

# 13 Sociality in Lizards

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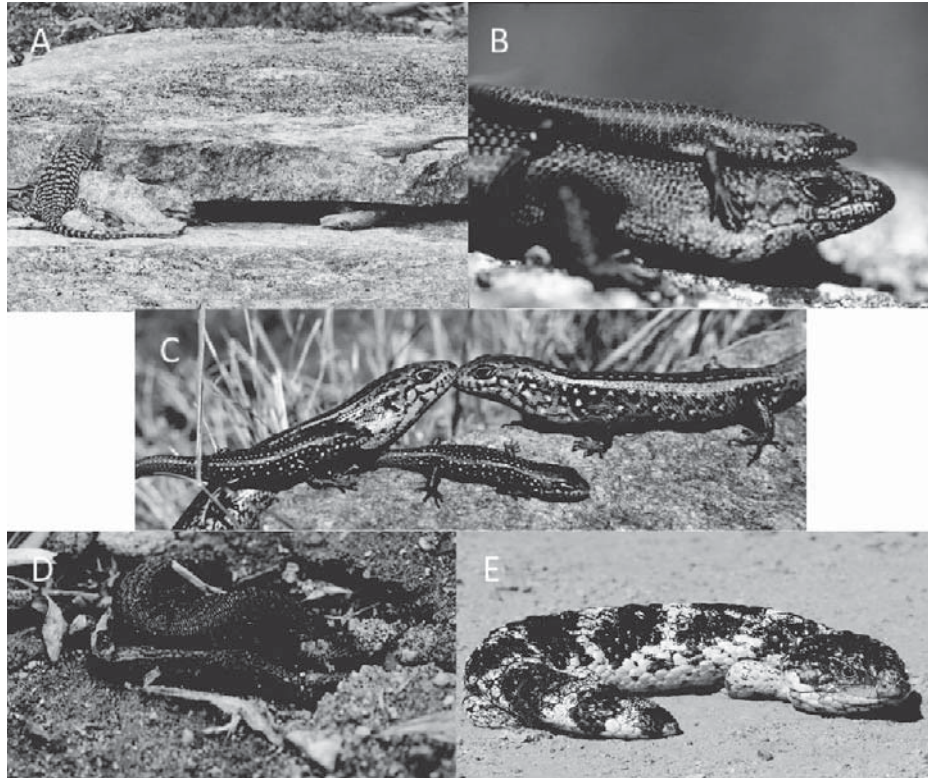
## Overview

Lizards, snakes and amphisbaenians (worm lizards) form a monophyletic group (the squamate reptiles), which contains 9,712 species (Uetz & Hošek, 2015) in 61 families (Wiens, *et al.*, 2012). New species are constantly being described, particularly with the advent of modern molecular systematics and improved access to remote regions. Consequently, this group is likely to be considerably larger in the future (Pyron, *et al.*, 2013). Not only is this a taxonomically diverse group of terrestrial vertebrates, but species occupy a wide range of habitats and ecosystems, and occur on all continents except Antarctica. Furthermore, they span a wide range of body sizes and forms from miniature chameleons and geckos that perch comfortably on a matchstick, to reticulated pythons in excess of 6 m in length. While snakes have traditionally been viewed as a group separate from lizards (e.g. different suborders in traditional taxonomic terms), they are in fact embedded within lizards such that some lizards are more closely related to snakes than they are to other lizards (Wiens, *et al.*, 2012; Pyron, *et al.*, 2013).

Squamate reptiles display a wide array of life history strategies, reproductive tactics, and social behaviors that frequently bring males and females into conflict and which are invariably further influenced by high levels of male contest competition (Baird, 2013). As a consequence, most species are polygynous, polyandrous, or both (polygynandry), and many are territorial (Stamps, 1977). However, some species also occur in stable social aggregations (Gardner, *et al.*, 2016). Of these, a small proportion live in family groups with a socially and mostly genetically monogamous parental unit. Interestingly, a single radiation of lizards in Australia (*Egernia* group of scincid lizards) (Figure 13.1), commonly forms long-term pair bonds and have a particularly high incidence of family

We dedicate this chapter to the memory of Mike Bull, in recognition of his immense contribution to our understanding of lizard social systems and natural history in general.

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**Figure 13.1** Representative lizard species with different social organization. (A) *Egernia cunninghami* adult and juvenile on rock outcrop close to refuge, photo © Stewart MacDonald; (B) *Egernia saxatilis*: adult and offspring, photo © David O'Connor; (C) *Egernia whitii* family: adult pair and offspring, photo © Geoff While; (D) *Xantusia vigilis*: adult female and juvenile, photo © Alison Davis Rabosky (see Davis, *et al.*, 2011); and (E) *Tiliqua rugosa* (sleepy lizard), photo © Stewart MacDonald. All these species live in family groups except the sleepy lizard, which pairs up before and during the breeding season and which has lifelong pair bonds.

living (Chapple, 2003; While, *et al.*, 2015; Gardner, *et al.*, 2016). The *Egernia* group is a Melanesian-Australian radiation (Gardner, *et al.*, 2008) consisting of seven genera (*Egernia*, *Liopholis*, *Lissolepis*, *Bellatorias*, *Cyclodomorphus*, *Tiliqua*, and *Corucia*), and is so called because the former *Egernia* genus was paraphyletic and split into four monophyletic genera. This review will focus primarily upon the evolution of kin-based sociality in lizards with a heavy emphasis on the *Egernia* group. We draw upon data from snakes only when it helps inform the evolution of kin-based sociality in “typical” lizards. Our review is therefore admittedly biased towards lizards because our overall goal is to advance our understanding of the evolution of sociality in general, but kin-based sociality in particular.

