Australian lizards are outstanding models for reproductive biology research

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Abstract

Australian lizards are a diverse group of animals distributed across the continent and inhabiting a wide range of environments. Together, they exhibit a remarkable diversity of reproductive morphologies, physiologies, and behaviours that is broadly representative of vertebrates more generally. Importantly, many of these reproductive traits have evolved independently in multiple Australian lizard groups, and these groups are closely related to taxa that exhibit ancestral forms of these traits. Australian lizards are thus outstanding model organisms for testing hypotheses about how reproductive traits function and evolve and they provide an important basis of comparison with other animals that exhibit similar traits. Here, we highlight how research on Australian lizard reproduction has contributed to answering broader evolutionary and ecological questions that apply to all animals. We review reproductive traits exhibited by Australian lizards that are important areas of current research. We highlight important questions that emerge from an understanding of this body of research when considered as a whole. Finally, we identify additional research questions that Australian lizards are well-suited for reproductive biologists to address.

Introduction

Australia is home to about 13 % of the world's lizard biodiversity (~850 of ~7,000 species; Uetz 2010), despite containing only 5 % of the world's land area. Australian lizards are taxonomically distributed across seven families: Carphodactylidae, Diplodactylidae, Gekkonidae, Pygopodidae (all from the infraorder Gekkota), Scincidae, Agamidae, and Varanidae (Cogger 2018). Of these, the Scincidae are the most diverse Australian lineage, with ~460 species (Wilson and Swan 2021). The Carphodactylide are endemic to Australia, and Australia is home to large proportions of the world's Diplodactylidae (~65 %), Pygopodidae (~97 %), Scincidae (~30 %), and Varanidae (~50 %). These species numbers and proportions are not exact, however, because the taxonomy of Australian lizards is still developing. Together, Australian lizards are distributed across the entire continent, and experience habitats ranging from cool temperate forests and alpine meadows to hot deserts and tropical rainforests (Figure 1; Cogger 2018). Most of the lizard species in Australia exist in only a few of these habitats, but some, like the pygopodid *Lialis burtonis* and the scincid *Tiliqua scincoides*, thrive across a range of habitat types. Australia's diverse environments, and the abilities of different lizard taxa to specialise or generalise to survive within them, are likely major reasons for Australia's high lizard biodiversity (Pianka 1969; Skeels *et al.* 2020).

Australian lizard biodiversity, and its distribution across such variable environments, provides important opportunities for testing hypotheses about how traits evolve and function. In particular, Australian lizards exhibit multiple evolutionary origins of key innovations related to reproduction, including social behaviours (Gardner *et al.* 2016), signalling and reproductive tactics (Dong CM 2021; Stuart-Fox *et al.* 2021), viviparity (live birth; Blackburn 2015), and transitions in sex determination (Sarre *et al.* 2004). The multiple origins of these traits provide natural replication for robust tests of key evolutionary hypotheses (Garland and Adolph 1994): do the physiological and genetic functions of these traits evolve in the same ways? How do their functions change in species that are distributed across variable environments (Figure 1)? The wide, overlapping distributions of some Australian lizard taxa (Cogger 2018) exhibiting variation in these traits provides a framework for answering these questions across species, and sometimes even within single species. Furthermore, many of these traits are shared with other animals, so the results gained from lizard research provide a basis for comparison with those other taxa (Tinkle *et al.* 1970).

In addition to their utility for answering scientific questions, lizards are tractable research models. Many species are an ideal size to study using both captive and field-based approaches. They are big enough to carry dataloggers, yet small enough to house in captivity with relative ease and low costs (McDiarmid *et al.* 2012). Several Australian skinks and dragons exhibit high population densities, which enables the sample sizes required for robust ecological analyses. For these reasons, lizards around the world have been important model organisms for research in ecology, physiology, and life history evolution since the 1950s (Huey *et al.* 1983; Milstead 1967; Vitt and Pianka 1994). Early research on Australian lizards contributed particular advances in understanding how placentas and viviparity evolve (Weekes 1935), and in community ecology (Pianka 1969; Pianka 1989).

Our objective with this review is to highlight the reproductive traits exhibited by Australian lizards that are of particular interest to biologists and students focused on broader evolutionary and ecological questions that apply to all animals. Many Australian lizard experts contributed their expertise to highlight some important areas where Australian lizards have, or could, contribute to answering broader questions in reproductive biology. We structured our review by covering topics in the sequence in which they occur during a reproductive cycle: behaviours and signalling involved in courtship; mechanisms involved in mating, egg production, and sperm competition; nesting and gestation; sex determination; and finally, birth in viviparous species.

1: Pair bonds and sociality

Social behaviour can be as simple as an interaction between two individuals that briefly meet, or complex social interactions among multiple individuals that form large stable groups that interact over extended periods of time. Such social groups emerge as the result of either family members remaining together (e.g. fraternal societies) or through non-random associations of unrelated individuals (e.g. egalitarian societies). Both cases can result in individuals becoming mutually dependent on one another, sometimes forgoing their own reproduction and instead assisting with the reproduction of others. The origin of complex social behaviour and societies has been highlighted as a major evolutionary transition (Maynard Smith and Szathmáry 1997). Thus, understanding the factors responsible for the evolutionary origins of such societies is a key challenge for biologists.

Traditionally, the flagship vertebrate taxa for understanding the evolution of complex sociality have been co-operatively breeding birds and mammals, organisms that live in complex societies (Rubenstein and Abbot 2017). Lizards, in contrast, have been largely ignored. However, a new social paradigm has emerged in lizards based on the recently-recognised presence of stable, long-term, and sometimes complex social associations in multiple, independent taxa (Doody *et al.* 2013; Doody *et al.* 2021a; Gardner *et al.* 2016; Halliwell *et al.* 2017b). The best example of such complex social organisation comes from an Australian group of scincid lizards, the Egerniinae. The Egerniinae include 62 species in 8 genera (*Egernia, Liopholis, Bellatorias, Lissolepis, Tiliqua, Cyclodomorphus, Corucia*, *Tribolonotus*) (Gardner *et al.* 2008; Uetz 2010). Many species in the Egerniinae are characterised by the presence of long-term social associations both between adults, and between adults and their offspring, which result in the formation of stable family groups (Gardner *et al.* 2016; While *et al.* 2019; Whiting and While 2017). Crucially, the presence of these stable social associations and the diversity of social organisation (solitary, pair-bonds, facultative family living, obligate family living) makes the Egerniinae an outstanding model system for understanding the factors that have facilitated the origin and elaboration of complex social organisation.

The key foundation of social organisation in the Egerniinae is the presence of long-term pair-bonds that form between males and females. Pair-bonds were first identified in sleepy lizards (*Tiliqua rugosa*) (Bull 1988; Bull 2000), where they are stable and may be life-long (Bull *et al.* 2017; Leu *et al.* 2015). Similar long-term pairings underpin social organisation across most social Egerniinae (Chapple 2003; Whiting and While 2017). The nature of these pair-bonds can be variable across species. Indeed, while the predominant form of pair-bonding within Egerniinae is monogamy, in some species, males form bonds with multiple females (Chapple and Keogh 2006; While *et al.* 2019; While *et al.* 2009b; While *et al.* 2011).

In other species, social bonding can extend to multiple adults of both sexes (Duffield and Bull 2002; Gardner *et al.* 2002a; Gardner *et al.* 2001), although often only a small number of individuals within these groups actually mate (Gardner *et al.* 2012). Long-term data on pair bonding are relatively sparse for most species, except *T. rugosa*. However, pair stability over multiple breeding seasons has been identified for *Egernia cunninghami* (Stow and Sunnucks 2004), *E. saxatilis* (O'Connor and Shine 2003), *E. stokesii* (Duffield and Bull 2002; Gardner *et al.* 2002b), and possibly *E. striolata* (Riley unpubl. data) and *Liopholis whitii* (While et al. unpubl. data). While the occurrence of these long-term pair-bonds is well-established, we know relatively little about their functional significance. The reproductive benefits of maintaining a stable pair-bond compared to switching partners (but see Bull 2000; Leu *et al.* 2015), the short and long-term trade-offs between maintaining single versus multiple social bonds, and the factors that initiate pair separation, remain largely unknown. Addressing these questions has the potential to reveal the factors that promote and maintain the initial emergence of long-term pair-bonds, which is relevant to other vertebrates in which family life is based upon the maintenance of social monogamy (e.g. Young *et al.* 2019).

Stable social associations between males and females in the Egerniinae vary not only in their nature but in the extent to which they correspond to patterns of paternity acquisition. On average, members of the Egerniinae exhibit some of the lowest levels of female polyandry (i.e. mating with one or more males) in lizards (Uller and Olsson 2008), with genetic monogamy the most pervasive mating system. Despite the low levels of polyandry, most species exhibit at least some multiple mating and/or extra-pair mating. In social *Egernia* species, this ranges from 2.6 % of litters including extra-pair paternity in *E. cunninghami* (Stow and Sunnucks 2004) to 10 – 30 % for other species (e.g. Bull *et al.* 1998b; Chapple and Keogh 2005a; Gardner *et al.* 2001; O'Connor and Shine 2003; While *et al.* 2014; While *et al.* 2009b). In contrast, Egerniinae species that do not live in social groups exhibit higher levels of genetic polyandry. For example, 75 % of *Tiliqua adelaidensis* litters show evidence of multiple mating (Schofield *et al.* 2014). Differences in the proportions of polyandry among species, coupled with variation in the extent of social complexity (see below), make the Egerniinae an excellent model for testing hypotheses about the role that genetic monogamy has played in the evolution of social organisation (e.g. Cornwallis *et al.* 2010; Hughes *et al.* 2008; Lukas and Clutton-Brock 2012).

