deprivation and salt loading. More tellingly, incubations of adrenal tissue in vitro had also failed to show any stimulatory effect of the pituitary gland on rates of steroid hormone secretion by the adrenal cortex and the natural conclusion was thus that reptiles lacked an adrenocorticotrophic hormone (ACTH). Pituitary cytologists had also misidentified the corticotroph in the reptilian *pars distalis* as a gonadotroph, an error that was not to be rectified until the 1980s.

The great legacy of Cowles' and Bogert's 1944 study of the thermal relations of a variety of reptiles in their natural habitat was the gradual appreciation of the extent to which these animals are able to maintain high and relatively constant body temperatures when active. That this is achieved through the behavioural exploitation of sources and sinks of heat in their immediate surroundings, rather than by purely physiological means, was a revelation to many physiologists and helped explain the anomalous results obtained at that time in many laboratory studies with reptiles. Reptiles were routinely studied in the laboratory at "room temperature", somewhere close to 20 °C, because they were thought to be "cold-blooded". At this body temperature, most terrestrial species respond very lethargically, if at all, to a great variety of physiological stimuli.

Research over the past three decades has left no doubt that reptiles osmoregulate, thermoregulate, maintain constant levels of glucose in their blood etc., in very analogous if not quite identical ways with other vertebrates. What has never been fully explored is the extent to which their homeostatic capacities are limited by their structural peculiarities; the fact, for example, that although they possess a metanephric kidney they are unable to elaborate an hyperosmotic urine. Effective homeostasis necessitates effector organs as well as sensors and it is at this level that one can observe some of the limitations that are imposed upon reptiles through their shared phylogeny.

Osmoregulation is a good case in point. Once it became clear that lizards in the field with grossly elevated plasma sodium concentrations were not dehydrated but loaded with excess sodium ions that were sequestered within the extracellular fluid, their lack of choice became apparent. The absence of a countercurrent osmotic multiplier in their kidney means that any dietary items ingested that have an electrolyte concentration greater than the lizard's own body fluids translates immediately into a water deficit in terms of the ultimate ability of the animal to excrete these same ions. The situation is exactly analogous to that of humans attempting to drink sea water for any length of time: the ionic concentration of the sea water is greater than the maximal concentrating capacity of our kidneys and, even if the salt could be excreted with the loss of body water, that loss would further concentrate the electrolytes remaining in the body. Hypernatraemia is thus the inevitable result of ingesting salt solutions above the maximal concentrating capacity of the osmoregulatory effector of any animal and there is nothing aberrant or unusual about the response of the reptile to this situation. What is unusual is that it happens on a regular basis to reptiles, especially those living in desert environments where water is in short supply and electrolyte levels in the diet may be high.

Many reptiles thus experience major excursions or deviations of their milieu intérieur from that which may be considered desirable or optimal for activity, especially in summer, but this should not be interpreted as evidence of their abandoning for a time their normal homeostatic strategies in the interests

of long-term survival. In fact they have no choice in the matter and must tolerate such perturbations of their milieu intérieur if they are to survive at all in such a habitat. What is remarkable is the extent to which they are able to tolerate such perturbations which would be lethal for birds and mammals, and it is in this enhanced physiological tolerance that one may perhaps discern the effects of natural selection.

Whether Claude Bernard ever envisaged such possibilities is not clear from his writings, but his most famous adage

“La fixité du milieu intérieur est la condition de la vie libre, indépendante.”

certainly takes account of such cases. Unfortunately, this has usually been rather poorly translated to mean that the constancy of the internal environment is a hallmark of the vertebrate condition. In fact Claude Bernard meant quite clearly that this is an essential *condition* of independence and ultimate liberty from the constraints of the environment. In this sense, reptiles are chained to their environment due to their constitutive inability to maintain the constancy of the internal environment in such instances.

When one asks the question whether the milieu intérieur of reptiles is identical to that of other vertebrates, small differences are apparent even amongst the different groups of reptiles if the available data are examined carefully. Lizards, for example, have a larger extracellular fluid volume than both crocodiles and snakes and their plasma volume is also significantly greater than that of crocodiles and chelonians. Both lizards and snakes have plasma sodium concentrations that are higher than those of crocodiles and chelonians and plasma potassium concentrations are higher in chelonians than in any other group.

The significance of these differences is obscure at this stage and, garnered as they have been from the literature as a whole, they could be the result of systematic bias in the particular species studied, the habitats represented, whether primarily laboratory or field-based studies etc. It is nonetheless unusual to find such apparent differences in a broadly based database and the suspicion is hard to dispel that they represent real variations. If so, these data suggest that the milieu intérieur of lizards is not identical with that of crocodiles or of chelonians and that homeostatic processes in the various reptiles do not operate around common set-points. Although not reviewed in this monograph, plasma glucose concentrations, for example, vary significantly between the different groups of reptiles and are typically low in snakes, for example, but are routinely as high as $18\text{--}20\text{ mmol l}^{-1}$ in agamid lizards such as *Ctenophorus nuchalis*. The metabolic significance of having several such different but apparently well-regulated set-points is quite unknown.

Selye recognised that set-points may be bypassed under certain circumstances without loss of regulation, and he coined the term “heterostasis” to account for the establishment and maintenance of balances in abnormal states. By and large this concept does not appear to have been widely employed by physiologists (as with his “general adaptation syndrome”) but the recent use

by Mrosovsky of the term "rheostasis" to describe regulation around shifting set-points suggests that there is a need.

I would suggest that one needs to go even further in an attempt to clarify what is meant by a set-point, which is one of the crucial elements of the concept of homeostasis. The analysis of thermoregulatory behaviour in reptiles makes it unlikely that they adhere to a single set-point in regulating their body temperature and there would appear to be at least two set-points, an upper and a lower, which are by no means invariant. A number of recent studies using operant-conditioning techniques has pointed the way and suggest that a much deeper understanding is needed than implied by the normally accepted on-off models of thermoregulatory behaviour in the literature.

The central role of hormones as important modulators of physiological and behavioural processes in reptiles has been emphasised in this monograph but it is clear that there are still very large gaps in our knowledge. The function, for example, of the steroid hormone corticosterone, which is secreted by the adrenal cortex of all reptiles, is quite obscure and there is evidence suggesting that it may be both natriferic (sodium-saving) and natriuretic (sodium-excreting) at the level of the kidney in different species. One might also expect it to act metabolically, increasing blood glucose levels through an effect on peripheral rates of glucose uptake, and assist with the breakdown of muscle protein in times of need, but this is still disputed.

Aldosterone, the other major secretory product of the reptilian adrenal cortex, does appear to function as a classic mineralocorticoid hormone, promoting sodium reabsorption and potassium excretion, as in mammals. It is important to note, however, that we are only sure of this in one species of lizard and its complementary effects on the nasal salt-excreting gland are based on much less direct experimentation. The extraordinarily high levels of aldosterone reported in the blood of sea snakes also suggest that it may have other functions in this unusual group of reptiles.

Evidence is mounting for the peptide hormone arginine vasotocin (AVT) functioning as a physiological antidiuretic hormone in reptiles, modulating rates of water excretion from the kidney. Receptors for this hormone have only just been localised within the nephron of the kidney of one species of lizard and they provide an intriguing insight into the possible mechanism of action of this hormone. The data are consistent with the hormone affecting both rates of salt reabsorption and water reclamation from the ultrafiltrate, but far more work needs to be done to substantiate this. It is also sobering to realise that circulating levels of AVT have only been measured in three species of reptiles to date, two lizards and a marine turtle. So far as one is aware, the related peptide mesotocin is also secreted by the pituitary of all reptiles but, to date, there is no clue as to its physiological function.

Perhaps most surprising is the recent discovery that AVT may also have a profound effect on behavioural phenomena, such as thermoregulation. The effects of salt loading, dehydration and hypovolaemia on temperature selec-

tion by lizards in thermal gradients may all be mediated by AVT, secreted from the *pars nervosa* of the pituitary gland. This adds a new dimension to our understanding of the ways in which lizards balance thermoregulatory costs and benefits. It is to be hoped that future work will focus more on how hormones such as AVT and melatonin co-ordinate thermoregulatory responses and apparently alter homeostatic end-points to meet varying ecological demands.

When approaching the question, posed in the Introduction, of whether

“desert-living species of reptiles may enhance their chances of survival during critical periods by abandoning or “loosening” homeostatic constraints, albeit at some cost.”,

the answer would appear to be yes, but only under extreme duress. We have thus seen how the iguanid chuckwalla lizard may spend periods of as long as 9 months in the Mojave desert without feeding, where the only input of water is from the catabolism of muscle and other tissues. Under such circumstances, the animal abandons all activity and does not thermoregulate and the picture is similar, although less extreme, in agamid lizards such as the ornate dragon lizard in Australia.

The chronic hypernatraemia experienced on a seasonal basis by many reptiles that feed on salt-rich dietary items is not such a case, however, and results simply from the fact that they lack a suitable effector organ to cope with such eventualities. It is often assumed that the cephalic salt-secreting organs found in many reptiles have evolved to contend with just this osmoregulatory problem, but the reality is more complex. The Australian agamid lizards of the genus *Ctenophorus* (*Amphibolurus*) could be seen, for example, as the lizards most in need of sodium-secreting nasal salt glands, in view of the extraordinarily high levels to which blood sodium levels rise in late summer, and yet they have none. The large Saharan desert agamid *Uromastix acanthinurus* does possess a very active nasal salt gland, but it secretes primarily potassium ions rather than sodium and this species still experiences severe hypernatraemia during the summer and autumn months in Algeria. In fact, very few of those reptiles that possess a salt gland are able to eliminate sodium ions at a high rate and, with obvious exceptions such as the Galapagos marine iguana and the green sea turtle, these glands appear to have evolved in herbivorous species in which the large intake of potassium ions is a major problem.

Potassium intake appears to pose a major problem for the desert tortoises in the United States, and this may be the reason that, in general, blood potassium levels appear higher in chelonians than in other reptiles. Recent studies with these tortoises have highlighted the fact that they never appear to achieve balance states in the wild and they would appear to represent the best case to date of reptiles abandoning homeostatic dictates in the interests of survival. This situation is unusual, however, when compared with other reptiles and there is speculation that these desert reptiles are only just managing to cope with what has become, relatively recently, a marginal habitat for them.

The question of stress is a difficult one with which to deal, if only because there is no general consensus as to how it should be detected and measured. I have suggested as an operational definition that one may be able to discern stress states by the combination of a significantly altered milieu intérieur in association with maximal deployment of normal regulatory mechanisms, i.e. a change of state despite the animal's best efforts to oppose this. It is too early to know whether this definition will help resolve some of the semantic difficulties that currently cloud the stress concept, but its application in the case of reptiles does enable us to reach some clear conclusions.

Desert reptiles appear to encounter thermal stress very rarely and they normally operate within very wide safety margins. The panting threshold in lizards would appear to be a reasonable index for the onset of thermal stress and most workers agree that this is rarely observed in species that have been observed intensively in the field. Stress provoked by obvious imbalances in water and electrolyte fluxes is another matter, however, and it is difficult to imagine that reptiles manifesting high levels of hypernatraemia and hyperkalaemia are not adversely affected by these changes in their water and electrolyte balance. These are often associated with non-adaptive changes in behaviour and enhanced rates of adrenal corticosteroidogenesis, which are normally considered to be indicative of stress, and it is hoped that future work with reptiles will focus on such changes.

Perhaps one of the more puzzling aspects of such phenomena is, if they are so obviously deleterious for the animals concerned, why has there not been natural selection to obviate or vitiate their influence? This is another area in which issues are clouded by a lack of adequate theory but stress again may be of great significance if, as has been suggested by some workers, adaptive evolutionary changes only occur as a consequence of some prior destabilisation of the genome (McDonald 1983).

Another fundamental question, of perhaps even greater significance, is the inherent stability of the taxon Reptilia itself, and there is reasonable doubt as to whether chelonians, crocodiles, snakes and lizards, the tuatara and Amphisbaenians can be all considered as forming part of a single monophyletic group. From a rigorously cladistic viewpoint, reptiles do not exist, being definable only as those amniotes that are neither birds nor mammals (Molnar 1991). This particular taxonomic perspective, if generally accepted, could have considerable bearing on attempts, such as in this monograph, to compare and understand the evolution of homeostatic and other adaptive responses of the various members of the Class. Recent cladistic analyses have also made it very likely that, within the Reptilia, a group such as the Lacertilia, which is currently made up of lizards, is in fact a paraphyletic group which gave rise to the snakes and the Amphisbaenians (Rage 1992). Following strict cladistic principles, this name should no longer be retained as a taxon or, if it is, it should also include both the snakes and Amphisbaenia and would then become a synonym for the squamates.

Cladists differ in how intransigent one should be in eliminating a paraphyletic taxon with such obvious utility as lizards, and an analogous situation may occur with the Sauria, which some systematists argue should also include the birds. Many of these difficulties will hopefully be resolved in the coming years, with the greater application of cladistic methodologies to approach the question of the systematic relatedness of the various reptilian groups. This should lead, ultimately, to a better appreciation of the phylogenetic relationships of the animals that we currently call reptiles and this can only enhance our understanding of the ways in which their unique physiological and behavioural attributes have evolved over time.

References

- Abel JH, Ellis RA (1966) Histochemical and electron microscopic observations on the salt secreting lacrymal glands of marine turtles. *Am J Anat* 118:337–358
- Ambrose SJ, Bradshaw SD (1988) The water and electrolyte metabolism of free-ranging and captive White-Browed scrubwrens, *Sericornis frontalis* (Acanthizidae) from arid, semi-arid and mesic environments. *Aust J Zool* 36:29–51
- Atsatt SR (1939) Color changes as controlled by temperature and light in lizards of the desert regions of southern California. *Univ Calif Publ Zool* 1:237–276
- Avery RA (1982) Field studies of body temperature and thermoregulation. In: Gans C, Pough FH (eds) *Biology of the Reptilia*, 12C. Academic Press, New York, pp 93–166
- Badia P, Lorenzo A, Diaz M, Gomez T (1987) Mechanism of transport of Na and Cl in the lizard colon. *Comp Biochem Physiol* 87A:883–887
- Baker LA, White FN (1970) Redistribution of cardiac output in response to heating in *Iguana iguana*. *Comp Biochem Physiol* 35:253–262
- Baker LA, Weathers WW, White FN (1972) Temperature induced peripheral blood flow changes in lizards. *J Comp Physiol* 80:313–323
- Bakken GS (1989) Aboreal perch properties and the operative temperature experienced by small animals. *Ecology* 70:922–930
- Bakken GS (1992) Measurement and application of operative and standard operative procedures in ecology. *Am Zool* 32:194–216
- Bakker HR, Bradshaw SD (1977) The effect of hypothalamic lesions on water metabolism of the toad *Bufo marinus*. *J Endocrinol* 75:161–172
- Bakker HR, Bradshaw SD (1989) Water turnover and electrolyte balance of the Spectacled Hare Wallaby (*Lagorhastes conspicillatus*) on Barrow Island. *Comp Biochem Physiol* 92A: 521–529
- Balment RJ, Loveridge JP (1993) Endocrines and osmoregulatory mechanisms in the Nile crocodile, *Crocodylus niloticus*. *Gen Comp Endocrinol* 73:361–367
- Barber BJ, Crawford EC (1977) A stochastic dual-limit hypothesis for behavioral thermoregulation in lizards. *Physiol Zool* 50:53–60
- Barnitt AE (1972) The effects of hyperkalemic stress on the cytology, histology and histochemistry of the nasal (salt) glands of the lizard *Sauromalus obesus* (Baird). PhD Thesis, University of Rhode Island
- Bartholomew GA (1964) The roles of physiology and behavior in the maintenance of homeostasis in the desert environment. *Symp Soc Exp Biol* 18:7–19
- Bartholomew GA (1982) Physiological control of body temperature. In: Gans C, Pough FH (eds) *Biology of the Reptilia*, 12C. Academic Press, New York, pp 167–211
- Bartholomew GA, Tucker VA (1963) Control of changes in body temperature, metabolism and circulation in the agamid lizard, *Amphibolurus barbatus*. *Physiol Zool* 36:199–218
- Bartholomew GA, Tucker VA (1964) Size, body temperature, thermal conductance, oxygen consumption, and heart rate in Australian varanid lizards. *Physiol Zool* 37:341–354
- Baverstock PR, Bradshaw SD (1975) Variation in rate of growth and adrenal corticosteroidogenesis in field and laboratory populations of the lizard *Amphibolurus ornatus*. *Comp Biochem Physiol* 52A:557–566
- Bellamy D, Chester-Jones I (1961) Studies on *Myxine glutinosa*. I. The chemical composition of the tissues. *Comp Biochem Physiol* 3:175–183

