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Variations upon a theme: Australian lizards provide insights into the endocrine control of vertebrate reproductive cycles

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ABSTRACT

Australian lizards exhibit a broad array of different reproductive strategies and provide an extraordinary diversity and range of models with which to address fundamental problems in reproductive biology. Studies on lizards have frequently led to new insights into hormonal regulatory pathways or mechanisms of control, but we have detailed knowledge of the reproductive cycle in only a small percentage of known species. This review provides an overview and synthesis of current knowledge of the hormonal control of reproductive cycles in Australian lizards. Agamid lizards have provided useful models with which to test hypotheses about the hormonal regulation of the expression of reproductive behaviors, while research on viviparous skinks is providing insights into the evolution of the endocrine control of gestation. However, in order to better understand the potential risks that environmental factors such as climate change and endocrine disrupting chemicals pose to our fauna, better knowledge is required of the fundamental characteristics of the reproductive cycle in a broader range of lizard species.

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1. Introduction

Australian lizards provide an extraordinary diversity and range of models with which to address fundamental problems in reproductive biology. Representing approximately 650 species, they are distributed across a wide range of climatic zones, from cool-temperate regions to hot deserts, and exhibit correspondingly diverse life history characteristics and seasonal patterns of reproduction (Shine, 1985). Furthermore, while sex is genetically determined (GSD) in most squamate reptiles, some lizards exhibit temperature-dependent sex determination (TSD) (Lovern, 2011) or even a combination of TSD and GSD, as in the Australian viviparous skinks *Eulamprus tympanum* (Robert and Thompson, 2001) and *Niveoscincus ocellatus* (Pen et al., 2010).

Research on Australian viviparous lizards has provided important insights into the evolution of viviparity in amniotes (Thompson et al., 2002). Nearly half of Australia's lizard species are skinks (Family Scincidae), with approximately 370 species in 33 genera (Wilson and Swan, 2003). Although the majority are oviparous, they include viviparous species with a wide range of placental types, from simple (e.g. *Egernia* and *Tiliqua*) to complex placentae (e.g. *Pseudomoia* and *Niveoscincus*) (Thompson et al., 2002). Indeed, the first systematic examination of placentation in viviparous reptiles was conducted on Australian skinks by Claire Weekes (Weekes, 1935) at the University of Sydney. In more recent years, Michael Thompson and his colleagues have focussed on the *Eugongylus* group of skinks as models for testing hypotheses on the evolution of amniote viviparity, focussing on placental structure and function (Thompson et al., 2002). Their physiological approach complements the depth and breadth of ecologically-focussed research into the evolution of viviparity that was initiated early in the twentieth century and continues to represent one of the 'big questions' in biological research (Shine, 2014).

Lizards also provide a rich variety of models for comparative endocrinologists. Lovern (2011) commented that studies on lizards have frequently led to new insights into hormonal regulatory pathways or associations between endocrine patterns and physiological or behavioral events. Our current understanding of behavioral neuroendocrinology owes much to research on lizards which has, in particular, uncovered the phenomena of dissociated reproductive strategies and hormone-independent behaviors, and highlighted the importance of progesterone (P) as a "male hormone" that both organizes and activates sexual behavior in males (Crews and Moore, 2005).

This review provides an overview and synthesis of current knowledge of the hormonal control of reproduction in Australian lizards. It illustrates how fundamental endocrine patterns have been modified as reproductive strategies have evolved in response to the different environmental challenges faced by this diverse and

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widespread group, and comments upon how such studies provide insights into the evolution of the hormonal control of reproduction.

2. Hormones and reproduction in lizards: a brief overview

The fundamental aspects of the endocrinology of reproduction in lizards have recently been reviewed (Jones, 2011; Kumar et al., 2011; Lovern, 2011; Ramírez-Pinilla et al., 2015) so only a brief overview is provided here in the context of variations in plasma hormone concentrations through the reproductive cycle.

2.1. Hypophysial regulation of reproduction in lizards

Surprisingly little is known of hypothalamo-pituitary regulation of the gonadal cycle. Reptile brains contain several variants of gonadotropin-releasing hormone (GnRH) although a gonadotropin release-inhibiting hormone (GRIH) has yet to be identified. Squamate reptiles appear to have only a single gonadotropin (GTH) that combines follicle-stimulating hormone (FSH) and luteinising hormone (LH) activity, representing a divergence from the typical pattern in tetrapod vertebrates (Jones, 2011).