Lizards provide a unique opportunity to understand the early evolution of vertebrate sociality because (1) social behavior is relatively simple and easily quantifiable, (2) social behavior is not obligate (e.g. most species exhibit facultative or temporary forms

of group living), and (3) there is enough variation in social strategies, both within and between species, to allow for meaningful tests. In lizards, mating systems vary from monogamy to polygynandry, parental care if present is typically through parent-offspring association (i.e. presence of parent deters potential predators, particularly conspecific adults), with social bonds and interactions between parents and offspring typically less complex than in many avian and mammalian systems (While, *et al.*, 2014a). As such, they offer great potential as models for understanding transitions to more complex forms of social structure and for uncovering the mechanisms that triggered the initial origins as well as the maintenance of family living and sociality in animals (Chapple, 2003; Doody, *et al.*, 2013; While, *et al.*, 2015). To understand the evolution of kin-based sociality in lizards, it is important to first consider the nature of social interactions in lizards more generally, since social selection (*sensu* Lyon & Montgomerie, 2012) acts on all aspects of social interactions that might lead to pair bonding and group formation (Kavaliers & Choleris, 2013).

## I SOCIAL DIVERSITY

Social systems have previously been organized into three broad categories: (1) social organization; (2) social structure; and (3) mating system (Kappeler & van Schaik, 2002; Kappeler, *et al.*, 2013). Much of what we know about the social and reproductive behavior of lizards is through studies of social structure and mating systems (Brattstrom, 1974; Fox, *et al.*, 2003). Specifically, lizards are excellent models for studies of territorial behavior, alternate reproductive tactics, and sexual selection more generally because they are frequently diurnal, easy to catch and follow, and exhibit strong site fidelity (Fox, *et al.*, 2003). In fact, the first significant publication of lizard behavior was a monograph of lizard mating behavior and sexual selection by Noble & Bradley (1933). Studies of lizard social structure have focused mainly on: (1) contest competition and rival recognition (Stamps, 1977; Fox & Baird, 1992; Whiting, 1999; Whiting, *et al.*, 2003; Whiting, *et al.*, 2006; Carazo, *et al.*, 2008; Sacchi, *et al.*, 2009; Umbers, *et al.*, 2012); (2) male alternate reproductive tactics (hereafter ARTs) (Wikelski, *et al.*, 1996; Sinervo & Lively, 1996; Whiting, *et al.*, 2009; Noble, *et al.*, 2013); (3) mate preference and mate choice (Olsson, *et al.*, 1994; Olsson & Madsen, 1995; Tokarz, 1995); and (4) communication in the form of static and dynamic visual signals, chemical signals/cues, and sometimes vocal signals (Martins, 1993; Ord, *et al.*, 2002; Ord & Martins, 2006; Hibbitts, *et al.*, 2007).

In addition to this large body of literature on social structure, lizards are increasingly becoming the focus of sexual selection studies using genetic parentage testing (Uller & Olsson, 2008; Wapstra & Olsson, 2014). From this work, we have detailed knowledge of mating systems, and in numerous cases, spatial and social organization. Lizards are therefore particularly useful organisms for studying the extent to which sexual selection influences patterns of social organization and social behavior. However, our understanding of social complexity in lizards – the extent to which they are capable of true individual recognition, kin recognition, forming associations

and alliances, and tracking of third party relationships – is in its infancy compared to studies in other taxonomic groups.

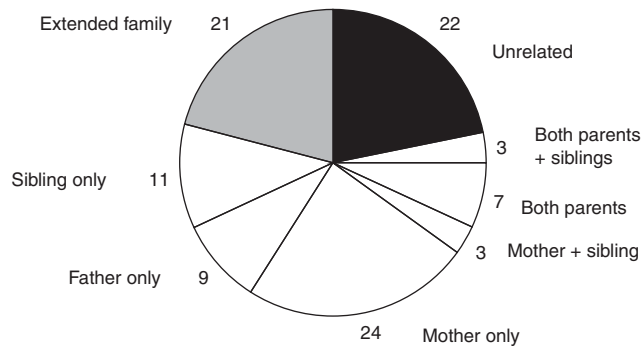
### 13.1 How Common is Sociality in Lizards?

Some form of aggregation has been documented in 94 species from 22 families, while stable social aggregations have been documented in 18 species from 7 families (Graves & Duvall, 1995; Mouton, *et al.*, 1999; Mouton, 2011; Gardner, *et al.*, 2016). However, our knowledge of the relatedness of individuals in these groups is generally scant. In some species, aggregations may be daily/nightly sleeping refuges or occur seasonally, and social bonds within these species are presumably weak, absent, or potentially strong (e.g. female rattlesnakes at rookeries with related females and offspring, Schuett, *et al.*, 2016). The vast majority of lizards, particularly those that experience any form of sexual conflict or sexual selection (e.g. contest competition), are expected to form social bonds with other individuals in their neighborhood independently of relatedness (e.g. Strickland, *et al.*, 2014). In this context, population social structure occurs when individuals are linked through non-random associations with one another (Whitehead, *et al.*, 2005; Croft, *et al.*, 2008; Strickland, *et al.*, 2014).