- Bennett AF (1982) The energetics of reptilian activity. In: Gans C, Pough FH (eds) *Biology of the Reptilia*, 13D. Academic Press, New York, pp 155–199
- Bennett AF, Dawson WR (1972) Aerobic and anaerobic metabolism during activity in the lizard *Dipsosaurus dorsalis*. *J Comp Physiol* 81:289–299
- Bennett AF, Dawson WR (1976) Metabolism. In: Gans C, Dawson WR (eds) *Biology of the Reptilia*, 5A. Academic Press, New York, pp 127–223
- Bennett AF, Licht P (1972) Anaerobic metabolism during activity in lizards. *J Comp Physiol* 81:277–288
- Bentley PJ (1959) Studies on the water and electrolyte metabolism of the lizard *Trachysaurus rugosus*. *Nature (Lond)* 145:37–47
- Bentley PJ (1962) Studies on the permeability of the large intestine and urinary bladder of the tortoise (*Testudo graeca*) with special reference to the effects of neurohypophysial and adrenocortical hormones. *Gen Comp Endocrinol* 2:323–328
- Bentley PJ (1971) Endocrines and osmoregulation. Springer, Berlin Heidelberg New York
- Bentley PJ (1976) Osmoregulation. In: Gans C, Dawson WR (eds) *Biology of the Reptilia*, 5A. Academic Press, New York, pp 365–412
- Bentley PJ, Blumer WFC (1962) Uptake of water by the lizard *Moloch horridus*. *Nature (Lond)* 194:699–700
- Bentley PJ, Bradshaw SD (1972) Electrical potential difference across the cloaca and colon of the Australian lizards *Amphibolurus ornatus* and *Amphibolurus inermis*. *Comp Biochem Physiol* 42A:465–471
- Bentley PJ, Schmidt-Nielsen K (1965) Permeability to water and sodium of the crocodilian *Caiman sclerops*. *J Cell Comp Physiol* 66:303–309
- Bentley PJ, Schmidt-Nielsen K (1970) Comparison of water exchange in two aquatic turtles, *Trionyx spinifer* and *Pseudemys scripta*. *Comp Biochem Physiol* 32:363–364
- Benyajati S, Yokota SD, Dantzler WH (1985) Renal function in sea snakes II. Sodium, potassium and magnesium excretion. *Am J Physiol* 249:R237–R245
- Berk ML, Heath JE (1975a) An analysis of behavioral thermoregulation in the lizard *Dipsosaurus dorsalis*. *J Therm Biol* 1:15–22
- Berk ML, Heath JE (1975b) Effects of preoptic, hypothalamic and telencephalic lesions on thermoregulation in the lizard, *Dipsosaurus dorsalis*. *J Therm Biol* 1:65–78
- Bernard C (1878) *Leçons sur les phénomènes de la vie communs aux animaux et aux végétaux*. Baillière et Fils, Paris
- Berry KH (ed) (1984) *The status of the desert tortoise (Gopherus agassizii) in the United States*. US Fish and Wildlife Service, Sacramento
- Beuchat CA (1986) Reproductive influences on the thermoregulatory behavior of a live-bearing lizard. *Copeia* 1986:971–979
- Beuchat CA (1988) Temperature effects during gestation in a viviparous lizard. *J Therm Biol* 13:135–142
- Beuchat CA, Ellner S (1987) A quantitative test of life history theory: thermoregulation by a viviparous lizard. *Ecol Monogr* 57:45–60
- Beuchat CA, Vleck D, Braun EJ (1986) Role of the urinary bladder in osmotic regulation of neonatal lizards. *Physiol Zool* 59:539–551
- Beyenbach KW (1984) Water permeable and impermeable barriers of snake distal tubules. *Am J Physiol* 246:F290–F299
- Beyenbach KW, Dantzler WH (1978) Generation of transepithelial potentials by isolated perfused renal distal tubules. *Am J Physiol* 248:F238–F246
- Beyenbach KW, Koeppen BM, Dantzler WH, Helman SI (1980) Luminal Na concentration and the electrical properties of the snake distal tubule. *Am J Physiol* 239:F412–F419
- Bickham JW (1981) Two-hundred-million-year-old chromosomes: deceleration of the rate of karyotypic evolution in turtles. *Sciences (NY)* 212:1291–1293
- Bindslev N, Skadhauge E (1971) Sodium chloride absorption and solute-linked water flow across the epithelium of the coprodaeum and large intestine of the normal and dehydrated fowl (*Gallus domesticus*). *In vivo* perfusion studies. *J Physiol (Lond)* 216:753–768
- Binyon EJ, Twigg GI (1965) Seasonal changes in the blood and thyroid of the grass snake, *Natrix natrix*. *Nature (Lond)* 207:779–780

- Bishop JE (1959) A histological and histochemical study of the kidney tubule of the common garter snake, *Thamnophis sirtalis*, with special reference to the sexual segment in the male. *J Morphol* 104:307–357
- Bock W (1980) The definition and recognition of biological adaptation. *Am Zool* 20:217–227
- Bons N (1983) Immunocytochemical identification of the mesotocin- and vasotocin-producing systems in the brain of temperate desert lizard species and their modifications by cold. *Gen Comp Endocrinol* 52:56–66
- Borst JGG, De Vries LA, Van Leeuwen AM, Ottolander GJH, Cejka V (1960) The maintenance of circulatory stability at the expense of volume and electrolyte stability. *Clin Chim Acta* 5:887–914
- Borut A, Horowitz M, Castel A (1972) Blood volume regulation in the spiny mouse: capillary changes due to dehydration. *Symp Zool Soc Lond* 31:175–189
- Bour R, Dubois A (1984) *Xerobates agassiz*, 1857, synonyme plus ancien de *Scaptochelys* Bramble, 1982 (Reptilia, Chelonii, Testudinidae). *Bull Soc Linn Lyon* 53:30–32
- Boyer DR (1965) Ecology of the basking habit in turtles. *Ecology* 46:99–118
- Bradshaw FJ, Bradshaw SD (1996) Arginine vasotocin: locus of action along the nephron of the Ornate Dragon Lizard, *Ctenophorus ornatus*. *Gen Comp Endocrinol* 103:281–289
- Bradshaw SD (1970) Seasonal changes in the water and electrolyte metabolism of *Amphibolurus* lizards in the field. *Comp Biochem Physiol* 36:689–718
- Bradshaw SD (1971) Growth and mortality in a field population of *Amphibolurus* lizards exposed to seasonal cold and aridity. *J Zool (Lond)* 165:1–25
- Bradshaw SD (1972) The endocrine control of water and electrolyte metabolism in desert reptiles. *Gen Comp Endocrinol [Suppl]* 3:360–373
- Bradshaw SD (1975) Osmoregulation and pituitary-adrenal function in desert reptiles. *Gen Comp Endocrinol* 25:230–248
- Bradshaw SD (1976) Effect of hypothalamic lesions on kidney and adrenal function of the lizard *Amphibolurus ornatus*. *Gen Comp Endocrinol* 29:285
- Bradshaw SD (1978a) Aspects of hormonal control of osmoregulation in desert reptiles. In: Gaillard PJ, Boer HH (eds) *Comparative endocrinology*, 1. Elsevier North-Holland Biomedical Press, Amsterdam, pp 213–216
- Bradshaw SD (1978b) Volume regulation in desert reptiles and its control by pituitary and adrenal hormones. In: Jorgensen CB, Skadhauge E (eds) *Osmotic and volume regulation*. Munksgaard, Copenhagen, pp 38–59
- Bradshaw SD (1981) Ecophysiology of Australian desert lizards: studies on the genus *Amphibolurus*. In: Keast A (ed) *Biogeography and ecology in Australia*, 2. Junk, Den Haag, pp 1395–1434
- Bradshaw SD (1985) Hydro-mineral balance in reptiles and its hormonal control. In: Lofts B, Holmes WN (eds) *Current trends in comparative endocrinology*, 2. Hong Kong University Press, Hong Kong, pp 939–943
- Bradshaw SD (1986a) Ecophysiology of desert reptiles. Academic Press, Sydney
- Bradshaw SD (1986b) Hormonal mechanisms and survival in desert reptiles. In: Assenmacher I, Boissin J (eds) *Endocrine regulations as adaptive mechanisms to the environment*, 1. Centre National de la Recherche Scientifique (CNRS), Bordeaux, pp 415–440
- Bradshaw SD (1988) Desert reptiles: a case of adaptation or pre-adaptation? *J Arid Environ* 14:155–174
- Bradshaw SD (1992a) Ecophysiology of desert reptiles. In: Adler K (ed) *Herpetology: current research on the biology of amphibians and reptiles*. Cornell University, Ithaca, New York, pp 121–139
- Bradshaw SD (1992b) Le problème du stress dans les études écophysiologiques: stratégies de mesure et de contrôle. *Bull Soc Ecophysiol (Paris)* 17:69–76
- Bradshaw SD (1996) Effect of the neurohypophysial peptide, arginine vasotocin (AVT) on behavioral thermoregulation in the agamid lizard *Ctenophorus (Amphibolurus) ornatus*. (in prep)
- Bradshaw SD, De'ath G (1991) Variation in condition indices due to climatic and seasonal factors in an Australian desert lizard, *Amphibolurus nuchalis*. *Aust J Zool* 39:373–385
- Bradshaw SD, Grenot CJ (1976) Plasma aldosterone levels in two reptilian species, *Uromastix acanthinurus* and *Tiliqua rugosa*, and the effect of several experimental treatments. *J Comp Physiol* 111:71–76

- Bradshaw SD, Main AR (1968) Behavioural attitudes and regulation of temperature in *Amphibolurus* lizards. *J Zool (Lond)* 154:193–221
- Bradshaw SD, Rice GE (1981) The effects of pituitary and adrenal hormones on renal and post-renal reabsorption of water and electrolytes in the lizard *Varanus gouldii* (Gray). *Gen Comp Endocrinol* 44:82–93
- Bradshaw SD, Shoemaker VH (1967) Aspects of water and electrolyte changes in a field population of *Amphibolurus* lizards. *Comp Biochem Physiol* 20:855–865
- Bradshaw SD, Waring H (1969) Comparative studies on the biological specificity of melanin-dispersing hormone (MDH). In: Fontaine M (ed) *La spécificité zoologique des hormones hypophysaires et de leurs activités*, 177. Centre National de la Recherche Scientifique, Paris, pp 135–152
- Bradshaw SD, Shoemaker VH, Nagy KA (1972) The rôle of adrenal corticosteroids in the regulation of kidney function in the desert lizard *Dipsosaurus dorsalis*. *Comp Biochem Physiol* 43A:621–635
- Bradshaw SD, Lemire M, Vernet R, Grenot CJ (1984a) Aldosterone and the control of secretion by the nasal gland of the North African desert lizard, *Uromastix acanthinurus*. *Gen Comp Endocrinol* 54:314–323
- Bradshaw SD, Tom JA, Bunn SE (1984b) Corticosteroids and control of nasal salt gland function in the lizard *Tiliqua rugosa*. *Gen Comp Endocrinol* 54:308–313
- Bradshaw SD, Saint Girons H, Naulleau G, Nagy KA (1987) Material and energy balance of some captive and free-ranging reptiles in western France. *Amphib Reptilia* 8:129–142
- Bradshaw SD, Saint Girons H, Bradshaw FJ (1991a) Patterns of breeding in two species of agamid lizards in the arid sub-tropical Pilbara region of Western Australia. *Gen Comp Endocrinol* 82:407–424
- Bradshaw SD, Saint Girons H, Bradshaw FJ (1991b) Seasonal changes in material and energy balance associated with reproduction in the Green Lizard *Lacerta viridis* in western France. *Amphib Reptilia* 12:21–32
- Braña F (1993) Shifts in body temperature and escape behavior of female *Podarcis muralis* during pregnancy. *Oikos* 66:216–222
- Brattstrom BH (1965) Body temperatures of reptiles. *Am Midl Nat* 73:376–422
- Braun EJ, Dantzler WH (1987) Mechanism of hormone actions on renal function. In: Chester-Jones I, Ingleton P, Phillips JG (eds) *Vertebrate endocrinology: fundamentals and biomedical implications*, 2. Academic Press, New York, pp 189–210
- Braysher M (1971) The structure and function of the nasal salt gland from the Australian sleepy lizard *Trachydosaurus* (formerly *Tiliqua*) *rugosus*: Family Scincidae. *Physiol Zool* 44:129–136
- Braysher M, Green B (1970) Absorption of water and electrolytes from the cloaca of an Australian lizard, *Varanus gouldii* (Gray). *Comp Biochem Physiol* 35:607–614
- Brewer KJ, Ensor DM (1980) Hormonal control of osmoregulation in the Chelonia. 1. The effects of prolactin and interrenal steroids in freshwater chelonians. *Gen Comp Endocrinol* 42:304–309
- Brodsky WA, Schilb TP (1960) Electrical and osmotic characteristics of the isolated turtle bladder. *J Clin Invest* 39:574–575
- Brodsky WA, Schilb TP (1965) Osmotic properties of isolated turtle bladder. *Am J Physiol* 208:46–57
- Burgess WW, Harvey AM, Marshall EK (1933) The site of the antidiuretic action of pituitary extracts. *J Pharmacol Exp Ther* 210:1293–1298
- Burian RM (1983) Adaptation. In: Grene M (ed) *Dimensions of Darwinism*. Cambridge University Press, London, pp 287–314
- Burton TM, Likens GE (1975) Energy flow and nutrient cycling in salamander populations in the Hubbard Brook Experiment Forest, New Hampshire. *Ecology* 58:1068–1080
- Butler DG (1972) Antidiuretic effect of arginine vasotocin in the Western Painted Turtle (*Chrysemys picta belli*). *Gen Comp Endocrinol* 18:122–125
- Butler DG, Knox WH (1970) Adrenalectomy of the Painted Turtle (*Chrysemys picta belli*): effect on ion regulation and tissue glycogen. *Gen Comp Endocrinol* 14:551–566
- Cabanac M (1979) Le comportement thermorégulateur. *J Physiol (Paris)* 75:115–178
- Cabanac M, Hammel HT, Hardy JD (1967) *Tiliqua scincoides*: temperature sensitive units in the lizard brain. *Sciences (NY)* 158:1050–1051