Social aggregations in the Egerniinae are not just underpinned by prolonged associations between males and females, but also by prolonged associations between parents and their offspring. Indeed, offspring often delay dispersal and remain in their parents' refuge, sometimes for several years. The number and duration of these parent-offspring associations varies across the Egerniinae - from species in which these associations are absent [e.g. *T. rugosa* (Bull and Baghurst 1998)], to species in which parents exhibit facultative associations with a single cohort of offspring [e.g. *L. whitii* (Chapple and Keogh 2006; While *et al.* 2009b), *Liopholis slateri* (Fenner *et al.* 2012), *Egernia saxatilis*, (O'Connor and Shine 2003)], to species that live in large social groups with multiple cohorts of young. For example, *E.*

cunninghami and *E. stokesii* can have up to five generations of offspring co-occurring in a single-family group (Gardner *et al.* 2001; Stow *et al.* 2001). Even in the mostly solitary *T. adelaidensis*, offspring can stay in natal burrows for several days before dispersing (Pearson *et al.* 2016). The associations between parents and offspring within the Egerniinae have several functional consequences that may constitute simple forms of parental care. For example, offspring gain increased access to basking sites, foraging opportunities, and retreat sites (Bull and Baghurst 1998; Munch *et al.* 2018; O'Connor and Shine 2004), which may result in an increase in early growth and survival (Botterill-James *et al.* 2016). Offspring also benefit from extended parent–offspring associations via a reduction in the risk of conspecific aggression and infanticide (O'Connor and Shine 2004; Sinn *et al.* 2008) and/or predation (Masters and Shine 2002; Watson *et al.* 2020). For example, the presence of a parent *E. saxatilis* eliminates aggression displayed toward offspring by unrelated adults (O'Connor and Shine 2004), and female *E. cunninghamii* actively chase off predatory snakes in the presence of their offspring (Watson *et al.* 2020). Finally, offspring may inherit territories via prolonged parent–offspring associations, as suggested by the high levels of genetic relatedness within social groups of *E. stokesii* (Gardner *et al.* 2001) as well as the long term residency of individuals in groups (Pearson *et al.* 2016).

Results from the Egerniiae clearly highlight the diversity in social traits that exist within the group. Future research needs to combine our understanding of diversity in social complexity with experimental tests that target the factors that mediate the expression and nature of these simple forms of social behaviour (e.g. Halliwell *et al.* 2017a; Halliwell *et al.* 2017b) in a phylogenetic context. This combination will allow us to connect plasticity in social behaviour at the individual level with evolutionary divergence of social complexity at the population and species level. Such research has the potential to generate an understanding of how different social entities (males, females, offspring, siblings) initially come together, how such social associations are maintained in the face of inevitable conflicts that arise, and ultimately, how the stabilisation of these associations provides a foundation for the elaboration of social behaviour. The growing appreciation that simple social behaviour, based around family life, has emerged independently in other lizard families (e.g. Cordylidae, Xantusiidae) (Gardner *et al.* 2016; Halliwell *et al.* 2017b) means that we can apply our understanding of social evolution in the Egerniinae to identify commonalities across transitions to social life in other social lizards. Furthermore, the Egerniinae is ideally placed to integrate a detailed understanding of the phenotypic convergence in social evolution with neurological, genomic and developmental approaches that tell us how social traits converge at a mechanistic level. Combined, this approach has the potential to place the Egerniinae alongside other emerging socio-genomic/neuro-molecular vertebrate models, such as cichlids, frogs, butterfly fishes, birds, and mammals (e.g. Bukhari *et al.* 2019; Fischer *et al.* 2019; Nowicki *et al.* 2020; O'Connell *et al.* 2012) as a major future contributor to our understanding of what it takes to make an organism social.

2: Pheromones and reproduction in Australian squamates

Pheromones are chemicals that elicit a behavioural or physiological response in others of the same species (Karlson and Lüscher 1959; although see distinctions of Wyatt 2010), and are important to the social behaviour of squamates, including behaviour tied to reproduction. Pheromones influence behaviours such as locating, recognising, and choosing mates; antagonistic interactions that can determine the availability of mates; and parent–offspring recognition (reviewed by Houck 2009; Martín and López 2011; Mason and Parker 2010). Production of pheromones involved in reproductive signalling is controlled by reproductive hormones in squamate reptiles (Parker and Mason 2012; Parker and Mason 2014). Conceivably, pheromones could influence cryptic female choice after mating has already happened (e.g. choosing to use or reject sperm from certain males). Additionally, pheromones could act as 'primers' that influence hormonal responses in the receiver (Bradbury and Vehrencamp 2011); for example, pheromones could induce or suppress sexual receptivity in the receiver (Mason and Parker 2010). However, many of the details of pheromones and reproductive behaviour remain to be tested in squamates.

Squamates produce pheromones from various regions of the body. Pheromones can be secreted from the skin (e.g. Mouton *et al.* 2014; Mouton *et al.* 2010; Van Wyk and Mouton 1992), including from specialised epidermal glands, such as generation glands and follicular pores (Cole 1966; Maderson 1972; Mayerl *et al.* 2015), or from specialised glands within the cloaca (Cooper and Grastka 1987; Cooper and Trauth 1992; Siegel *et al.* 2014). Pheromones identified from the scats of several Australian Egerniinae (Bull *et al.* 1999a; Bull *et al.* 2000; Bull *et al.* 1999b) are likely produced from glands in the cloaca and deposited onto the surface of the faeces, although this hypothesis remains untested. Variation in the presence of cloacal glands across squamates has not been widely assessed, but epidermal glands, which are visible to the naked eye and thus better known, vary widely in their presence among squamate lineages (García-Roa *et al.* 2017). Epidermal glands can vary between sexes, typically with glands being better developed or only present in males (Mayerl *et al.* 2015). In some Australian lizards, such as *Amalosia* and *Nactus* geckos, the presence and absence of male epidermal pores vary even among closely related populations (Zozaya and Hoskin pers. obs.). Variation in femoral pore size and extent covaries with environmental variation in the *Ctenophorus maculatus* species complex, (Edwards *et al.* 2015), suggesting ecological factors may influence the evolution of epidermal glands in these species. Evolutionary trade-offs with other signalling modalities, such as visual displays, could also explain some variation in chemical signalling investment and the presence and extent of epidermal pores (e.g., *Sceloporus*; Campos *et al.* 2020; Ossip-Klein *et al.* 2013) but has yet to be explored in

Australian lizards. The drivers of anatomical variation in pheromone production, and its consequences for behaviour, are poorly understood areas ripe for further study, with agamids and *Amalosia* and *Nactus* geckos being potentially good models.

While most research on pheromones in squamates has focused on European and New World species, there are a number of studies on Australasian taxa that have focused on pheromone-mediated discrimination (Table 1). These studies do not conclusively demonstrate a pheromonal role in reproduction, but they do suggest the potential for influencing mate choice and antagonistic behaviours that could lead to assortative mating. The link between pheromone variation and reproductive behaviours remains to be explicitly tested in most Australian taxa, except for in the sea krait genus *Laticauda* (Shine *et al.* 2002c). Assessing female receptivity (Head *et al.* 2005), and recognising and trailing mates (Bull *et al.* 1993a; Bull and Lindle 2002; Olsson and Shine 1998) are key for identifying, finding, and guarding potential or actual mates. Additionally, the capacity for reciprocal mother–offspring recognition (Head *et al.* 2008) is important to mediate post-natal conflict and care. Beyond these areas, more in-depth studies are needed to determine the precise ways in which pheromones influence behaviour and reproduction.

Pheromonal research in Australia has focussed heavily on skinks, particularly those in the subfamily Egerniinae (Table 1), which exhibit complex sociality (Whiting and While 2017). However, pheromones are likely important to many squamate taxa. In fossorial taxa (e.g. *Anomalopus, Lerista, Aprasia,* blind snakes), pheromones are probably the most important, if not the only, signalling trait facilitating the finding and choosing of mates. Furthermore, recent work showing divergence in the chemical blends of epidermal pore secretions among morphologically similar, but genetically divergent, gecko lineages suggests pheromones may be important for mediating reproductive isolation in ‘cryptic species’ complexes (Zozaya *et* *al.* 2019). Continued research into the form and function of squamate pheromone systems is needed to better understand their influence on reproduction and their evolutionary consequences (e.g. speciation, evolution of sociality). Australia's extraordinary squamate diversity — with its corresponding diversity in morphology (for example in epidermal pores), ecology, social systems, and behaviour, and the presence of several clades with worldwide distributions — present multiple potential model systems for pursuing lizard pheromone research.

3: Colour polymorphisms and alternative reproduction tactics in *Ctenophorus* spp.

Intraspecific variation in male colour and reproductive traits

Colour polymorphism is the co-existence of two or more distinct, heritable morphs within an interbreeding population, with the rarest occurring too frequently to be solely the result of recurrent mutation (Huxley 1955). Colour polymorphic species are valuable for examining the relationships between traits under both natural and sexual selection because the colour morphs are a convenient visual indicator of specific reproductive behaviours and often carry physiological costs (Stuart-Fox *et al.* 2021). Trade-offs between body size, colouration, aggressiveness, and postcopulatory sexual selection often occur in polymorphic species in which males compete for reproductive success using alternative mating tactics, for example, where one morph is most successful in monopolising females through territoriality and another morph is more successful in fertilization through subterfuge (Sinervo and Lively 1996). Australia has two lizard species that have been used as model systems for such research: *Ctenophorus pictus* (painted dragon) and *C. modestus* (swift dragon). Male *C. pictus* are polymorphic in two aspects: head colour [(red, orange, yellow, or blue (Olsson *et al.* 2007b)], and the presence or absence of a yellow gular bib (Olsson *et al.* 2009a).

Similarly, male *C. modestus* are polymorphic for throat colour [orange, yellow, yellow with an orange centre, and grey (Teasdale *et al.* 2013)]. Colour traits in both species correspond to alternative behavioural, physiological, and life-history traits. Both species have been used to study different aspects of alternative reproductive tactics and sexual selection, with *C. pictus* as a model system for demonstrating the physiological costs associated with each morph, and *C. modestus* as a model for behaviour and aspects of coloration (e.g. visual conspicuousness, genetic and biochemical basis).

Colour traits in *C. pictus* are associated with trade-offs between investments in male aggressiveness, metabolism, condition loss, postcopulatory success, and telomere maintenance (a biomarker of stress and ageing) (Olsson *et al.* 2018; Olsson *et al.* 2017), which are mediated by oxidative stress (Friesen *et al.* 2017a; Friesen *et al.* 2020b; Friesen *et al.* 2021; Friesen *et al.* 2017b; Healey and Olsson 2009; Healey *et al.* 2007; McDiarmid *et al.* 2017; Olsson *et al.* 2007a; Olsson *et al.* 2009a; Rollings *et al.* 2017). Bibbed and red-headed males invest more in traits that aid in precopulatory sexual selection, whereas yellow and non-bibbed males invest more in traits that aid in postcopulatory sexual selection, including sperm competition (Friesen *et al.* 2020a) (see Section 6). Red-headed and/or bibbed males tend to be more aggressive, and more likely to win male-male contests (Healey *et al.* 2007; McDiarmid *et al.* 2017). Bibbed males are also more attractive to females (McDiarmid *et al.* 2017). In contrast, yellow and non-bibbed males share similar reproductive tactics that include having larger testes (Olsson *et al.* 2009b) that produce more and faster sperm (Friesen *et al.* 2020c), but with significantly shorter copulation durations than either red or bibbed males (Friesen *et al.* 2020c; Olsson *et al.* 2009b). Although overall rates of multiple paternity are relatively low (~15 % in the wild), yellow males have three times greater paternity success in head-to-head sperm competition trials over red males (Olsson *et al.* 2009b).