In contrast, kin-based (i.e. family) groups have only been identified in a single higher-level group of lizards (Scincoidea, *sensu* Pyron, *et al.*, 2013). Within this group or lineage are an additional four lineages that constitute major families: Xantusiidae (three subfamilies), Gerrhosauridae (two subfamilies), Cordylidae (two subfamilies), and Scincidae (three subfamilies). Kin-based sociality has thus far only been documented in the Xantusiidae and Scincidae, but it could very well be present in the remaining two families because species are known to live in stable conspecific aggregations but relatedness has not yet been tested. Only a single species of xantusiid, *Xantusia vigilis*, has been shown to have kin-based sociality (Figure 13.2) while nine species of the *Egernia* group in three genera (*Egernia*, *Liopholis*, *Bellatorias*) have thus far been confirmed to live in stable family groups (Figure 13.1, Table 13.1). However, field observations of lizard groups found in burrows, rock crevices, tree cavities, and underneath cover items which specifically consist of a single adult pair and associated juveniles have been reported from at least eight additional species representing four more squamate families (reviewed in Chapple, 2003; Davis, *et al.*, 2011; Gardner, *et al.*, 2016). Thus, future relatedness studies may uncover a more widespread distribution of kin-based sociality across lizards.

### 13.2 Forms of Sociality in Lizards

Lizard societies take a number of forms that include groups without kin structure, monogamous pairs with kin-based family living, and extended parent-offspring associations.



**Figure 13.2** Frequency of group composition according to relatedness in the desert night lizard (*Xantusia vigilis*). Reproduced from Davis, *et al.* (2011).

### 13.2.1 Social Organization and Structure Independent of Kin

Examining the link between social organization and mating system is a good first step towards understanding the different forms of sociality in lizards. In terms of mating systems, multiple mating is common in lizards and appears to be the case for almost every lizard species examined (Uller & Olsson, 2008; Wapstra & Olsson, 2014). In this respect, most territorial species have traditionally been classified as polygynous (Bull, 2000) because a subset of males appear to secure the majority of paternity. However, this type of categorization ignores the fact that in almost every species for which there has been genetic paternity testing of offspring, females have been shown to mate multiply (Uller & Olsson, 2008). Most species are therefore polygynandrous rather than polygynous. Polyandry in lizards has been suggested to be driven by indirect (genetic) benefits, despite little actual evidence for this (Uller & Olsson, 2008). More recently, it has been proposed that polyandry may have evolved in lizards through the combined effects of mate encounter frequency and sexual conflict over mating rates. Females are less likely to resist mating with multiple males if the costs are relatively low (Uller & Olsson, 2008) and/or if females are able to exclude the sperm of less desirable males through postcopulatory means (Olsson, *et al.*, 1994). In these systems, there is no pair bond or association, and females may mate with close kin but avoid the costs of inbreeding through sperm selection (Olsson, *et al.*, 1994).

In classical territorial systems, more than one female may occupy a male's territory. However, while residents may keep rival males at bay and exclude them from their territory, they cannot prevent females from visiting other males or copulating with sneaker males out of view (Wikelski, *et al.*, 1996). In these systems, the social organization is not kin-based, but there are social bonds and therefore there is social structure. However, it is unclear whether territoriality is driving sociality (a common assumption in lizard studies), or even the degree to which it influences sociality in lizards. For example, in the non-family living Australian eastern water dragon, *Intellagama lesueurii*, there are social bonds within and between the sexes. The strongest bonds

**Table 13.1** A summary of family living in lizards defined by long-term, stable groups consisting of a parental unit and one or more generations of offspring. Parental units are largely monogamous for at least the season and often across seasons. We have not included species that have parent-offspring associations <6 months in duration and/or studies in which there is no genetic confirmation of group membership such as in the Cordylidae. This list is therefore less inclusive than Davis, *et al.* (2011). We have not indicated levels of extra-pair paternity because of differences in the way these data have been collected (see text). The sleepy lizard, *Tiliqua rugosa*, does not associate with its offspring but is included here because it forms life-long stable pairs and is part of the clade containing the *Egernia* group. We also include the few members of the *Egernia* group that we know are solitary. *Cyclodomorphus* is the only member of the clade containing the *Egernia* group not listed here because family living has not been reported (or properly tested for).

Family	Species	Solitary	Nuclear family	Extended family	Group size	Reference	
Scincidae	<i>Liopholis inornata</i>	X			N/A	Chapple, 2003	
	<i>Liopholis kintorei</i>		X			McAlpin, <i>et al.</i> , 2011	
	<i>Liopholis whitii</i>		X		2–6	Chapple & Keogh 2005, 2006; While, <i>et al.</i> , 2009b, 2011	
	<i>Tiliqua rugosus</i>	X			2		
	<i>Tiliqua adelaidensis</i>	X			N/A		
	<i>Bellatorias major</i> *		?	?	3–8	Osterwalder, <i>et al.</i> , 2004	
	<i>Bellatorias frerei</i>			X (genetic evidence)		Fuller, <i>et al.</i> , 2005	
	<i>Egernia kingii</i> **			X		Masters & Shine, 2003	
	<i>Egernia cunninghami</i>			X	2–27	Stow & Sunnock, 2004; Stow, <i>et al.</i> , 2001	
	<i>Egernia saxatilis</i>		X		2–14	O’Connor & Shine, 2003	
	<i>Egernia striolata</i>		X		2–4	Duckett, <i>et al.</i> , 2012; Bull & Bonnett, 2004	
	<i>Egernia stokesii</i>				X	2–17	Duffield & Bull, 2002; Gardner, <i>et al.</i> , 2001, 2002, 2007
	<i>Lissolepis coventryi</i>	X				N/A	Chapple, 2003
	<i>Gnypetoscincus queenslandiae</i>			X (loose)		2–9	Sumner, 2006
	<i>Corucia zebrata</i> ***	X				2–5	Hagen, <i>et al.</i> , 2013
	Xantusiidae	<i>Xantusia vigilis</i> ****		X	X	2–20	Davis, <i>et al.</i> , 2011; Zweifel & Lowe, 1966