- Callard IP, Callard GV (1978) The adrenal gland in Reptilia. Part 2. Physiology. In: Chester-Jones I, Henderson IW (eds) General, comparative and clinical endocrinology of the adrenal cortex, 2. Academic Press, London, pp 370–418
- Campbell JD (1985) The influence of metabolic cost upon the level and precision of behavioral thermoregulation in an eurythermic lizard. *Comp Biochem Physiol* 81A:597–601
- Cannon WB (1929) Homeostasis. *Physiol Rev* 9:399–422
- Cannon WB (1939) The wisdom of the body. Norton and Co., New York
- Case TJ (1972) Thermoregulation and evaporative cooling in the chuckwalla, *Sauromalus obesus*. *Copeia* 1972:145–160
- Case TJ (1976) Seasonal aspects of thermoregulatory behavior of the chuckwalla, *Sauromalus obesus obesus* (Reptilia, Lacertilia, Iguanidae). *J Herpetol* 10:85–95
- Chan DKO, Callard IP, Chester-Jones I (1970) Observations on the water and electrolyte composition of the iguanid lizard *Dipsosaurus dorsalis* (Baird and Girard) with special reference to the control by the pituitary gland and the adrenal cortex. *Gen Comp Endocrinol* 15:374–387
- Chelazzi G, Calzolari R (1986) Thermal benefits from familiarity with the environment in a reptile. *Oecologia* 68:557–558
- Clarke BC, Nicolson SW (1994) Water, energy, and electrolyte balance in captive Namib sand-dune lizards (*Angolosaurus skoogi*). *Copeia* 1994:962–974
- Cloudsley-Thompson JL (1971) The temperature and water relations of reptiles. Merrow Publishing, Watford, England
- Cloudsley-Thompson JL (1988) Strategies for survival of desert reptiles. In: Gosh PK, Prakash I (eds) Ecophysiology of desert vertebrates. Scientific Publishers, Jodhpur, India, pp 187–288
- Cogger HG (1974) Thermal relations of the mallee dragon, *Amphibolurus fordii* (Lacertilia: Agamidae). *Aust J Zool* 22:319–339
- Cordier R (1928) Etudes histophysiologiques sur le tube urinaire des reptiles. *Arch Biol (Liège)* 38:109–170
- Cothran ML, Hutchison DH (1979) Effect of melatonin on thermal selection by *Crotaphytus collaris* (Squamata: Iguanidae). *Comp Biochem Physiol* 63A:461–466
- Coulson RA, Hernandez T (1964) Biochemistry of the alligator: a study of metabolism in slow motion. Louisiana State University Press, Baton Rouge
- Coulson RA, Hernandez T (1970) Nitrogen metabolism and excretion in the living reptile. In: Campbell JW (ed) Comparative biochemistry of nitrogen metabolism. Academic Press, New York, pp 639–710
- Cowan FBM (1974) The ultrastructure of the of the lachrymal “salt” gland and the harderian gland in the euryhaline *Malaclemys* and some closely related stenohaline emydines. *Can J Zool* 49:691–687
- Cowan FBM (1985) Short term acclimation of *Malaclemys terrapin* to seawater. *Comp Biochem Physiol* 68A:55–59
- Cowles RB (1958) Possible origin of dermal temperature regulation. *Evolution* 12:347–357
- Cowles RB, Bogert CM (1944) A preliminary study of the thermal requirements of desert reptiles. *Bull Am Mus Nat Hist* 83:265–296
- Crawford EC (1972) Brain and body temperatures in a panting lizard. *Science (NY)* 177:431–433
- Crawford EC, Barber BJ (1974) Effect of core, skin, and brain temperature on panting in the lizard *Sauromalus obesus*. *Am J Physiol* 226:569–573
- Crawford EC, Kampe G (1971) Physiological responses of the lizard *Sauromalus obesus* to changes in ambient temperature. *Am J Physiol* 220:1256–1260
- Crawford K, Spotila J, Standora E (1983) Operative environmental temperatures and basking behavior of the turtle *Pseudemys scripta*. *Ecology* 64:989–999
- Crisp M, Cook LM, Hereward FV (1979) Color and heat balance in the lizard *Lacerta dugesii*. *Copeia* 1979:220–258
- Crowe JH, Nagy KA, Francis C (1970) Structure of lizard salt glands. *Am Zool* 10:556
- Crowley SR (1987) The effect of desiccation upon the preferred body temperature and activity level of the lizard *Sceloporus undulatus*. *Copeia* 1987:25–32
- Curry-Lindahl K (1957) Behaviour of the tropical rock lizard *Agama cyanogaster* (Rüppel) in hot environments. *Ann Soc R Zool Belg* 87:45–74
- Curry-Lindahl K (1979) Thermal ecology of the tree agama (*Agama atricollis*) in Zaire with a review of heat tolerance in reptiles. *J Zool (Lond)* 188:185–220

- Dagognet F (1984) Préface. Introduction à l'étude de la médecine expérimentale. Flammarion, Paris, pp 9–28
- Dantzler WH (1967) Glomerular and tubular effects of arginine vasotocin in water snakes (*Natrix sipedon*). *Am J Physiol* 212:83–91
- Dantzler WH (1968) Effects of metabolic alkalosis and acidosis on tubular urate secretion in water snakes. *Am J Physiol* 215:747–751
- Dantzler WH (1970) Kidney function in desert vertebrates. In: Benson GK, Phillips JG (eds) *Hormones and the environment*, 18. Cambridge University Press, London, pp 157–190
- Dantzler WH (1976) Renal function (with special emphasis on nitrogen excretion). In: Gans C, Dawson WR (eds) *Biology of the Reptilia*, 5A. Academic Press, New York, pp 447–503
- Dantzler WH (1978) Some renal glomerular and tubular mechanisms involved in osmotic and volume regulation in birds and reptiles. In: Jorgensen CB, Skadhauge E (eds) *Osmotic and volume regulation*. Munksgaard, Copenhagen, pp 87–201
- Dantzler WH (1980) Renal mechanisms for osmoregulation in reptiles and birds. In: Gilles R (ed) *Animals and environmental fitness: physiological and biochemical aspects of adaptation and ecology*. Pergamon Press, Oxford, pp 91–110
- Dantzler WH (1982) Reptilian glomerular and tubular functions and their control. *Fed Proc* 41:2371–2376
- Dantzler WH (1989a) *Comparative physiology of the vertebrate kidney*. Springer, Berlin Heidelberg New York
- Dantzler WH (1989b) The nephron in reptiles. In: Kinne RKH (ed) *Structure and function of the kidney*, 1. Karger, Basel, pp 143–193
- Dantzler WH, Bentley SK (1978a) Fluid absorption with and without sodium in isolated perfused snake proximal tubule. *Am J Physiol* 234:F68–F78
- Dantzler WH, Bentley SK (1978b) Lack of effect of potassium on fluid absorption in isolated, perfused snake proximal renal tubules. *Renal Physiol* 1:268–274
- Dantzler WH, Braun EJ (1980) Comparative nephron function in reptiles, birds, and mammals. *Am J Physiol* 239:R197–R213
- Dantzler WH, Holmes WN (1974) Water and mineral metabolism in reptiles. In: Florkin M, BT Scheer (eds) *Chemical zoology IX*. Academic, New York, pp 277–336
- Dantzler WH, Schmidt-Nielsen B (1966) Excretion in fresh-water turtle (*Pseudemys scripta*) and desert tortoise (*Gopherus agassizii*). *Am J Physiol* 210:198–210
- Dantzler WH, Shaffner DP, Chiu PJS, Sawyer WH (1970) Probenecid inhibition of arginine vasotocin in snakes, frogs, and on frog bladders *in vitro*. *Am J Physiol* 218:929–936
- Daut EF, Andrews RM (1993) The effect of pregnancy on thermoregulatory behavior of the viviparous lizard *Chalcides ocellatus*. *J Herpetol* 27:6–13
- Davis LE, Schmidt-Nielsen B (1967) Ultrastructure of the crocodile kidney (*Crocodylus acutus*) with special reference to electrolyte and fluid transport. *J Morphol* 121:255–276
- Davis LE, Schmidt-Nielsen B, Stolte H (1976) Anatomy and ultrastructure of the excretory system of the lizard *Sceloporus cyanogenys*. *J Morphol* 121:255–276
- Dawson WR, Templeton JR (1963) Physiological responses to temperature in the lizard *Crotaphytus collaris*. *Physiol Zool* 36:219–236
- Dawson WR, Templeton JR (1966) Physiological responses to temperature in the alligator lizard, *Gerrhonotus multicarinatus*. *Ecology* 47:760–765
- de Rouffignac C (1990) The urinary concentrating mechanism. In: Kinne RKH (ed) *Urinary concentrating mechanisms*, 2. Karger, Basel, pp 31–102
- de Witt CB (1967a) Behavioral thermoregulation in the desert iguana. *Sciences (NY)* 158:809–810
- de Witt CB (1967b) Precision of thermoregulation and its relation to environmental factors in the desert iguana, *Dipsosaurus dorsalis*. *Physiol Zool* 40:49–66
- de Witt CB, Friedman RM (1979) Significance of skewness in ectotherm regulation. *Am Zool* 19:195–209
- Diaz M, Lorenzo A (1989) Modulation of active potassium transport by aldosterone. *Comp Biochem Physiol* 95A:79–85
- Diaz M, Lorenzo A (1991) Regulation of amiloride-sensitive Na⁺ absorption in the lizard (*Gallotia galloti*) colon by aldosterone. *Comp Biochem Physiol* 100A:63–68

- Diaz M, Lorenzo A, Badia P, Gomez T (1994) The role of aldosterone on water and electrolyte transport across the colonic epithelium of the lizard *Gallotia galloti*. *Comp Biochem Physiol* 91A:71–77.
- Diefenbach CODC (1973) Integumentary permeability to water in *Caiman crocodilus* and *Crocodylus niloticus* (Crocodylia: Reptilia). *Physiol Zool* 46:72–78
- Dmi'el R (1972) Effect of activity and temperature on metabolism and water loss in snakes. *Am J Physiol* 223:510–516
- Dmi'el R, Borut A (1972) Thermal behaviour, heat exchange and metabolism in the desert snake *Spalerosophis cliffordi*. *Physiol Zool* 45:78–94
- Dmi'el R, Zilber B (1971) Water balance in a desert snake. *Copeia* 1971:754–755
- Doucet A (1988) Function and control of Na-K-ATPase in single nephron segments of the mammalian kidney. *Kidney Int* 34:749–760
- Doucet A, Katz AI, Morel F (1979) Determination of Na-K-ATPase activity in single segments of the mammalian nephron. *Am J Physiol* 237:F105–F113
- Douglas JF, Layne JN (1978) Activity and thermoregulation of the gopher tortoise (*Gopherus polyphemus*) in southern Florida. *Herpetologica* 34:359–374
- Dousa TP (1974) Effects of hormones on cyclic AMP formation in kidneys of nonmammalian vertebrates. *Am J Physiol* 226:1193–1197
- Dreisig H (1985) A time budget model of thermoregulation in shuttling ectotherms. *J Arid Environ* 8:191–205
- Dryden G, Green B, King D, Losos J (1990) Water and energy turnover in a small monitor lizard, *Varanus acanthurus*. *Aust Wildl Res* 17:641–646
- Dubuis A, Faurel L, Grenot CJ, Vernet R (1971) Sur le régime alimentaire du lézard saharien *Uromastix acanthinurus* Bell. *CR Acad Sci (Paris)* 273:500–503
- Duggan RT, Lofts B (1978) Adaptation to fresh water in the sea snake, *Hydrophis cyanocinctus*: tissue electrolytes and peripheral corticosteroids. *Gen Comp Endocrinol* 36:510–520
- Duggan RT, Lofts B (1979) The pituitary-adrenal axis in the sea snake, *Hydrophis cyanocinctus* Daudin. *Gen Comp Endocrinol* 38:374–383
- Dunson WA (1968) Salt gland secretion in the pelagic sea snake *Pelamis*. *Am J Physiol* 215:1512–1517
- Dunson WA (1969a) Reptilian salt glands. In: Bothelo SV, Brooks FP, Shelley WB (eds) *Exocrine glands*. University of Pennsylvania Press, Philadelphia, pp 83–103
- Dunson WA (1969b) Electrolyte excretion by the salt gland of the Galàpagos marine iguana. *Am J Physiol* 216:995–1002
- Dunson WA (1970) Some aspects of the water and electrolyte balance in three estuarine reptiles, the Diamondback terrapin, American and “salt water” crocodiles. *Comp Biochem Physiol* 32:161–174
- Dunson WA (1974) Salt gland excretion in a mangrove monitor lizard. *Comp Biochem Physiol* 47A:1245–1255
- Dunson WA (1976) Salt glands in reptiles. In: Gans C, Dawson WR (eds) *Biology of the Reptilia*, 5A. Academic Press, New York, pp 413–445
- Dunson WA (1979) Control mechanisms in reptiles. In: Gilles R (ed) *Mechanisms of osmoregulation in animals*. Wiley and Sons, Chichester, pp 273–322
- Dunson WA (1980) The relation of sodium and water balance to survival in sea water of estuarine and freshwater races of the snakes *Nerodia fasciata*, *Nerodia sipedon* and *Nerodia valida*. *Copeia* 1980:268–280
- Dunson WA (1982) Salinity relations of crocodiles in Florida Bay. *Copeia* 1982:374–385
- Dunson WA (1985) Effect of water salinity and food salt content on growth and sodium efflux of hatching diamondback terrapins (*Malaclemys*). *Physiol Zool* 58:736–747
- Dunson WA, Dunson MK (1973) Convergent evolution of sublingual salt glands in the marine file snake and the true sea snakes. *J Comp Physiol* 86:193–208
- Dunson WA, Dunson MK (1974) Interspecific differences in fluid concentration and secretion rate of sea snake salt glands. *Am J Physiol* 227:430–438
- Dunson WA, Dunson MK (1979) A possible new salt gland in a marine homalopsid snake (*Cerberus rhynchops*). *Copeia* 1979:661–672
- Dunson WA, Heatwole H (1986) The effect of relative shell size in turtles on water and electrolyte composition. *Am J Physiol* 250:R1133–R1137

