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Endocrinology of osmoregulation and thermoregulation of Australian desert tetrapods: A historical perspective

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ABSTRACT

Many Australian tetrapods inhabit desert environments characterised by low productivity, unpredictable rainfall, high temperatures and high incident solar radiation. Maintaining a homeostatic *milieu intérieur* by osmoregulation and thermoregulation are two physiological challenges faced by tetrapods in deserts, and the endocrine system plays an important role in regulating these processes. There is a considerable body of work examining the osmoregulatory role of antidiuretic hormones for Australian amphibians, reptiles and mammals, with particular contributions concerning their role and function for wild, free-living animals in arid environments. The osmoregulatory role of the natriuretic peptide system has received some attention, while the role of adrenal corticosteroids has been more thoroughly investigated for reptiles and marsupials. The endocrinology of thermoregulation has not received similar attention. Reptiles are best-studied, with research examining the influence of arginine vasotocin and melatonin on body temperature, the role of prostaglandins in heart rate hysteresis and the effect of melanocyte-stimulating hormone on skin reflectivity. Australian mammals have been under-utilised in studies examining the regulation, development and evolution of endothermy, and there is little information concerning the endocrinology of thermoregulation for desert species. There is a paucity of data concerning the endocrinology of osmoregulation and thermoregulation for Australian desert birds. Studies of Australian desert fauna have made substantial contributions to endocrinology, but there is considerable scope for further research. A co-ordinated approach to examine arid-habitat adaptations of the endocrine system in an environmental and evolutionary context would be of particular value.

1. Introduction

Evolutionary adaptations of desert vertebrates have long been a source of interest to physiologists, as it is in arid environments that vertebrates must contend with conditions far removed from the aquatic habitats in which they originated (Williams and Tieleman, 2001). The most characteristic feature of the Australian landmass is widespread aridity; 80% of the Australian landmass is semi-arid or arid (Bradshaw, 1986; Heatwole, 1987), therefore a significant proportion of Australian tetrapods inhabit desert environments. For example, the distribution of >40% of Australian mammal species includes semi-arid or arid regions, and >20% are restricted to these regions (Withers et al., 2004). All continents have deserts, but Australian deserts have especially low productivity (Bradshaw, 1986, 2003) due to particularly variable and unpredictable rainfall coupled with ancient impoverished soils (Morton et al., 2011). Therefore, Australian deserts are particularly challenging environments for terrestrial vertebrates. As such, studies of the physiological mechanisms by which vertebrates persist in Australian deserts have been particularly important in improving knowledge of the adaptations of vertebrate animals to extreme environments in a global context.

Australia's fauna and its unique evolutionary history provide an ideal natural laboratory for examining the evolution of adaption to extreme arid environments. The ancient Gondwanan elements of Australia's tetrapod fauna, such as marsupials, ratites, chelid turtles and diplodactyline geckos, evolved in relative isolation on the Australian continent after the break-up of the supercontinent Gondwana during the Early Cretaceous (Heatwole, 1987). These taxa diversified to fill a wide range of niches occupied by quite different and distantly related taxa on other continents, and such convergent evolution highlights common adaptations that address similar physiological challenges. Over time, this Gondwanan faunal element also had to adapt to a changing climate, as the Australian continent drifted northwards and became drier. In the Cenozoic, the Australian continent had a warm and humid climate, which

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underwent progressive drying throughout the Eocene and Oligocene. The first major step in the transition towards aridity was in the mid-Miocene, by which time paleo-drainage systems in north-western Australia had ceased to flow. This aridity spread into the centre of the continent throughout the remaining Miocene. The primarily arid and semi-arid climate of modern Australia was established by the end of the Pliocene, with arid glacial and humid interglacial cycles occurring throughout the Pleistocene. At present there is a particularly dry interglacial phase, reflecting the very dry preceding glacial maximum (Heatwole, 1987; Martin, 2006; Morton et al., 2011). In addition to a warmer and drier climate, Australia's northward drift has also brought the continent into close proximity with southeast Asia, and a considerable proportion of Australia's current fauna including rodents, most lizards and snakes, and many birds, represents more recent invasions from southeast Asia since the Tertiary (Heatwole, 1987). Many of these groups have adapted to desert environments and have become a conspicuous element of Australia's desert fauna. Finally, human-introduced invasive species such as cane toads, house mice, rabbits, goats, camels, donkeys and cats provide another more recently introduced faunal element for examination of a more recent response to Australia's desert habitats.

Maintaining a homeostatic internal environment (*milieu intérieur*) by the processes of osmoregulation and thermoregulation are two particular physiological challenges faced by terrestrial animals in desert environments. Deserts by their very definition are arid habitats where evaporation exceeds precipitation (Williams and Tieleman, 2001), therefore osmoregulation, or the maintenance of water and solute levels constant or within the range of tolerance (Shoemaker and Nagy, 1977) is an obvious physiological challenge. This is especially true in Australian deserts where there may be many years of extreme aridity interspersed by occasional heavy rain and flooding (Morton et al., 2011). Australian deserts are also hot deserts (Bradshaw, 1986; Williams and Tieleman, 2001), and the extreme ambient temperatures and high incident solar radiation experienced by Australian desert vertebrates are exacerbated by the paucity of free water; this impacts on the capacity for evaporative heat loss at high ambient temperatures. Thus Australian desert vertebrates also face considerable thermoregulatory challenges.

