# Stable Social Grouping in Lizards

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# INTRODUCTION

Social behavior is extremely diverse. It ranges from simple and brief interactions between two individuals for the purposes of mating to complex interactions between individuals that occur within large cooperative societies (Szekely et al. 2010; Rubenstein and Abbot 2017). Because of the near ubiquity of social behavior across sexually reproducing animal species, and the fact that our own species is one of the most social of all organisms, there has been a fundamental interest in understanding its ecological and evolutionary causes and consequences.

In a very broad sense, social behavior can be compartmentalized into a number of key components. Social structure describes patterns of social interactions and relationships between individuals, while the mating system describes the resulting reproductive consequences of such interactions. Social organization, on the other hand, describes the structure of associations between individuals within a population (e.g., groups), the size of these associations, and their spatial and temporal cohesion. Such social organization can result in the emergence of stable social groups which form the basis from which more elaborate forms of social behavior (including cooperation) can evolve. Stable social groups can emerge either as a result of non-related individuals aggregating together (egalitarian social groups) or as a result of individuals delaying dispersal and remaining within their natal home range, creating strong kin structure (fraternal social groups) (*sensu* Strassmann and Queller 2010). As we discuss below, whereas lizards have contributed substantially to our understanding of social structure and mating systems (e.g., Stamps 1983; Fox et al. 2003; Uller and Olsson 2008; Whiting and While 2017), it is only in the past few decades that biologists have begun to appreciate their potential to also contribute to our understanding of the evolution of stable social groups (Bull 2000; Gardner et al. 2016; Whiting and While 2017).

In this chapter, we provide an overview of research on stable social grouping in lizards, focusing on recent contributions and future directions. In doing so, our aim is not to provide a comprehensive review of all aspects of lizard social behavior itself, as this is clearly beyond the scope of a single chapter. For readers interested in lizard social behavior per se, we point them toward the other chapters in this book that explicitly focus on this topic (e.g., Chapters 9, 10, and 12–14). Instead, we provide a detailed overview of patterns of stable social grouping in lizards and outline the factors which may have led to their emergence, maintenance, and diversification within this structural grade of squamates. We then discuss the role that lizards may play in our continued quest to understand when, where, and why animals live together.

# SOCIAL BEHAVIOR IN LIZARDS

Social behavior per se has been relatively well studied in lizards, beginning with Noble and Bradley's (1933) monograph of lizard mating behavior and sexual selection. Since then much of the research focus has been on lizard social structure and the resultant mating systems (Brattstrom 1974; Fox et al. 2003). Indeed, lizards have served as excellent model systems for this task as they are frequently diurnal, are easy to catch and follow, and exhibit strong site fidelity (Fox et al. 2003). As a result, lizards have contributed substantially to our understanding of territorial behavior (Stamps 1983; Wikelski et al. 1996), contest competition (Stamps 1977; Fox and Baird 1992; Whiting 1999; Whiting et al. 2003, 2006; Carazo et al. 2008), alternate reproductive tactics (Wikelski et al. 1996; Sinervo and Lively 1996; Whiting et al. 2009; Noble et al. 2013), and communication (e.g., static and dynamic visual signals, chemical signals/cues, vocal signals; Martins 1993; Ord et al. 2002; Ord and Martins 2006; Hibbitts et al. 2007).

Lizards have also been the focus of a wide range of sexual selection studies. Stemming from this work, we now have detailed knowledge of the mating systems of many lizard species and an understanding of the consequences of this for variation in male and female reproductive success. For

almost all species for which there has been genetic paternity testing of offspring, females have been shown to exhibit high levels of polyandry (e.g., multiple mating; Uller and Olsson 2008; Wapstra and Olsson 2014). Thus, while the majority of territorial species have traditionally been classified as being polygynous (Bull 2000), in reality, most are polygynandrous (see Kamath and Losos 2017 for discussion of this in anoles). The high incidence of female polyandry in lizards appears largely to be the outcome of mate encounter rates (Uller and Olsson 2008). Indeed, where the costs of mating to females are low, as they are in most species, patterns of paternity are driven largely by a male's opportunity to acquire multiple copulations. There are a few exceptions to this, however. For example, in sand lizards (*Lacerta agilis*), where the population structure elicits strong costs associated with mating with the wrong individual, female multiple mating increases hatching success and lowers the incidence of deformities (Olsson et al. 1994). In general, however, it appears that female multiple mating evolved in lizards in the absence of indirect female benefits via strong selection on males, and that benefits arise only secondarily due to population-specific characters, such as low genetic variation and a high degree of inbreeding depression (Uller and Olsson 2008).

## SOCIAL GROUPINGS IN LIZARDS

While reptiles have been used extensively to study social structure and mating systems, the extent to which they have been used to study social organization and specifically the evolution of stable social groups, has been limited. This is, in part, because it has been assumed that lizard social organization is restricted to territorial overlap and/or nonrandom associations related to mating (see above). However, work over the past three decades has begun to refute this idea. Indeed, following on from Michael Bull's seminal work in the 1980s (Bull 1988), social groupings have now been documented for 66 lizard species across 18 families, and stable social aggregations have been documented for 16 species across 5 families (Gardner et al. 2016). Importantly, the taxonomic and functional diversity of stable lizard social grouping is similar to that found in many other taxa (e.g., fish and amphibians); taxa which have been used extensively to study the evolution of social complexity (Mank et al. 2005; Summers et al. 2006; Brown et al. 2010). Thus, lizards have the potential to be excellent model organisms for understanding the factors responsible for the emergence, maintenance, and diversification of social groups.