- Dunson WA, Taub AM (1967) Extrarenal salt excretion in sea snakes (*Laticauda*). *Am J Physiol* 213:975-982
- Dunson WA, Weymouth RD (1965) Active uptake of sodium by softshell turtles (*Trionyx spinifer*). *Science* 149:67-69
- Dunson WA, Packer RK, Dunson MK (1971) Sea snakes: an unusual salt gland under the tongue. *Sciences* (NY) 173:437-441
- Dunson WA, Dunson MK, Keith AD (1978) The nasal gland of the Montpellier snake *Malpolon monspessulanus*: fine structure, secretion composition and a possible role in reduction of dermal water loss. *J Exp Zool* 203:461-474
- Dupré RK, Crawford EC (1985a) Behavioral thermoregulation during dehydration and osmotic loading of the desert iguana. *Physiol Zool* 58:357-363
- Dupré RK, Crawford EC (1985b) Control of panting in the desert iguana: roles for peripheral temperatures and the effect of dehydration. *J Exp Zool* 235:341-347
- Dupré RK, Crawford EC (1986) Elevation of the panting threshold of the desert iguana, *Dipsosaurus dorsalis*, during dehydration: potential roles of changes in osmolality and body fluid volume. *J Comp Physiol* 156B:377-381
- Dworkin LD, Ichikawa I, Brenner BM (1983) Hormone modulation of glomerular function. *Am J Physiol* 244:F95-F104
- Edmonds CJ, Pilcher D (1969) Sodium transport mechanisms of the large intestine. In: Burland WL, Samuels PD (eds) *Transport across the intestine*. Churchill-Livingstone, Edinburgh, pp 43-57
- Elizondo RS, LeBrie SJ (1969) Adrenal-renal function in water snakes *Natrix cyclopion*. *Am J Physiol* 217:419-425
- Ellis RA, Abel JH (1964) Intercellular channels in the salt-secreting glands of marine turtles. *Sciences* (NY) 144:1340-1343
- Ellis RA, Goertemiller CC (1974) Cytological effects of salt-stress and localisation of transport adenosine triphosphatase in the lateral nasal glands of the desert iguana, *Dipsosaurus dorsalis*. *Anat Rec* 180:285-298
- Ellis RA, Goertemiller CC, Stetson DL (1977) Significance of extensive "leaky" cell junctions in the avian salt gland. *Nature* (Lond) 268:555-556
- Ellis TM (1981) Tolerance of seawater by the American crocodile, *Crocodylus acutus*. *J Herpetol* 15:187-192
- Ellis TM, Chappell MA (1987) Metabolism, temperature relations, maternal behavior, and reproductive energetics in the ball python (*Python regius*). *J Comp Physiol* 157B:393-402
- Ellis TM, Evans DH (1984) Sodium balance in the American alligator. *J Exp Zool* 231:325-329
- Ellner LR, Karasov WH (1993) Latitudinal variation in the thermal biology of Ornate box turtles. *Copeia* 1993:447-455
- Else PL, Hulbert AJ (1985) An allometric comparison of the mitochondria of mammalian and reptilian tissues: the implications for the evolution of endothermy. *J Comp Physiol* 156B:3-11
- Else PL, Hulbert AJ (1987) Evolution of mammalian endothermic metabolism: "leaky" membranes as a source of heat. *Am J Physiol* 253:R1-R7
- Engbretson GA (1992) Neurobiology of the lacertilian parietal eye system. *Ethol Ecol Evol* 4:89-107
- Engbretson GA, Hutchinson VH (1976) Parietalectomy and thermal selection in the lizard *Sceloporus magister*. *J Exp Zool* 198:29-38
- Ernst SA (1972) Transport adenosine triphosphate cytochemistry. II. Cytochemical localisation of ouabain-sensitive, potassium-dependent phosphatase activity in the secretory epithelium of the avian salt gland. *J Histochem Cytochem* 20:22-38
- Ernst SA, Mills JW (1977) Basolateral plasma membrane localization of ouabain-sensitive sodium transport sites in the secretory epithelium of the avian salt gland. *J Cell Biol* 75:74-94
- Evans DH, Ellis TM (1977) Sodium balance in the hatchling American crocodile, *Crocodylus acutus*. *Comp Biochem Physiol* 58A:159-162
- Fänge R, Fugelli K (1962) Osmoregulation in chimaeroid fish. *Nature* (Lond) 196:689
- Felsenstein J (1985) Phylogenies and the comparative method. *Am Nat* 125:1-15
- Fergusson B, Bradshaw SD (1991) Plasma arginine vasotocin, progesterone and luteal development during pregnancy in the viviparous lizard, *Tiliqua rugosa*. *Gen Comp Endocrinol* 82:140-151

- Fergusson B, Bradshaw SD (1992) In vitro contractions in the viviparous lizard *Tiliqua rugosa*: effects of gestation and steroid pre-treatment *in vivo*. Gen Comp Endocrinol 86:203–210
- Figler RA, MacKenzie DS, Owens DW, Licht P, Amoss MS (1989) Increased levels of arginine vasotocin and neurophysin during nesting in sea turtles. Gen Comp Endocrinol 73:223–232
- Firth BT, Heatwole H (1976) Panting thresholds of lizards. The role of the pineal complex in panting responses in an agamid, *Amphibolurus muricatus*. Gen Comp Endocrinol 29:388–401
- Firth BT, Kennaway DJ (1980) Plasma melatonin levels in the scincid lizard *Trachydosaurus rugosus*. The effects of parietal eye and lateral eyes impairment. J Exp Biol 85:311–321
- Firth BT, Kennaway DJ (1987) Melatonin content of the pineal, parietal eye and blood plasma of the lizard, *Trachydosaurus rugosus*: effect of constant and fluctuating temperature. Brain Res 404:313–318
- Firth BT, Turner JS (1982) Sensory, neural and hormonal aspects of thermoregulation. In: Gans C, Pough FH (eds) Biology of the Reptilia, 12. Academic Press, London, pp 213–274
- Firth BT, Ralph CL, Boardman TJ (1980) Independent effects of the pineal and a bacterial pyrogen in behavioral thermoregulation in lizards. Nature (Lond) 285:399–400
- Firth BT, Maudlin RE, Ralph CL (1988) The role of the pineal complex in behavioral thermoregulation in the collared lizard, *Crotaphytus collaris*. Physiol Zool 61:176–185
- Firth BT, Thompson MB, Kennaway DJ, Belan I (1989a) Thermal sensitivity of reptilian melatonin rhythms: “cold” tuatara vs. “warm” skink. Am J Physiol 256:R1160–R1163
- Firth BT, Turner JS, Ralph CL (1989b) Thermoregulatory behaviour in two species of iguanid lizards (*Crotaphytus collaris* and *Sauromalus obesus*): diel variation and the effect of pinealectomy. J Comp Physiol 159:13–20
- Foà A, Janik DS, Minutini L (1992) Circadian rhythms of plasma melatonin in the ruin lizard *Podarcis sicula*: effects of pinealectomy. J Pineal Res 12:109–113
- Foà A, Monteforti G, Minutini L, Innocenti A, Quagliari C, Flamini M (1994) Seasonal changes of locomotor activity patterns in ruin lizards *Podarcis sicula* I. Endogenous control of the circadian rhythm. Behav Ecol Sociobiol 34:267–274
- Fox H (1976) The urinogenital system of reptiles. In: Gans C, Parsons TS (eds) Biology of the Reptilia, 6. Academic Press, New York, pp 1–157
- Fraser S, Grigg GC (1984) Control of thermal conductance is insignificant to thermoregulation in small reptiles. Physiol Zool 57:392–400
- Fraser SP (1985) Variability of heating and cooling rates during radiant heating in a scincid lizard, *Egernia cunninghami*. Comp Biochem Physiol 80A:281–286
- Friar W, Ackman RG, Mrosovsky N (1972) Body temperatures of *Dermochelys coriacea*: warm turtles from cold water. Sciences (NY) 177:791–793
- Fruton JS (1979) Claude Bernard the scientist. In: Robin ED (ed) Claude Bernard and the internal environment: a memorial volume. Marcel Dekker, New York, pp 35–41
- Gabe M, Saint Girons H (1976) Contributions à la morphologie comparée des fosses nasales et de leurs annexes chez les lépidosauriens. Mem Mus Natl Hist Nat Paris A98:1–87
- Gaffney ES, Hutchison JH, Jenkins FA, Meeker LJ (1987) Modern turtle origins: the oldest known Cryptodire. Science (NY) 237:289–292
- Galli-Gallardo SM, Oguro C, Pang PKT (1979) Renal responses of the Chilean toad, *Calyptocephalella caudiverbera*, and the mudpuppy, *Necturus maculosus*, to mesotocin. Gen Comp Endocrinol 37:134–136
- Gans C (1979) Momentarily excessive construction as the basis for protoadaptation. Evolution 33:227–233
- Gans C (1988) Adaptation and the form-function relation. Am Zool 28:681–697
- Gans C (1993) On the merits of adequacy. Am J Sci 293A:391–406
- Gans C, Merlin R, Blumer WFC (1982) The water-collecting mechanism of *Moloch horridus* re-examined. Amphib Reptilia 3:57–64
- Garland HO, Henderson IW, Brown JA (1975) Micropuncture study of the renal responses of the urodele amphibian *Necturus maculosus* to injections of arginine vasotocin and anti-aldoosterone compound. J Exp Biol 63:249–264
- Garrick LD (1974) Reproductive influences on behavioral thermoregulation in the lizard *Sceloporus cyanogenys*. Physiol Behav 12:85–91
- Garrick LD (1979) Lizard thermoregulation: operant responses for heat at different thermal intensities. Copeia 1979:258–266

- Gatten RE (1985) The uses of anaerobiosis by amphibians and reptiles. *Am Zool* 25:945–954
- Geiser F (1990) Influence of polyunsaturated and saturated dietary lipids on adipose tissue, brain and mitochondrial fatty acid composition of a mammalian hibernator. *Biochim Biophys Acta* 1046:159–166
- Geiser F (1991) The effect of unsaturated and saturated dietary lipids on the pattern of daily torpor and the fatty acid composition of tissues and membranes of the deer mouse *Peromyscus maniculatus*. *J Comp Physiol* 161B:590–597
- Geiser F, Kenagy GJ (1987) Polyunsaturated lipid diet lengthens torpor and reduces body temperature in a hibernator. *Am J Physiol* 252:R897–R901
- Geiser F, Firth BT, Seymour RS (1992a) Polyunsaturated dietary lipids lower the selected body temperature of a lizard. *J Comp Physiol* 162B:1–4
- Geiser F, Stahl B, Leramonth RP (1992b) The effect of dietary fatty acids in the pattern of torpor in a marsupial. *Physiol Zool* 65:1236–1245
- Gerwein RW, John-Alder HB (1992) Growth and behaviour in thyroid-deficient lizards. *Gen Comp Endocrinol* 87:312–324
- Gibbons JW (1987) Why do turtles live so long? *Bioscience* 37:262–269
- Gilles M, Chauvet J, Chauvet M-T, Clarke C, Bern HA, Acher R (1993) Chemical identification of the mammalian oxytocin in a Holocephalean fish, the rat fish (*Hydrologus coliei*). *Gen Comp Endocrinol* 92:260–264
- Gilles-Baillien M (1969) Seasonal changes in the permeability of the isolated vesical epithelium of *Testudo hermanni hermanni* Gmelin. *Biochim Biophys Acta* 193:129–136
- Gilles-Baillien M (1970) Urea and osmoregulation in the diamondback terrapin *Melaclemys centrata centrata* (Latreille). *J Exp Biol* 52:691–697
- Gilles-Baillien M (1973) Hibernation and osmoregulation in the diamondback terrapin *Malaclemys centrata centrata* (Latreille). *J Exp Biol* 59:45–51
- Gilles-Baillien M, Schoffeniels E (1965) Variations saisonnières dans la composition du sang de la tortue Greque *Testudo hermanni* Gmelin. *Ann Soc R Zool Belg* 95:75–79
- Glaser R (1958) Increase in locomotor activity following shielding of the parietal eye in night lizards. *Sciences (NY)* 128:1577–1578
- Goff GP, Stenson GB (1988) Brown adipose tissue in leatherback sea turtles: a thermogenic organ in an endothermic reptile? *Copeia* 1988:1071–1075
- Gonzalez CF, Shamoo YE, Wyssbrod HR, Solinger RE, Brodsky WA (1967) Electrical nature of sodium transport across the isolated turtle bladder. *Am J Physiol* 213:333–340
- Gordon MS (1965) Intracellular osmoregulation in skeletal muscle during salinity adaptation in two species of toads. *Biol Bull (Woods Hole)* 128:218–229
- Gordon MS, Schmidt-Nielsen K, Kelly HM (1961) Osmotic regulation in the crab-eating frog (*Rana crancrivora*). *J Exp Biol* 38:659–678
- Gould SJ, Lewontin RC (1979) The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme. *Proc R. Soc Lond B* 205:581–598
- Gould SJ, Vrba ES (1982) Exaptation – a missing term in the science of form. *Paleobiology* 8:4–15
- Grant BW (1990) Trade-offs in activity time and physiological performance for thermoregulating desert lizards, *Sceloporus merriami*. *Ecology* 71:2323–2333
- Grant BW, Dunham AE (1988) Thermally imposed time constraints on the activity of the desert lizard *Sceloporus merriami*. *Ecology* 69:167–176
- Grantham JJ, Burg MB (1966) Effect of vasopressin and cyclic AMP on permeability of isolated collecting tubules. *Am J Physiol* 211:255–259
- Green B (1972a) Aspects of renal function in the lizard *Varanus gouldii*. *Comp Biochem Physiol* 43A:747–756
- Green B (1972b) Water losses of the sand goanna (*Varanus gouldii*) in its natural environment. *Ecology* 53:452–457
- Green B, King D, Butler WH (1986) Water, sodium and energy turnover in free-living Perenties, *Varanus giganteus*. *Aust Wildl Res* 13:589–595
- Green B, Dryden G, Dryden K (1991a) Field energetics of a large carnivorous lizard, *Varanus rosenbergi*. *Oecologia* 88:547–551
- Green B, King D, Braysher M, Saim A (1991b) Thermoregulation, water turnover and energetics of free-living Komodo dragons, *Varanus komodoensis*. *Comp Biochem Physiol* 99A:97–101

- Greene HW (1988) Antipredator mechanisms in reptiles. In: Gans C, Huey RB (eds) *Biology of the Reptilia*, 16, No. 1. Liss, New York, pp 3–152
- Greger R (1985) Ion transporting mechanisms in thick ascending limb of Henle's Loop of mammalian nephron. *Physiol Rev* 65:760–797
- Greger R, Schlatter E (1984) Mechanism of secretion in the rectal gland of spiny dogfish (*Squalus acanthias*). I. Experiments in isolated *in vitro* perfused rectal gland tubules. *Pflügers Arch* 402:63–75
- Greger R, Schlatter E, Lang F (1983) Evidence for electroneutral sodium chloride cotransport in the cortical thick ascending limb of Henle's loop of rabbit kidney. *Pflügers Arch* 396:308–314
- Grene M (1959) Two evolutionary theories. *Br J Philos Sci* 9:110–193
- Grenot CJ (1967) Observations physio-écologiques sur la régulation thermique chez le lézard agamidé *Uromastix acanthinurus* Bell. *Bull Soc Zool Fr* 92:51–66
- Grenot CJ (1968) Sur l'excrétion nasale de sels chez le lézard saharien *Uromastix acanthinurus*. *CR Acad Sci (Paris)* 226:1871–1874
- Grenot CJ (1976) Ecophysiologie du lézard saharien *Uromastix acanthinurus* Bell 1825 (Agamidae, herbivore). *Publ Lab Zool Ecole Normale Supérieure Paris* 7:1–323
- Grenot CJ (1988) Réponses écophysiologiques des reptiles aux contraintes hydriques dans les écosystèmes méditerranéens arides. In: Castri FD, Floret C, Rambal S, Roy J (eds) *Time scales and water stress: 5th Int Conf on Mediterranean ecosystems (Medecos V)*. Montpellier, France, 1987. IUBS, France 1988:29–51
- Grenot CJ, Vernet R (1973) Sur une population d'*Uromastix acanthinurus* Bell isolée au milieu du Grand Erg Occidental (Sahara algérien). *CR Acad Sci (Paris)* 276:1349–1352
- Grigg GC (1981) Plasma homeostasis and cloacal urine composition in *Crocodylus porosus* caught along a salinity gradient. *J Comp Physiol* 144:261–270
- Grigg GC, Drane CR, Courtice GP (1979) Time constants of heating and cooling in the eastern water dragon, *Physignathus lesuerii*. *J Therm Biol* 44:354–360
- Grigg GC, Johansen K, Harlow P, Beard LA, Taplin LE (1986a) Facultative aestivation in a tropical freshwater turtle *Chelodina rugosa*. *Comp Biochem Physiol* 83A:321–323
- Grigg GC, Taplin LE, Green B, Harlow P (1986b) Sodium and water fluxes in *Crocodylus porosus* free-living in marine and brackish conditions. *Physiol Zool* 59:240–253
- Grime JP (1989) The stress debate: symptom of impending synthesis? *Biol J Linn Soc* 37:3–17
- Grubb B, Bentley PJ (1987) Aldosterone-induced amiloride-inhibitable short-circuit current in the avian ileum. *Am J Physiol* 253:G211–G216
- Guillette LJ (1979) Stimulation of parturition in a viviparous lizard (*Sceloporus jarrovi*) by arginine vasotocin. *Gen Comp Endocrinol* 38:457–460
- Guppy M, Davison W (1982) The hare and the tortoise: metabolic strategies in cardiac and skeletal muscles of the skink and the chameleon. *J Exp Zool* 220:289–295
- Guppy M, Bradshaw SD, Fergusson B, Hansen IA, Atwood C (1987) Metabolism in lizards: low lactate turnover and advantages of heterothermy. *Am J Physiol* 22:R77–R82
- Hadj-Bekkouché F, Cherifa A, Cherifa D, Saidi A (1993) Variations nycthémerales de l'aldostéronémie et de la corticostéronémie chez la tortue terrestre, *Testudo mauritanica*, Dumer (Chelonia, Testudinidae). *Gen Comp Endocrinol* (in press)
- Hailey A, Rose CA, Pulford E (1987) Food consumption, thermoregulation and ecology of the skink *Chalcides bedriagai*. *Herpetol J* 1:144–153
- Hall DA, Varney DM (1980) Effect of vasopressin on electrical potential difference and chloride transport in mouse medullary thick ascending limb of Henle's loop. *J Clin Invest* 66:792–802
- Hamilton WJI (1973) *Life's color code*. McGraw-Hill, New York
- Hamilton WJI, Coetzee CG (1969) Thermoregulatory behaviour of the vegetarian lizard *Angolosaurus skoogi* on the vegetationless northern Namib desert dunes. *Sci Pap Namib Desert Res Stn* 47:95–103
- Hammerson GA (1987) Thermal behaviour of the snake *Coluber constrictor* in west-central California. *J Therm Biol* 12:195–197
- Hammerson GA (1989) Effects of weather and feeding on body temperature and activity in the snake *Masticophis flagellum*. *J Therm Biol* 14:219–224
- Hanwell A, Linzell JL, Peaker M (1971) Salt-gland secretion and blood flow in the goose. *J Physiol (Lond)* 213:373–387