Hormones are chemical messengers released into the bloodstream by endocrine glands, in response to specific stimuli. Hormones act on specific target organs that have the appropriate receptor molecules and elicit a wide range of responses. The endocrine system plays a role both in the chronic regulation of, and acute response to, a wide range of physiological processes, including osmoregulation and thermoregulation, and therefore the endocrinological control of water, salt and thermal balance is of particular importance to desert vertebrates. Examining the response of Australian desert vertebrates to the extreme osmoregulatory and thermoregulatory challenges of their environment can enlighten us about not only the mechanisms, but also the environmental function and evolution of homeostatic systems and processes. I review here how studies of Australian desert terrestrial vertebrates have contributed to, and continue to, advance our knowledge of the endocrinological control of osmoregulation and thermoregulation of terrestrial vertebrates.

2. Amphibians

Amphibians represent the transition of tetrapod vertebrates from an aquatic to a terrestrial environment and so their osmoregulatory strategies are of particular interest to physiologists. The osmoregulation of amphibians differs substantially from both aquatic fish and terrestrial amniotes, with their general use of cutaneous aerial respiration and subsequent requirement for a permeable skin impacting greatly on their osmoregulatory requirements and processes (Bentley, 2002). Four hormonal systems, the hypothalamo-neurohypophysial system, the renin/angiotensin/aldosterone system, the adrenocorticotrophic (ACTH)/corticosteroid system and the natriuretic peptide system, play a primary role in amphibian osmoregulation, with lesser roles for hormones including insulin, prolactin, hydrins and guanylins (Uchiyama and Konno, 2006). Amphibians' capacity for thermoregulation is relatively poorly developed compared to other tetrapods due to their highly permeable skin, but some species, such as "waterproof" frogs including *Litoria*, do show some regulation of body temperature (T_b) relative to ambient temperature.

Of the three extant amphibian orders, only the anurans inhabit Australia. There are two major, widespread families of native Australian anurans, the Hylidae or tree frogs and the Myobatrachidae or southern ground frogs. The ancient myobatrachid frogs in particular have radiated to fill a wide variety of niches, but are typically a xerophilous group that have become a conspicuous element of Australia's deserts (Bentley, 2002). Studies of the endocrinology of these myobatrachid frogs can reveal adaptive strategies that have allowed these unlikely desert inhabitants to become such a successful element of Australia's arid zone fauna, but surprisingly, these studies are few, reflecting the generally limited knowledge concerning comparative endocrinology of amphibians worldwide (Uchiyama and Konno, 2006) and preventing the informative analysis of endocrine function in an ecological and phylogenetic context necessary to fully explore the evolutionary significance of variation in amphibian osmoregulation.

2.1. Osmoregulation

The most spectacular adaption of Australian myobatrachid desert frogs to surviving the inhospitable desert conditions of high temperatures and little free water is their ability to withstand long periods of aestivation, burrowed below the desert substrate. Some burrowing desert frogs, including the genera *Neobatrachus* and *Cyclorana*, form a cocoon of shed skin layers providing a barrier to evaporative water loss from the skin (Withers, 1995). Others such as *Heleioporus*, *Notaden*, *Arenophryne* and *Myobatrachus* burrow into soil with a favourable water potential (Cartledge et al., 2006a,b; Thompson et al., 2005). Behaviours such as aestivation and cocoon formation are presumably under hormonal control, but hormonal changes that reduce activity, prevent consumption of shed skin layers and possibly contribute to metabolic depression have not yet been identified (Bentley, 2002); this is an important direction for future research.

The only studies of the major osmoregulatory hormone arginine vasotocin (AVT) for Australian desert frogs are for the burrowing myobatrachid frogs *Cyclorana platycephala*, *Neobatrachus aquilonius* and *Notaden nichollsi*. The interrelationship between aestivation period, plasma and urine osmolality and plasma AVT concentration was examined for the arid-habitat, cocooning, water-holding frog *C. platycephala* by Cartledge et al. (2008), for frogs aestivating in the laboratory for up to 15 months. During this period, plasma osmolality increased from initial levels of 250–487 mOsm after 9 months, then remained stable for the rest of the aestivation period. Urine osmolality, however, continued to increase until 15 months aestivation, by which time it was iso-osmotic (469 ± 31.3 mOsm) with the plasma (501 ± 31.2 mOsm), indicating that frogs were re-absorbing water from the bladder to replace that lost by evaporation. Despite the general role of AVT contributing to osmoregulation by controlling the excretion of water from the kidneys in response to increased plasma osmolality (Bentley, 2002; McCormick and Bradshaw, 2006), there was no clear relationship between plasma AVT concentrations and osmolality during the