\* Male-female bonds, some association with juveniles, telemetry study.  
 \*\* Based on one family observed for 10 years.  
 \*\*\* Mostly solitary, some mixed groups.  
 \*\*\*\* 22% (26/117 groups) occur in unrelated groups, 57% (67/117 groups) in nuclear families, and 21% (25/117 groups) in extended families.



are between females, although males and females form relatively strong bonds (Strickland, *et al.*, 2014). While females may show social affiliation with a particular male, they still mate multiply and fertilization favors males with higher levels of heterozygosity (i.e. less inbred males, Frère, *et al.*, 2015). Sociality in lizard systems that are not kin-based is likely more complex than we think, and not simply an artefact of territoriality.

### 13.2.2 Monogamous Pair Bonds and Kin-based Family Living

A much less common form of social organization in lizards is a single, long-term monogamous pair. There are two forms of long-term monogamy in lizards: (1) a single social unit consisting of a male and female but with no association to their offspring; and (2) a parental unit and one or more generations that live together over the long-term. In the former option, there is one well documented example of a male and female unit with no offspring association: the sleepy lizard, *Tiliqua rugosa* (Figure 13.1), which has been studied by Bull and colleagues for more than thirty years (Bull, 1994; Leu, *et al.*, 2015). This species forms long-term pair bonds that frequently exceed 10 years and one particular pair currently stands at more than 27 years as of 2013 (Leu, *et al.*, 2015). Males and females pair-up six to eight weeks before they copulate and then separate shortly thereafter. However, there is no parental care or parent-offspring association (Leu, *et al.*, 2011). Pairs that have been together longer tend to come together earlier in the breeding season, breed sooner, and are thought to co-ordinate their reproductive behaviors more effectively (Leu, *et al.*, 2015). In the lizard group *Egernia*, sociality consisting of a parental unit and kin is common. The *Egernia* group consists of three genera in which stable family groups with sometimes multiple cohorts of offspring have been documented (Table 13.1, Figure 13.1). Additionally, kin-based family groups have also been documented in the North American desert night lizard (Xantusiidae: *Xantusia vigilis*). Groups in this species typically consist of kin and at least one parent that refuge together in decaying logs or under rocks (Davis, *et al.*, 2011; Davis Rabosky, *et al.*, 2012).

### 13.2.3 Nest Attendance, Brooding, and Parent-Offspring Associations

Solitary species that do not readily fall into a sociality category may nevertheless exhibit parental care and form short-term bonds with their offspring during a brief postpartum phase. Among squamate reptiles, these species may be oviparous or viviparous. Egg-laying species will either actively brood their eggs or simply remain at the nest and many species will actively defend their nests against potential predators (Somma, 2003; Huang, 2006; Stahlschmidt & DeNardo, 2011; While, *et al.*, 2014a). In the lizard *Eutropis longicauda*, females cannot recognize their own eggs but they defend their nests as an extension of territorial behavior (Huang & Pike, 2011). Parental care then ceases immediately, or shortly after the emergence of young. In viviparous species (and some oviparous species), there can be a more prolonged association between offspring and parents that may persist from days (in some snakes) to a few years (in some members of

the *Egernia* group, Greene, *et al.*, 2002, Chapple, 2003; Somma, 2003; While, *et al.*, 2014a). For example, gravid female live-bearing North American pitvipers (more than 33 species in 8 genera) are particularly well-known for firstly aggregating at rookeries to give birth and secondly for forming mother-offspring associations. These associations typically last until they first shed their skin, sometime in the second week following birth (Greene, *et al.*, 2002). Female rattlesnakes are also more aggressive during the time that they are in association with their offspring (Greene, *et al.*, 2002). In timber rattlesnakes, gravid females are more likely to associate with female kin when they aggregate at rookeries, while neonates stay close to their mother (Clark, 2004). Timber rattlesnakes are also capable of kin recognition (Clark, 2004). Collectively, these and other snake species show the hallmarks of sociality but do not form stable long-term groups. Nonetheless, they may prove valuable for understanding the early evolution of parental care and sociality in reptiles (Schuett, *et al.*, 2016).

