Ecophysiology of Australian Arid-Zone Reptiles

S. Don Bradshaw

Introduction

The Australian arid zone supports a diverse lizard and snake fauna that is significantly more species-rich than that of other arid regions in the world (Pianka 1986; Morton and James 1988; Powney et al. 2010). The precise origins of this fauna are, however, still the subject of research and some dispute. There is clear evidence for a Gondwanan origin for many components of the Australian fauna, e.g., monotremes, marsupials, passerine birds, parrots, ratites and chelid turtles, but the case for lizards and snakes is less clear. The arid zone was also not always arid, and it is only since the early Miocene that it started to take its present form (Martin 2006). A case for the Gondwanan origin of agamid lizards, with a 150-million-year divergence date between Southeast Asian and Australasian agamids based on mitochondrial DNA, was made by Schulte et al. (2003). The study was criticised, however, for methodological flaws, and a reanalysis of their data, along with the addition of nuclear (c-*mos*) sequences, pushed the date of this implied separation back to approximately 30 MYA (Hugall and Lee 2004). This would make an Asian origin for the Australian agamids by rafting and island hopping plausible, as the Australasian tectonic plate approached the Asian continent. Amongst the Australian agamids, two species stand out as being basal to the radiation and much older than other groups: the chameleon dragon, *Chelosonia brunnea*, and the mountain devil, *Moloch horridus* (Hugall et al. 2008), with the latter invading the developing arid zone long before any other agamid. The current consensus is in favour of an Asian origin for the agamids, dating to the early Miocene, which was followed by an extensive adaptive radiation of the group in the arid zone. There is one group of

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lizards, however, where a case for Gondwanan origin is compelling: the geckos and pygopodids (Oliver and Sanders 2009; Oliver and Bauer 2011). Molecular phylogenies indicate that at least five Australian lineages of diplodactyloid gecko, with wide distributions in the arid zone, are as old or older than elapid snakes and agamids. The snake-like pygopodids appear to have radiated before Australia was occupied by snakes, and recent research suggest that the Australian elapids have evolved from primitive sea kraits (*Laticaudia*) that may have swum the sea gap from Asia and come ashore in a snake-deficient continent (Scanlon and Lee 2004; Underwood 1957).

A strong case for an Asian, rather than Gondwanan origin, can also be made for the varanid lizards (Fuller et al. 1998). Molecular analyses reveal the existence of three monophyletic clades: an African, Indo-Asian and an Indo-Australian clade. Within the Indo-Australia clade, the endemic dwarf monitors (*Odatria*) form a clade sister to the large Australian monitors (the *gouldii* group) (Ast 2001). These studies thus indicate that the squamate fauna of the Australian arid zone is composed of both old Gondwanan (geckos and pygopodids) and more recent Asian elements (agamid lizards, skinks, elapid snakes and varanids).

Despite this wide diversity displayed in their phylogenetic origins, all of the reptiles inhabiting the Australian arid zone must contend with the same environmental contingencies that characterise arid environments worldwide, viz.:

(a) High day temperatures through summer that must be tolerated, regulated, or avoided
(b) A deficiency of available free water that renders difficult
(c) The regulation of water and electrolyte balance
(d) Seasonal deficiencies of nitrogen (protein), phosphorus and energy (carbohydrate) essential for growth and reproduction

Temperature Regulation

Following the pioneering study of Cowles and Bogert on North American desert lizards (Cowles and Bogert 1944), early publications on Australian lizards in the arid zone focused on thermoregulation. The concept of 'ectotherms' with an 'eccritic' or 'preferred body temperature' (PBT), resulting from active choice on the part of the animal in a thermal gradient, was established, and early surveys compared mean body temperatures of lizards active in the field (MBT) with their PBT determined in the laboratory (Licht et al. 1966; Heatwole 1970; Bradshaw and Main 1968). Although originally thought to be an unvarying and conservative feature of the thermal biology of different reptilian taxa, detailed field studies showed that the MBT actually represents a compromise between physiological preferences and ecological opportunities (Avery 1982; Cogger 1974). Various studies aimed at measuring the accuracy of thermoregulation of arid-zone species have shown, however,

that this can be quite precise. A single specimen of Australia's largest terrestrial reptile, the perentie, *Varanus giganteus*, which is widespread in the arid zone, was radio-tracked for a period of 7 days by King et al. (1989) on Barrow Island. The authors found that its body temperature during the day was relatively constant, averaging 35.8 °C when active, similar to that of other varanid species (Pianka 1986). The body temperature did not fall below 30 °C at night, however, due to the thermal buffering of its large body mass (8.8 kg).