- Harlow P, Grigg G (1984) Shivering thermogenesis in a brooding diamond python, *Python spilotes spilotes*. *Copeia* 1984:959–965
- Harris EJ (1960) Transport and accumulation in biological systems. Butterworths, London
- Harris VA (1964) The life of the rainbow lizard. Hutchinson, London
- Harvey PH, Pagel MD (1991) The comparative method in evolutionary biology. Oxford University Press, London
- Harvey PH, Purvis A (1991) Comparative methods for explaining adaptations. *Nature (Lond)* 351:619–624
- Hays RM (1990) Water transport in epithelia. In: Kinne RKH (ed) *Urinary concentrating mechanisms*, 2. Karger, Basel, pp 1–30
- Heath JE (1964a) Head-body temperature differenced in horned lizards. *Physiol Zool* 37:237–239
- Heath JE (1964b) Reptilian thermoregulation: evaluation of field studies. *Science (NY)* 146:784–785
- Heath JE (1965) Temperature regulation and diurnal activity in horned lizards. *Univ Calif Publ Zool* 64:97–136
- Heath JE (1970) Behavioral regulation of body temperature in poikilotherms. *Physiologist* 13:399–410
- Heatwole H (1970) Thermal ecology of the desert dragon, *Amphibolurus inermis*. *Ecol Monogr* 40:425–457
- Heatwole H (1976) Reptile ecology. University of Queensland Press, Queensland, Australia
- Hebert SC, Andreoli TE (1984) The effects of antidiuretic hormone on cellular conductive pathways in mouse medullary thick ascending limbs of Henle. II. Determinants of the ADH-mediated increases in transepithelial voltage and in net Cl^- absorption. *J Membr Biol* 80:221–233
- Henle K (1992) Predation pressure, food availability, thermal environment, and precision of thermoregulation in a desert population of the skink *Morethia boulengeri*, with a comment on measuring thermoregulatory precision. *Zool Jahrb Syst* 119:405–412
- Hentschel H, Elger M (1987) The distal nephron in the kidney of fishes. *Adv Anat Embryol Cell Biol* 108:1–151
- Hentschel H, Elger M (1989) Morphology of glomerular and aglomerular kidneys. In: Kinne RKH (ed) *Structure and function of the kidney*, 1. Karger, Basel, pp 1–72
- Henzell RP (1972) Adaptation to aridity in lizards of the *Egernia whitei* species group. PhD Thesis, University of Adelaide
- Hertz PE, Huey RB, Garland T (1988) Time budgets, thermoregulation, and maximal locomotor performance: are reptiles olympians or boy scouts? *Am Zool* 28:927–938
- Hertz PE, Huey RB, Stevenson RD (1993) Evaluating temperature regulation by field-active ectotherms: the fallacy of the inappropriate question. *Am Nat* 142:796–818
- Hochachka PW (1973) Multiple end products of anerobiosis in diving vertebrates. *Physiologist* 16:373
- Holmes WN, McBean RL (1964) Some aspects of electrolyte excretion in the Green turtle *Chelonia mydas mydas*. *J Exp Biol* 41:81–90
- Holmes WN, Phillips JG (1985) The avian salt gland. *Biol Rev* 60:213–256
- Holmes WN, Butler DG, Phillips JG (1961) Observations on the effect of maintaining glaucous-winged gulls (*Larus glaucescens*) on fresh water and sea water for long periods. *J Exp Biol* 48:487–508
- Horowitz M, Borut A (1970) Effect of acute dehydration on body fluid compartments in three rodent species: *Rattus norvegicus*, *Acomys cahirinus* and *Meriones crassus*. *Comp Biochem Physiol* 35:283–290
- Horowitz M, Borut A (1973) Blood volume regulation in dehydrated rodents: plasma colloid osmotic pressure, total osmotic pressure and electrolytes. *Comp Biochem Physiol* 44A:1261–1265
- Horowitz M, Borut A (1975) Blood volume regulation in dehydrated rodents: plasma protein turnover and sedimentation coefficients. *Comp Biochem Physiol* 51A:827–831
- Huey RB (1982) Temperature, physiology, and the ecology of reptiles. In: Gans C, Pough FH (eds) *Biology of the Reptilia*, 12C. Academic Press, New York, pp 25–91
- Huey RB, Kingsolver JG (1993) Evolution of resistance to high temperature in ectotherms. *Am Nat* 142:S21–S46

- Huey RB, Slatkin M (1976) Cost and benefit of lizard thermoregulation. *Q Rev Biol* 51:363–383
- Huey RB, Peterson CR, Arnold SJ, Porter WP (1989) Hot rocks and not-so-hot rocks: retreat site selection by garter snakes and its thermal consequences. *Ecology* 70:931–944
- Hulbert AJ (1978) The thyroid hormones: a thesis concerning their action. *J Theor Biol* 73:81–100
- Hulbert AJ (1988) Metabolism and the development of endothermy. In: Tyndale-Biscoe CH, Jannsens PA (eds) *The developing marsupial*. Springer, Berlin Heidelberg New York, pp 148–161
- Hulbert AJ, Else PL (1989) Evolution of mammalian endothermic metabolism: mitochondrial activity and cell composition. *Am J Physiol* 256:R63–R69
- Hulbert AJ, Else PL (1990) The cellular basis of endothermic metabolism: a role for “leaky” membranes. *NIPS* 5:25–28
- Huot-Daubremont C, Grenot C, Bradshaw SD (1996) Temperature regulation in Hermann’s tortoise (*Testudo hermanni hermanni*), studied with indwelling probes. *Amphib Reptilia* 17:91–102
- Hutchinson VH, Kosh RJ (1974) Thermoregulatory function of the parietal eye in the lizard *Anolis carolinensis*. *Oecologia* 16:173–177
- Hutchinson VH, Dowling HG, Vinegar A (1966) Thermoregulation in a brooding female Indian python, *Python molurus bivittatus*. *Sciences (NY)* 151:694–696
- Ichikawa I, Brenner BM (1977) Evidence for glomerular actions of ADH and dibutyryl cyclic AMP in the rat. *Am J Physiol* 233:F102–F117
- Imbert-Teboul M, Champigneulle A, Siga E (1993) Segmental distribution of V_{1a} - and V_2 -receptor mediated effects along the nephron. In: Gross P, Robertson GL (eds) *Vasopressin*, 1. John Wiley, Eurotext, New York, pp 275–287
- Imbert M, Chabardès D, Montegut M, Clique A, Morel F (1975) Vasopressin dependent adenylate cyclase in single segments of rabbit kidney tubule. *Pflügers Arch* 357:173–186
- Innocenti A, Minutini L, Foà A (1994) Seasonal changes of locomotor activity patterns in ruin lizards *Podarcis sicula* II. Involvement of the pineal. *Behav Ecol Sociobiol* 35:27–32
- Izard Y, Detrait J, Bouquet P (1961) Variations saisonnières de la composition du sang de *Vipera aspis*. *Ann Inst Pasteur (Paris)* 100:539–545
- Jard S (1983) Vasopressin isoreceptors in mammals: relation to cyclic AMP-dependent and cyclic AMP-independent mechanisms. In: Kleinzeller A, Martin BR (eds) *Current topics in membrane and transport*, 18. Academic Press, New York, pp 255–285
- Jard S, Morel F (1963) Actions of vasotocin and some of its analogues on salt and water excretion by the frog. *Am J Physiol* 204:222–226
- John-Alder HB (1984) Seasonal variations in activity, aerobic energetic capacities and plasma thyroid hormones (T3 and T4) in an iguanid lizard. *J Comp Physiol* 109B:175–189
- Johnson CR (1972) Head-body temperature difference in *Varanus gouldii* (Sauria: Varanidae). *Comp Biochem Physiol* 43A:1025–1029
- Johnson CR (1974) Thermoregulation in crocodilians – I. Head-body temperature control in the Papuan-New Guinea crocodiles, *Crocodylus novaeguineae* and *Crocodylus porosus*. *Comp Biochem Physiol* 49A:3–28
- Jones MEE, Bradshaw SD, Fergusson B, Watts R (1990) The effect of available surface water on levels of anti-diuretic hormone (lysine vasopressin) and water and electrolyte metabolism of the Rottnest Island quokka (*Setonix brachyurus*). *Gen Comp Endocrinol* 77:75–87
- Joos B, John-Alder HB (1990) Effects of thyroxine on standard and total metabolic rates in the lizard *Sceloporus undulatus*. *Physiol Zool* 63:873–885
- Junqueira LCU, Malnic G, Monge C (1966) Reabsorptive function of the ophidian cloaca and large intestine. *Physiol Rev* 39:151–159
- Kar A, Chandola-Saklani A (1985) Circulating thyroid hormone concentrations in relation to seasonal events in the male garden lizard, *Calotes versicolor*. *Gen Comp Endocrinol* 60:14–19
- Katz AI, Doucet A, Morel F (1979) Na-K-ATPase activity along the rabbit, rat, and mouse nephron. *Am J Physiol* 237:F114–F120
- Kingsbury BA (1994) Thermal constraints and eurythermy in the lizard *Elgaria multicarinata*. *Copeia* 1994:266–273
- Kirschner LB (1977) The sodium chloride excreting cells in marine vertebrates. In: Gupta BL, Moreton RB, Oschman JL, Wall BJ (eds) *Transport of ions and water in animals*. Academic Press, London, pp 427–452

- Kleiber M (1961) *The fire of life*. Wiley and Sons, New York
- Kluger MJ, Tarr RS, Heath JE (1973) Posterior hypothalamic lesions and disturbances in behavioral thermoregulation. *Physiol Zool* 46:79–84
- Knowles HC (1956) Hypernatraemia. *Metabolism* 5:508–518
- Koike TL, Pryor LR, Neldon HL, Venable RS (1977) Effect of water deprivation on plasma radioimmunoassayable arginine vasotocin in conscious chickens (*Gallus domesticus*). *Gen Comp Endocrinol* 33:359–364
- Komadina S, Solomon S (1970) Comparison of renal function of bull and water snakes (*Pituophis melanoleucus* and *Natrix sipedon*). *Comp Biochem Physiol* 32:333–343
- Kulshreshtha VV, Khan RA (1988) Effect of masking of parietal eye on cloacal temperature in *Varanus monitor*. *Indian J Exp Biol* 26:790–791
- Kutcher C (1967) Plasma volume change during water deprivation in gerbils, hamsters, guinea pigs and rats. *Comp Biochem Physiol* 25:929–936
- La Pointe JL (1969) Effects of ovarian steroids and neurohypophysial hormones on the oviduct of the viviparous lizard *Klauberina riversiana*. *J Endocrinol* 43:197–205
- La Pointe JL (1977) Comparative physiology of neurohypophysial hormone action on the vertebrate oviduct-uterus. *Am Zool* 17:763–773
- Lacher TE, Alho CJR, Pereira IGT (1986) The relation between cloacal temperature and ambient temperature in five species of Brazilian turtles. *Rev Bras Biol* 46:563–566
- Langlois J (1902) La régulation thermique chez les poikilothermes. *J Physiol Pathol* 4:249–256
- Lauren DJ (1985) The effect of chronic saline exposure on the electrolyte balance, nitrogen metabolism and corticosterone titer in the American alligator, *Alligator mississippiensis*. *Comp Biochem Physiol* 81A:217–223
- LeBrie SJ (1972) Endocrines and water and electrolyte balance in reptiles. *Fed Proc* 31:1599–1608
- LeBrie SJ, Elizondo RS (1969) Saline loading and aldosterone in water snakes *Natrix cyclopion*. *Am J Physiol* 217:426–430
- Lecomte J, Clobert J, Massot M (1993) Shift in behaviour related to pregnancy in *Lacerta vivipara*. *Rev Ecol (Terre Vie)* 48:99–107
- Lee AK, McDonald IR (1985) Stress and population regulation in small mammals. *Oxford reviews of reproductive biology*, 7. Oxford University Press, Oxford, pp 261–304
- Lee JC (1980) Comparative thermal ecology of two lizards. *Oecologia* 44:171–176
- Lee MSY (1993) The origin of the turtle body plan: bridging a famous morphological gap. *Science (NY)* 261:1716–1720
- Le Fevre ME (1973) Effects of aldosterone on the isolated substrate-depleted turtle bladder. *Am J Physiol* 225:1252–1256
- Legler JM (1960) Natural history of the Ornate box turtle, *Terrapene ornata* Agassiz. *Univ Kans Publ Mus Nat Hist* 11:527–669
- Lemire M (1983) Contribution à l'étude des structures nasales des Sauriens. Structure et fonction de la glande "à sels" des lézards déserticoles. Thèse de Doctorat d'Etat, Université de Pierre et Marie Curie, Paris VI
- Lemire M, Vernet R (1982) Effects of different loads on the nasal gland secretion of the lizard *Uromastix acanthinurus* (Agamidae) and relations with its functions. *Comp Biochem Physiol* 72A:65–72
- Lemire M, Vernet R (1983) Acclimation of nasal salt secretion in the lizard *Uromastix acanthinurus* (Agamidae). Effects of repetitive salt loads. *J Arid Environ* 6:145–153
- Lemire M, Deloince R, Grenot CJ (1970) Etudes des cavités nasales du Léopard Fouette-Queue, *Uromastix acanthinurus* Bell. *CR Acad Sci (Paris)* 270:817–820
- Lemire M, Deloince R, Grenot CJ (1972) Etude histoenzymologique de la glande "à sels" du lézard saharien *Uromastix acanthinurus* Bell. *CR Acad Sci (Paris)* 274:3414–3416
- Lemire M, Grenot CJ, Vernet R (1979) La balance hydrique d'*Uromastix acanthinurus* Bell (Sauria, Agamidae) au Sahara dans des conditions semi-naturelles. *CR Acad Sci (Paris)* 288:359–362
- Lemire M, Grenot CJ, Vernet R (1980) Electrolyte excretion by the nasal gland of an herbivorous Saharan lizard, *Uromastix acanthinurus* (Agamidae). Effects of single NaCl and KCl loads. *J Arid Environ* 3:325–330
- Lemire M, Grenot CJ, Vernet R (1982) Water and electrolyte balance of free-living Saharan lizards, *Uromastix acanthinurus*. *J Comp Physiol* 146:81–93