### 13.3 Why Lizards Form Social Groups

A wide range of lizard and snake species aggregate for ecological reasons (reviewed in Graves & Duvall, 1995; Gardner, *et al.*, 2016). These aggregations range in size from just a few individuals to several thousand and occur either because optimal refuges are limited and/or because of the physiological benefits of grouping (Graves & Duvall, 1995; Lancaster, *et al.*, 2006; Mouton, 2011). The types of shelters that promote aggregations in squamates are those that offer thermal benefits (Shah, *et al.*, 2003; Shah, *et al.*, 2004), refuge from predators (Mouton, 2011), hibernacula in temperate regions with cold winters (Gregory, 1984; Graves & Duvall, 1995), or oviposition/rookery sites (Graves & Duvall, 1995; Doody, *et al.*, 2009). While the primary reason for an aggregation may be ecological (e.g. refuge) or physiological (e.g. temperature/water loss), there could still be social benefits from grouping. Furthermore, it has been hypothesized that grouping behavior as a result of abiotic factors could act as an initial trigger for the evolution of sociality (Graves & Duvall, 1995; Shah, *et al.*, 2003; Lancaster, *et al.*, 2006; Davis Rabosky, *et al.*, 2012). Several studies have tested whether lizards will still group when offered an abundance of shelters under uniform environmental conditions in the lab. The results from these studies are mixed. For example, the cordylid lizard *Platysaurus broadleyi* occupies communal refuges consisting of more than 100 individuals in the wild (M. Whiting, *unpublished data*) but does not group in captivity and males avoid sharing refuges. Conversely, both the gecko *Nephruerus milii* and the cordylid *Ouroborus cataphractus* will continue to aggregate under uniform conditions in the lab (Shah, *et al.*, 2003; Visagie, *et al.*, 2005). At present, the potential role of environmental factors in enhancing social affiliation, and thereby potentially favoring sociality, is poorly understood.

In contrast, explanations for the emergence, maintenance and diversification of more stable social organization (i.e. those found in the *Egernia* group) have focused mostly on explanations analogous to those put forward for family-living birds and mammals (e.g. Komdeur, 1992; Koenig, *et al.*, 1992; Hatchwell & Komdeur, 2000). Simply put,



social organization emerges as a result of constraints imposed by the availability of key habitat features such as permanent retreat sites. Thus, while there may be additional benefits of grouping together similar to those identified for other less stable aggregations of lizards (and other organisms), it is unlikely that these benefits are the source of selection on lizards' social organization itself. However, *X. vigilis* that aggregated had both higher reproductive success and survival compared to solitary individuals (Davis Rabosky, *et al.*, 2012), suggesting that a key feature can also be the simple presence of the conspecifics themselves. Below, we address the potential benefits of aggregating first, before detailing the important role that ecology plays in mediating the evolution of social organization within the *Egernia* group and *X. vigilis*.

### 13.3.1 Resource Acquisition and Use

A key component of the ecology of the *Egernia* group is its reliance on permanent shelter sites (Table 13.2). These shelter sites are either established structures such as rock outcrops or tree hollows (Chapple, 2003; Michael, *et al.*, 2010), or they have been constructed via the excavation of deep and complex burrow systems, sometimes by multiple generations of the same family (McAlpin, *et al.*, 2011). These structures tend to be patchily distributed across the landscape and separated from other such outcrops by unsuitable habitat (Duffield & Bull, 2002; O'Connor & Shine, 2003). However, the extent of heterogeneity in habitat availability differs markedly between species. In burrowing species, suitable habitat can be relatively homogenous, separated by a matter of meters. In contrast, for species that live on rocky outcrops (e.g. *E. striolata* and *E. stokesii*; Table 13.2), patches of suitable habitat can be separated by distances of 50 meters and often much more (Gardner, *et al.*, 2001), providing considerable barriers to dispersal. As a consequence of this patchy distribution, acquisition of shelter sites has been suggested to be the key factor that influenced the emergence and diversification of social organization in the *Egernia* group. Indeed, most of the family-living species live on either rock outcrops or trees (Table 13.2) with only one exception (*L. kintorei*). In contrast, all the *Tiliqua* are solitary except *T. rugosa*, which has life-time pair bonds during the breeding season, and do not live in discrete habitats.

The majority of studies on the role of permanent shelter sites on the emergence of social organization have focused on the extent to which habitat availability constrains dispersal. However, some authors have suggested that group organization may influence the ability of individuals to acquire high quality shelter sites. For example, Michael, *et al.* (2010) found group size in *Egernia striolata* to be positively correlated with habitat quality (independently of crevice size), with larger social groups found in the highest quality areas of the rock outcrops (e.g. the top, with greatest access to basking sites and reduced predation risk). They suggested that larger groups of lizards might be better able to defend high-quality home ranges than solitary individuals. However, an equally likely scenario is that more extensive habitat supports more individuals and therefore has larger groups. Interestingly, there is the possibility that family groups can usurp other groups and gain access to higher quality resources such as basking areas. *Egernia saxatilis* families will control basking areas at the expense

**Table 13.2** Ecological characteristics of family living lizards. All species are viviparous. See Greer (1989) and Chapple (2003) for additional ecological information. Age at maturity is the year in which individuals become sexually mature. We include the same solitary species from Table 13.1 here. All species are in the family Scincidae except *X. vigilis*, which is in the Xantusiidae.