Thermoregulatory precision in monitor lizards was studied by Christian and Weavers (1996), who developed an index of thermal exploitation (Ex), based on an earlier study on North American reptiles (Hertz et al. 1993). The Ex parameter is a ratio calculated by dividing the time that a lizard spends within its set-point range by the time available for the animal to exploit this temperature range and describes the thermoregulatory characteristics of ectotherms in a heterogeneous thermal environment. In their study of three species of varanids, Ex varied from 1.0 (perfect regulation) to negative (no thermoregulation) with the most active species, *Varanus panoptes*, being the 'better' regulator over all seasons. *Varanus gouldii*, a species whose range also extends into the arid zone, was a perfect regulator in the wet season of the year, but Ex became negative in the dry season, when all activity ceased and they remained in their burrows (Christian and Weavers 1996). A more recent attempt to correlate active body temperatures and microhabitat occupation in central Australian agamids is that of Melville and Schulte II (2001), with thermal factors playing a considerable role.

A critical question is whether arid-zone reptiles are ever forced to endure body temperatures significantly above their PBT, and, therefore, likely to induce stress responses leading to decreased fitness (Bradshaw 1997, 2017). An early analysis with a range of agamids of the genus *Ctenophorus* (then *Amphibolurus*) established that increasing aridity of the habitat was associated with MBTs significantly above the PBT, and this was attributed to the greater amount of time more arid-living species were forced to spend in high-temperature-avoidance behaviour patterns (Bradshaw 1988). This repetitive exposure to higher than 'preferred' body temperatures entrained an increased thermal resistance, measured as the critical thermal maximum (CTMax), which was lost after acclimation to laboratory conditions. Greer (1980, 1990) found that the CTMax of arid-living species of scincid lizards was also higher than that of mesic species, assuming these differences to be genetic, but the effect of acclimation was not investigated. Today, one also needs to consider the possibility of epigenetic effects (Hoppeler 2015). When considered in relation to the CTMax for each species, however, the highest body temperatures recorded in the field are invariably some 5–6 °C below the CTMax, and lizards (both in Australia and in North America) thus experience wide safety margins in the field (Huey 1982; Bradshaw 1988). Many reptiles commence 'panting' with a gaping mouth when apparently suffering from heat stress, and the panting threshold (PT) is positively correlated with the CTMax in 14 species of North American lizards (Whitfield and Livezey 1973). Panting thresholds for the few species of Australian lizards that have been studied are, however, well above the maximum body temperature ever recorded in the field (Stebbins and Barwick 1968; Heatwole 1976). Dehydration and increases

in plasma osmolality, however, have a significant impact on the PT of the North American desert iguana (Dupré and Crawford 1985a) and also impact on its thermoregulation (Dupré and Crawford 1985b). Hypernatraemia (see glossary) also significantly depresses the PBT of the rock-living agamid, *Ctenophorus ornatus*, operating through the pituitary peptide hormone, arginine vasotocin (AVT) (Bradshaw et al. 2007).

So far as I am aware, there has been no study to date on the thermoregulation of any snake inhabiting the Australian arid zone. It is thus not possible to reach any conclusions regarding their thermoregulatory abilities and potential exposure to thermal stress. An early paper documented PBTs in a number of Australian snakes in the laboratory, ranging from 29.6 to 34.5 °C (Lillywhite 1980). Only one of these, the Western brown snake *Pseudonaja nuchalis*, is common in the arid zone, and its PBT was 34.0 ± 1.2 °C. Suggestions in the literature that the PBT of snakes is generically invariant (Rosen 1990) have been contested by careful studies involving telemetry. A 4-year study, for example, of the Australian blacksnake, *Pseudechis porphyriacus* (not an arid-zone species, however) showed excellent thermoregulatory capacities, maintaining a body temperature between 28 and 31 °C over a variety of seasons (Shine 1987). Available CTMax data for North American snakes also show a 6.8 °C differential when compared with maximum-recorded body temperatures in the field (Bradshaw 1988; Huey 1982), suggesting that thermal stress is never a problem. The most notable feature about snakes in the arid zone is their behavioural use of nocturnality as a means of avoiding high day temperatures (Greer 2000). Dehydration and hypernatraemia also depress the PBT by some 6–7 °C of the Western tiger snake, *Notechis scutatus* (also not an arid-zone species) operating also through AVT and lowering rates of evaporative water loss (Ladyman and Bradshaw 2003; Ladyman et al. 2003, 2006). There are some chelid species that occur in the arid zone (e.g. the flat-shelled turtle, *Chelodina steindachneri*), but nothing is known of their ecophysiology or how they survive for long periods in dry river beds (Kuchling 1999).