## WHAT CHARACTERIZES SOCIAL GROUPINGS IN LIZARDS?

Social groups in lizards take several forms, in terms of both their genetic makeup and the extent to which they represent stable entities. At a very broad level, lizard social organization assumes two main forms: (1) egalitarian social groups, which emerge as a result of nonrandom associations between unrelated individuals, and (2) fraternal social groups, which form as a result of closely related individuals remaining together. With regard to the latter, social groups can take a range of forms spanning from those that are characterized simply by prolonged parent (usually maternal)–offspring associations, to those comprising large communal family groups in which there are stable adult pair bonds and multiple cohorts of young.

### Egalitarian Social Groupings

Egalitarian social groups, in which unrelated individuals aggregate together, are relatively common among lizards, having been identified across 13 families within four major lizard suborders (the Gekkota, Iguania, Lacertoidea, and Scincoidea; Gardner et al. 2016). Group size can range from a few individuals to several thousand. Group composition may be relatively transient, both in

terms of its stability (e.g., the extent to which such groups dissolve) and its makeup (e.g., the specific individuals within the group). However, this is not necessarily the case. For example, in the Eastern Water Dragon (*Intellagama lesueurii*), individuals form relatively stable associations (independent of relatedness) (Strickland et al. 2014). With the relatively recent emergence of social network analysis of animals, there is great potential for the exploration of lizard sociality, more generally, in non-kin-based systems.

Many species of lizard also aggregate in greater numbers, although such aggregations may manifest only at daily/nightly sleeping refuges. As a result, the social bonds between individuals within these social aggregations are presumably weak or absent. While the function of these social associations is unknown in most instances, there are a number of ecological reasons that have been suggested as to why lizards may group in this way. For example, individuals from a range of taxa, including thick-tailed geckos (*Underwoodisaurus milli*), bearded dragons (*Pogona vitticeps*), and marine iguanas (*Amblyrhynchus cristatus*), have been shown to aggregate for thermoregulatory benefits (e.g., Wikelski 1999; Shah et al. 2003, 2004; Khan et al. 2010). Similarly, individual banded geckos that aggregate have been shown to exhibit a third less water loss than do solitary geckos suggesting substantial hydrostatic benefits are associated with grouping (Lancaster et al. 2006). Additional benefits suggested to promote the occurrence of egalitarian grouping behavior in lizards include a reduction of predation risk (Mouton 2011), increased foraging efficiency (Barry et al. 2014), and increased access to mates (Lemos-Espinal et al. 1997; Mouton 2011). Alternatively, it has been suggested that such social aggregations form as a result of limited availability of key habitat, for example, the availability of suitable hibernacula (Gregory 1984; Graves and Duvall 1995) or oviposition/rookery sites (Graves and Duvall 1995; Doody et al. 2009), which result in the coming together of individuals at certain times of year. Importantly, while the primary reasons for these aggregations may be ecological (e.g., refugia) or physiological (e.g., temperature/water loss), social benefits could still accrue from the resultant grouping. Furthermore, such grouping behavior, driven by abiotic factors, could act as an initial trigger for the emergence of more stable social aggregations (Graves and Duval 1995; Shah et al. 2003; Lancaster et al. 2006; Davis Rabosky et al. 2012).

## Fraternal Social Groupings

In contrast to the taxonomic diversity of egalitarian social groups, fraternal (kin-based) social groupings (with the exception of those that exhibit only parent–offspring associations) have been identified in only one higher level group of lizards, the Scincoidea. Within the Scincoidea, kin-based sociality has been documented in two families: the Xantusiidae and Scincidae. Members of both the Gerrhosauridae and Cordylidae have been suggested to live in social aggregations, but kin structure is yet to be confirmed (Gardner et al. 2016). The vast majority of the kin-based social aggregations within the Scincidae occur within a single Australasian lineage, the subfamily Egerniinae (hereafter referred to as the *Egernia* group), a monophyletic assemblage of skinks consisting of the genera *Egernia*, *Liopholis*, *Lissolepis*, *Bellatorias*, *Cyclodomorphus*, *Tiliqua*, and *Corucia* (Gardner et al. 2008). In total, 11 species of the *Egernia* group, representing four genera, have been confirmed to live in stable social groups, with anecdotal evidence of social grouping in a further 17 species (Gardner et al. 2016). In contrast to this, a single species of the family Xantusiidae, *Xantusia vigilis*, has been shown to exhibit kin-based sociality (Davis et al. 2011). Field observations of lizards found in burrows, rock crevices, tree cavities, and underneath cover items that specifically consist of a single adult pair and associated juveniles, however, have been reported for a large number of additional lizard species (reviewed by Chapple 2003; Davis et al. 2011; Gardner et al. 2016), suggesting that kin-based sociality may be more widespread than is currently appreciated (see below).