Bibbed male *C. pictus* do not lose paternity to neighbouring males in the field, probably because of effective territorial defence and mate guarding (Healey and Olsson 2009; Olsson *et al.* 2009a). Their investment in precopulatory traits carries a cost: both red-headed and bibbed males have significantly shorter blood cell telomeres (a potential marker of ageing and stress) than yellow-headed males and non-bibbed males (Friesen *et al.* 2019; Friesen *et al.* 2017a; Olsson *et al.* 2007a). In contrast, their sperm telomeres are longer (Friesen *et al.* 2020c). Sperm telomere length is negatively related to sperm swimming velocity (Friesen *et al.* 2020c). The potential for sperm telomere length to influence sperm competitiveness or biases in female sperm storage are exciting ideas that remain to be tested (Friesen *et al.* 2020c; Olsson *et al.* 2018; Olsson *et al.* 2017), as they may have implications for sperm competition across animals.

The male morphs of *C. modestus* exhibit different reproductive behavioural strategies, with orange as the most aggressive and grey as the least aggressive. The aggression level of yellow and orange-yellow morphs is conditional on the competitor's morph, where they are more aggressive to yellow and orange than to grey. The grey morph is the least bold, with similar boldness across the remaining morphs (Yewers *et al.* 2016). Differences in morph behavioural strategy correspond to differences in circulating baseline concentrations of androgen hormones. The aggressive orange morph has higher concentrations of androgens than either grey or yellow morphs (Yewers *et al.* 2017).

Although both *C. modestus* and *C. pictus* exhibit colour polymorphisms, the two species differ in their geographic distributions of morphs. All populations of *C. modestus* contain the same four morph types, but morph frequencies vary greatly among populations. There is evidence that spatial variation in selection shapes morph frequency patterns in *C. modestus*, given strong relationships between morph frequencies and mean annual aridity index and vegetation cover, with no relationships between genetic similarity or geographic distance (McLean *et al.* 2015). In contrast, colour traits in *C. pictus* vary in abundance geographically. It is unclear if the apparent costs and benefits of alternative strategies influence fluctuations in morph frequency across years. From research on *Uta stansburiana* in the USA, fluctuations of morphs may be driven by female preference (Alonzo and Sinervo 2001) from year to year, but they also vary across geographic space from monomorphic to trimorphic (Corl *et al.* 2010b). Explanations for this variation centre on sexual selection as the cause of variance in morph number, given a positive relationship between sexual size dimorphism and morph number in *U. stansburiana* (Corl *et al.* 2010a). However, this relationship may not be indicative of variation in sexual selection (Chelini *et al.* in review). Instead, it may be driven by common environmental drivers, which each independently influence the proportion of sexual size dimorphism and the number of morphs in a population (Chelini *et al.* in review). Environmental variables similarly influence the proportion of morphs in *C. modestus* (Mclean *et al.* 2015), but this has not yet been explored in *C. pictus*. By what mechanisms the environment regulates morph frequencies in polymorphic species is yet to be determined. It is possible that alternate numbers of morphs represent alternate resolutions of sexual conflict over mating dictated by environmental conditions (Svensson *et al.* 2020).

Intraspecific variation in female reproductive traits

Lizard species also exhibit variation in reproductive output, including egg size, egg number, and reproductive frequency, which collectively determine total per-year fecundity. *Ctenophorus modestus* and *C. decresii* (tawny dragon) are sister species within the *C. decresii* species complex (Dong *et al.* 2021; McLean *et al.* 2014) which differ in maternal reproductive strategy. *Ctenophorus modestus* females exhibit higher fecundity over a breeding season and produce larger clutches with lower individual egg masses and more clutches per season (Dong CM 2021). In contrast, *C. decresii* females produce smaller clutches of larger eggs, and seldom more than one clutch per season. *Ctenophorus modestus* clutches also have longer incubation periods than do *C. decresii*.

The differing reproductive strategies of the species may be attributable to environment-mediated selection. Both species are endemic to South Australia: *Ctenophorus modestus* occurs in the Flinders and Olary Ranges, whereas *C. decresii* occurs in the Mount Lofty Ranges, on the Fleurieu Peninsula, and on Kangaroo Island. The two species were long considered ‘lineages’ of *C. decresii sensu lato,* but were recently elevated to separate species on the basis of morphological and genetic differentiation (Dong *et al.* 2021). Lineage divergence may have resulted from local adaptation to separate refugia during glacial-interglacial Pleistocene cycles (Byrne 2008; McLean *et al.* 2014). The evolution of differences in reproductive characteristics between the two species presents an opportunity to investigate the potential influence of environment-mediated selection on reproductive and other life history traits.

Longer active seasons may allow for a higher laying frequency in *C. modestus*, and conversely, shorter active seasons constrain the breeding season of *C. decresii*. A shorter active season also restricts the time for embryonic development and selects for a higher investment in the first clutch. This difference in reproductive output aligns with predictions that cold environments at high latitudes favour the production of fewer and larger eggs to increase offspring survival (Fischer *et al.* 2003; Morrison and Hero 2003; Yampolsky and Scheiner 1996). However, patterns of reproductive traits in lizards are not always globally congruent (Meiri *et al.* 2020; Sun *et al.* 2013). Counter-gradient variation in patterns of reproductive biology may be driven by many additional abiotic and biotic factors beyond latitude and climate (e.g. resource availability, predation risk, microhabitat preferences; Angilletta 2009; Mesquita *et al.* 2016). Furthermore, lizards may compensate for environmental factors in ways such as adjusting seasonal timing of reproduction (Warner and Shine 2007) or developmental mechanisms such as embryonic development rates (Niewiarowski and Angilletta 2008; Oufiero and Angilletta Jr. 2006), physiological pathways (Sun *et al.* 2013), and switching between semelparity and iteroparity (Eckhardt *et al*. 2017). Australia's diversity of lizard species and geography presents an ideal model for testing hypotheses about how lizard reproductive traits evolve to cope with the constraints caused by different environments, because some species are distributed across a variety of environment types (Cogger, 2018; Wilson and Swan, 2021). The examples of geographic differences in reproductive output we present for *Ctenophorus* species are likely to also occur in other species with large distributions across varied environments, such as *Lialis burtoni*, *Varanus gouldi*, and *Tiliqua scincoides.*

4: Sexual selection on the neural control of reproduction

One of the few areas in neuroscience where lizards have made significant contributions is the neural control of reproductive behaviour (Lovern *et al.* 2004; Wade 2011). Across all vertebrates, two of the key brain regions controlling reproductive behaviour are the medial preoptic nucleus and the ventromedial hypothalamic nucleus, both located in an area called the diencephalon. The medial preoptic nucleus drives male sexual behaviour while the ventromedial hypothalamic nucleus drives female behaviour (Numan 2014), and the interaction between hormones and these two brain regions largely governs reproductive behaviour. Environmental influences, such as time of year and presence of conspecifics, affect reproductive behaviour in part by driving temporary changes to the size and the activity of these brain regions (Beck *et al.* 2008; Wade *et al.* 1993). In Australian agamid lizards, selection can drive more permanent changes in these brain regions over evolutionary time (Hoops *et al.* 2017).

Agamids are a particularly attractive lineage in which to study evolutionary changes in brain structure. They have the lowest known coefficient of brain allometry amongst lizards, and the highest known encephalisation quotient (Black 1983). Brain allometry is a measure of how closely changes in body size are paralleled by changes in brain size, while the encephalisation quotient estimates how “enlarged” a brain is relative to a standard brain for a given body size (Platel 1979). The net result is that agamids have unusually large brains (for lizards) and relatively little variation in brain volume based on body size, which provides an opportunity for research.

Sexual selection drives both an increase in the volume of the medial preoptic nucleus and a decrease in the volume of the ventromedial hypothalamic nucleus in male *Ctenophorus* spp. dragons (Hoops *et al.* 2017). Thus, sexual selection possibly increases motivation and drive to perform male reproductive behaviours. However, brain region volumes do not differ across female *Ctenophorus* species, suggesting that sexual selection does not drive changes in their female reproductive behaviour. This suggests a passive role for females in reproduction, and is consistent with behavioural studies in some species of *Ctenophorus* (Jansson *et al.* 2005; Lebas 2001; Olsson 2001). In other lizard species, however, females can play very active roles in reproduction, including female-specific evolutionary changes in behaviour and motivation. For example, the female Lake Eyre dragon (*Ctenophorus maculosus*) displays unique reproductive colouration and behaviour that signals to males whether she is receptive to a male’s advances (Olsson 1995). However, the brain structure of *C. maculosus* has not been compared to those of species with more passive reproductive behaviour. A behavioural innovation like that in female *C. maculosus* is presumably the product of neuroevolutionary innovation, and presents an opportunity to further understand how sexual selection can alter the brain.

Additional studies of brain anatomy across Australian lizards have great potential to develop our understanding of brain evolution. Approaches examining similar patterns of brain evolution with respect to sexual selection could reveal how generalizable the findings in the study of *Ctenophorus* species are to other lizards, and tease apart specific behaviours and ecological factors (such as territoriality, seasonality, or life history) that may influence how sexual selection shapes brain structure. There are additional topics, such as pair bonding (Section 1) and parental care, where Australian lizards have the potential to make seminal contributions to our understanding of the neural underpinnings of reproductive behaviour, and how these traits evolve. The strength of Australian lizards as models for study of brain anatomy and function is the breadth of diversity of reproductive strategies, how our intimate understanding of this diversity can be leveraged towards understanding the underlying neural control, and what that means for the evolution of diverse reproductive strategies across vertebrates. The findings presented here represent the first step forward; the potential in this area is almost limitless.

5: Genital variation

Postcopulatory sexual selection is likely the main evolutionary force driving diversification in genital morphology in most animals (Brennan and Prum 2015; Simmons 2014). Understanding intrasexual and intersexual variation in genital morphology is critical for understanding mating-system dynamics, sexual conflict, and cryptic female choice. This knowledge is especially important given the diversity of mating systems within Australian lizards, each representing different opportunities for conflict and postcopulatory choice.

Genital traits may also have an underappreciated role in understanding species diversification in lizards (Klaczko *et al.* 2015), as these traits are often involved in the development of reproductive isolation among putative species. Most of our understanding of genitalia in Australian lizards comes from work describing genital development in relation to sex determination (Whiteley *et al.* 2017b). In squamates, males have hemipenes, whereas females may or may not have analagous structures called hemiclitores (Böhme 1995; Martínez-Torres *et al.* 2015).