Water Turnover and Osmoregulation

Reptiles possess a metanephric kidney but lack the countercurrent multiplier mechanism of birds and mammals needed to elaborate an hyperosmotic urine (Dantzler and Bradshaw 2009; O'Shea et al. 1993). This renders them particularly vulnerable to significant perturbations of their *milieu intérieur* should they be faced with high electrolyte intakes or lack sufficient free water needed to excrete dietary salts (Cooper 2017). Some species possess cephalic salt-secreting glands that help in the maintenance of osmotic homeostasis (e.g. most varanids and many scincid lizards (Bradshaw 1986)), but they are absent in Australian agamids and terrestrial snakes (Saint Girons and Bradshaw 1987; Saint Girons et al. 1981).
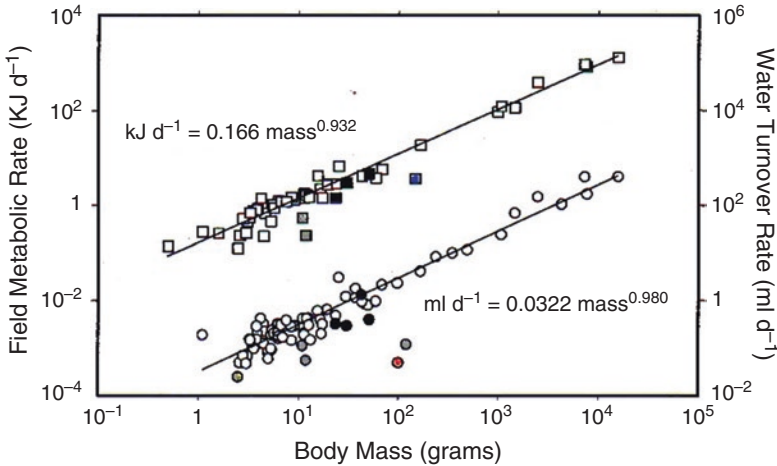
Fig. 1 Allometric relationship between body mass and field metabolic rate in kJ.d^{-1} (FMR, squares) and water turnover rate in mL.d^{-1} (circles) for semiarid- and arid-zone lizards. (Adapted from Withers and Bradshaw, 1995)

The increased availability of tritiated water and liquid scintillation counters in the 1970s and '80s led to the first measurements of rates of water turnover of free-living lizards in North America, followed soon after by those of Australian arid-zone species. When compared with rates in tropical and subtropical species, those in arid-zone species were significantly lower, reflecting their overall enhanced water economy (Nagy 1982). Water turnover increases virtually linearly with body mass, and Nagy's regression for arid-zone species of mL.d^{-1} = 20.5 kg$^{0.91}$ was updated to 32.2 kg$^{0.98}$ by Withers and Bradshaw (1995) and is close to the allometric relationship for free-ranging varanids with mL.d^{-1} = 38 kg$^{1.19}$ (Bradshaw 1997). In all three cases, the exponent of the equation does not differ significantly from 1.0 (Fig. 1).

Interspecific regression equations such as these, which are based on average values for a wide range of species, can, however, mask more subtle differences between species that may only be apparent when intraspecific regression equations are compared. A comparative study of the relationship between body mass and rate of evaporative water loss in several skinks, geckos and an agamid lizard found large and significant differences in the values of '*a*' and '*b*' in the allometric relationship $y = ax^b$ where y is water loss and x is body mass in grammes (Fig. 2). These data from an early preliminary study suggest that there are substantial differences in the value of the constant '*a*', which represents the rate of water loss of a 1 g (or 1 kg) animal depending on the scale. The gecko *Gehyra variegata* has a very high '*a*' value of 8.71 and thus will have a high rate of water loss when small, but the low value of the exponent '*b*' of 0.26 means that its rate of evaporative water loss will decrease, relative to its body mass, as it grows in size. The barking gecko, *Underwoodisaurus milii*, on the other hand, with $b = 0.97$, does not benefit from any relative increase in its water economy as it grows. The agamid, *Ctenophorus*

Fig. 2 A plot of mean
values for '*a*' and '*b*' from
the respective allometric
equations ($y = ax^b$)
describing the relationship
between body mass (*x*) and
rate of evaporative water
loss (*y*) for six species of
Australian lizards from
three families. (Adapted
from Bradshaw, 1986, and
references therein. NB
*Ctenotus lesueuri* = *C.
australis*)
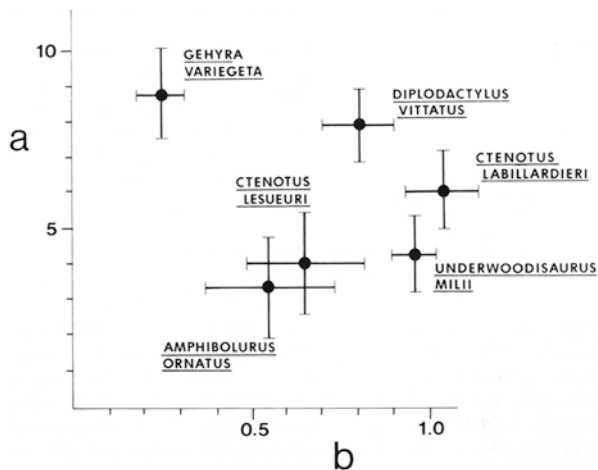
(formerly *Amphibolurus*) *ornatus*, is the 'best' adapted in terms of water economy,
with *a* = 3.16 and *b* = 0.55, and it is evident that lizards such as *Ctenotus labillard-
ieri* and *Diplodactylus vittatus* must, if they are to survive, restrict their movements
to moist habitats because of their coupled high '*a*' and '*b*' values and potential for
desiccation.

In the absence of a renal concentrating system, increases in water economy in
reptiles can only be achieved by either reducing intake of water or by limiting losses.
Under extreme conditions of salt loading, some lizards close down kidney function,
cease filtering and become temporarily anuric (Bradshaw 1997), but reduction in
rates of respiratory and cutaneous water loss underpins their enhanced water econ-
omy (Lillywhite 2006; Zucher 1980).