Species	Rock-dwelling	Semi-arboreal	Terrestrial	Longevity (yrs)	Litter size	Age at maturity (yrs)	Refuge type	Habitat	Reference
<i>Liopholis inornata</i> *			X		1–4	2	Burrow	Sandy, xeric	Chapple, 2003
<i>Liopholis kintorei</i>			X		1–7	2	Burrow	Sandy, xeric	McAlpin, <i>et al.</i> , 2011; Chapple, 2003
<i>Liopholis whitii</i>			X	13	1–4	2	Rock crevices, logs	Coastal heath, grasslands, dry sclerophyll forest, open woodland	Chapple & Keogh, 2005, 2006; White, <i>et al.</i> , 2009b, 2011
<i>Tiliqua rugosus</i> **			X	>50	1–3	5	Burrows, vegetation	Chenopod shrubland, xeric	Bull, <i>et al.</i> , 1993; Leu, <i>et al.</i> , 2011; M. Bull <i>unpublished data</i>
<i>Tiliqua adelaidensis</i> *			X	9	1–4	2	Burrow	Grassland, spider burrows	Milne, <i>et al.</i> , 2002; Schoefield, <i>et al.</i> , 2014; Hutchinson, <i>et al.</i> , 1994
<i>Bellatorias major</i>			X	11–23	3–7		Hollow logs	Rainforest, wet sclerophyll forest	Osterwalder, <i>et al.</i> , 2004; Shea, 1999
<i>Bellatorias frerei</i>			X				Burrows, hollow logs	Well-watered forest, seasonally dry forest	Fuller, <i>et al.</i> , 2005
<i>Egernia kingii</i>			X	>10	2–11	3	Rock crevice	Heath	Masters & Shine, 2003; Chapple, 2003
<i>Egernia cunninghami</i>	X			>50***	4–8	5	Rock crevice	Open <i>Eucalyptus</i> woodland, exposed rock outcrops	Stow & Sunnocks, 2004; Stow, <i>et al.</i> , 2001
<i>Egernia saxatilis</i>	X	X			1–4		Rock crevice	Open <i>Eucalyptus</i> woodland, exposed rock outcrops	O'Connor & Shine, 2003

Table 13.2 (cont.)

Species	Rock-dwelling	Semi-arboreal	Terrestrial	Longevity (yrs)	Litter size	Age at maturity (yrs)	Refuge type	Habitat	Reference
<i>Egernia striolata</i>	X	X			1-7	2-3	Crevices in rock, logs, tree hollows	Open <i>Eucalyptus</i> woodland, temperate semi-arid woodland	Duckett, <i>et al.</i> , 2010; Bull & Bonnett, 2004
<i>Egernia stokesii</i>	X	X		>12	1-8	5-6	Rock crevice	Rocky outcrops in grassland	Duffield & Bull, 2002; Gardner, <i>et al.</i> , 2001, 2002, 2007
<i>Lissolepis coventryi</i> *			X	>8	1-4	2-3	Vegetation, burrows	Wetlands, swampy heath	Clemenn, <i>et al.</i> , 2004; Chapple, 2003
<i>Gnypetoscincus queenslandiae</i>			X	ca. 10	1-5	6.5	Rotting logs	Rainforest	Summer, 2006
<i>Corucia zebrata</i>		arboreal			1		Tree hollows	Rainforest	Hagen, <i>et al.</i> , 2013
<i>Xantusia vigilis</i>			X	8-10	1-2	2-3	Logs, under rocks	Joshua tree woodland, desert	Davis, <i>et al.</i> , 2010; Zweifel & Lowe, 1966

\* Solitary species.

\*\* Pairs up before and during breeding season.

\*\*\* Based on one captive animal; see text.

of a rival family during staged trials in the lab (O'Connor & Shine, 2004), but the degree to which this might occur in the wild is unknown.

In addition to asking why and how sociality, and in particular, family living evolved, we should also ask why family living is so rare among squamate reptiles. The answer to the latter question may have something to do with diet and foraging mode. Almost all species are primarily insectivorous (Vitt, *et al.*, 2003) and adopt either a sit-and-wait foraging mode or an active/wide-foraging mode although these differences are not always clear-cut (McBrayer, *et al.*, 2007). Actively foraging lizards move through the landscape and use vomerolfaction (i.e. the ability to detect prey chemicals through tongue-flicks and processing of chemical cues in the Jacobsen's organ in the roof of the mouth) to find hidden prey, which they then retrieve (Cooper, 1994). For these species, there is likely to be less competition for a food source that is mostly scattered if they forage alone. Furthermore, there may be additional costs to coordinating with other individuals such as attracting the attention of predators and any cognitive and behavioral constraints associated with coordinating movements. Furthermore, active foragers have significantly higher metabolic rates than ambush foragers (Brown & Nagy, 2007). This foraging-centric lifestyle may preclude group or family living, although this idea has received no significant attention in the literature and would be difficult to test beyond a correlation or comparative analysis.

Ambush foraging lizards that are group living have the added challenge of localized competition for food. To some degree, this competition may be ameliorated through excursions to prey patches away from the group. For example, the armadillo lizard, *Ouroborus* (formerly *Cordylus*) *cataphractus*, lives in stable, large aggregations (commonly 2 to 6, but up to 55 individuals, Effenberger & Mouton, 2007) and is thought to reduce food competition by binge feeding at termite foraging ports away from the group, particularly during the dry season (Shuttleworth, *et al.*, 2008, 2013). The family-living members of the *Egernia* group are typically omnivorous or even, herbivorous, as adults (Chapple, 2003). Although we know very little about their foraging behavior, they are not active foragers although they likely make short excursions to feed on plant matter. Furthermore, they are frequently confined to rock outcrops or trees, which are discrete units of habitat normally associated with sit-and-wait foraging lizards. While their foraging mode and diet may be an outcome of non-social factors and may have preceded family living, being bound to a discrete resource in the case of ambush foragers, could facilitate kin-based sociality.

### 13.3.2 Predator Avoidance

The stable social aggregations observed in the *Egernia* group have also been suggested to provide benefits in terms of reduced predation risk. Enhanced vigilance and reduced predation risk were first proposed to explain the prolonged associations between male and female *T. rugosa* (Bull & Pamula, 1998). Positive benefits of group organization on anti-predatory behavior have also been documented in large *Egernia* social groups. For example, groups of both *E. stokesii* and *E. cunninghami* have been shown to detect predators earlier than solitary individuals (Eifler, 2001;

Lanham & Bull, 2004). The complex burrow and crevice networks used by many species are likely to reduce predation risk further.