Research on hemipenal morphology is limited in Australian lizards. In a broadscale study across *Varanus*, including Australian species, hemipenal morphology is more phylogenetically informative than non-genital morphological characters; this pattern could also be indicative of faster evolving genitalia like that seen in *Anolis* species (Klaczko *et al.* 2015). Understanding such variation in Australian lizards may be important for understanding diversification dynamics in rapidly-radiating Australian lizard lineages. Anecdotally, Australian agamids have larger hemipenes (relative to SVL) compared to other ecologically-similar lizard families on other continents (i.e., phrynosomatids; D.L. Edwards pers. obs.). Greater hemipenal lengths are associated with greater copulation frequencies between species of *Anolis* lizards (Johnson *et al.* 2011). Differences in relative hemipenal size could therefore suggest fundamental differences in mating frequencies across lizard families. In *Liolaemus* species, hemipenal eversion is part of conspecific male-male aggressive displays (Ruiz-Monachesi *et al.* 2019). The potential for hemipenal morphology to play a similar role in Australian lizards remains to be investigated.

In contrast to males, very little is known about female genital evolution in squamates. Female genitals in squamates can be present as a rudimentary structure (Neaves *et al.* 2006), as hemiclitores (Böhme 1995; Martínez-Torres *et al.* 2015), or as miniaturized hemipenes

(Telemeco 2015). Even when present, they can also exhibit different coloration from conspecific male hemipenes (Valdecantos and Lobo 2015). The functional role of female genitalia in squamates, and its variability, is unknown. *Varanus* spp., which are especially diverse across Australia, exhibit morphological diversity in hemiclitores (Böhm *et al.* 2013; Böhme 1995; Böhme and Ziegler 2009; Ziegler *et al.* 2005; Ziegler *et al.* 2007), yet a comprehensive exploration of hemiclitoral morphology or even presence/absence in any Australian lizard genus, including *Varanus* (but see (King and Green 1999), is currently lacking. Hemiclitoral morphology may relate to cryptic and post-mating female control of reproduction. A prevailing paradigm is that precopulatory female choice is rare in lizards (Olsson 2001; Olsson and Madsen 1995; but see Sullivan and Kwiatkowski 2007). Variation in the presence/absence of cloacal glands, sensory innervation, epithelial wall thickness, and presence/absence of sperm crypts in lizards suggests that females have morphologically variable structures capable of providing them with the opportunity for postcopulatory choice (Sánchez-Martínez *et al.* 2007). Hemiclitori may have been retained for similar roles, such as expulsion of sperm. Studies should be undertaken using lizards with different mating systems and morphologies to determine the extent to which female lizards are able to control copulation duration and fertilisation in association with hemiclitoral and cloacal-vaginal morphology, which would determine mating biomechanics, sexual conflict over mating and the evolution of postcopulatory female choice (Brennan 2016; Firman *et al.* 2017; Friesen *et al.* 2016; Friesen *et al.* 2014).

Work stemming from understanding genital development in relation to sex determination mode have provided some understanding of how lability in hemiclitoral structure develops. The central hypothesis is that genital variation occurs through differences in developmental programming among species. *Pogona vitticeps* exhibits temporary pseudohermaphrodism (TPH), whereby both ovaries and hemipenes are present at hatching (Whiteley *et al.* 2017a;

Whiteley *et al.* 2018). Females exhibit more lability in phenotype than males, which is not associated with temperature-dependent sex determination (Whiteley *et al.* 2017a). Thermostability of sex differentiation may play a role in an extended period of TPH, because other species with temperature-dependent or thermal influenced sex determination also show extended periods of TPH (Whiteley *et al.* 2018). While TPH complicates sex assignment based on hemipene eversion at birth in *P. vitticeps* (Whiteley *et al.* 2018)*,* other Australian lizards (*Carinascincus* [formerly *Niveoscincus*] *ocellatus*) show clear genital differentiation at birth (Neaves *et al.* 2006). Resolving these differences among species is important for efforts to use genitalia to identify sex at birth. Given the diversity of sex determining mechanisms present within Australian lizards (Section 10), especially agamids, it is important to understand how genitalia develop in these different systems.

6: Multiple paternity, sperm competition, and postcopulatory sexual selection

Polyandrous mating systems are widespread throughout animal and plant taxa (Jennions and Petrie 2000; Pizzari and Wedell 2013; Taylor *et al.* 2014). Squamate reptiles are no exception (Friesen *et al.* 2020a; Uller and Olsson 2008), and are excellent models to test critical questions about female promiscuity. Except for sperm, male lizards and snakes do not directly provide females with resources during courtship, mating, or after offspring are hatched/born, although females of territorial species may receive benefits from residing on a resource-rich site (Uller *et al.* 2010). Thus, the evolution of polyandry in lizards and snakes is simplified compared to other vertebrates with parental care (mammals and birds), so the fundamental costs and benefits of polyandry can be isolated (Kvarnemo and Simmons 2013; Uller and Olsson 2008). One benefit of polyandry is to ensure that a female has enough sperm to fertilize her ova. Sperm limitation may drive multiple mating in common lizards (*Zootoca vivipara*) (Uller and Olsson 2005). Multiple mating is associated with higher fecundity in lizards (LaDage *et al.* 2008; Noble *et al.* 2013; Uller and Olsson 2005; York and Baird 2019), but more studies specifically designed to tease apart the effects of sperm limitation and benefits of polyandry are needed in lizards. Social skinks and agamids with colour traits that may function in pre-copulatory sexual selection are ideal model systems, and both occur in Australia (Section 3).

A consequence of polyandry is that the battle for reproductive success does not always end after intrasexual competition for mates (usually males) or intersexual selection of mates (usually by females)—which together evolve as a result of precopulatory sexual selection (Andersson 1994; Darwin 1871). Instead, sexual selection continues within the reproductive tracts of promiscuous females, where the sperm of different males compete to fertilise eggs (Parker 1970; Parker and Pizzari 2010), and where female traits bias the contest for fertilisation success of different males (Arnqvist 2014; Eberhard 1996; Thornhill 1983). Together, these phenomena evolve as a result of postcopulatory sexual selection. Sperm competition is the post-mating analogue of male-male competition for mates, which occurs when the ejaculates of more than one male overlap within the reproductive tract of a polyandrous female (Parker 1998). Sperm competition between multiple males usually results in multiple paternity when there is no complete bias towards a single competitor. Multiple paternity is pervasive in squamates studied thus far, with more than 50 % of clutches/litters exhibiting multiple paternity in the wild (Uller and Olsson 2008). Within lizards, rates of multiple paternity depend on how well males can monopolise access to females (Uller and Olsson 2008; Uller et al. 2010). Rates of multiple paternity are generally low (4 – 30 %) in Australian territorial agamids (Table 2), but higher in non-social skinks (43 – 94 %; Uller and Olsson 2008). The levels of polyandry in agamids (Table 2) contrast with ecologically-similar families of lizards where multiple paternity is much higher (40 – 80 %), for example, in the genera *Lacerta* in Europe (Fitze *et al.* 2005), and *Uta*, *Crotaphytus*, and *Sceloporus* in

North America (Abell 1997; Haenel *et al.* 2003; Peterson and Husak 2006; Zamudio and Sinervo 2000).

Female sperm storage, where females store sperm for weeks to years after mating, increases the chance that sperm from different males will compete (Parker 1970). Sperm competition for fertilisation produces strong selection on sperm and ejaculate traits (Lüpold *et al.* 2020), which may impose energetic costs and concomitant trade-offs with precopulatory traits (body size, aggressiveness, colouration) as we find in some Australian lizards (Section 3). Indeed, females of some Australian dragons store sperm across multiple clutches, creating the situation in which males may sire young posthumously (Olsson *et al.* 2009b). Female sperm storage could therefore shift male investment towards early-season mating success (Zamudio and Sinervo 2000). As a result, the evolution of female sperm storage, sperm longevity, and male lifespan are likely linked in some species. Females could select for sons that mature earlier, with longer-lived sperm, but die younger due to investments in early maturity. This pattern could be common in short-lived annual lizards common in Australia, like *Ctenophorus pictus* and *C. fordi* but has yet to be investigated.

Polyandry also has indirect genetic benefits in lizards and snakes (Wapstra and Olsson 2014), including positive fitness effects linked to offspring survival (Eizaguirre *et al.* 2007; Madsen *et al.* 1992), offspring dispersal (Laloi *et al.* 2009), improved heterozygosity for inbreeding avoidance, and "trading-up" to a better mate (Laloi *et al.* 2011; Olsson *et al.* 1996b; While *et al.* 2014). Post-copulatory processes and conditions within the female reproductive tract may allow females to select sperm from males less-related to themselves (Olsson *et al.* 1996a; Olsson *et al.* 2004; Olsson *et al.* 1997), or, in species with XX/XY chromosomal sex determination, allow females to select sperm to determine the sexes of their offspring in a sex-biased environment (Cox and Calsbeek 2010; Olsson *et al.* 2007b). Nevertheless, the effects of multiple mating on offspring phenotypes are not always positive in lizards (Keogh *et al.* 2013; Noble *et al.* 2013), but these effects could also be cryptic in studies that do not analyse genetic interactions between the individuals participating in staged matings. In future work involving the assignment of parentage using molecular techniques, we encourage researchers to include enough markers to allow examination of genetic effects on the probability of paternity (e.g. relatedness) as well as male traits (genitalia, sperm, ejaculates) that may be used as cues by females to select paternity. Nearly nothing is known about female morphology, physiology, or behaviours that generate biases due to relatedness of their partners. Any polyandrous Australian species of lizard with a moderate length of sperm storage that demonstrates regular individual male-female interactions would be an ideal model for teasing apart the mechanisms of cryptic female choice. Dissociated mating and female sperm storage are relatively common in Australian skinks, including the genera *Carinascincus*, *Hemiergis*, and *Pseudemoia*, so these taxa might be useful models (Murphy *et al.* 2006).

7: Nesting Ecology in Australian Goannas

Most reptiles lack parental care and desert their eggs after depositing them in an excavated ground nest, burrow, or under objects such as rocks, logs, bark, or vegetation. For example, only a very small proportion of lizards attend their eggs (Shine 1988; Somma 2003), fuelling a perception that reproducing reptiles rarely engage in social behaviour after mating (but see Section 1). Moreover, excavating and backfilling shallow ground nests is conserved across many lizard families (Doody *et al.* 2009), with eggs predictably deposited in shallow nests in areas that are warm enough for successful development. In contrast, 'deep-nesting' Australian monitor lizards ('goannas') highlight that the ecology and evolution of nest site choice behaviour in lizards is anything but stereotypical or conserved.