The role of the pituitary hormone arginine vasotocin (AVT) in controlling kidney
function in three species of agamid lizards was investigated by Ford and Bradshaw
(2006) who posited an 'adaptationist' scenario (sensu Gould and Lewontin (1979)),
testing whether desert species would display enhanced renal responses to dehydra-
tion and salt loading when compared with mesic species. In fact, they found little
support for this hypothesis, apart from a primarily glomerular rather than tubular
response to salt loading in the mesic species, *Pogona minor*. Surprisingly, AVT lev-
els in the desert species, *Ctenophorus nuchalis*, showed no significant correlation
with changes in plasma osmolality, although increasing levels of AVT were associ-
ated with a marked antidiuresis that was both glomerular and tubular in nature. This
study thus supports the conclusion that desert-living reptiles are 'exapted' rather
than adapted to the exigencies characteristic of the arid zone (Bradshaw 1986, 1988).

The Western netted dragon, *Ctenophorus nuchalis*, is widespread in sandy areas
of the arid zone in Australia and was the subject of a long-term ecophysiological
and population study at Shark Bay in Western Australia (Bradshaw 1986). An
unexpected discovery to emerge from mark-and-recapture data with this large (up
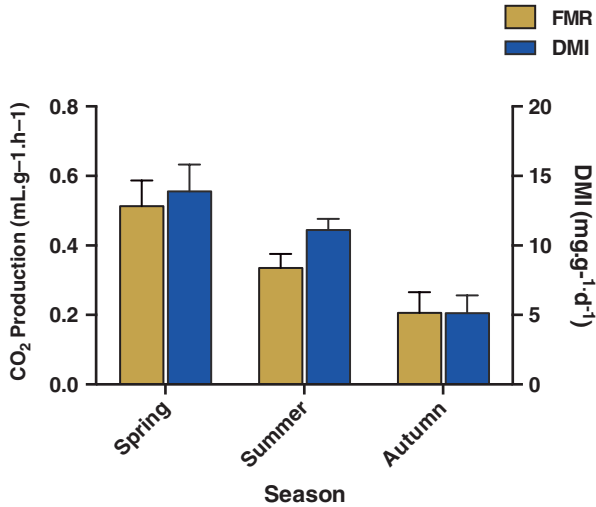
Fig. 3 Seasonal changes in field metabolic rate (FMR) measured as CO_2 production in $mL.g^{-1}.h^{-1}$ and estimated dry matter intake (DMI) in $mg.g^{-1}.d^{-1}$ in the Western netted dragon, *Ctenophorus nuchalis*, in Shark Bay, Western Australia. (Adapted from Nagy and Bradshaw, 1995)

to 60 g), fast-growing lizard is that it is an annual species, along with many other species in the genus. Following winter rains, they breed and lay eggs in spring, then progressively lose condition and die during summer such that, by autumn, few if any adults in the population survive and the young emerge to colonise what is an 'empty' environment (Bradshaw 1981). A detailed study of seasonal changes in body condition, with modelling of daily changes in thermoregulatory activity, established that coping with high environmental temperatures in summer precludes the lizards from feeding adequately (even though food is available) and thus leads to their demise (Bradshaw and De'ath 1991). Their gradual slide into negative water balance as summer progresses, with a corresponding catastrophic decline in field metabolic rate (FMR) and dry matter intake (DMI), measured with doubly labelled water, is shown in Fig. 3.

A closely related species, the ringtail dragon, *Ctenophorus caudicinctus*, is a rock-dweller and lives sympatrically with *C. nuchalis* in the arid Pilbara region of Western Australia. This species breeds invariably in autumn, following cyclonic rains, and a study of the two species together found that *C. nuchalis* deferred breeding in spring in some years when winter rains failed, survived the summer period and bred in autumn with *C. caudicinctus* (Bradshaw et al. 1991). This implies that the summer death seen with *C. nuchalis* at Shark Bay is a post-reproductive phenomenon, and both *C. nuchalis* and *C. caudicinctus*, like *C. fordi* (Cogger 1978), are thus semelparous species (Henle 1991; Dickman et al. 1999). The reasons why there is a breakdown in the ability to maintain homeostasis following reproduction in
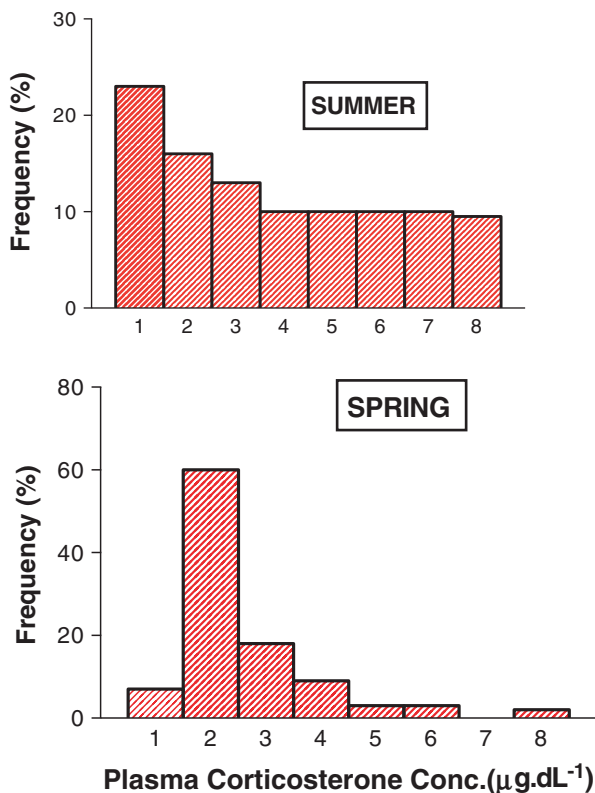
Fig. 4 Frequency distribution of plasma corticosteroid concentrations in the agamid lizard *Ctenophorus nuchalis* injected with adrenocorticotrophic hormone (ACTH) after dexamethasone blockade in spring and summer at Shark Bay in Western Australia. The aberrant, non-Gaussian response of the lizards in late summer to the ACTH challenge is evident. (Adapted from Bradshaw 1986)