As with other social species, fraternal social groupings in lizards are characterized by long-term stable adult pair bonds and delayed juvenile dispersal, resulting in the formation of family groups

consisting of adults and their offspring (Chapple 2003; While et al. 2015; Gardner et al. 2016; Whiting and While 2017). Although such traits are relatively consistent across species, there is considerable variation in group size and composition, both within and among species. For example, within the *Egernia* group, social organization includes species that are largely solitary (e.g., *Tiliqua adelaidensis*, Schofield et al. 2014; *Liopholis inornata*, Daniel 1998; *Lissolepis coventryi*, Taylor 1995), those in which adults pair bond during the breeding season (e.g., *Tiliqua rugosa*, Bull 2000), those which live in small family groups (e.g., *Liopholis whitii*, *Egernia saxatilis*, O'Connor and Shine 2003; Chapple and Keogh 2005; While et al. 2009a), and those species which live in large stable extended family groups (e.g., *E. cunninghami*, Stow and Sunnucks 2004; *E. stokesii*, Gardner et al. 2001).

### Stable Adult Pair Bonds

One of the key characteristics of lizard fraternal social groups is the presence of long-term, stable, usually monogamous, pair bond between a male and a female. Perhaps the best example of this comes from the sleepy lizard (*Tiliqua rugosa*) (Bull 2000). A long-term study documented 31 partnerships that lasted for more than 15 years, 110 pairs that exceeded 10 years, and 1 pair that has been together for at least 27 years (ongoing) (Leu et al. 2015; Bull et al. 2017). Such extended long-term monogamy within and between seasons has since been shown to form the basis for social organization across most species in the *Egernia* group (Chapple 2003), as well as for *Xantusia vigilis* (Davis et al. 2011).

Although the majority of species in the *Egernia* group exhibit social monogamy, polygynous social groups, in which some males form pair bonds with multiple females, are also known. Such social groups often exist at a lower frequency than monogamous pair bonds. For example, 30% of social groups in *Liopholis whitii* are characterized by a single male sharing his crevice site with up to three females (Chapple and Keogh 2006; While et al. 2009a, 2011). This variation in social organization is closely tied to crevice site availability. Indeed, experimental work has shown that the structure of available habitat, along with high levels of female–female aggression, plays a crucial role in mediating social organization in this species (Halliwell et al. 2017a). Similar arguments have been suggested to explain variation in social organization in other *Egernia* group species (Duffield and Bull 2002; Chapple 2003). Variation in social organization within the *Egernia* group can also include aggregations of multiple adults of both sexes. For example, in *E. stokesii*, stable social groups can consist of up to 11 adults (both males and females) sharing the same crevice site (Gardner et al. 2001, 2002; Duffield and Bull 2002). Other species, such as *E. cunninghami*, *E. mcpheei*, and *E. striolata*, have also been reported to live in large communal groups containing multiple adults (Stow et al. 2001; Chapple 2003; Stow and Sunnucks 2004). Similarly, in *Xantusia vigilis*, group size varies from 2 to 18 individuals, with social organization being represented by both nuclear families and extended family groups (Davis et al. 2011).

Monogamous, polygynous, and polygynandrous pair bonds all exhibit surprising stability within and between seasons. Besides the likely lifelong pair bonding of Sleepy Lizards (*T. rugosa*), in *Liopholis whitii* pairs also exhibit considerable stability across years, with some pairs having been together for the majority of their reproductive lifespan (e.g., 10 years; G. While, unpublished data). While long-term data for the majority of other systems is relatively sparse, studies over several breeding seasons have confirmed strong pair stability between years for *Egernia cunninghami* (Stow and Sunnucks 2004), *E. saxatilis* (O'Connor and Shine 2003), and *Egernia stokesii* (Duffield and Bull 2002; Gardner et al. 2002). Thus, pair stability appears to be prevalent among social *Egernia* species. Unsurprisingly, pair separation is extremely rare in these systems. In *L. whitii*, only 15% of pairs exhibit separation by choice (i.e., not via the mortality of one individual; G. While, unpublished data). Social groups of *Xantusia vigilis* also show moderate levels of stability, with 29% of groups stable across consecutive years (Davis et al. 2011).

Although lizards in general tend to exhibit relatively high levels of female polyandry (Uller and Olsson 2008), high levels of genetic monogamy appears to be the rule for lizards that exhibit strong social organization (Gardner et al. 2016; Whiting and While 2017). This is not to say that genetic monogamy is ubiquitous, as all species exhibit some level of extra-pair mating. Interestingly, levels of extra-pair paternity differ considerably both within and among populations/species. In *Egernia cunninghami*, only 2.6% of litters include extra-pair offspring (Stow and Sunnucks 2004). Levels of extra-pair paternity are also relatively low for other species including 12%–26% for *Liopholis whitii* (Chapple and Keogh 2005; While et al. 2009b, 2014a), 20% for *E. saxatilis* (O'Connor and Shine, 2003), 25% for *E. stokesii* (Gardner et al. 2001), and 19% for *Tiliqua rugosa* (Bull et al. 1998). Although the data are currently limited, species exhibiting less social, nonfamily behavior appear to exhibit considerably higher levels of genetic polyandry. For example, for *Tiliqua adelaidensis*, 75% of offspring within litters result from multiple mating (Schofield et al. 2014).