### 13.3.3 Homeostasis

In addition to general habitat constraints, much of the behavior and life history of lizards and snakes more broadly is driven by thermal requirements dictated by their environment (Pianka & Vitt, 2003). For example, temperature has a profound effect on growth rates, as well as reproductive mode, frequency, and activity (Vitt & Seigel, 1985; James & Shine, 1988; Warner & Shine, 2007; Radder, *et al.*, 2008). Furthermore, in more temperate regions there are a limited number of suitable over-wintering sites and this results in aggregations of individuals in hibernation or during temperatures unsuitable for activity. The close proximity of these individuals as a consequence of physiological constraints may have a bearing on sociality that is little appreciated. Thermoregulatory benefits have been associated with social aggregations in *Egernia* and *X. vigilis*. In winter, *X. vigilis* that aggregated, and juveniles in particular, experienced significant thermal benefits that translated into higher fitness (Davis Rabosky, *et al.*, 2012). In *E. stokesii*, group size has a positive effect on heat retention, with larger groups maintaining higher nighttime body temperatures than smaller groups (Lanham, 2001). Grouping behavior in *Egernia* group species may also have indirect effects on homeostasis by allowing increased investment in thermoregulatory behavior due to decreased investment in other behaviors like vigilance. For example, *Egernia stokesii* exhibit reduced vigilance behavior and flight initiation distances in groups, which allowed individuals more time to bask (Lanham & Bull, 2004). Finally, the reliance on permanent shelter and crevice sites also provides individuals homeostatic benefits as burrows act to both reduce temperature oscillations as well as enhance humidity (Henzell, 1972; Webber, 1979).

### 13.3.4 Mating

Mating benefits are not only one of the key drivers of social behavior observed in many lizard species (Graves & Duvall 1995), but they are also thought to be responsible for the relatively simple polygynous mating systems based on territoriality or dominance hierarchies, characteristic of the majority of reptile social systems (Stamps, 1983). As detailed earlier, social organization in the *Egernia* group emerges as a result of restricted dispersal rather than direct benefits associated with increased access to mates. Nevertheless, variation in social organization within populations largely emerges as a result of a male's ability to monopolize areas that can attract multiple females. For example, *Liopholis whitii* (Figure 13.1) males that occupy areas with high rock crevice availability are more likely to acquire multiple female partners (e.g. polygynous social groups) than those in areas with fewer rock crevices (Chapple & Keogh, 2006; G. While, *personal observations*). In *X. vigilis*, social behavior greatly impacts male reproductive success. Of 230 neonates molecularly assigned to 123 sires, none were the offspring of males that were known to be solitary the preceding winter (approximately a third of all males, Davis Rabosky, *et al.*, 2012).

Seasonal monogamy can be driven by a wide variety of factors including obligate parental care or a shortage of receptive females, which in turn may drive mate-guarding behavior (Lukas & Clutton-Brock, 2013). However, different factors could be driving long-term monogamy. The mate familiarity hypothesis suggests that long-term monogamy is adaptive because it results in better coordination of reproductive behavior, particularly in organisms exhibiting biparental care (e.g. Black, 1996; Black, 2001; Mariette & Griffith, 2012). Nevertheless, long-term monogamy in non-avian taxa that do not provision their young could still be adaptive if it facilitates the priming and/or coordination of male and female reproductive cycles and behavior. For example, in the sleepy lizard, *Tiliqua rugosa*, long-term partners pair up earlier in the season and have their young earlier in the year (Leu, *et al.*, 2015). Although this could give juveniles a head start, and therefore, a potential fitness advantage, this hypothesis remains untested. Similarly, there may be benefits to stable long-term monogamy in coordinating reproduction in the *Egernia* group. To our knowledge, the benefits of mate familiarity and coordinated reproduction have never previously been considered for lizard systems other than the sleepy lizard. This element could be important in explaining some of the variance in fitness benefits of monogamy and should be considered in future studies.

### 13.3.5 Offspring Care

Although the level of parent–offspring interaction in lizards that exhibit kin-based social organization is substantially lower than in other vertebrate species (e.g. full parental provisioning, Clutton-Brock, 1991), it nevertheless shows a greater level of parent–offspring interaction than previously reported in the majority of squamate species. For example, delayed juvenile dispersal is a key feature of both *X. vigilis* (Davis, *et al.*, 2011) and *Egernia* group social organization (Gardner, *et al.*, 2001; O'Connor & Shine, 2003; Stow & Sunnucks, 2004; Davis, *et al.*, 2011). Thus, the emergence of sociality within these groups is closely linked to the benefits of delayed dispersal of offspring. Moreover, lizards are capable of social learning and in water skinks, *Eulamprus quoyii*, young lizards are more likely to pay attention to social information than older individuals (Noble, *et al.*, 2014). For species that live in family groups, there could be significant benefits to social learning, particularly in juveniles and subadults.