these lizards is not clear, although parallels with small semelparous dasyurid marsupials are obvious (Bradley 2003). Changes in circulating levels of corticosteroid-binding globulin (CBG) and free and bound concentrations of the adrenal steroid, corticosterone, have been implicated in stress reactivity studies of the North American lizard, *Urosaurus ornatus* (Jennings et al. 2000), but have yet to be measured in these Australian species. What has been documented in *C. nuchalis* is a marked change in the normal adrenal response in spring to the stress of confinement, or injections of adrenocorticotrophic hormone (ACTH), when repeated after breeding in late summer at Shark Bay, with the majority of individuals failing to respond, whilst others show an aberrant overresponse to the stressor (Bradshaw 1997, 2017) (Fig. 4).

A number of studies have been conducted in the wet/dry tropics of Australia, using doubly-labelled water to document the energetics of agamid and varanids lizards which are very informative, linking activity, thermoregulation and foraging patterns. Two species of varanid lizards, for example, were studied along the South Alligator River in the Northern Territory of Australia and displayed divergent patterns of activity and resource exploitation (Christian et al. 1995). Rates of energy expenditure and water turnover were faster in *Varanus gouldii* than in *V. panoptes*, but levels were higher in both species in the wet/dry tropics than in other varanids, such as *Varanus giganteus* occupying the arid zone (Green et al. 1986). *Varanus gouldii*, for example, with an average water influx of 50.7 mL.kg^{-1}.d^{-1}, was turning over approximately 8% of its total body water content per day (TBW), compared with only 3.9% for *V. giganteus* on Barrow Island (King and Green 1999). The frilled-neck lizard, *Chlamydosaurus kingii*, is a large 600 g agamid that is common in the tropical north of Australia. It ceases activity in the dry season of the year, spending it perched on tree trunks. Rates of water turnover are rapid, as would be expected in the wet season with a mean annual rainfall of 1600 mm in Darwin, but water turnover rates fall to 13.6 mL.kg^{-1}.d^{-1} in the early dry season which is only approximately 2% of the TBW per day; later in the dry season, this falls even further to 5.6 mL.kg^{-1}.d^{-1} (2.9 mL.d^{-1}) (Christian and Green 1994). This is, however, still substantially greater than the rate of metabolic water production for a lizard of this size (ca. 0.3 mL.d^{-1}), showing that whilst apparently inactive, the lizards are still feeding sporadically. The only other study of an arid-living varanid is that of the small (12 g) arboreal *Varanus caudolineatus* in the Murchison region of Western Australia (Thompson et al. 1997). Water influx in summer averaged 31.6 mL.kg^{-1}.d^{-1}, and FMR was 0.46 mL CO_2.g^{-1}.h^{-1}, which enables a calculation of the 'Water Economy Index' (WEI) of 0.14 (Nagy and Peterson 1988). This is considerably less than that reported for any other varanid species.

There is a single published study of energetics and water flux rates of a free-ranging gecko, the marbled velvet gecko, *Oedura marmorata*, in both tropical regions and in central Australia (Christian et al. 1998). As would be expected, both FMR and rates of water influx are much lower in the arid population than in the geckos from the tropical locations. The FMR of arid geckos in spring was 40.1 kJ.d^{-1}, compared with FMRs ranging from 109.8 to 148.9 kJ.d^{-1} for the tropical geckos. The authors do raise the possibility that the two populations may not in fact be from the one species, and a recent paper on the systematics of the *Oedura* complex confirms this with the arid population currently listed as *Oedura aff. Marmorata* (P Doughty pers. comm.). Rates of metabolism and water flux have been reported in the northern death adder, *Acanthophis praelongus*, again not an arid-zone species, with a similar tropical pattern of reduced rates in the dry season compared with that in the wet (Christian et al. 2007).