### Delayed Juvenile Dispersal and Prolonged Parent–Offspring Associations

The second defining feature of fraternal lizard social groups is that of delayed offspring dispersal, which results in prolonged associations between parents and their progeny. As with pair bonding, the extent of such prolonged associations varies considerably, both within and among species. For example, in the *Egernia* group, such association ranges from species in which parents do not associate at all with their offspring (e.g., *Liopholis inornata*, Daniel 1998; *Tiliqua rugosa*, Bull and Baghurst 1998), through those in which parents associate predominantly with a single offspring or cohort of offspring (e.g., *L. whitii*, Chapple and Keogh 2006; While et al. 2009a; *L. slateri*, Fenner et al. 2012), to those in which parents associate with multiple cohorts of offspring (e.g., *Egernia cunninghami*, Stow et al. 2001; *E. saxatilis*, O'Connor and Shine 2003; *E. stokesii*, Gardner et al. 2001). In the most extreme cases, this results in large communal groups of up to 30 related individuals, including nonbreeding adults who stay within their parents' social group. For example, in large social groups of *E. stokesii*, within-group relatedness between adult females is extremely high (between $r = 0.25$ and $r = 0.55$), suggesting that these groups comprise mothers and their adult daughters (Gardner et al. 2001).

The prolonged parent–offspring association exhibited by fraternal lizard societies raises questions about the extent to which such associations represent a form of parental care. There are several potential functions of parent–offspring associations that may constitute simple forms of parental care. For example, offspring may gain increased access to basking locations, foraging opportunities, and retreat sites (Bull and Baghurst 1998; O'Connor and Shine 2004; but see Langkilde et al. 2007), which may result in an increase in early growth and survival (Botterill-James et al. 2016). Alternatively, offspring may benefit from extended parent–offspring associations via a reduction in the risk of infanticide and conspecific aggression (O'Connor and Shine 2004; Sinn et al. 2008). Members of the *Egernia* group frequently live in highly saturated environments whereby aggression toward conspecifics is common, and infanticide is a potentially significant source of offspring mortality (Post 2000; Lanham and Bull 2000; O'Connor and Shine 2004). As the parents of most such species aggressively defend their home range from conspecifics (Chapple 2003; O'Connor and Shine 2004), offspring that reside within those territories may gain significant (albeit indirect) benefits. Experimental evidence concerning *E. saxatilis* has shown that the presence of a parent almost eliminates aggression displayed toward offspring by unrelated adults (O'Connor and Shine 2004), and females of both *Liopholis whitii* and *E. saxatilis* have been shown to exhibit heightened aggression during periods of postpartum parent–offspring association, presumably when offspring are most at risk (O'Connor and Shine 2004; Sinn et al. 2008). Finally, offspring may gain from prolonged parent–offspring associations through the inheritance of territories, as suggested by the presence of high levels of genetic relatedness within social groups of *Egernia stokesii* (see above). Therefore, although levels of parent–offspring interaction are lower than those exhibited by other vertebrate

species (e.g., full parental provisioning; Clutton-Brock 1991), they nevertheless show a greater level of interaction than previously appreciated and, importantly, may provide a key social context from which more elaborate forms of parental care could evolve (While et al. 2014b; Halliwell et al. 2017c).

Parental care and prolonged parent–offspring associations are also evident in a number of lizard species that do not exhibit long-term monogamous pair bonds (e.g., fraternal social groups characterized only by extended parent–offspring associations). Such species may be oviparous or viviparous. The function of such parental care is diverse. In oviparous species it includes selection of nest sites (based on drought, desiccation, temperature extremes, hypoxia, predation, and parasitism), the brooding of eggs, and the defense of nests and eggs against potential predators (Somma 2003; Huang 2006; While et al. 2014b). For example, in *Eutropis longicauda*, females defend their nests as an extension of territorial behavior (Huang and Pike 2011). In viviparous species (and some oviparous species), this association between parents and offspring can occur post-birth/hatching and may persist from days to a few years. Such prolonged parent–offspring associations have now been documented for 95 species across 23 families and vary in their form, duration, and whether juveniles associate with females only or with adults of both sexes (Halliwell et al. 2017c). The function of such associations between group members ranges from passive tolerance of juveniles within adult home ranges to defense of offspring from conspecifics and predators (e.g., Halloy et al. 2007; Masters and Shine 2003).

## THE EVOLUTION OF LIZARD SOCIAL GROUPING

Social groups form, first and foremost, when individuals regularly encounter and interact with one another. Once these interactions stabilize, a new social context emerges, from which more complex forms of social behavior and social organization can evolve. Thus, when trying to understand the evolutionary processes that have led to the diversity in social behavior evident among lizards (or indeed any taxa) we must ask (1) what are the factors that facilitate the initial emergence of social interactions that form the foundation of social groups, (2) what are the factors that maintain social interactions and groups once they emerge, and (3) what influences the further refinement and diversification of social behavior and grouping.

### Factors That Influence the Emergence of Lizard Social Grouping

#### *Life History Traits*

Life history traits have long been suggested to provide a fundamentally important precursory context for the emergence of social organization across a wide range of organisms. Long lifespans, delayed maturity, and high relative investment in offspring have been suggested as phenomena underlying transitions to social life in birds, mammals, and insects (Arnold and Owens 1998; Covas and Griesser 2007). Such traits are likely to have also been important for such transitions in lizards. Indeed, social grouping in lizards, particularly that associated with fraternal social groups, appears to be accompanied by several of these life history traits.