Where the yellow-spotted monitor, *Varanus panoptes*, and its sister species, Gould's monitor, *V. gouldii*, lay their eggs has only recently been identified. Aboriginal women suspected that eggs were laid in 'warrens', areas denuded of vegetation with multiple burrow entrances (Figure 2) (Christian 2004), which was confirmed by excavation beyond the terminus of open burrows. These warrens contain communal nests, solitary nests (with mothers returning to the same nest site year after year), nests with complex structures, and the deepest vertebrate nests in the world [up to 4 m deep; (Doody *et al.* 2015; Doody *et al.* 2014; Doody *et al.* 2018a; Doody *et al.* 2018b)]. Moreover, the burrows provide refuges, foraging sites, aestivation sites and nesting sites for many other animals, which is the first demonstrated case of ecosystem engineering in lizards (Doody *et al.* 2021b).

Each warren contains multiple nests for the present (communal nesting) and previous years' nesting (which may indicate traditional solitary nesting). For example, one portion of a *V. gouldii* warren contained 97 nests, including 21 nests with eggs (the rest were nests from previous years) (Doody *et al.* 2018a). Similarly, a *V. panoptes* warren contained 110 nests, including 11 with incubating eggs (Doody *et al.* 2018b). Extrapolation to the area of the entire *V. gouldii* warren predicted 53 nests with eggs, which implicates many mothers, despite the potential for multiple clutches per annum. When well-fed in captivity, *V. panoptes* mothers can produce multiple clutches (D. Kirschner, unpubl. data), but this is less likely in nature, especially in a food-limited desert ecosystem (Doody *et al.* 2018b). Communal and traditional solitary nesting in these species may be related to the ease in constructing deep nesting burrows in soil that has been loosened by conspecifics within and among years, or some other benefit to mothers, eggs or hatchlings (Doody *et al.* 2009).

Both *V. panoptes* and *V. gouldii* nests are the deepest for any vertebrate: mean nest depths are 2.3-2.5 m (range 1.0 – 3.6 m; N=162) for *V. panoptes* and 3.0 m (range 1.8 – 4.0 m; N=103) for *V. gouldii* (Doody *et al.* 2015; Doody *et al.* 2014; Doody *et al.* 2020; Doody *et al.* 2018a; Doody *et al.* 2018b). Most ground-nesting reptiles deposit their eggs at depths of 20 – 250 mm, and even the gigantic leatherback sea turtle nests at depths averaging < 1 m (Doody *et al.* 2014). These two goanna species probably nest deeply to maintain moist conditions during the long (~8 month) incubation period that spans the entire dry season, rather than depth being related to temperature (Doody *et al.* 2015). *Varanus panoptes* nests are deeper in a desert site than in a woodland site with higher rainfall (Doody *et al.* 2018b), and *V. panoptes* mothers nest deeper in drier years (Doody *et al.* 2021b). Decoupling of temperature from moisture in reptile nests (Doody *et al.* 2021b) demonstrates plasticity in depth due to a soil moisture gradient; in all other (shallower) reptile nests, shallower nesting means warmer but drier conditions, complicating the isolation of whether temperature or moisture is the cue for plasticity in nest depth.

Nesting is complex in both *V. panoptes* and *V. gouldii*, which construct elaborate helical burrows consisting of straight sections to a depth of about 1.5 m, followed by 2 – 7 tight spirals descending straight down and terminating in a slightly enlarged egg chamber. Fossil helical burrows date back to 255 Mya [*Diictodon*, a mammal-like therapsid; (Smith 1987)] and more recently from 22 – 34 Mya [*Palaeocastor*, a terrestrial beaver; (Martin and Bennett 1977)]. Extant animal species with helical burrows include pocket gophers, prairie dogs, and scorpions (reviewed in Doody *et al.* 2015). The adaptive advantages of helical burrows are untested for any species, but may include an anti-predator function, improved drainage or hatchling escape, providing a more stable microclimate, an anti-crowding mechanism, or mechanical advantage (reviewed in Doody *et al.* 2015). Interestingly, hatchling goannas appear not to use the spirals to emerge from the nest, but rather excavate a straight vertical tunnel, often through resistant soils (Doody *et al.* 2018a).

These varanids serve as ecosystem engineers for small animals, including 28 species of lizards (geckos, skinks, goannas), snakes, frogs, mammals, and numerous invertebrates. One warren contained 418 individual frogs (mostly *Uperoleia spp*.) that were aestivating there during the dry season (Doody *et al.* 2021a). The warrens also provided nesting habitat for another goanna species (*V. acanthurus*) and the gecko *Strophurus ciliaris* (Böhm *et al.* 2013; Doody *et al.* 2017; Doody *et al.* 2021b). These two goanna species thus join the burrowing tortoises of North America (*Gopherus*) and perhaps mound-nesting crocodilians as reptilian ecosystem engineers (Kinlaw and Grasmueck 2012; Somaweera *et al.* 2020).

Deep, complex communal nesting would not be expected to have evolved in desert or dry-adapted lizard species with shorter incubation periods, because the short incubation period would preclude the need for incubation over the entire dry season. The evolution of helical nesting remains enigmatic. Without knowing its value (adaptive or not), we cannot make predictions about its evolution, or lack thereof, in other lizard species. No other lizard species constructs such deep, helical burrows, but we predict that a third large, desert-inhabiting goanna with a long incubation period, the perentie (*V. giganteus*), may also nest at great depths due to its ecological similarity to its congeners. Deep helical nesting may also occur in populations of *V. griseus* near the Sahara Desert. As for why these goannas nest communally, the energy required to construct such deep complex burrows, and for the young to escape the burrows through resistant soils using their own tunnels, could select for mothers returning to communal nesting areas to take advantage of loosened soils. Returning to these sites would reduce the energetic costs of digging for both mothers and offspring, and thus allow both easier nesting, and easier escape from nests.

8: Viviparity and placentation

Australia is one of the best places in the world to study the evolution of viviparity and placentation, using reptiles as a model. Viviparity has evolved here repeatedly in both skinks and snakes (Blackburn 2015), and Australia has 20 % of the reliably classified species that are bimodally reproductive: *Lerista bougainvillii* (Greer 1989; Qualls and Shine 1998), and *Saiphos equalis* (Smith and Shine 1997). In these species, individuals in some locations lay eggs, whilst those in other locations give birth to live young, providing a unique opportunity for comparative research on the evolution, costs, and mechanisms underpinning parity mode within a single species. Complex placentation and obligate placentotrophy have also evolved at least twice in Australian skinks, in the genera *Carinascincus* and *Pseudemoia* (Stewart and Thompson 2004; Weekes 1935). These represent 40 % of the known origins of placentotrophy in lizards. A third skink species, *Eulamprus quoyii*, also exhibits a modified chorioallantoic placenta (Murphy *et al.* 2011), though it is not highly placentotrophic (Thompson 1977; Thompson 1981). Together, viviparity and placentation represent some of the best opportunities for studying how novel complex traits evolve in vertebrates, because they have evolved repeatedly so many times (Griffith and Wagner 2017) and provide the phylogenetic replication necessary for comparisons to be statistically robust. In Australia, most research on viviparity and placentation has focused on a relatively small group of skink species: *Sphenomorphus* group (*Eulamprus* spp., *Lerista bougainvillii*, *Saiphos equalis*), *Eugongylus* group (*Carinascincus* spp., *Pseudemoia* spp.), and Egerniinae (*Egernia* spp., *Liopholis* spp., *Tiliqua* spp.). The parity mode of additional species has been assigned based on observations of reproductive behaviour or dissection of gravid female museum specimens (Blackburn 2000). It is unlikely that viviparity will be discovered in any lizard previously thought to be oviparous, but unexpected discoveries always have the potential to develop new avenues of research. For example, observation of both oviparity and viviparity *within an* *individual* (the first in a vertebrate) in *S. equalis* raises the possibility that reproductive mode may be plastic in some species (Laird *et al.* 2019).

All viviparous lizards studied so far have at least a simple placenta that provides respiratory gas exchange and a site of embryonic anchoring to the uterus (Blackburn 2015). Some species have more complex nutritive placentas, in which substantial quantities of organic nutrients are transported from the mother to embryos during pregnancy (obligate placentotrophy). Detecting this feature is more difficult than identifying viviparity alone. Placentotrophic species are identified by examination of the morphology of the placental tissues and comparisons of the dry masses of freshly-ovulated eggs to those of newborn offspring (matrotrophy index; Thompson *et al.* 2000). Placentotrophic embryos increase in dry mass during development as mothers allocate nutrients to them, whereas non-placentotrophic embryos decrease in dry mass as they catabolise nutrients from their yolk (Stewart 1989; Swain and Jones 2000; Thompson *et al.* 2000). Placental transport of nutrients has also been demonstrated in Australian skinks using stable and radioisotopes (Itonaga *et al.* 2012b; Jones and Swain 2006; Swain and Jones 1997; Thompson 1977). Within Australian lizards, placental structure and function have been most well-studied in the *Eugongylus* group skinks *Carinascincus* spp. and *Pseudemoia* spp. Even within these genera, the placental structures in *P. baudinii*, *P. rawlinsoni*, *C. palfreymani,* and *C. orocryptus* remain unstudied, and the degree of placental nutrient transport in *P. baudinii*, *P. rawlinsoni*, *C. greeni, C. palfreymani,* and *C. orocryptus* remains unknown. Furthermore, the amount of nutrients allocated across the placenta can vary within a species (Itonaga *et al.* 2012a; Thompson and Speake 2006; Van Dyke *et al.* 2014), so single estimates of matrotrophy index may not be representative of all individuals. The phylogenies for both *Carinascincus* and *Pseudemoia* remain poorly-resolved (Brandley *et al.* 2015; Hutchinson and Donnellan 1992). Basic studies of placental structure and function in these taxa, and a robust phylogeny, are needed to determine how the placenta has evolved in these species.