- Licht P (1984) Reptiles. In: Lamming GE (ed) Marshall's physiology of reproduction. Churchill Livingstone, London, pp 206–282
- Licht P, Bradshaw SD (1969) A demonstration of corticotropic activity and its distribution in the pars distalis of the reptile. *Gen Comp Endocrinol* 36:689–718
- Lillywhite HB (1987) Temperature, energetics, and physiological ecology. In: Seigel RA, Collins JT, Novak SS (eds) Snakes: ecology and evolutionary biology. McGraw-Hill, New York, pp 422–477
- Lorenzo A, Medina V, Badia P, Gomez T (1990) Effects of vasopressin on electrolyte transport in lizard intestine. *J Comp Physiol B* 159:745–751.
- Lowy RJ, Dawson DC, Ernst SA (1989) Mechanism of ion transport by avian salt gland primary cell cultures. *Am J Physiol* 256:R1184–R1191
- Lynn WG (1970) The thyroid. In: Gans C, Parsons TS (eds) Biology of the Reptilia, 3. Academic Press, New York, pp 201–234
- Macchi IA, Phillips JG (1966) In vitro effect of adrenocorticotropin or cortical secretion in the turtle, snake and bullfrog. *Gen Comp Endocrinol* 6:170–182
- Macfarlane WV (1978) The ecophysiology of water in desert organisms. In: McIntyre AK (ed) Water: planets, plants and people. Australian Academy of Science, Canberra, ACT, pp 108–143
- Macfarlane WV, Morris RJH, Howard B (1963) Turnover and distribution of water in desert camels, sheep, cattle and kangaroos. *Nature (Lond)* 197:270–271
- Marples BJ (1932) The structure and development of the nasal glands of birds. *Proc Zool Soc Lond* 1932:829–844
- Marshall AT (1984) The windowless energy dispersive X-ray detector: prospects for a role in biological X-ray microanalysis. *Scanning Electron Microsc* 1984:493–504
- Marshall AT, Hyatt AD, Phillips JG, Condrón RJ (1985) Isosmotic secretion in the avian nasal salt gland: X-ray microanalysis of luminal and intracellular ion distributions. *J Comp Physiol* 156B:213–227
- McDonald JF (1983) The molecular basis of adaptation: a critical review of relevant ideas and observations. *Annu Rev Ecol Syst* 14:77–182
- McGinnis SM (1966) *Sceloporus occidentalis*: preferred body temperature of the western fence lizard. *Science (NY)* 152:1090–1091
- McGinnis SM, Dickson LL (1967) Thermoregulation in the desert iguana *Dipsosaurus dorsalis*. *Science (NY)* 156:1757–1759
- McGinnis SM, Falkenstein M (1971) Thermoregulatory behavior in three sympatric species of iguanid lizards. *Copeia* 1971:552–554
- McGinnis SM, Voigt SG (1971) Thermoregulation in the desert tortoise, *Gopherus agassizii*. *Comp Biochem Physiol* 40A:119–126
- Medawar PB (1951) Problems of adaptation. *New Biology* 11:10–26
- Medica PA, Bury RB, Luckenbach R (1980) Drinking and construction of water catchments by the desert tortoise *Gopherus agassizii*, in the Mojave desert. *Herpetologica* 36:301–304
- Meek R (1984) Thermoregulatory behaviour in a population of Hermann's tortoise (*Testudo hermanni*) in southern Yugoslavia. *Br J Herpetol* 6:387–391
- Meek R (1988) The thermal ecology of Hermann's tortoise (*Testudo hermanni*) in summer and autumn in Yugoslavia. *J Zool (Lond)* 215:99–111
- Meek R, Avery RA (1988) Thermoregulation in chelonians. *Herpetol J* 1:253–259
- Meissl H, Dodt E (1981) Comparative physiology of pineal photoreceptor organs. In: Oksche A, Pévet P (eds) The pineal organ: photobiology, biochemistry, endocrinology. Elsevier North Holland, Amsterdam, pp 61–80
- Miller T, Bradshaw SD (1979) Adrenocortical function in a field population of a macropodid marsupial (*Setonix brachyurus*, Quoy and Gaimard). *J Endocrinol* 82:159–170
- Minnich JE (1967) Water procurement and conservation by desert reptiles in their natural environment. *Isr J Med Sci* 12:740–758
- Minnich JE (1970a) Water and electrolyte balance of the desert iguana, *Dipsosaurus dorsalis*, in its natural habitat. *Comp Biochem Physiol* 35:921–933
- Minnich JE (1970b) Evaporative water loss from the desert iguana, *Dipsosaurus dorsalis*. *Copeia* 1970:575–578
- Minnich JE (1971) Seasonal variation in weight-length relationships and fat body size in the desert iguana, *Dipsosaurus dorsalis*. *Copeia* 1971:359–362

- Minnich JE (1972) Excretion of urate salts by reptiles. *Comp Biochem Physiol* 41A:535–549
- Minnich JE (1977) Adaptive responses in the water and electrolyte budgets of native and captive desert tortoises, *Gopherus agassizi*, to chronic drought. *Desert Tortoise Council Symp Proc* 1977:102–129
- Minnich JE (1979) Reptiles. In: Maloij GMO (ed) *Comparative physiology of osmoregulation in animals*, 1. Academic Press, London, pp 393–641
- Minnich JE (1982) The use of water. In: Gans C, Pough FH (eds) *Biology of the Reptilia*, 12C. Academic Press, New York, pp 325–395
- Minnich JE, Piehl PA (1972) Spherical precipitates in the urine of reptiles. *Comp Biochem Physiol* 41A:551–554
- Minnich JE, Shoemaker VH (1970) Diet, behavior and water turnover in the desert iguana, *Dipsosaurus dorsalis*. *Am Midl Nat* 84:496–509
- Minnich JE, Shoemaker VH (1972) Water and electrolyte turnover in a field population of the lizard *Uma scoparia*. *Copeia* 1972:650–659
- Minnich JE, Ziegler MR (1976) Comparison of field water budgets in the tortoises *Gopherus agassizii* and *Gopherus polyphemus*. *Am Zool* 16:219
- Moberly WR (1968) The metabolic responses of the common iguana, *Uguana iguana* to activity and restraint. *Comp Biochem Physiol* 27:1–20
- Molnar RE (1991) Fossil reptiles in Australia. In: Vickers-Rich P, Monaghan JM, Baird RF, Rich TH (eds) *Vertebrate palaeontology of Australia*. Pioneer Design Studio and Monash University Publications Committee, Melbourne, pp 605–701
- Monod T (1973) *Les déserts*. Editions Horizons de France, Paris
- Morel F (1983) Regulation of kidney functions by hormones: a new approach. *Recent Prog Horm Res* 39:271–304
- Morel F, Doucet A (1986) Hormonal control of kidney functions at the cell level. *Physiol Rev* 66:377–468
- Morel F, Chabardès D, Imbert-Teboul M (1978) Methodology for enzymatic studies of isolated tubular segments: adenylate cyclase. In: Martinez-Maldonado M (ed) *Methods in pharmacology*, 4B. Plenum, New York, pp 297–323
- Morel F, Imbert-Teboul M, Chabardès D (1981) Distribution of hormone-dependent adenylate cyclase in the nephron and its physiological significance. *Annu Rev Physiol* 43:569–581
- Morgareidge KR, White FN (1969) Cutaneous vascular changes during heating and cooling in the Galápagos iguana. *Nature (Lond)* 223:587–591
- Mrosoovsky N (1990) Rheostasis: the physiology of change. Oxford University Press, New York
- Muchlinski AE, Stoutenburgh RJ, Hogan JM (1989) Fever response in laboratory maintained and free-ranging chuckwalla (*Sauromalus obesus*). *Am J Physiol* 257:R150–R155
- Muchlinski AE, Hogan JM, Stoutenburgh RJ (1990) Body temperature regulation in a desert lizard, *Sauromalus obesus*, under undisturbed field conditions. *Comp Biochem Physiol* 95A:579–583
- Munsick RA (1966) Chromatographic and pharmacological characterization of the neurohypophyseal hormones of an amphibian and a reptile. *Endocrinology* 78:591–599
- Murray RW, Potts WTW (1961) The composition of the endolymph, perilymph and other body fluids of elasmobranchs. *Comp Biochem Physiol* 2:65–75
- Murrish DE, Schmidt-Nielsen K (1970) Water transport in the cloaca of lizards: active or passive? *Science* 170:324–326
- Myrhe K, Hammel HT (1969) Behavioral regulation in internal temperature in the lizard. *Am J Physiol* 217:1490–1495
- Nagy KA (1972) Water and electrolyte budgets of a free-living desert lizard, *Sauromalus obesus*. *J Comp Physiol* 79:39–62
- Nagy KA (1973) Behavior, diet and reproduction in a desert lizard, *Sauromalus obesus*. *Copeia* 1973:93–102
- Nagy KA (1982a) Field studies of water relations. In: Gans C, Pough H (eds) *Biology of the Reptilia*, 12C. Academic Press, New York, pp 483–501
- Nagy KA (1982b) Energy requirements of free-living iguanid lizards. In: Burghardt GM, Rand AS (eds) *Iguanas of the world: their behaviour, ecology, and conservation*, Noyes Publications, Park Ridge, New Jersey, pp 45–59

- Nagy KA (1988) Seasonal patterns of water and energy balance in desert vertebrates. *J Arid Environ* 14:201–210
- Nagy KA, Bradshaw SD (1995) Energetics, osmoregulation and food consumption by free-living desert lizards, *Ctenophorus* (= *Amphibolurus*) *nuchalis*. *Amphib Reptilia* 16:25–35
- Nagy KA, Medica PA (1986) Physiological ecology of desert tortoises in southern Nevada. *Herpetologica* 42:73–92
- Nagy KA, Peterson CC (1988) Scaling of water flux rate in animals. *Univ Publ Zool* 120:1–172
- Nagy KA, Shoemaker VH (1975) Energy and nitrogen budgets of the free-living desert lizard *Sauromalus obesus*. *Physiol Zool* 48:252–262
- Nagy KA, Clarke RB, Seely MK, Mitchell DM, Lighton JRB (1991) Water and energy balance in Namibian desert sand dune lizards, *Angolosaurus skoogi* (Anderson 1916). *Funct Ecol* 5:731–739
- Nicholson SW, Lutz PL (1989) Salt gland function in the Green sea turtle *Chelonia mydas*. *J Exp Biol* 144:171–184
- Nishimura H (1985) Endocrine control of renal handling of solutes and water in vertebrates. *Renal Physiol* 8:279–300
- Norris KA (1967) Color adaptation in desert reptiles and its thermal relationships. In: Milstead W (ed) *Lizard ecology: a symposium*. University of Missouri Press, Columbia, pp 162–229
- Norris KS, Dawson WR (1964) Observations on the water economy and electrolyte excretion of Chuckwallas (*Lacertilia*, *Sauromalus*). *Copeia* 1964:638–646
- Nothstine SA, Davis JO, DeRoos RM (1971) Kidney extracts and ACTH on adrenal steroid secretion in a turtle and a crocodilian. *Am J Physiol* 221:726–732
- O'Connor MP, Spotila JR (1992) Consider a spherical lizard: animals, models and approximations. *Am Zool* 32:179–193
- Oelrich TM (1956) The anatomy of the head of *Ctenosaura pectinata* (Iguanidae). *Misc Publ Mus Zool Univ Mich* 94:1–122
- Oksche A (1984) Evolution of the pineal complex: correlation of structure and function. *Ophthalmic Res* 16:88–95
- Oksche A, Farner DS, Serventy DL, Wolff F, Nicholls CA (1963) The hypothalamo-hypophysial neurosecretory system of the zebra finch, *Taeniopygia castanotis*. *Z Zellforsch* 58:846–914
- O'Neil RG, Sansom SC (1984) Characterisation of apical cell membrane Na⁺ and K⁺ conductances of cortical collecting duct using microelectrode techniques. *Am J Physiol* 247:F14–F24
- O'Shea JE, Bradshaw SD, Stewart T (1993) The renal vasculature and excretory system of the agamid lizard *Ctenophorus ornatus*. *J Morphol* 217:287–299
- Osmolska H (1979) Nasal salt gland in dinosaurs. *Acta Palaeontol Pol* 24:205–215
- Owen R (1866) *On the anatomy of vertebrates*. Longman Green, London
- Pagel MD, Harvey PH (1988) Recent developments in the analysis of comparative data. *Q Rev Biol* 63:413–440
- Pang PKT, Sawyer WH (1978) Renal and vascular responses of the bullfrog (*Rana catesbeiana*) to mesotocin. *Am J Physiol* 235:F151–F155
- Pang PKT, Uchiyama M, Sawyer WH (1982) Endocrine and neural control of amphibian renal functions. *Fed Proc* 41:2365–2370
- Parent A (1979) Monoaminergic systems of the brain. In: Gans C, Northcutt RG, Ulinski P (eds) *Biology of the Reptilia*, 10. Academic Press, New York, pp 247–285
- Parvez S, Ventura MA, Parvez H (1979) Aldosterone antagonism. In: Agarwal MK (ed) *Antihormones*. Elsevier North-Holland, Amsterdam, pp 111–135
- Patterson JW, Davies PMC (1978) Preferred body temperature: seasonal and sexual differences in the lizard *Lacerta vivipara*. *J Therm Biol* 3:39–41
- Patterson R (1977) Growth and shell relationships in the desert tortoise. In: Trotter M (ed) *Symposium of the desert tortoise council Las Vegas, Nevada*. Desert Tortoise Council, San Diego, California 1977:158–166
- Peaker M (1971) Avian salt glands. *Philos Trans R Soc* 262B:289–300
- Peaker M (1978) Excretion of potassium from the orbital region in *Testudo carbonaria*: a salt gland in a terrestrial tortoise? *J Zool (Lond)* 184:421–422
- Peaker M, Linzell LJ (1975) *Salt glands in birds and reptiles*. Cambridge University Press, Cambridge