Conclusion

This short review serves to highlight how little we actually know of the ecophysiology of arid-zone reptiles in Australia. Despite having a reptilian fauna that is at least three times as rich in number of species as that of other desert regions of the world, ecophysiology has been little studied, and we only have speculations and hypotheses to account for reptile abundance and diversity (Morton and James 1988; Pianka 1986, 1989, 2014; Byrne et al. 2008). Although rates of water and energy turnover of arid-zone species are slower than those occurring in tropical regions of Australia, this does not appear to be the result of any specific adaptations of the former. In fact some species, such as the semelparous lizard *Ctenophorus nuchalis,* typically 'avoid' the exigencies of the arid zone by what may be thought of as the bizarre habit of breeding and depositing eggs in spring, only to die in the oncoming summer. The

population thus survives during the hottest period of the year in the egg phase, and juveniles emerge each autumn to a habitat devoid of adults. Natural selection also does not operate to enhance summer survival as the lizards are then post-reproductive. Longer-living lizards, such as the many varanids, have to survive during the summer months and, in most cases, do this by drastically reducing their activity and often retreating below ground. In common with reptiles living in other regions of the world, the reason for their abundance and diversity in desert areas is linked to their ectothermy and slow rates of resource utilisation, compared with those of birds and mammals, and better described as 'exaptations' (Gould and Vrba 1982), rather than adaptations (Bradshaw 1988).

Glossary

Ectotherm An animal that derives its body heat from an external source, such as the sun.
Eccritic or preferred body temperature (PBT) The mean body temperature maintained behaviourally by a reptile when placed in a thermal gradient.
Mean body temperature (MBT) The average body temperature of a reptile when active, which may differ from the PBT because of a lack of thermal resources.
Agamid A lizard belonging to the family Agamidae, also called dragon lizard, e.g. the ornate dragon lizard, *Ctenophorus ornatus*.
Varanid A lizard belonging to the family Varanidae, also called monitor lizards, e.g. the perentie, *Varanus giganteus*.
Index of thermal exploitation (Ex) A ratio calculated by dividing the time that a lizard spends within its set-point range by the time available for the animal to exploit this temperature range and describes the thermoregulatory characteristics of ectotherms in a heterogeneous thermal environment.
CTMax The critical thermal maximum, or highest body temperature, above which the animal is unable to recover.
FMR Field metabolic rate. The rate of metabolism of a free-ranging animal in its natural habitat measured as either the rate of oxygen consumption or carbon dioxide production, usually with the doubly-labelled water method.
Scincid A lizard belonging to the family Scincidae, also called skinks, e.g., the bobtail goanna, *Tiliqua rugosa*.
Vasotocin (AVT, arginine vasotocin) A peptide hormone released from the posterior lobe of the pituitary gland of reptiles that enhances water reabsorption from the kidney and also lowers the PBT.
Hypernatraemia An increase in the concentration of sodium ions in the blood above normal hydrated levels.
PT (panting threshold) The body temperature at which some lizards open their mouth (gape) and increase their respiratory rate (panting).
Metanephric kidney The structurally more complex kidney of higher vertebrates, which in the case of birds and mammals, is capable of producing an hyperosmotic urine (i.e. one with an osmotic pressure greater than the plasma).

Cephalic salt glands Specialised glands found in many reptiles that assist in osmoregulation by secreting a concentrated salt solution rich in either sodium or potassium. All are located in the head (nose, eye or tongue) and hence called 'cephalic'.

Anuric Ceasing to produce urine; seen in many lizards when feeding on diets rich in salt.

Semelparous Animals, such as salmon, that die after breeding only once. Named after the unfortunate Semelae, mother of Bacchus, who succumbed after a night of passion with the Greek God Zeus.

References

Ast JC (2001) Mitochondrial DNA evidence and evolution in Varanoidae (Squamata). Cladistics 17:211

Avery RA (1982) Field studies of body temperature temperatures and thermoregulation. In: Gans C, Pough FH (eds) Biology of the Reptilia. Academic Press, New York, pp 211–226

Bradley AJ (2003) Stress, hormones and mortality in small carnivorous marsupials. In: Jones ME, Dickman CR, Archer M (eds) Predators with pouches: the biology of carnivorous marsupials. CSIRO, Collingwood

Bradshaw SD (1981) Ecophysiology of Australian desert lizards: studies on the genus *Amphibolurus*. In: Keast A (ed) Biogeography and ecology in Australia. Junk, Den Haag

Bradshaw SD (1986) Ecophysiology of desert reptiles. Academic Press, Sydney

Bradshaw SD (1988) Desert reptiles: a case of adaptation or pre-adaptation? J Arid Environ 14:155–174

Bradshaw SD (1997) Homeostasis in desert reptiles. Springer, Berlin/Heidelberg

Bradshaw SD (2017) A state of non-specific tension in living matter? Stress in Australian animals. Gen Comp Endocrinol 244:118–129

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, Main AR (1968) Behavioural attitudes and regulation of temperature in *Amphibolurus* lizards. J Zool (Lond) 154:193–221