Research on Australian lizards underlies much of our understanding of how viviparity and placentation evolve and function in reptiles, and this work provides a basis for comparison with other viviparous taxa. Early in lizard pregnancies, a plasma membrane transformation (PMT) homologous to that of mammals occurs, which likely allows for embryos to anchor to the uterus (Murphy *et al.* 2000). This phenomenon was first recognised in Australian skinks. In *Pseudemoia* spp., the PMT is facilitated partially by changes in the distributions of desmosomes, tight junctions, occludins and cadherins in the uterine epithelium (Biazik *et al.* 2007; Biazik *et al.* 2008; Biazik *et al.* 2010; Wu *et al.* 2011). Once pregnancy begins, chorioallantoic and yolk sac placentas develop in all viviparous lizards, which facilitate contact between maternal and embryonic tissues (Thompson and Speake 2006). The functions of the two placentas likely vary across species, but the chorioallantoic placenta always exhibits dense capillary beds that presumably facilitate placental exchange, especially for respiratory gases. In *Eulamprus tympanum*, angiogenesis in uterine and embryonic components of the chorioallantoic placenta increases the density and apposition of capillaries in both tissues (Parker *et al.* 2010a; Parker *et al.* 2010b). In *Saiphos equalis*, angiogenesis is driven in part by vascular endothelial growth factors (VEGFs; Murphy *et al.* 2010; Whittington *et al.* 2015). Carbonic anhydrases in both uterine and embryonic components of the chorioallantoic placenta likely facilitate transport of carbon dioxide in *Pseudemoia entrecasteauxii* (Van Dyke *et al.* 2015). Most viviparous lizards also transport small amounts of nutrients to their developing embryos (Thompson *et al.* 2000), especially inorganic ions like calcium (Linville *et al.* 2010), which may replace the role of the eggshell as an ion reserve in oviparous species (Herbert *et al.* 2006). In Australian lizards, evidence of obligate placentotrophy of organic nutrients is so far limited to skinks in the genera *Carinascincus* and

Pseudemoia; candidate nutrient transporters in these taxa include lipoprotein lipase, and amino acid-transporting solute carriers (SLCs; Griffith *et al.* 2016; Griffith *et al.* 2013). Gene expression analyses, particularly transcriptomic studies, have identified thousands of genes that are likely to be involved in pregnancy in Australian lizards (Foster *et al.* 2020; Griffith *et al.* 2016; Griffith *et al.* 2017; Hendrawan *et al.* 2017). These genes likely contribute to key pregnancy-related functions including uterine remodelling, nutrient and respiratory gas transport, and immune regulation, and testing the functions of these genes is the next step in understanding their role in the evolution of viviparity.

Australian lizards also present an excellent opportunity to study the selective pressures that drive the evolution of viviparity and placentae, although these questions have received much less attention than the genetic, physiological, and morphological mechanisms that underpin both traits. Adaptive hypotheses for viviparity and placentation focus on the potential fitness benefits mothers gain by being able to continuously control the environment that developing embryos experience, and also on embryos' ability to impact maternal physiology to their own benefit (Crespi and Semeniuk 2004; Shine 1995; Tinkle and Gibbons 1977). Research integrating ecophysiological and molecular approaches is needed to test how viviparity and placentotrophy impact fitness, and whether the fitness benefits of these traits overrides their concomitant fitness costs. For example, viviparity may allow mothers to improve the fitness of their individual offspring, but it also reduces the number of reproductive events a single female can have per year, and increases the physical burden on the mother (Tinkle and Gibbons 1977). Australian skinks are ideal models to test these adaptive hypotheses given their diversity of reproductive modes, especially in taxa that overlap in distribution and ecology, as do the genera *Pseudemoia*, *Carinascincus*, *Bassiana*, and *Lampropholis.* The two reproductively bimodal species, *Lerista bougainvillii* and *Saiphos equalis*, also present an excellent opportunity to test how the fitness costs and benefits of reproductive mode vary with environment within single species. Simultaneously, they provide the opportunity to determine whether gene flow between viviparous and oviparous populations constrains the evolution of reproductive mode.

9: Sex Reversal

Sex determination and differentiation are two developmental processes that govern the dichotomous phenotype, male or female. This variation is constrained to produce either male or female phenotypes. A sex-determining factor initiates the sexual differentiation cascade, and results in individuals that possess either ovaries (female) or testes (male), as well as sex-specific behaviours, morphologies, and physiologies. Lizard sex determining factors could fall into diverse categories and we still have not identified a single sex determining gene for lizards. In many lizard species, sex chromosomes determine female or male development, and these genetic sex determination (GSD) systems can be either female heterogametic (ZZ/ZW) or male heterogametic (XX/XY) (Bull 1980). Temperature-dependent sex determination (TSD) is also common among lizards (Harlow 2004), whereby sex is determined by the temperature at which the embryo develops during a sensitive period of incubation. Although some lizard lineages possess stable and conserved sex chromosomes, others exhibit rapid sex chromosome evolution, including transitions between male and female heterogamety and turnover in the chromosome pair recruited to determine sex (Pennell *et al.* 2018; Sarre *et al.* 2011). Sex chromosomes are predicted to play a central role in lizard evolution, adaptation, and speciation; even though the same reproductive phenotypes are achieved (male or female), episodic turnover in sex chromosomes and sex determining systems has broad evolutionary consequences (Ezaz *et al.* 2009; Sarre *et al.* 2011). Many transitions have occurred between TSD and GSD across the lizard phylogeny (Janzen and Krenz 2004) (see also Section 10).

Sex determining systems exist as a continuum of genetic and environmental influence, with many species likely to occupy an intermediate position on the continuum from TSD to GSD (Sarre *et al.* 2004). Incubation temperatures are suspected of being capable of overriding genotypic sex-determining signals in ZZ/ZW and XX/XY systems in some species (Holleley *et al.* 2015; Holleley *et al.* 2016; Quinn *et al.* 2007; Shine *et al.* 2002a) in both oviparous and viviparous lizards (Cornejo-Páramo *et al.* 2020a; Dissanayake *et al.* 2021; Holleley *et al.* 2015; Holleley *et al.* 2016; Shine *et al.* 2002a; Wiggins *et al.* 2020). Discordance between genotypic and phenotypic sex is known as sex reversal (Weber and Capel 2018). Naturally occurring temperature-sex reversal has only been definitively identified in two vertebrates, both Australian lizards, which possess contrasting systems of GSD that simultaneously display temperature-dependent influences on sex. *Pogona vitticeps* is an agamid dragon lizard with a female heterogametic (ZZ/ZW) GSD system, but high incubation temperatures (> 32°C) result in reversal of the ZZ male genotype to a female phenotype (Holleley *et al.* 2015; Quinn *et al.* 2007). In contrast, *Bassiana duperreyi* has a male heterogametic (XX/XY) GSD system in which low incubation temperatures (< 20°C) result in reversal of the XX genotype to a male phenotype (Dissanayake *et al.* 2021; Radder *et al.* 2008; Shine *et al.* 2002a).

The occurrence of sex reversal in wild populations of *P. vitticeps* and *B. duperreyi* provide unique opportunities to study the distribution and dynamics of sex reversal under different selective pressures in Australia (Figure 3). Theoretical studies show that as the frequency of sex reversal increases in a population, and provided the reversed individuals are fertile, a likely response is the reduction and possible elimination of the W or Y chromosome under Fisher's frequency-dependent selection (Düsing ; Fisher 1930) and a transition to a pure TSD system (Bókony *et al.* 2017; Bull 1981; Dissanayake *et al.* 2021; Geffroy and Wedekind 2020; Grossen *et al.* 2011; Holleley *et al.* 2015; Schwanz *et al.* 2020). Alternatively, selection for the rarer sex may drive the evolution of higher temperature thresholds for sex reversal and the maintenance of GSD in this species (Schwanz *et al.* 2020). Across the natural range of *P. vitticeps*, sex reversal is spatially constrained, displaying no association with latitude or other environmental variables, which is contrary to expectation based on laboratory observations (Castelli *et al.* 2021). In *B. duperreyi,* rates of sex reversal increase with elevation (from zero to 18.46 % of XX individuals manifesting as phenotypic males; Dissanayake *et al*. 2021). This observation suggests that *B. duperreyi* has not been subject to selective pressures for rapid evolution in the threshold for sex reversal, and thus populations at high elevations may be susceptible to loss of the Y chromosome (Dissanayake *et al.* 2021). Evolution of the thermal threshold for sex reversal is possible in both species, and there exists some evolutionary capacity to buffer or moderate the effects of extreme climates (Castelli *et al.* 2021; Dissanayake *et al.* 2021).

Few species have been examined for instances of sex reversal in Australia or elsewhere [but see (Whiteley *et al.* 2021a; Wiggins *et al.* 2020)]. The widespread occurrence of homomorphic sex chromosomes in lizards means that instances of sex reversal are challenging to detect. New bioinformatics tools and methods make it possible to identify and characterize sex chromosomes, leading to unanswered questions in sex determination mechanisms in lizards (Cornejo-Páramo *et al.* 2020a; Dissanayake *et al.* 2020; Hill *et al.* 2018; Palmer *et al.* 2019). Sex reversal, although not currently confirmed, may occur in several other Australian lizards; the southern water skink *Eulamprus heatwolei* (Cornejo-Páramo *et al.* 2020a), spotted snow skink, *Carinascincus ocellatus* (Cornejo-Páramo *et al.* 2020a) (see Section 10)*,* Jacky dragon *Amphibolurus muricatus* (Whiteley *et al.* 2021b), and several overseas species, including the common collared lizard (*Crotaphytus collaris*)

(Wiggins *et al.* 2020), the multi-ocellated racerunner (*Eremias multiocellata*) (Wang *et al.* 2015), and the Japanese gecko (*Gekko japonicus*) (Tokunaga 1985).

So far, the molecular mechanisms of sex reversal in lizards are not fully understood (Castelli *et al.* 2021; Georges and Holleley 2018; Whiteley *et al.* 2021c). The tantalizing possibility that many traditionally regarded TSD species also have a cryptic underlying chromosomal component to sex determination is an important area of future research. Evolutionary modelling has shown that the Y or W chromosome can persist at low frequency despite high rates of sex reversal (Quinn *et al.* 2007; Schwanz *et al.* 2020). Beyond cryptic Y or W sex chromosomes, even more complex scenarios may exist that interact with thermal sex-determining cues, such as polygenic sex determination or *de novo* sex chromosomes (Mork *et al.* 2014). This is likely to be a very fruitful area of research using new genomic techniques. Finally, there are several evolutionary questions of interest concerning the transitions between GSD and TSD. For example, once the transition to TSD occurs, is there sufficient time for optimization of the thresholds for sex determination (pivotal temperature) to avoid catastrophic sex ratio skew and demographic extinction under climate change? There will no doubt be many more surprises. The recent media report of sex reversal in an adult Boyd's forest dragon (*Lophosaurus boydii*) in response to loss of the sole male in its captive population (Mannix 2020) is one such example. If confirmed, this will provide exciting new avenues of research and the interaction of cytogenetic and genetic aspects of developmental programming in lizards.