First, most lizard species that display stable social groupings are relatively long lived. For example, almost all the *Egernia* group for which there are data are thought to live for more than 10 years (Chapple 2003) and in some cases for more than 50 years (e.g., *Tiliqua rugosa*, Bull 1995; Bull et al. 2017; *E. cunninghami*, P.Harlow, unpublished data). *Xantusia vigilis* is also relatively long lived (at least 8–10 years) based on an absence of growth in older individuals (Zweifel and Lowe 1966; Davis et al. 2011). However, longevity per se may not be the actual causal mechanism linking life history to social groupings. Instead, several life history traits that are correlated with longevity, such as delayed maturity and high reproductive investment in relatively few offspring may be of significance

in driving the change (Covas and Griesser 2007; Blumstein and Moller 2008). Members of the *Egernia* group are not only long lived, but are also often slow to mature (typically 2–3 years, but up to 5 years), skip opportunities to reproduce (i.e., do not reproduce every year), and invest more than related taxa in individual offspring (Chapple 2003). *X. vigilis* shows the same patterns of small litter size (1–2 years, very rarely 3), of proportionately large offspring, late maturity (2–3 years), and intermittent reproduction especially in years of low rainfall (Miller 1951; Zweifel and Lowe 1966). Combined, these traits fit the prediction that post-hatching parent–offspring associations are linked to high-quality offspring in family-living species (Covas and Griesser 2007). However, the strong phylogenetic bias of the occurrence of fraternal social groups among lizards currently mitigates against formal tests of this hypothesis. Longevity and delayed maturity are also likely to promote the evolution of long-term pair bonds. For example, in the *Egernia* system, limited availability of suitable habitat (e.g., high habitat saturation; see below), strong territoriality, and relatively long lifespans create low breeder turnover and intense competition over access to limited permanent crevice sites (O'Connor and Shine 2004; Langkilde et al. 2005; While et al. 2009a). These factors heighten the risk of being left without a mate or territory when switching mates between breeding seasons (see also Choudhury 1995) and perhaps favors the evolution of stable social monogamy between seasons (see arguments presented by Botterill-James et al. 2017a).

A final trait that is likely to be particularly important in the emergence of fraternal social groups is viviparity. Giving birth to live young increases opportunities for interaction between parents and their offspring and, therefore, should promote transitions from solitary to group living. In support of this, postpartum parent–offspring associations are almost completely restricted to viviparous species (While et al. 2014b). Furthermore, phylogenetically controlled comparative analyses have shown that the evolution of viviparity has repeatedly preceded the emergence of parent–offspring associations in lizards (Halliwell et al. 2017c). Importantly, this has the potential to set the stage for the evolution of more complex forms of stable social aggregations (e.g., transitions from parent–offspring associations to family groups). Indeed, phylogenetic reconstructions suggest that live birth also preceded the evolution of more stable social groupings, in which individuals remain in groups across multiple seasons or years (Halliwell et al. 2017c). Interestingly, the evolution of viviparity is associated with cold climates because of the thermal control it affords the mother during embryonic development (Shine 2004, 2014). By extension, if kin-based sociality is dependent on viviparity, the distribution of kin-based sociality could be strongly tied to the geographic, as well as the phylogenetic, distribution of viviparity.

### *Ecology*

Whereas particular life history traits increase the probability that individuals will come into contact with one another, ultimately it is ecology that dictates whether this probability is realized. Extensive work founded on a broad range of social organisms suggests that resource availability (e.g., ecological constraints) plays a fundamental role in enhancing the probability of contact (Emlen 1982; Stacey and Ligon 1987; Komdeur 1992; Heg et al. 2004; Bach et al. 2006). This is also the case for lizards. Resource availability and ecological constraints are the primary factors that have been suggested to influence the emergence of both long-term pair bonding and delayed juvenile dispersal in *Egernia* group species (Duffield and Bull 2002; Chapple 2003; Halliwell et al. 2017b; Whiting and While 2017). For example, these species rely on permanent shelter sites that are either naturally occurring structures, such as rock outcrops or tree hollows (Chapple 2003; Michael et al. 2010), or the result of construction via the excavation of deep and complex burrow systems, sometimes by multiple generations of the same family (McAlpin, et al. 2011). Crucially, these structures tend to be patchily distributed across the landscape and separated from one another by unsuitable habitat (Duffield and Bull 2002; O'Connor and Shine 2003). The extent of heterogeneity in habitat availability differs markedly between species. For burrowing species, suitable habitat can be

relatively homogeneous, separated only by a matter of meters. In contrast, for species that live on rocky outcrops (e.g., *Egernia striolata* and *E. stokesii*), patches of suitable habitat can be separated by distances of 50 m or much more (Gardner et al. 2001). Such distances constitute considerable barriers to dispersal. These circumstances have the potential to impact both the availability of potential mates (see above), thus influencing the evolution of long-term pair bonding, and juvenile dispersal, thus influencing the extent of parent–offspring association (see Halliwell et al. 2017a, b for experimental evidence of this in *Liopholis whitii*). Importantly, a number of other lizard taxa which have been suggested to occur in stable family groups, such as certain cordylid lizards, and *Liolaemus* and *Oligosoma* skinks, occur in similar ecological circumstances with regard to their reliance on permanent shelter sites (Halloy and Halloy 1997; Mouton et al. 1999; Mouton 2011; Visagie et al. 2005; Berry 2006). This suggests that lizard social groupings may actually be more common than we currently appreciate, as long as the right ecological and life history conditions occur. However, targeted field and molecular work is required to confirm this.