Bradshaw SD, Saint Girons H, Bradshaw FJ (1991) 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, Ladyman M, Stewart T (2007) Effect of hypernatraemia and the neurohypophysial peptide, arginine vasotocin (AVT), on behavioural thermoregulation in the agamid lizard, *Ctenophorus ornatus*. Gen Comp Endocrinol 150:34–40

Byrne M, Yeates DK, Joseph L, Kearney M, Bowler J, Williams AJ, Cooper S, Donnellan SC, Keogh S, Leys R, Melville J, Murphy DJ, Porch N, Wyrwoll KH (2008) Birth of a biome: insights into the assembly and maintenance of the Australian arid zone biota. Mol Ecol 17:4398–4417

Christian KC, Green B (1994) Seasonal energetics and water turnover of the Frillneck Lizard, *Chlamydosaurus kingii*, in the wet-dry tropics of Australia. Herpetologica 50(3):274–281

Christian KA, Weavers BW (1996) Thermoregulation of monitor lizards in Australia: an evaluation of methods in thermal biology. Ecol Monogr 66(2):139–157

Christian CS, Corbett LK, Green B (1995) Seasonal activity and energetics of two species of varanid lizards in tropical Australia. Oecologia 103:349–357

Christian K, Bedford GS, Green B, Schultz T, Newgrain K (1998) Energetics and water flux of the marbled velvet gecko (*Oedura marmorata)* in tropical and temperate habitats. Oecologia 116:336–342

Christian K, Webb JK, Schultz T, Green B (2007) Effects of seasonal variation in prey abundance on field metabolism, water flux, and activity of a tropical ambush foraging snake. Physiol Biochem Zool 80:522–533

Cogger HG (1974) Thermal relations of the mallee dragon, *Amphibolurus fordii* (Lacertilia: Agamidae). Aust J Zool 22:319–339

Cogger HG (1978) Reproductive cycles, fat body cycles, and sociosexual behaviour in the Mallee dragon, *Amphibolurus fordi* (Lacertilia: Agamidae). Aust J Zool 26:653–672

Cooper CE (2017) Endocrinology of osmoregulation and thermoregulation of Australian desert tetrapods: a historical perspective. Gen Comp Endocrinol 244:186–200

Cowles RB, Bogert CM (1944) A preliminary study of the thermal requirements of desert reptiles. Bull Am Mus Nat Hist 83:265–296

Dantzler WH, Bradshaw SD (2009) Reptiles. In: Evans D (ed) Osmotic and ionic regulation: cells and animals. CRC Press (Taylor & Francis Group), New York

Dickman CR, Letnic M, Mahon PS (1999) Population dynamics of two species of dragon lizards in arid Australia: the effect of rainfall. Oecologia 119:357–366

Dupré KR, Crawford EC (1985a) 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 (1985b) Behavioral thermoregulation during dehydration and osmotic loading of the desert iguana. Physiol Zool 58:357–363

Ford SS, Bradshaw SD (2006) Kidney function and the rôle of arginine vasotocin (AVT) in three agamid lizards from differing habitats in Western Australia. Gen Comp Endocrinol 147:62–69

Fuller S, Baverstock PR, King D (1998) Biogeographic origins of goannas (Varanidae): a molecular perspective. Mol Phylogenet Evol 9:294–307

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

Green B, King D, Butler WH (1986) Water, sodium and energy turnover in free-living Perenties, *Varanus giganteus*. Aust Wildl Res 13:589–595

Greer AE (1980) Critical thermal maximum temperatures in Australian scincid lizards: their ecological and evolutionary significance. Aust J Zool 28:98–102

Greer AE (1990) The biology and evolution of Australian lizards. Surrey Beatty & Sons, Sydney

Greer AE (2000) The biology and evolution of Australian snakes. Q Rev Biol 75:67–68

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

Henle K (1991) Life history patterns in lizards of the arid and semiarid zone of Australia. Oecologia 88:347–358

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

Hoppeler H (2015) Epigenetics in comparative physiology. J Exp Biol 218:6

Huey RB (1982) Temperature, physiology, and the ecology of reptiles. In: Gans C, Pough FH (eds) Biology of the Reptilia. Academic Press, New York

Hugall AF, Lee SY (2004) Molecular claims of Gondwanan age for Australian agamid lizards are untenable. Mol Biol Evol 21:2102–2110

Hugall AF, Foster R, Hutchinson M, Lee SY (2008) Phylogeny of Australasian agamid lizards based on nuclear and mitochondrial genes: implications for morphological evolution and biogeography. Biol J Linn Soc 93:343–358

Jennings DH, Moore MC, Knapp R, Matthews L, Orchinick M (2000) Plasma steroid-binding globulin mediation of differences in stress reactivity in alternate male phenotypes in tree lizards, *Urosaurus ornatus*. Gen Comp Endocrinol 120:289–299

King D, Green B (1999) Goannas. UNSW Press, Sudney

King D, Green B, Butler H (1989) The activity pattern, temperature regulation and diet of *Varanus giganteus* on Barrow Island, Western Australia. Wildl Res 16:41–47