- Pearson OP (1977) The effect of substrate and skin color on the thermoregulation of a lizard. *Comp Biochem Physiol* 58A:353–358
- Pearson R, Pearson L (1976) The vertebrate brain. Academic Press, London
- Peek WD, McMillan DB (1979a) Ultrastructure of the tubular nephron of the garter snake *Thamnophis sirtalis*. *Am J Anat* 154:103–128
- Peek WD, McMillan WD (1979b) Ultrastructure of the renal corpuscle of the garter snake *Thamnophis sirtalis*. *Am J Anat* 155:83–101
- Peterson CC (1993) Physiological ecology of two Mojave desert populations of the desert tortoise *Xerobates agassizii*: effects of seasonal rainfall pattern and drought. PhD, University of California, Los Angeles
- Peterson CC (1996) Anhomeostasis: Seasonal water and solute relations in two populations of the desert tortoise (*Gopherus agassizii*) during chronic drought. *Physiol Zool* 69(6): in press
- Peterson CR (1987) Daily variation of the body temperatures of free-ranging garter snakes. *Ecology* 68:160–169
- Pianka ER (1986) Ecology and natural history of desert lizards. Princeton University Press, Princeton, New Jersey
- Pietruszka RD (1987) Maxithermy and the thermal biology of an herbivorous sand dune lizard. *J Arid Environ* 14:175–185
- Plummer MV (1993) Thermal ecology of arboreal green snakes (*Opheodrys aestivus*). *J Herpetol* 27:254–260
- Porter WC, Tracy CR (1983) Biophysical analyses of energetics, time-space utilization, and distributional limits. In: Huey RB, Pianka ER, Schoener TW (eds) *Lizard ecology: studies of a model organism*. Harvard University Press, Cambridge, Massachusetts, pp 55–83
- Pough FH (1980) The advantages of ectothermy for tetrapods. *Am Nat* 115:92–112
- Pough FH (1983) Amphibians and reptiles as low-energy systems. In: Aspey WP, Lustick SI (eds) *Behavioral energetics: the cost of survival in vertebrates*. Academic Press, New York, pp 141–188
- Pulford E, Hailey A, Stubbs D (1984) Thermal relations of *Testudo hermanni robertmertensi* Wermuth in S. France. *Amphib Reptilia* 5:37–41
- Quay WB (1979) The parietal eye-pineal complex. In: Gans C, Northcutt RG, Ulinski P (eds) *Biology of the Reptilia*, 9. Academic Press, New York, pp 245–406
- Rage J-C (1992) Phylogénie et systématique des lépidosauriens. Où en sommes-nous? *Bull Soc Herpetol Fr* 62:19–36
- Regamey J (1936) Les caractères sexuelles du lézard (*Lacerta agilis* L.). *Rev Suisse Zool* 42:87–168
- Regaud C, Policard A (1903) Sur l'existence de diverticules du tube urinaire sans relations avec les corpuscles de Malpighi, chez les serpents, et sur l'indépendance relative des fonctions glomérulaire et glandulaire du rein en général. *CR Soc Biol (Paris)* 55:1028–1029
- Rice GE (1982) Plasma arginine vasotocin concentrations in the lizard *Varanus gouldii* (Gray) following water loading, salt loading and dehydration. *Gen Comp Endocrinol* 47:1–6
- Rice GE, Bradshaw SD (1980) Changes in dermal reflectance and vascularity and their effects on thermoregulation in *Amphibolurus nuchalis* (Reptilia: Agamidae). *J Comp Physiol* 135:139–146
- Rice GE, Bradshaw SD, Prendergast FJ (1982) The effects of bilateral adrenalectomy on renal function in the lizard *Varanus gouldii* (Gray). *Gen Comp Endocrinol* 47:182–189
- Rismiller PD, Heldmaier G (1988) How photoperiod influences body temperature in *Lacerta viridis*. *Oecologia* 75:125–131
- Roberts JS, Schmidt-Nielsen B (1966) Renal ultrastructure and excretion of salt and water by three terrestrial lizard. *Am J Physiol* 211:476–486
- Robertson JD (1954) The chemical composition of the blood of some aquatic chordates, including members of the Tunicata, Cyclostomata and Osteichthyes. *J Exp Biol* 31:424–442
- Robinson GD, Dunson WA (1976) Water and sodium balance in the estuarine diamondback terrapin (*Malaclemys*). *J Comp Physiol* 105:129–152
- Rocha AS, Kokko JP (1977) Sodium chloride and water transport in the medullary thick ascending limb of Henle. Evidence for active chloride transport. *J Clin Invest* 52:612–623
- Rooke IJ, Bradshaw SD, Langworthy RA, Tom JA (1986) Annual cycle of physiological stress and condition of the silvereye, *Zosterops lateralis* (Aves). *Aust J Zool* 34:493–501

- Rosen PC (1990) Comparative field study thermal preferenda in Garter snakes (*Thamnophis*). J Herpetol 25:301–312
- Rosenbloom AA, Fisher DA (1974) Radioimmunoassay of arginine vasotocin. Endocrinology 95:1726–1732
- Roth JJ, Ralph CL (1976) Body temperature of the lizard (*Anolis corolinensis*): effect of parietectomy. J Exp Zool 198:17–28
- Ruby DE, Zimmerman LC, Bulova SJ, Salice CJ, O'Connor MP, Spotila JR (1994) Behavioral responses and time allocation differences in desert tortoises exposed to environmental stress in semi-natural enclosures. Herpetol Monogr 8:27–44
- Ruch TC, Fulton JF (1960) Medical physiology and biophysics, 18th edn. WB Saunders, Philadelphia
- Saint Girons H (1980) Thermoregulation in reptiles with special reference to the Tuatara and its ecophysiology. Tuatara 24:59–80
- Saint Girons H, Bradshaw SD (1981) Données histophysiologiques sur l'hypophyse de *Tiliqua rugosa* (Reptilia, Scincidae) et notamment la signification fonctionnelle des cellules gamma. ArchAnat Microsc Morphol Exp 70:129–140
- Saint Girons H, Lemire M, Bradshaw SD (1977) Structure de la glande nasale externe de *Tiliqua rugosa* (Reptilia, Scincidae) et rapports avec sa fonction. Zoomorphologie 88:277–288
- Saint Girons H, Rice GE, Bradshaw SD (1981) Histologie comparée et ultrastructure de la glande nasale externe de quelques Varanidae (Reptilia, Lacertilia). Ann Sci Nat Zool (Paris) 3(13):15–21
- Sandor T (1972) Corticosteroids in Amphibia, Reptilia and Aves. In: Idler DR (ed) Steroids in non-mammalian vertebrates. Academic Press, New York, pp 253–327
- Sandor T, Mehdi AZ (1980) Corticosteroids and their role in the extrarenal electrolyte excreting organs of nonmammalian vertebrates. In: Delrio G, Brachet J (eds) Steroids and their mechanism of action in non-mammalian vertebrates. Raven Press, New York, pp 33–49
- Sanford B, Stephens GA (1988) The effects of adrenocorticotropin hormone and angiotensin II on adrenal corticosteroid secretions in the freshwater turtle *Pseudemys scripta*. Gen Comp Endocrinol 72:107–114
- Sawyer WH, Pang PKT (1975) Endocrine adaptation to osmotic requirements of the environment. Endocrine factors in osmoregulation by lung fishes and amphibians. Gen. Comp. Endocrinol. 25:224–229
- Sawyer WH, Pang PKT (1979) Responses by vertebrates to neurohypophysial principles. In: Barrington EJ (ed) Hormones and evolution, 2. Academic Press, London, pp 493–523
- Sawyer WH, Sawyer MK (1952) Adaptive responses to neurohypophysial functions in vertebrates. Physiol Zool 25:84–98
- Scatchard G (1949) The attractions of proteins for small molecules and ions. Ann NY Acad Sci 51:660–672
- Schamberger ML, Turner FB (1986) The application of habitat modeling to the desert tortoise (*Gopherus agassizii*). Herpetologica 42:134–138
- Schmidt-Nielsen B (1979) Regulation of volume and composition of extracellular fluid. In: Robin ED (ed) Claude Bernard and the internal environment, 1. Marcel Dekker, New York, pp 191–206
- Schmidt-Nielsen B, Davis LE (1968) Fluid transport and tubular intercellular spaces in reptilian kidneys. Science 159:1105–1108
- Schmidt-Nielsen K, Dawson WR (1964) Terrestrial animals in dry heat: desert reptiles. In: Dill DB (ed) Handbook of physiology, section 4: adaptation to the environment, 4. American Physiological Society, Bethesda, Maryland, pp 467–480
- Schmidt-Nielsen K, Fänge R (1958) Salt glands in marine reptiles. Nature (Lond) 182:783–784
- Schmidt-Nielsen B, Schmidt D (1973) Renal function of *Sphenodon punctatum*. Comp Biochem Physiol 44:121–129
- Schmidt-Nielsen B, Skadhauge E (1967) Function of the excretory system of the crocodile (*Crocodylus acutus*). Am J Physiol 205:483–488
- Schmidt-Nielsen K, Borut A, Lee P, Crawford E (1963) Nasal salt excretion and the possible function of the cloaca in water conservation. Science (NY) 142:1300–1301
- Schultz SG (1977) The role of paracellular pathways in isotonic fluid transport. Yale J Biol Med 50:99–113

- Schwarzkopf L, Brooks RJ (1985) Application of operative environmental temperatures to analysis of basking behavior in *Chrysemys picta*. *Herpetologica* 41:206–212
- Secor SM, Nagy KA (1994) Bioenergetic correlates of foraging mode for the snakes *Crotalus cerastes* and *Masticophis flagellum*. *Ecology* 75:1600–1614
- Secor SM, Jayne BC, Bennett AF (1992) Locomotor performance and energetic cost of sidewinding by the snake *Crotalus cerastes*. *J Exp Biol* 163:1–14
- Seely MK, Roberts CS, McClain E (1988) Microclimate and activity of the lizard *Angolosaurus skoogi* on a dune slipface. *S Afr J Zool* 23:92–102
- Selye H (1952) The story of the adaptation syndrome. Acta Incorporated, Montreal, Canada
- Selye H (1972) Homeostasis and heterostasis. In: Brooks CM, Koizumi K, Pinkston JO (eds) The life and contributions of Walter B. Cannon 1871–1945: his influence on the development of physiology in the twentieth century. State University of New York Press, Albany, pp 108–112
- Simple RE, Sigsworth D, Stitt JT (1969) Composition and volume of fluids in winter and summer turtles native to Ontario, Canada. *J Physiol (Lond)* 204:39P–40P
- Simple RE, Sigsworth D, Stitt JT (1970) Seasonal observations on the plasma, red cell, and blood volumes of two turtle species native to Ontario, Canada. *Can J Physiol Pharmacol* 48:282–290
- Seshadri C (1957) Water conservation in *Uromastix hardwickii* (Gray) with a note on the presence of Müllerian ducts in the male. *J Zool Soc India* 9:103–113
- Sherbrooke W (1990) Rain-harvesting in the lizard, *Phrynosoma cornutum*: behaviour and integumental morphology. *J Herpetol* 24:302–308
- Sherbrooke WC (1993) Rain-drinking behaviours of the Australian Thorny Devil (Sauria: Agamidae). *J Herpetol* 27:270–275
- Shine R (1987) Intraspecific variation thermoregulation, movements and habitat use by Australian Blacksnakes, *Pseudechis porphyriacus* (Elapidae). *J Herpetol* 21:165–177
- Shine R (1988) Parental care in reptiles. In: Gans C, Huey RB (eds) *Biology of the Reptilia*, 16. Alan Liss, New York, pp 275–330
- Shine R (1994) Allometric patterns in the ecology of Australian snakes. *Copeia* 1994:851–867
- Shine R, Lambeck R (1990) Seasonal shifts in the thermoregulatory behaviour of Australian Blacksnakes, *Pseudechis porphyriacus* (Serpentes: Elapidae). *J Therm Biol* 15:310–305
- Shoemaker VH (1964) The effects of dehydration on electrolyte concentrations in a toad, *Bufo marinus*. *Comp Biochem Physiol* 13:261–271
- Shoemaker VH, Nagy KA (1977) Osmoregulation in amphibians and reptiles. *Annu Rev Physiol* 39:449–471
- Shoemaker VH, Nagy KA (1984) Osmoregulation in the Galápagos marine iguana, *Amblyrhynchus cristatus*. *Physiol Zool* 57:291–300
- Shoemaker VH, Licht P, Dawson WR (1966) Effects of temperature on kidney function in the lizard *Tiliqua rugosa*. *Physiol Zool* 39:244–252
- Shoemaker VH, Nagy KA, Bradshaw SD (1972) Studies on the control of electrolyte excretion by the nasal gland of the lizard *Dipsosaurus dorsalis*. *Comp Biochem Physiol* 42A:749–757
- Shuttleworth TJ, Thompson JL, Dantzler WH (1987) Potassium secretion by nasal glands of desert lizard *Sauromalus obesus*. *Am J Physiol* 253:R83–R90
- Sievert LM, Hutchison VH (1991) The influence of photoperiod and position of light source on behavioral thermoregulation in *Crotaphytus collaris* (Squamata: Iguanidae). *Copeia* 1991:105–110
- Silveira PF, Schiripa LN, Carmona E, Picarelli ZP (1992) Circulating vasotocin in the snake *Bothrops jararaca*. *Comp Biochem Physiol* 103A:59–64
- Skadhauge E (1967) *In vivo* perfusion studies of the cloacal water and electrolyte resorption in the fowl (*Gallus domesticus*). *Comp Biochem Physiol* 23:483–501
- Skadhauge E (1969) The mechanism of salt and water reabsorption in the intestine of the eel (*Anguilla anguilla*) adapted to waters of various salinities. *J Physiol (Lond)* 204:135–158
- Skadhauge E (1977) Excretion in lower vertebrates: function of gut, cloaca and bladder in modifying the composition of the urine. *Fed Proc* 36:2487–2492
- Skadhauge E (1978a) Hydromineral regulation in lower vertebrates. In: Gaillard PJ, Boer HH (eds) *Comparative endocrinology*. Elsevier, Amsterdam, pp 197–207
- Skadhauge E (1978b) Osmoregulation and hormones in reptiles. In: Assenmacher I, Farner D (eds) *Environmental endocrinology*. Springer, Berlin Heidelberg New York, pp 217–221