## Factors That Influence the Maintenance of Lizard Social Grouping

Once social interactions emerge, the extent to which they are stabilized and form the foundation from which more complex forms of social behavior can evolve are dependent on (1) the recurrence of the ecological conditions which promoted their initial emergence and (2) the strength of selection favoring social interactions once they arise. Kin selection is fundamentally important in this context. Indeed, the maintenance of the social interactions that underpin social groups will be promoted when the benefits of those social interactions outweigh their costs, mediated by the level of relatedness between group members (Hamilton 1964). Where groups are made up of largely unrelated individuals (e.g., egalitarian societies), social groups are maintained by a straight cost/benefit scenario, mediated, in some instances, by mutualistic benefits between group members. Fraternal societies, in contrast, have the added advantage of kin structure. This means that individuals have the potential to gain both direct *and* indirect fitness benefits from social interactions. Therefore, the stability of social groupings in lizards, as for other taxa, depends primarily on factors that influence the components of Hamilton's rule ($rB - C > 0$, where $r$ is the level of relatedness between the actor and recipient of a behavior $r$, $B$ is the benefit of the behavior conferred to the recipient, and $C$ is the cost of the behavior to the actor; Hamilton 1964), and the extent to which these mediate the level of conflict versus cooperation between group members. These social interactions are all mediated through communication, where recognition of kin or siblings is required (see Section "The Role of Communication" for details) and which helps maintain long-term stable associations.

### *Relatedness*

Central to Hamilton's rule is relatedness. In instances where relatedness between group members is high, kin selection can promote and maintain cooperative social behavior. This has largely been studied in the context of the elaborate social behaviors exhibited by cooperatively breeding birds, mammals, and eusocial insects (Hughes et al. 2008; Cornwallis et al. 2010; Lukas and Clutton-Brock 2012). However, relatedness is also important for maintenance of relatively simple social behavior. In such systems, the basal level of cooperation is represented by simple interactions between family members, specifically between parents and their offspring and between siblings (Queller 1994). Lessening of relatedness within groups should therefore result in reduced cooperation and increased conflict, leading to decreased social structure and complexity at the population level. Conversely, high levels of relatedness should increase the benefits of investing in parental care and for cooperation among brood mates. Such interactions ultimately promote transitions to more advanced social behavior, such as long-term stable pair bonds and greater interaction within and between cohorts of offspring (While et al. 2009a). Importantly, these traits are the precursors

for the evolution of more highly derived forms of sociality, such as cooperative breeding and euso-ciality, present in species showing more advanced socialized interactions (Queller 1994; Field and Brace 2004).

Relatedness between group members is influenced primarily by the extent of natal philopatry, which means that related individuals remain within the vicinity of one another (see above). However, for a given level of natal philopatry, female mating behavior will have fundamental implications for the structure of relatedness of social groups. Specifically, low levels of female polyandry (high levels of monogamy) increase the relatedness between group members, favoring cooperation between individuals. Empirical support for this derives from observations that the distribution of complex sociality across the animal kingdom is closely correlated with low levels of polyandry (e.g., Hughes et al. 2008; Cornwallis et al. 2010; Lukas and Clutton-Brock 2012). Similar arguments are likely to explain the maintenance of social grouping across lizards. For example, there are considerable (albeit low) levels of polyandry across the *Egernia* group and in some species this has been shown to influence the composition of the family group by promoting enhanced dispersal of extra-pair off-spring (While et al. 2009b). Although the behavioral mechanisms mediating these responses have not been directly studied, recent research has suggested that they are most likely influenced by the extent to which conflicts of interest between family members are introduced (Botterill-James et al. 2017a, b). Such conflict is then likely to mediate the extent to which offspring remain versus disperse out of the natal range. Over evolutionary time, this may influence the stability of social living.

### The Costs and Benefits of Social Behavior

For a given level of relatedness, the level of conflict versus cooperation between group members is dictated by the costs and benefits of expressing a particular social behavior. The main factor that influences these costs and benefits is resource availability. When resources are low, the tolerance of offspring by parents, and of siblings, may have significant costs, reducing access to resources and therefore growth and survival. We may, therefore, predict that under resource poor conditions greater conflict between group members will occur, resulting in increased dispersal with resultant smaller group sizes. Conversely, when resource availability is high, competition will be decreased, and group members may even gain kin selected benefits by tolerating other individuals, leading to reduced dispersal and the emergence of larger group sizes. While resource availability, in terms of crevice sites, has been shown to be important in mediating social grouping in lizards at a broad scale (e.g., Halliwell et al. 2017a), the extent to which more fine scale variation in resource avail-ability (e.g., food availability) influences levels of conflict and cooperation and ultimately family dynamics is still relatively unexplored. The one exception is for *Liopholis whitii*, wherein yearly variation in resource availability (dictated by rainfall patterns) has been shown to be a strong predic-tor of the level of parent–offspring association (Botterill-James 2014). Future experimental, work in which fine-scale resource availability is manipulated in large-scale experimental setups, will provide opportunities to examine these ideas further.