Kuchling G (1999) The reproductive biology of the Chelonia. Springer, Heidelberg

Ladyman M, Bradshaw SD (2003) The influence of dehydration on the thermal preferences of the Western Tiger snake, Notechis scutatus. J Comp Physiol B 173:239–246

Ladyman M, Bradshaw SD, Bradshaw FJ (2003) Hypernatraemia and its effect on temperature regulation and levels of the hormone aginine vasotocin in the Western Tiger snake, *Notechis scutatus*. J Comp Physiol B

Ladyman MT, Bradshaw SD, Bradshaw FJ (2006) Physiological and hormonal control of thermal depression in the Tiger snake, *Notechis scutatus*. J Comp Physiol B 176:547–557

Licht P, Dawson WR, Shoemaker VH, Main AR (1966) Observations on the thermal relations of Western Australian lizards. Copeia 1966:97–110

Lillywhite HB (1980) Behavioural thermoregulation in Australian elapid snakes. Copeia 1980:452–458

Lillywhite H (2006) Water relations of tetrapod integument. J Exp Biol 209:200–226

Martin HA (2006) Cenozoic climatic change and the development of the arid vegetation in Australia. J Arid Environ 66:533–563

Melville J, Schulte Ii JA (2001) Correlates of active body temperatures and microhabitat occupation in nine species of central Australian agamid lizards. Austral Ecol 26:660–669

Morton SR, James CD (1988) The diversity and abundance of lizards in arid Australia: a new hypothesis. Am Nat 132:237–256

Nagy KA (1982) Field studies of water relations. In: Gans C, Pough H (eds) Biology of the Reptilia. Academic Press, New York

Nagy KA, Bradshaw SD (1995) Energetics, osmoregulation and food consumption by free-living desert lizards, *Ctenophorus (=Amphibolurus) nuchalis*. Amphibia-Reptilia 16:25–35.

Nagy KA, Peterson CC (1988) Scaling of water flux rate in animals. Univ Calif Publ Zool 120:1–172

Oliver PM, Bauer AM (2011) Systematics and evolution of the Australian knobtail geckos (*Nephrurus,* Carphodactylidae, Gekkota): pleisomorphic grades and progressive biome shifts through the Miocene. Mol Phylogenet Evol 59:664–674

Oliver PM, Sanders KL (2009) Molecular evidence for Gondwanan origins of multiple lineages within a diverse gecko radiation. J Biogeogr 36:2044–2055

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

Pianka ER (1986) Ecology and natural history of desert lizards. Princeton University Press, Princeton

Pianka E (1989) Desert lizard diversity: additional comments and some data. Am Nat 134:344–364

Pianka E (2014) Rarity in Australian desert lizards. Austral Ecol 13:214–224

Powney GD, Grenyer, Orme CDL, Owens IPF, Meiri S (2010) Hot, dry and different: Australian lizard richness is unlike that of mammals, amphibians and birds. Glob Ecol Biogeogr 19:386–396

Rosen PC (1990) Comparative field study thermal preferenda in garter snakes (*Thamnophis*). J Herpetol 25:301–312

Saint Girons H, Bradshaw SD (1987) Aspects of variation in histology and cytology of the external nasal glands of Australian lizards. J R Soc West Aust 69:117–121

Saint Girons H, Rice GE, Bradshaw SD (1981). Histologie comparée et ultrastructure de la glande nasale externe de quelques Varanidae (Reptilia, Lacertilia). Annales Scientifiques et Naturelles en Zoologie de Paris, 3, 13ème Ser.:15–21

Scanlon JD, Lee MSY (2004) Phylogeny of Australasian venomous sea snakes (Colubridae, Elapidae, Hydrophiinae) based on phenotypic and molecular evidence. Zool Scr 33:335–366

Schulte J, Melville J, Larson A (2003) Molecular phylogenetic evidence for ancient divergence of lizard taxa on either side of Wallace's line. Proc R Soc Lond B 270:597–603

Shine R (1987) Intraspecific variation thermoregulation, movements and habitat use by Australian blacksnakes, *Pseudechis porophyriacus* (Elapidae). J Herpetol 21:165–177

Stebbins RC, Barwick RE (1968) Radiotelemetric study of thermoreulation in a lace monitor. Copeia 1968:541–547

Thompson GG, Bradshaw SD, Withers PC (1997) Energy and water turnover rates of a free-living and captive goanna, *Varanus caudolineatus* (Lacertilia: Varanidae). Comp Biochem Physiol 116A:105–111

Underwood G (1957) On lizards of the family Pygopodidae: a contribution to the morphology and phylogeny of the Squamata. J Morphol 100:207–268

Whitfield CL, Livezey RL (1973) Thermoregulatory patterns in lizards. Physiol Zool 46:285–296

Withers PC, Bradshaw SD (1995) Water and energy balance of the mountain devil *Moloch horridus*: is the devil a sloth? Amphibia-Reptilia 16:47–54

Zucher A (1980) Procedural and anatomical considerations of the determination of cutaneous water loss in reptiles. Copeia 1980:425–439