- Skadhauge E, Bradshaw SD (1973) Salt and water excretion in the Australian Zebra Finch. *Acta Physiol Scand Suppl* 396:127(Abstr)
- Skadhauge E, Bradshaw SD (1974) Drinking of saline, and cloacal excretion of salt and water in the Australian zebra finch. *Am J Physiol* 52A:1236–1267
- Skadhauge E, Duvdevani I (1977) Cloacal absorption of NaCl and water in the lizard *Agama stellio*. *Comp Biochem Physiol* 56A:275–279
- Skinner DC (1991) Effect of intraperitoneal melatonin injections on thermoregulation in the Transvaal girdled lizard, *Cordylus vittifer*. *J Therm Biol* 16:179–184
- Slip DJ, Shine R (1988) Reptilian endothermy: a field study of thermoregulation by brooding diamond pythons. *J Zool (Lond)* 216:367–378
- Slobodkin LB, Rapoport A (1974) An optimal strategy for evolution. *Q Rev Biol* 49:181–200
- Smith HW (1930) Metabolism of the lungfish *Protopterus aethiopicus*. *J Biol Chem* 88:97–130
- Smits AW (1985) Correlates of activity, diet, and body water flux in the chuckwalla lizard *Sauromalus hispidus*. *Physiol Zool* 58:166–174
- Smits AW (1986) Accessory lymph sacs and body fluid partitioning in the lizard *Sauromalus hispidus*. *J Exp Biol* 121:165–177
- Smits AW, Kozubowski MM (1985) Partitioning of body fluids and cardiovascular responses to circulatory hypovolaemia in the turtle, *Pseudemys scripta elegans*. *J Exp Biol* 116:237–250
- Smits AW, Lillywhite HB (1985) Maintenance of blood volume in snakes: transcapillary shifts of extravascular fluid during acute hemorrhage. *J Comp Physiol* 155:305–310
- Smits AW, Ward J, Lillywhite H (1986) Effects of hyperkalemia on thermoregulatory and feeding behaviors of the lizard, *Sauromalus obesus*. *Copeia* 1986:518–520
- Sokabe H, Ogawa M (1974) Comparative studies of the juxtaglomerular apparatus. *Int Rev Cytol* 37:271–327
- Spotila JR, O'Connor MP, Zimmerman LC, Ruby DE (1994) Introduction: conservation biology of the desert tortoise, *Gopherus agassizii*. *Herpetol Monogr* 8:1–4
- Stebbins RC (1960) Effects of pinealectomy in the western fence lizard, *Sceloporus occidentalis*. *Copeia* 1960:276–283
- Stebbins RC, Eakin RM (1958) The role of the “third eye” in reptilian behaviour. *Am Mus Novit* 1870:1–40
- Steinberg MB, Finelli AL, Gerwein RW, John-Alder HB (1993) Behavioral effects of thyroxine in a lizard (*Ameiva undulata*: Teiidae). *Physiol Zool* 66:148–165
- Stern JT (1970) The meaning of “adaptation” and its relation to natural selection. In: Dobzhansky T, Hecht MK, Steere WC (eds) *Evolutionary biology*, 4. Appleton-Century-Crofts, New York, pp 39–66
- Stevenson RD (1985) The relative importance of behavioral and physiological adjustments controlling body temperature in terrestrial ectotherms. *Am Nat* 126:362–386
- Stitt JT, Semple RE, Sigsworth DW (1970) Effects of changes in body temperature on circulating plasma volumes of turtles. *Am J Physiol* 219:683–686
- Stolte H, Schmidt-Nielsen B, Davis L (1977) Single nephron function in the kidney of the lizard *Sceloporus cyanogenys*. *Zool Jahrb Physiol Bd* 81:S219–244
- Stoner LC (1977) Isolated, perfused amphibian renal tubules: the diluting segment. *Am J Physiol* 283:F438–F444
- Stoner LC (1985) The movement of solutes and water across the vertebrate distal nephron. *Renal Physiol* 8:237–248
- Storr GM (1967) Geographic races of the agamid lizard *Amphibolurus caudicinctus*. *J R Soc West Aust* 50:49–56
- Storr GM (1982) Revision of the bearded dragons (Lacertilia: Agamidae) of Western Australia with notes on the dismemberment of the genus *Amphibolurus*. *Rec West Aust Mus* 10:199–214
- Taplin LE (1984) Homeostasis of plasma electrolytes, sodium and water pools in the estuarine crocodile, *Crocodylus porosus*, from fresh, saline and hypersaline waters. *Oecologia* 63:63–70
- Taplin LE (1985) Sodium and water budgets of the fasted estuarine crocodile, *Crocodylus porosus*. *J Comp Physiol* 155B:501–513
- Taplin LE (1988) Osmoregulation in crocodiles. *Biol Rev* 63:333–377
- Taplin LE, Grigg GC (1981) Salt glands in the tongue of the estuarine crocodile *Crocodylus porosus*. *Science (NY)* 212:1045–1047

- Taplin LE, Loveridge JP (1988) Nile crocodiles, *Crocodylus niloticus* and estuarine crocodiles, *Crocodylus porosus*, show similar osmoregulatory responses on exposure to seawater. *Comp Biochem Physiol* 89A:443–448
- Taplin LE, Grigg GC, Harlow P, Ellis TM, Dunson WA (1982) Lingual salt glands in *Crocodylus acutus* and *Crocodylus johnstoni* and their absence from *Alligator mississippiensis* and *Caiman crocodilus*. *J Comp Physiol* 149:43–47
- Taplin LE, Grigg GC, Beard L (1985) Salt gland function in fresh water crocodiles: evidence for a marine phase in eusuchian evolution? In: Grigg GC, Shine R, Ehmann H (eds) *Biology of Australian frogs and reptiles*. Surrey Beatty and Sons, Sydney, pp 403–410
- Templeton JR (1960) Respiration and water loss at higher temperatures in the desert iguana, *Dipsosaurus dorsalis*. *Physiol Zool* 33:136–145
- Templeton JR (1964) Nasal salt excretion in terrestrial lizards. *Comp Biochem Physiol* 11:223–229
- Templeton JR (1970) Reptiles. In: Whittow GC (ed) *Comparative physiology of thermoregulation*. Academic Press, New York, pp 167–221
- Templeton JR (1972) Salt and water balance in desert lizards. *Symp Zool Soc Lond* 31:61–77
- Templeton JR, Murrish DE, Randall ER, Mugaas JN (1968) The effect of aldosterone and adrenalectomy on nasal salt excretion by the desert iguana *Dipsosaurus dorsalis*. *Am Zool* 8:818–819 (Abstract)
- Templeton JR, Murrish DE, Randall EM, Mugaas JN (1972a) Salt and water balance in the desert iguana, *Dipsosaurus dorsalis* I. The effect of dehydration, rehydration and full hydration. *Z Vgl Physiol* 76:245–354
- Templeton JR, Murrish DE, Randall EM, Mugaas JN (1972b) Salt and water balance in the desert iguana, *Dipsosaurus dorsalis* II. The effect of aldosterone and adrenalectomy. *Z Vgl. Physiol* 76:255–269
- Thaysen JH (1979) The lacrimal gland. In: Gielbisch G (ed) *Transport organs*, 4B. Springer, Berlin Heidelberg New York, pp 415–433
- Thomas DH, Skadhauge E (1979) Chronic aldosterone therapy and the control of transepithelial transport of ions and water by the colon and coprodaeum of the domestic fowl (*Gallus domesticus*) *in vivo*. *J Endocrinol* 83:239–250
- Thomas DH, Skadhauge E, Read MV (1979) Acute effects of aldosterone on water and electrolyte transport in the colon and coprodaeum of the domestic fowl (*Gallus domesticus*) *in vivo*. *J Endocrinol* 83:229–237
- Thorson TB (1968) Body fluid partitioning in Reptilia. *Copeia* 1968:592–601
- Tinkle DW (1967) The life and demography of the side-blotched lizard, *Uta stansburiana*. *Misc Publ Mus Zool Univ Mich* 132:1–182
- Tosini G, Avery RA (1995) Occlusion of the parietal eye induces a transient wavelength-dependent shift in lizard thermoregulatory set points. *J Exp Zool* 269:84–87
- Tosini G, Avery R (1996) Dermal photoreceptors regulate basking behavior in the lizard *Podarcis muralis*. *Physiol Behav* 59:195–198
- Tosini G, Lanza B, Bacci M (1991) On the thermoregulatory significance of microinsular melanism in the lizard of genus *Podarcis*. In: Ghiara G (ed) *Symposium on the evolution of terrestrial vertebrates*. Mucchi, Modena, Italy, pp 613–629
- Tosini G, Jones S, Avery R (1995) Infra-red irradiance and set point temperatures in behaviourally thermoregulating lacertid lizards. *J Therm Biol* 20:497–503
- Tracy CR (1982) Biophysical modeling in reptilian physiology and ecology. In: Gans C, Pough FH (eds) *Biology of the Reptilia*, 12C. Academic Press, New York, pp 275–321
- Trobec TN, Stanley JG (1971) Uptake of ions and water by painted turtle, *Chrysemys picta*. *Copeia* 1971:537–542
- Turner FB, Hayden P, Burge BL, Roberson JB (1986) Egg production by the desert tortoise (*Gopherus agassizii*) in California. *Herpetologica* 42:93–104
- Turner JC (1987) On the transient temperatures of ectotherms. *J Therm Biol* 12:207–214
- Turner JS (1987) The cardiovascular control of heat exchange: consequences of body size. *Am Zool* 27:69–79
- Uchiyama N (1994) Sites of action of arginine vasotocin in the nephron of the bullfrog kidney. *Gen Comp Endocrinol* 94:366–373
- Underwood H (1984) The pineal and circadian rhythms. In: Reiter RJ (ed) *The pineal gland*. Raven Press, New York, pp 221–251

- Underwood H (1985) Pineal melatonin rhythms in the lizard *Anolis carolinensis*: effects of light and temperature cycles. *J Comp Physiol* 157A:57–65
- Uva B, Vallarino M, Mandich A, Isola G (1982) Plasma aldosterone levels in the female tortoise *Testudo hermanni*. *Gen Comp Endocrinol* 46:116–123
- Valenti G, Cheavlier J, Hugon J, Bourguet J (1987) Membrane structure and water permeability in renal-like epithelia. In: Kirsch R, Lahlou B (eds) *Comparative physiology of environmental adaptations*, 1. Karger, Basel, pp 67–75
- van Berkum FH, Huey RB, Adams BA (1986) Physiological consequences of thermoregulation in a tropical lizard (*Ameiva festiva*). *Physiol Zool* 59:464–472
- van Devender TR, Moodie KB (1977) The desert tortoise in the late Pleistocene with comments about its earlier history. *Proc Symp Desert Tortoise Council*. Las Vegas, Nevada, pp 41–45
- van Devender TR, Moodie KB, Harris AH (1976) The desert tortoise (*Gopherus agassizi*) in the Pleistocene of the northern Chihuahuan desert. *Herpetologica* 32:298–304
- van Lennep EW, Komnick H (1970) Fine structure of the nasal gland in the desert lizard *Uromastix acanthinurus*. *Cytobiologie* 2:47–67
- van Lennep EW, Young JA (1979) Salt glands. In: Giebisch G (ed) *Transport organs*, 4B. Springer, Berlin Heidelberg New York, pp 675–692
- van Mierop LHS, Barnard SM (1976) Thermoregulation in a brooding female *Python molurus bivittatus*. *Copeia* 1976:398–401
- van Mierop LHS, Barnard SM (1978) Further observations on thermoregulation in the brooding python *Python molurus* (Serpentes: Boidae). *Copeia* 1978:615–621
- Vernet R. (1977) Recherches sur l'écologie de *Varanus griseus* dans les écosystèmes sableux du Sahara Nord-Occidental (Algérie) Thèse du Troisième Cycle, Université de Pierre et Marie Curie, Paris VI
- Vernet R, Lemire M, Grenot CJ (1988a) Field studies on activity and water balance of a desert monitor *Varanus griseus* (Reptilia, Varanidae). *J Arid Environ* 15:81–90
- Vernet R, Lemire M, Grenot CJ, Francz J-M (1988b) Ecophysiological comparisons between two large Saharan lizards, *Uromastix acanthinurus* (Agamidae) and *Varanus griseus* (Varanidae). *J Arid Environ* 14:187–200
- Vinson GP, Whitehouse BJ, Goddard C, Sibley CP (1979) Comparative and evolutionary aspects of aldosterone secretion and zona glomerulosa function. *J Endocrinol* 81:5P–24P
- Walton BM, Bennett AF (1993) Temperature-dependent color change in Kenyan chameleons. *Physiol Zool* 66:270–287
- Warburg MR (1965) The influence of ambient temperature and humidity on the body temperature and water loss from two Australian lizards, *Tiliqua rugosa* (Gray) (Scincidae) and *Amphibolurus barbatus* Cuvier (Agamidae). *Aust J Zool* 13:331–350
- Watson GE (1962) Notes on copulation and distribution of Aegean land tortoises. *Copeia* 1962:317–321
- Weathers WW (1971) Some cardiovascular aspects of temperature regulation in the lizard *Dipsosaurus dorsalis*. *Comp Biochem Physiol* 40A:503–515
- Webb GJW, Johnson CR (1972) Head-body temperature differences in turtles. *Comp Biochem Physiol* 43A:593–611
- Webb GJW, Johnson CR, Firth BT (1972) Head-body temperature differences in lizards. *Physiol Zool* 45:130–142
- Werner Y (1990) Do gravid females of oviparous gekkonid lizards maintain elevated body temperatures? *Hemidactylus frenatus* and *Lepidodactylus lugubris* on Oahu. *Amphib Reptilia* 5:375–393
- Werner Y, Whitaker AH (1978) Observations and comments on the body temperatures of some New Zealand reptiles. *N Z J Zool* 11:20–24
- White FN (1976) Circulation. In: Gans C, Dawson WR (eds) *Biology of the Reptilia*, 5A. Academic Press, New York, pp 275–334
- Whitfield CL, Livezey RL (1973) Thermoregulatory patterns in lizards. *Physiol Zool* 46:285–296
- Whybren PJ (1981) Evidence for the presence of nasal salt glands in the Hadrosauridae (Ornithischia). *J Arid Environ* 4:43–57
- Will PC, Cortright RN, Groseclose RG, Hopfer U (1985) Amiloride-sensitive salt and fluid absorption in small intestine of salt-depleted rats. *Am J Physiol* 248:G124–G132

- Willemssen RE (1991) Differences in thermoregulation between *Testudo hermanni* and *Testudo marginata* and their ecological significance. *Herpetol J* 1:559–567
- Williams GC (1966) Adaptation and natural selection: a critique of some current evolutionary thought. Princeton University Press, Princeton, New Jersey
- Williams GC (1992) Natural selection. Domains, levels and challenges. Oxford University Press, New York
- Withers KW, Hulbert AJ (1987) The influence of dietary fatty acids and hypothyroidism on mitochondrial fatty acid composition. *Nutr Res* 7:1139–1150
- Withers PC (1993) Cutaneous water acquisition by the Thorny Devil (*Moloch horridus*: Agamidae). *J Herpetol* 27:265–270
- Withers PC, Bradshaw SD (1995) Water and energy balance of the mountain devil *Moloch horridus*: is the devil a sloth? *Amphib Reptilia* 16:47–54
- Withers PC, Campbell JD (1985) Effects of environmental cost on thermoregulation in the desert iguana. *Physiol Zool* 58:329–339
- Withers PC, Dickman CR (1995) Role of the diet in determining water, energy and salt intake in the mountain devil *Moloch horridus* (Lacertilia: Agamidae). *J R Soc West Aust* 78:3–11
- Woolley P (1959) The effect of posterior lobe pituitary extracts on blood pressure in several vertebrate classes. *J Exp Biol* 36:453–458
- Wright A, Chester-Jones I (1957) The adrenal gland in lizards and snakes. *J Endocrinol* 15:83–99
- Wright J, Steer E, Hailey A (1988) Habitat separation in tortoises and the consequences for activity and thermoregulation. *Can J Zool* 66:1537–1544
- Yokota SD, Benyajati S, Dantzler WH (1985) Renal function in sea snakes I. Glomerular filtration rate and water handling. *Am J Physiol* 18:R228–R236
- Zarnick B (1910) Vergleichende Studien über den Bau der Niere von *Echidna* und der Reptilienniere. *Jena Z Naturwiss* 45:113–224
- Zimmerman LC, Tracy CR (1989) Interactions between the environment and ectothermy and herbivory in reptiles. *Physiol Zool* 62:374–409
- Zimmerman LC, O'Connor MP, Kemp SA, Spotila JR (1992) Thermoregulation by desert tortoises (*Gopherus agassizii*) at the Desert Tortoise Conservation Center, Las Vegas, Nevada: preliminary results. *Proc Symp Desert Tortoise Council*, Las Vegas, Nevada, pp 103–117
- Zimmerman LC, O'Connor MP, Bulova SJ, Spotila JR, Kemp SJ, Salice CJ (1994) Thermal ecology of desert tortoises in the eastern Mojave desert: seasonal patterns of operative and body temperatures, and microhabitat utilisation. *Herpetol Monogr* 8:45–59

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