Several other ecological factors may also be important in mediating group dynamics within social lizards. Reduction of predation risk has been suggested to be an important benefit of group living for some *Egernia* group species. For example, groups of both *E. stokesii* and *E. cunninghami* are able to detect predators sooner than solitary individuals (Eifler 2001; Lanham and Bull 2004). Social groupings may also provide thermoregulatory benefits. For example, individuals of *Xantusia vigilis* that aggregate experience significant thermal benefits that translate into higher fitness (Davis Rabosky et al. 2012). For *Egernia stokesii*, group size has a positive effect on heat retention, with larger groups maintaining higher nighttime body temperatures than smaller groups (Lanham 2001). Lastly, increased risk of parasite transmission has been suggested to exert significant selective pres-sure on the maintenance of stable social grouping (Altizer et al. 2003). For both *Tiliqua rugosa* and *Egernia stokesii* (Godfrey et al. 2006, 2009; Leu et al. 2010), group structure and social behavior

increase the rate at which parasites spread between individuals. For *E. stokesii*, an individual's position within a transmission network (based upon shared shelter sites) along with the level of within-group relatedness are strongly related to the risk of infection from parasites (Godfrey et al. 2006, 2009). Conversely, group living may also decrease parasite transmission in lizards through either dilution effects (Mooring and Hart 1992), cooperation with regard to ectoparasite removal (Wikelski 1999), or the minimization of contact with individuals outside the social group that may carry novel parasites (Bull and Burzacott 2006; Godfrey et al. 2009).

### *The Role of Communication*

The final factor central to the maintenance of group living is communication. Indeed, some form of recognition, either mate recognition, parent–offspring recognition, or sibling–sibling recognition, must, to some degree, mediate all levels of social interaction that facilitate the maintenance or dissolution of social grouping. Social lizards tend to lack the overtly visual displays exhibited by their nonsocial counterparts. For example, territorial lizards are often (but not always) conspicuously colored (males) and use dynamic visual signals to communicate at a distance (Ord and Martins 2006). The lack of such overt social behavior has been suggested to be one of the primary reasons for the current lack of appreciation of lizards as model systems for social behavior research (Doody et al. 2013). Instead, social species appear to rely heavily on chemical communication. Members of the *Egernia* group, and many species of lizards generally, tongue-flick to acquire social information. In some instances, this information is acquired directly from individuals during interactions. However, a number of *Egernia* group species have also been shown to mark their territories with scat piles (Duffield and Bull 2002; Chapple 2003; Fenner and Bull 2011). Importantly, many of these species have been suggested to exhibit quite sophisticated kin recognition mechanisms (Bull et al. 1994, 1999, 2000, 2001; Main and Bull 1996; O'Connor and Shine 2006), although the principal mechanisms underlying this are still the subject of much debate. Early experimental data suggested that kin recognition may be the outcome of genetic matching (e.g., Bull et al. 2002), providing a means by which the fine-scale ability to recognize individuals of close genetic relatedness could occur, as suggested by patterns of mate choice and offspring dispersal in the wild (e.g., While et al. 2009b, 2014a; Bordogna et al. 2016). However, experimental evidence is equivocal and few studies have convincingly been able to fully eliminate other potential explanatory causes, such as familiarity, in mediating these interactions (but see Bull et al. 2001). Clearly, experimental and comparative work exploring the coevolutionary dynamics between mechanisms of communication and social complexity in lizards provides an exciting avenue for future research.

## Factors That Influence the Diversification of Lizard Social Grouping

Once lizard social groups have emerged, the diversification of social organization will depend upon the extent to which environmental conditions mediate the emergence of additional social interactions between individuals. For example, the communal family groups exhibited by some *Egernia* group species (e.g., *E. cunninhami* and *E. stokesii*; Stow and Sunnucks 2004; Gardner et al. 2001), which incorporate multiple cohorts of young, presumably emerged from nuclear family groups via the extended tolerance of young-of-the-year under particular environmental conditions. Thus, the same conditions that promoted the initial emergence and maintenance of social organization continue to play a role in its diversification. Furthermore, where such social groups are stabilized by selection they provide a novel social context within which additional traits can be co-opted to function in various ways, resulting in the refinement and elaboration of social behavior. For example, once simple parent–offspring associations emerge and are stabilized, any parental trait (such as aggression or forms of feeding) that provides (indirect) benefits to the offspring can be the subject of selection. Indeed, theoretical models suggest that once these relatively simple forms of social

behavior evolve the elaboration of social behavior and complexity can proceed relatively rapidly (Gardner and Smiseth 2011). Although we do not yet have data for testing these ideas in the majority of systems, lizards offer an exciting opportunity to explore the relatively simple steps that may have contributed to social diversification (see below).

## LIZARDS AS MODEL ORGANISMS FOR UNDERSTANDING THE EVOLUTIONARY ECOLOGY OF COMPLEX SOCIALITY

We hope that we have provided substantive evidence that there is broad taxonomic and functional diversity in stable lizard social organization, equivalent to that seen in other social taxa. With this in mind, we believe that lizards provide an outstanding opportunity for addressing fundamental questions relating to the early evolution of complex sociality. In particular, the fact that social groupings are (1) relatively simple and easily quantifiable, (2) not obligate (e.g., most species exhibit facultative or temporary forms of group living), and (3) exhibit sufficient variation in social organization (both within and among species) to allow for meaningful tests, make lizards a promising assemblage for uncovering the mechanisms that trigger the initial origins, and ongoing maintenance, of stable social grouping in animals (Chapple 2003; Doody et al. 2013; While et al. 2015; Whiting and While 2017). Indeed, much of the work on mammal and bird sociality is focused on the far end of social complexity trajectory, such as complex social tactics (e.g., punishment in primates), alliance formation, and cooperative breeding. In contrast, there has been little attention given to the early evolution and emergence of family living and kin-based sociality in vertebrates more generally. Lizards have the added advantage of being amenable to large-scale experimental studies, allowing us to design targeted experiments to tease apart causal relationships between key biotic and abiotic factors that have been suggested to influence the emergence and maintenance of social organization (e.g., Botterill-James et al. 2016; Halliwell et al. 2017a, b; Botterill-James et al. 2017b). This is not possible for the majority of bird and mammal systems.