2.2. Oviparous female lizards

Follicular development typically involves the deposition of large amounts of yolk for embryonic nutrition. In oviparous reptiles, estradiol-17β (E2) produced by the maturing follicle stimulates vitellogenesis and shell gland recruitment. High plasma E2 concentrations are therefore expected during the vitellogenic stage of the reproductive cycle, while late vitellogenesis and ovulation are associated with peak plasma concentrations of E2 and high concentrations of progesterone (P) and testosterone (T) (Jones, 2011; Ramírez-Pinilla et al., 2015). All reptiles, whether oviparous or viviparous, develop true secretory corpora lutea. Ovulation therefore marks a transition from the estrogen-dominated vitellogenic phase to the progesterone-dominated luteal phase. Oviparous squamates characteristically have a short-lived peri-ovulatory peak in plasma P concentrations. Concentrations decline after luteolysis and oviposition which typically occurs after approximately one third to half of embryonic development has taken place *in utero* (Albergotti and Guillette, 2011).

2.3. Viviparous female lizards

Most viviparous lizards are relatively lecithotrophic: they produce large yolky eggs and support embryonic development via both yolk and placenta. The percentage of matrotrophic contributions via the placenta varies between species according to placental type and complexity (Blackburn, 2014). As in oviparous lizards, vitellogenesis is characterized by increasing plasma E2 concentrations. After ovulation, gestation is supported by P, and the corpora lutea remain active for longer than in oviparous reptiles. Although the specific pattern of plasma P concentrations varies between species, most exhibit a peak in mid- to late-gestation (Albergotti and Guillette, 2011; Jones, 2011).

2.4. Male lizards

In male lizards, as in other vertebrates, spermatogenesis is under the control of androgens produced by the Leydig cells of the testis. Androgens also control development of the secondary sex organs (including epididymis and renal sexual segment) and sexual behavior, while estrogens are involved in post-spermatogenic testicular regression. Two types of annual testicular cycle are recognized: prenuptial and postnuptial. In species with prenuptial cycles, spermatogenesis occurs before or during the breeding season, and there is a single annual peak of plasma T coincident with the culmination of spermatogenesis, when mating occurs. In postnuptial species, on the other hand, spermatogenesis takes place after the mating season and sperm are stored in male (or female) accessory ducts until the next mating season. In these animals, peak plasma T concentrations occur when the seminiferous tubules are regressed (Kumar et al., 2011).

3. Australian lizards as model species for reproductive endocrinology

Australian lizards provide a wide range of appropriate models for reproductive endocrinologists because they cover a climatic range that includes the deserts of the interior, the wet tropics and cool-temperate alpine regions. They therefore exhibit a diversity of life history strategies with concomitant variations in parity mode and the timing of key reproductive events. In temperate lizards, temperature is the main proximate cue regulating the timing of reproduction, but in tropical species there appears to be little relationship between seasonal environmental variations and the timing of breeding (Whittier, 1994); instead, the initiation of gonadal development and reproductive activity appears to be regulated by exposure to solar radiation (Clerke and Alford, 1993). At the other end of the environmental spectrum, females of some lizards found in the cool alpine regions of Tasmania (the island state of Australia) typically exhibit biennial breeding: gestation is extended through hibernation and parturition timed so that young are born in spring (Girling et al., 2002a; Olsson and Shine, 1999).

Such variations in reproductive biology will be mirrored by differences in annual cycles of key reproductive hormones. Despite underlying commonalities in the fundamental role(s) of particular hormones across vertebrates (Norris, 2007), documenting and describing subtle species-specific differences in hormone profiles can elucidate fundamental endocrine mechanisms such as environmental regulation of the hypothalamo-pituitary-gonadal axis or the timing of parturition (Girling et al., 2002a). However, at the world-wide scale, relationships between plasma hormones and the reproductive cycle have been documented for a very few lizard species representing only eight of 32 families. Indeed, endocrine profiles and reproduction been well-characterized only in the two genera *Tiliqua* and *Niveoscincus* (Lovern, 2011) which are both Australian scincid taxa.

Although the Australian fauna includes members of the families Scincidae (skinks), Agamidae (dragons) and Varanidae (monitors and goannas) (Wilson and Swan, 2003), the Gekkonidae, Diplodactylidae and Carphodactylidae (geckoes) and Pygopodidae (flap-footed lizards) (Han et al., 2004), only skinks and dragons have been studied from an endocrinological perspective. This review therefore takes a 'case study' approach: it highlights how research on particular Australian lizard species or species groups has contributed to our current understanding of vertebrate endocrine physiology in the specific context of understanding the hormonal control of key reproductive events.

4. Hormones and reproduction in Australian dragon lizards (Agamidae)

The dragons, Family Agamidae, are most common in the arid to dry tropics, with only one species, *Rankinia diemensis*, extending as far south as Tasmania. Dragons are wholly oviparous: females excavate burrows in which they lay their clutches of 2–30 eggs. Agamids are notable for the range of complex courtship, territorial and sometimes spectacular defensive behaviors exhibited by many species (Wilson and Swan, 2003). Although endocrine-focussed

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