10: Evolution of sex determination systems

Sex determination is so fundamental to reproduction that it is expected to be under strong purifying selection with highly conserved processes (Uller *et al.* 2007). Indeed, conserved GSD systems exist in therian mammals (male heterogamety; XX/XY) and birds (female heterogamety; ZZ/ZW)(Bachtrog *et al.* 2014; Vicoso *et al.* 2013). In contrast, reptilian sex determination mechanisms vary in a phylogenetically complex manner, which suggests multiple evolutionary transitions (Janzen and Phillips 2006; Pokorna and Kratochvil 2009). In lizards, there is GSD (both XX/XY and ZZ/ZW are both common), TSD, and interactions between genes and temperature (GSD+EE or thermosensitive GSD) (Sarre *et al.* 2004). Sex chromosomes range from highly differentiated to morphologically indistinct pairs in lizards with GSD. Sex determination in lizards may be dosage dependent, where the homogametic sex (ZZ or XX) possesses two copies of a sex determining gene and acquires a threshold for sexual phenotype, whilst the heterogametic sex (XY or ZW) possesses one copy and does not reach the threshold (Quinn *et al.* 2007). In addition, patterns of TSD are diverse: high temperatures can produce excess males (‘FM’ pattern), excess females (‘MF’ pattern) or an excess of females at both high and low temperatures with males produced at intermediate temperatures (‘FMF’ pattern; Figure 4). Finally, reaction norms to temperature can be steep, where the switch between male and female producing temperatures can occur over a small pivotal range (Figure 4a-c), or shallow (Figure 4d), where sex ratios vary gradually over a broad range of temperatures.

Work on Australian lizards has led to the important re-defining of sex determination as existing as a continuum of states between pure GSD and pure TSD, rather than a dichotomous trait (Sarre *et al.* 2004). However, questions remain about how and why transitions between systems of sex determination occur. The drivers and mechanisms acting at the time of transitions are difficult to determine due to the divergence between lizard groups with different sex determining systems. Australian lizards are central to understanding the evolutionary drivers of transitions, the mechanisms that underpin transitions and their consequences to species and populations. The adaptive benefit of GSD versus TSD has been the subject of extensive research in Australia (Pen *et al.* 2010; Shine 1999; Shine *et al.* 1995;

Wapstra and Warner 2010; Warner and Shine 2005; Warner and Shine 2008). TSD should be favoured when there are sex-specific advantages resulting from development at temperatures that produce an excess of the sex that benefits (Charnov and Bull 1977; but see Uller and Olsson 2006). GSD typically produces 50:50 sex ratios and is therefore favoured when seasonal temperature fluctuations are high and might otherwise produce sex ratio biases that are maladaptive for some individuals (Bulmer and Bull 1982; but see Cornejo-Páramo *et al.* 2020b; Dooren and Leimar 2003). Species with TSD may be particularly vulnerable to climate change because of the effect that highly-skewed sex ratios can have on population persistence if one sex becomes rare to the point of limiting mating frequency (Boyle *et al.* 2014; Le Galliard *et al.* 2005; Valenzuela *et al.* 2019; Wedekind 2017). While selection can favour biased sex ratios when sex-specific fitness benefits occur with incubation temperature (Charnov and Bull 1977), populations with sex ratios that are consistently biased towards one sex can experience deterioration of genetic diversity and therefore have reduced adaptive potential, with consequences for species distributions (Le Galliard *et al.* 2005; Mitchell and Janzen 2010; Mitchell *et al.* 2008). However, such population-wide skews are rare and often transient, because frequency-dependent selection favours females (or parents) producing the under-represented sex (Fisher 1958), which concomitantly can select for mechanisms to balance skews (Uller *et al.* 2007).

In reptiles, TSD was first discovered in *Agama agama* more than 50 years ago (Charnier 1966; Steele *et al.* 2018), followed by observations in turtles (Pieau 1972; Yntema 1976), the leopard gecko (Viets *et al.* 1993), and the tuatara (Cree *et al.* 1995), all of which are oviparous. Because viviparous females can behaviourally buffer the effects of temperature on offspring development, TSD was considered incompatible with viviparity (Bull 1980), but temperature effects on offspring sex have since been demonstrated in two viviparous Australian lizards (Robert and Thompson 2001; Wapstra *et al.* 2004). These viviparous species differ from typical TSD species because they have distinctly shallow reaction norms best characterised by Figure 4d. Australia has considerable lizard diversity, scientific expertise, and exceptional species amenable to advancing our understanding of evolutionary transitions in sex determination. One such species (*C. ocellatus*) is undergoing an incipient transition in sex determination, offering a rare opportunity to unravel the causes and consequences of such transitions.

An Australian model system for transitions in sex determination: Carinascincus ocellatus

The viviparous spotted snow skink, *C. ocellatus* (Figure 5a) is a rare example of a viviparous species undergoing incipient divergence in sex determination (Cunningham *et al.* 2017; Pen *et al.* 2010; Wapstra *et al.* 2004). This small Tasmanian-endemic skink has a broad geographic and climatic distribution across Tasmania, with concomitant variation in life history (Wapstra and Swain 2001; Wapstra *et al.* 1999; Wapstra *et al.* 2001). In a warm, low elevation population, maternal basking opportunity (and therefore developmental temperature) influences the sex of her offspring; warm environmental conditions lead to an excess of female offspring in the population and cool conditions lead to an excess of males. In a high elevation population, sex ratios remain at parity regardless of environmental conditions and maternal basking opportunity (Cunningham *et al.* 2017; Pen *et al.* 2010) (Figure 5b,c). The sex ratio response to temperature, initially observed in the laboratory in females from the low elevation population through altered basking opportunity (Wapstra *et al.* 2004), has since been demonstrated in the wild (Wapstra *et al.* 2009). There are potentially important consequences for this population-specific effect of environmental temperatures on offspring sex ratios (5c) and for our understanding of the impact of climate change on species with TSD (especially where they follow a relatively rare shallow reaction norm) (Cunningham *et al.* 2020). Because warm temperatures produce a female-biased sex ratio in *C. ocellatus*, climate warming may result in population growth rather than decline as temperatures warm, as long as males do not become limiting (Cunningham *et al.* 2017; Rankin and Kokko 2007; Wapstra *et al.* 2009).

In *C. ocellatus*, divergence in sex determination could be driven by a combination of population-specific selection on how mothers allocate the sexes of their offspring (resulting in thermosensitive sex determination at low elevation) along with selection against strongly biased sex ratios in variable, unpredictable environments [resulting in GSD at high elevation (Pen *et al.* 2010), Figure 5d]. Specifically, in warm lowland populations, individual females that produce daughters under warmer conditions potentially have higher fitness because female offspring born early reach sexual maturity earlier and have a higher lifetime reproductive output than those born late. This situation selects for a link between gestational temperature, birth date, and offspring sex. Conversely in the cold highlands, selection does not occur because cooler conditions lead to slower growth with later sexual maturity, which creates a dissociation between temperature-dependent development, birth date, size at maturity, and sex-specific fitness benefits to mothers from sons or daughters. The high annual fluctuation in temperature in the cold highlands further selects against temperature effects in this model, because of the resultant frequency-dependent selection against the large skews in sex ratios (Figure 5d).

The theoretical model (Figure 5) established a potential adaptive explanation for the intra-specific variation in sex determination in *C. ocellatus*, but its mechanistic predictions (emergence/loss of genes of major effect at high/low elevation) require testing. Sex chromosomes and sex-linked DNA in *C. ocellatus* differ only slightly between the populations (Hill *et al.* 2021a; Hill *et al.* 2018) and these populations diverged during the Pleistocene with negligible gene flow since divergence (Hill *et al.* 2021b). Specifically, and in contrast to some of the model predictions, both populations have XY heterogamety with morphologically undifferentiated X and Y sex chromosomes (Hill *et al.* 2021a) (Figure 5e), and both populations largely share sex-linked genetic sequences (Hill *et al.* 2018). In addition, each population also possesses unique sex-linked genetic sequences. The *C. ocellatus* system highlights that only minor changes to the sex-linked genome are required for transitions in sex determination to occur: the high elevation population has more repeat and heterochromatin accumulation on the Y chromosome than the low elevation population (Hill *et al.* 2021a) and recombination among the sex-linked loci shared among populations is more suppressed in the high elevation population (Hill *et al.* 2018). This molecular work demonstrates that rather than loss/gain of genes of major effect as predicted, population-specific sex ratio responses to temperature are underpinned by sex-linked genes important for sex determination in both populations. However, the theoretical model (Figure 5) is useful because it establishes testable hypotheses for how sex determination evolves in viviparous lizards, and could easily be applied to other Australian viviparous species that exhibit temperature effects on offspring sex, like *Eulamprus tympanum* (Robert and Thompson 2001). Indeed, the model predictions are consistent for taxa starting with either XY or ZW chromosomal sex determination. The diversity of viviparous lizards in Australia may provide several useful models for further research if temperature is found to affect offspring sex in additional species.

11: Control over timing of birth

Most viviparous animals give birth to their offspring synchronously (within minutes or hours), although some lizard species complete the act of birth over several days. This phenomenon has been termed ‘birthing asynchrony’ and is defined as a spread in births separated by a minimum of 12 hours [i.e., not within the same day; (While *et al.* 2007a)].

Birthing asynchrony is analogous to hatching asynchrony in birds, whereby the eggs of a clutch are laid and hatch over several days (Amundsen and Slagsvold 1996; Magrath 1990; Stenning 1996; Stoleson and Beissinger 1995). However, unlike hatching asynchrony, birthing asynchrony appears not to result from developmental asynchrony - birds are constrained to produce one embryo at a time and thus, to lay one egg at a time. In contrast, lizards that exhibit birthing asynchrony retain fully-developed offspring and give birth to them one at a time (While *et al.* 2007b), even when multiple offspring are present within the same uterus. This reproductive strategy occurs in multiple species within the Egerniinae, as well as four species within the African lizard family Cordylidae (Table 3).

The presence of birthing asynchrony raises several interesting questions relating to the proximate and ultimate mechanisms that facilitate this behaviour. Most work to date has focussed on the latter. Analogous hatching patterns in birds may be a mechanism that allows parents to mediate intra-brood conflict during times of limited resource availability (Lack 1947; Stienen and Brenninkmeijer 2006). In Egerniinae, birthing asynchrony may provide a similar advantage by influencing the competitive environment of the brood and thus mediating offspring growth, survival or dispersal (While and Wapstra 2009). Like hatching asynchrony in birds, birthing asynchrony results in a size hierarchy in a litter. While this size hierarchy does not impact the competitive ability of each offspring, it does alter the level of competition present within a single litter (While *et al.* 2009a; While and Wapstra 2009). Social Egerniinae often live in saturated habitats that include intense competition for resources, high levels of conspecific aggression and high juvenile mortality (Chapple 2003). Birthing asynchrony may operate as a trade-off between offspring mortality/dispersal and offspring mass/growth as a result of size hierarchy (While and Wapstra 2009). Indeed, when offspring are kept together in captivity, smaller individuals, which are frequently attacked by conspecifics, grow at a slower rate and behavioural development differs between dominant and submissive individuals (Riley *et al.* 2017). In the wild, such behaviour may facilitate the dispersal of the subdominant individual, allowing parents to modify the number of offspring they tolerate in their home range during periods of resource limitation. Interestingly, the only other family of lizards in which birthing asynchrony has been documented, the African Cordylidae, also include group-living species (Mouton 2011). The co-occurrence of these traits across potentially two independent transitions to simple family life makes the links between the evolution of complex sociality and that of birthing asynchrony hard to ignore. However, the functional consequences of birthing asynchrony and the size hierarchies it produces remain to be investigated.