Despite this, data on reptile sociality remain scarce. The primary impediment to future studies is, therefore, a lack of information regarding the extent of social behavior for most species. One potential reason for this is that reptiles generally lack overt social displays (as detailed above), whereupon social behavior tends to remain relatively cryptic (Doody et al. 2013). Even for lizard species exhibiting the most overt social organization (such as *Egernia*), key social traits, such as parent–offspring associations, are often only identifiable using molecular techniques and detailed field studies (Gardner et al. 2001; Stow et al. 2001; Chapple and Keogh 2005; While et al. 2009a, b). Future research should therefore target systems in which analogous conditions to those outlined above may have facilitated the convergent emergence of family living. There are several candidate groups for such studies: the Cordylidae of sub-Saharan Africa, the liolaemid iguanids of South America, the oligosomid skinks, and Duvaucel's Gecko (*Hoplodactylus duvaucelii*) of New Zealand. All of these display complex social behavior, including postpartum parental care and social aggregations of adults and juveniles (Halloy and Halloy 1997; Mouton et al. 1999; Mouton 2011; Visagie et al. 2005; Berry 2006; Barry et al. 2014). We hope that a growing appreciation that lizards can play a fundamental role in understanding the early evolution of complex sociality, coupled with the advent of more sophisticated molecular and field techniques (e.g., pit tagging and data loggers), will lead behavioral and evolutionary ecologists to pay greater attention to documenting the diversity of social behavior exhibited by lizards.

Ultimately, to infer broad evolutionary patterns, the field and experimental studies outlined above need to be combined with comparative analyses of social traits across species. Such an approach will allow us not only to identify the causes and consequences of variation in social behavior in ecological settings but also to translate this understanding into a set of general principles that adequately describe the variation we see across species (Halliwell 2016). This can be achieved in

several ways using lizards. First, comparisons between species within lineages will reveal how closely related species can take widely divergent social paths. Importantly, the most comprehensive and informative insights will be gained by focusing research efforts on taxonomic groups that allow us both to form clear predictions of phylogenetic patterns in trait distribution and to explicitly test hypotheses of functional links between traits. There are a number of lizard lineages, such as the *Egernia* group, that have the potential to be particularly important in this regard. Second, studies across broadly disparate lizard groups will allow us to incorporate information on ecology and life history to evaluate common factors that have been important in driving the emergence, maintenance, and diversification of social traits among groups. This approach has been an extremely fruitful avenue of research into social evolution in other taxa (Mank et al. 2005; Summers et al. 2006; Hughes et al. 2008; Cornwallis et al. 2010, 2017; Lukas and Clutton-Brock 2012). Recent research using similar approaches in lizards promises to provide equally informative insights (e.g., Gardner et al. 2016; Halliwell et al. 2017c).

## CONCLUSIONS

In summary, lizards exhibit a wide range of social behavior and organization, ranging from short-term associations for the purpose of mating to large communal family groups which in some instances contain nonbreeding adults. We argue here that a suite of traits and abiotic factors correlate with kin-based sociality in lizards. These include a range of life history traits and the reliance on key habitat requirements. These, in combination, appear to be an important precursor for kin-based sociality, but additional work targeting species that exhibit similar traits is required to reduce the phylogenetic bias currently present in the data. The maintenance of social organization and social dynamics, more generally, is dictated primarily by subtle changes in environmental conditions that mediate the key components of Hamilton's rule, namely, relatedness and the costs and benefits of cooperating versus competing. If these conditions seem familiar, it is because many of the arguments that we advance for the evolution of kin-based sociality in lizards are analogous to those proposed to explain the evolution of advanced forms of social behavior (e.g., cooperative breeding, eusociality) in other systems (Hughes et al. 2008; Cornwallis et al. 2010; Lukas and Clutton-Brock 2012). Indeed, evolution often results in convergent outcomes, and complex social organization tends to emerge when ecological and life history conditions impose constraints that cause closely related kin to interact. Lizards are no different, but what sets them apart is their ability to provide for an enhanced understanding of the very early stages of social evolution. Recent research has suggested that to ultimately understand why social groups evolved, we need to move away from traditional model systems in which sociality is highly derived, and in which individuals exhibit obligate or permanent forms of group living (Smiseth et al. 2003; Falk et al. 2014). By focusing on identifying the nature of social behavior and organization in species that exhibit facultative and/or temporary forms of social grouping (Whiting and While 2017), we can understand more about the early evolution of social grouping. Lizards offer an outstanding model system for this purpose, and we anticipate that they will feature more prominently in the social behavior literature in the future.

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