While considerable work has attempted to understand the function of birthing asynchrony, we know almost nothing about how it is achieved mechanistically in either lizard clade. The answer is likely to lie in the co-option of the mechanisms that underpin the birthing process itself. These mechanisms span hormonal, neuronal, and embryonic effects, all of which interact to initiate and maintain the process of parturition. Lizards with asynchronous birth may have co-opted these mechanisms to finely control when birth is initiated for each individual offspring while simultaneously preventing the birth of the remainder of the litter. For example, hormones actively influence the parturition process within the mother (Chaim and Mazor 1998) by way of their presence in the bloodstream and through changes in receptor expression in uterine tissue (Blanks and Thornton 2003). Additionally, dynamic changes in uterine innervation and neuronal receptor expression could facilitate the isolation of a single embryo within the uteri of a female. This type of regionally-specific neuronal fluctuation is readily evident in the mammalian cervix at term pregnancy (Boyd *et al.* 2009; Chávez-Genaro *et al.* 2006) and exemplifies the capacity for the uterine environment to change rapidly and with precision. These mechanisms are further impacted by the presence of the developing embryos, and maternal-foetal hormone signalling provides an avenue for each embryo to influence the timing of its own birth (Challis *et al.* 2000; Liggins 2000). While all the above mechanisms present intriguing targets for co-option during the evolutionary refinement of live birth, none yet have come under empirical scrutiny.

The integration of physiological, histological, and molecular techniques provides an opportunity to tease apart these competing mechanisms and generate a holistic understanding of the parturition process, and, more explicitly, how timing of birth is controlled by mothers and/or offspring. Specifically, the use of contraction bioassays to measure uterine contractile responses to key hormones (Paul *et al.* 2020), in combination with measuring changes in neuronal density across regions of the uterus to gauge the capacity for uterine relaxation, have the potential to demonstrate how this behaviour is achieved. Furthermore, combining contractile assays with transcriptomic data will allow identification of the regions of the genome that are associated with the contractile and relaxation responses. Such information should be compared across clades to examine whether similar mechanisms have been co-opted in independent lineages in a convergent pattern. Combined, this will enhance our understanding of how systemic reproductive innovations emerge, and will provide fundamental knowledge of how the process of live birth itself evolved. These results would have implications for a broad range of disciplines including evolutionary biology, conservation biology, and even human health.

Conclusions

We have identified a number of areas where research on Australian lizards has provided key advances in our understanding of animal reproduction, and areas where their potential as models for research has been under-utilised. Australian lizards are particularly important models for studying the origins and mechanisms underlying sociality and mating systems. They exhibit a continuum of social behaviours, from largely solitary to highly social, which provides a framework for understanding how sociality first evolves. Lizards communicate using chemical and/or visual signals, and these signals correlate with their mating behaviours. Thus, how their signals and mating behaviours coevolve is a potentially rich field for future research, especially given the diversity Australian lizards exhibit between communal sociality and solitary life. Furthermore, their mating behaviours feed into a complex arena of sexual conflict, where males and females both exhibit potential adaptations to increase their own fitness at the expense of their mates'. The fitness consequences of mating systems, as well as post-mating mechanisms like cryptic female choice and sperm competition, thus provide a basis for understanding how mechanisms of communication might provide a starting point for more complex social behaviours to evolve.

Australian lizards are also important models for post-fertilisation components of reproduction, especially the evolution of nesting decisions, viviparity, placentation, sex determination mechanisms, and asynchronous birth. Each of these traits has important consequences for how animal species survive in the face of environmental change. Our review shows how nesting decisions, TSD, and viviparity allow females to manipulate and potentially optimize their offspring fitness in response to environmental conditions like temperature, moisture, and population sex ratio. Placentation may provide a mechanism for females to maintain fetal survival in response to changes in food abundance during reproductive events. Birthing asynchrony allows the timing of parturition to be modified, possibly in response to social or environmental cues, so that all offspring are not born into the same environment.

Although we have covered many key topics, many questions and areas of investigation where Australian lizards would provide excellent models for study remain. We have highlighted a list of outstanding key questions that were illuminated by our review in Table 4. It is not an exhaustive list, but we highlight questions that emerged after considering the review of all our topics. For example, communication, sociality, and environment-dependent variation (or fitness) are key topics that appear repeatedly in our review, and have major consequences for several areas of investigation. Our review demonstrates the utility of Australian lizards for addressing these questions.

In addition to the questions that emerged from our review, we also catalogued several topics that our review did not cover (Table 5). These topics were neglected by necessity rather than by choice, because no authors responded to our initial invitation to the Australian Society of Herpetologists listserv to cover these topics. There are certainly active research projects focusing on these topics that we did not review sufficiently here as a result. However, the lack of response for these topics may indicate that these fields are areas for which lizards are relatively under-utilised. We have suggested possible outstanding questions for which lizards would be ideal models to address.

Our reviews clearly highlights that the Australian dragons (Agamidae) and skinks (Scincidae) have contributed to understanding broad biological questions, in part because of their large number of species, and their special features such as sexual colour dimorphisms and reproductive modes. By contrast, we have highlighted only one study on goannas (Varanidae), and none on any of the gekkotans (Carphodactylidae, Diplodactylidae, Gekkonidae, Pygopodidae). Despite this fact, it seems unlikely that the latter families do not offer potential opportunities for significant research on broad reproductive questions. For example, the gekkonids are unusual for laying calcareous-shelled eggs, which provides a good comparison with the flexible-shelled eggs of species in the other gekkotan families, with implications for embryonic physiology and development (Andrews et al, 2013). Apart from the research on deep-nesting varanid lizards (Section 7), little is known about nests and nesting (nest sites, nest structure and environmental features, especially temperatures and water potentials) in most Australian lizards. Nest sites, nest structure, and environmental features, especially temperatures and water potentials, remain unknown for most species. Given the range of potential nest environments in Australia, from extreme aridity to moist temperate regions, investigations of nest and nesting behaviours, and their impact on embryonic physiology, are likely to be informative for development of the understanding of the evolution of reproductive strategies (viviparity, sex determination, incubation periods, rates of development and so on), and for predicting future effects of climate change. Gekkotans will be equally as important in these investigations as are dragons and skinks.

In summary, Australian lizards are speciose and diverse, providing opportunities for exciting research in reproductive biology. We have highlighted key areas of research that are ongoing, emerging, and relatively neglected. We hope that new generations of reproductive biologists and ecologists will be inspired by our review to consider these topics for their own research careers. To encourage students who are excited by the topics in our review, we have provided a list of the authors responsible for each section in our supplementary materials (Supplementary Table 1). We urge readers to contact the relevant authors for research opportunities in the topics that they find interesting. Australian lizards offer excellent opportunities to test important hypotheses in vertebrate reproductive biology. Their abundance and the diversity of environments they inhabit provide an important resource for ongoing ecological and evolutionary research.

Acknowledgements. We thank Professor Paul Cooper for the invitation to prepare this review *in lieu* of a plenary presentation by MBT at the 2020 meeting of the Australian and New Zealand Society of Comparative Physiology and Biochemistry, which was cancelled because of the COVID-19 pandemic. We acknowledge the use of the Atlas of Living Australia, grid.506668.b.

Conflicts of Interest

The authors declare no conflicts of interest.

Declaration of Funding

This research did not receive any specific funding.

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Figure Titles

Figure 1. Species richness map for Australian lizards. Colour coding represents the number of species in a 50 km x 50 km pixel, with cooler colours indicating fewer species (down to 4) and warmer colours indicating more species (up to 88; Reproduced from Cogger 2018 with permission from CSIRO Publishing).

Figure 2. Gould's monitor lizard (*V. gouldii*) communal nesting warren before excavation. Note the multiple entrances (photograph by Stephen Zozaya).

Figure 3. Sex reversal in the Australian lizard species *Bassiana duperreyi* and *Pogona vitticeps*. (A) Distribution of sex reversal across the ranges of *P. vitticeps* (Castelli et al. 2021) and *B. duperreyi* (Dissanayake et al. 2021). The species range is indicated by the shaded areas. (B) Graphical representation of sex reversal characteristics (not to scale); top – *P. vitticeps*: sex reversal occurs when an individual with a male genotype (ZZ) is incubated at temperatures above 32 °C, causing it to develop as a phenotypic female (ZZf) (Holleley et al. 2015); bottom – *B. duperreyi*: an individual with a female phenotype (XX) incubated at low temperatures will reverse its sex and develop as a phenotypic male (XXm) (Shine et al. 2002; Radder et al. 2008). (C) Sex reversal frequency of *B. duperreyi* along an elevational gradient (Dissanayake et al. 2021). Underlying map generated using ArcGIS 10.5.1 (http://www.esri.com) and data from the Digital Elevation Model (Geoscience Australia) made available under Creative Commons Attribution 3.0 Australia (https://creativecommons.org/licenses/by/3.0/au/legalcode, last accessed 21-Dec-20). The species range is indicated by the shaded areas (Data from the Atlas of Living Australia website at http://www.ala.org.au. Accessed 3 January 2021). (https://creativecommons.org/licenses/by/3.0/au/legalcode, last accessed 21-Dec-20).

Figure 4. Patterns of temperature dependent sex determination (TSD). FM pattern (a,d) where males are produced at high temperatures; MF pattern (b) where females are produced at high temperatures; or FMF pattern (c) where males are produced at an intermediate temperature and females are produced either side of this temperature. Reaction norms can be steep (a-c) or shallow (d).

Figure 5. *Carinascincus ocellatus* (a) high (1200 metres above sea level (masl), GSD, blue) and low (50 masl, GSD+EE, red) elevation populations (b) with population specific sex-ratio responses to incubation temperature (c). A life history model parameterised with long-term field data predicts loss of sex determining genes at low elevation and emergence of sex determining genes at high elevation (adapted from Pen et al. 2010) (d). Sex chromosomes (e), labelled here with *C. ocellatus*-specific Y-linked probe (Hill, et al. 2021a), are undifferentiated in both populations.