Offspring may benefit from associations with parents in a number of ways. First, offspring may gain increased access to basking locations, foraging opportunities, and retreat sites (Bull & Baghurst, 1998; O'Connor & Shine, 2004; but see Langkilde, *et al.*, 2007). Furthermore, the presence of high levels of genetic relatedness within social groups in species such as *E. stokesii* suggests that offspring may gain from prolonged parental care through the inheritance of territories (Gardner, *et al.*, 2001). Alternatively, offspring may benefit from extended parent–offspring interactions via a reduction in the risk of infanticide and conspecific aggression (O'Connor & Shine, 2004; Sinn, *et al.*, 2008). *Egernia* group species frequently live in highly saturated environments whereby aggression towards conspecifics is common. Indeed, infanticide has been identified as a key cause of offspring mortality in a number of these species (Post, 2000; Lanham & Bull, 2000; O'Connor & Shine, 2004). Parents of most species vigorously and



aggressively defend their home range from conspecifics (Chapple, 2003; O'Connor & Shine, 2004), providing a significant benefit to the offspring who reside within it. Experimental evidence from *E. saxatilis* has shown that the presence of a parent nearly eliminates all of the aggression displayed towards its offspring by unrelated adults (O'Connor & Shine, 2004). Work on both *E. saxatilis* and *L. whitii* has shown that female aggression is heightened during periods of post-partum parent offspring association, when offspring are presumably most at risk (O'Connor & Shine, 2004; Sinn, *et al.*, 2008). As a consequence, the extent of aggression a female displays towards a conspecific is the key predictor of offspring survival in *L. whitii* (Sinn, *et al.*, 2008).

### 13.3.6 Other Reasons: Parasites and Infection Risk

One additional potential factor suggested to explain the emergence of social living in the *Egernia* group is parasite prevalence and risk of infection. Parasites have been suggested to select both for and against social living. For example, group living can increase the risk of infection by providing parasites with easy transmission between individuals (Altizer, *et al.*, 2003). Alternatively, group living can decrease parasite transmission through dilution effects (Mooring & Hart, 1992), cooperation in ectoparasite removal (Wikelski, 1999), or through minimizing contact with individuals outside the social group whom may carry novel parasites (Bull & Burzacott, 2006; Godfrey, *et al.*, 2009). In the *Egernia* group, early work suggested that long-term monogamy played a crucial role in reducing the risk of parasite transmission by minimizing interactions with other individuals. Studies of “divorce” (i.e. planned separation) in *T. rugosa* provide some evidence for this hypothesis: males who separated from partners one season to the next had significantly higher parasite prevalence than males who retained partners (Bull & Burzacott, 2006). In contrast, parasite prevalence in *E. stokesii* had no effect on group size (Godfrey, *et al.*, 2006). However, both an individual’s position within a transmission network (based upon shared shelter sites) as well as the level of within-group relatedness have been shown to be strongly related to the risk of infection from parasites (Godfrey, *et al.*, 2006, 2009). Work on other social and less social species is required to fully appreciate the role that parasite prevalence, along with some of the other factors detailed above, play in mediating social organization.

## 13.4 The Role of Ecology in Shaping Sociality in Lizards

As mentioned above, ecology is likely to have played a central role in mediating the evolution of social organization in lizards, particularly within the *Egernia* group.

### 13.4.1 Habitat and Environment

Habitat constraints are fundamental to explaining the emergence of kin based social organization within the *Egernia* group and potentially lizards more generally. While life

history traits may act as a powerful precursor to social living, variation in habitat characteristics are likely to ultimately influence between and within species variation in sociality (Duffield & Bull, 2002). As detailed above, species in the *Egernia* group are typically found in close association with permanent shelter and crevice sites from which they undertake the majority of their basking, feeding, and social activities (Chapple, 2003, Table 13.2). Because of a dependence on such sites, populations are typically highly saturated with intense competition over a limited number of patchily distributed retreat sites that results in high levels of conspecific aggression and high juvenile mortality (Chapple, 2003; O'Connor & Shine, 2004; Langkilde, *et al.*, 2005). Habitat heterogeneity is therefore likely to influence the two key components of social organization in the *Egernia* group: the composition of long-term stable pair bonds and delayed juvenile dispersal.

Many species of *Egernia* (e.g. *E. stokesii*, *E. cunninghami*, *E. saxatilis* and *E. striolata*) live in rocky outcrops, isolated from other species and populations by unsuitable habitat (Duffield & Bull, 2002). Given that large scale dispersal is generally low within the genus (Stow, *et al.*, 2001; Duffield & Bull, 2002; Chapple & Keogh, 2005), a lack of available crevice sites within an outcrop means that the only option open for individuals is to share crevices (Duffield & Bull, 2002; Chapple, 2003). The resulting social heterogeneity will in turn dictate the mating system by influencing the extent to which males can monopolize females (monogamy versus polygyny), the opportunity for extra-pair copulations (Uller & Olsson, 2008; Wapstra & Olsson, 2014), and the costs of undertaking extra-pair copulations. Importantly, social density and resource availability related to habitat suitability are also likely to influence patterns of offspring dispersal by mediating the costs and benefits of delayed dispersal for offspring and prolonged care for parents. Kin selection could then influence tolerance of offspring within the natal home range, as opposed to the crevices of other individuals, ultimately resulting in the formation of closely related family groups (While, *et al.*, 2009a).

An obvious prediction is that higher levels of social organization should evolve where dispersal between available habitat patches is limited. This prediction can be tested both empirically (e.g. by carrying out large-scale field experiments in enclosures where habitat availability is manipulated) and by comparing social organization between populations of the same species that use different habitats (e.g. *E. striolata*, which lives on trees or rocks). A study across 44 populations of *E. striolata* confirmed a strong environmental component to variation in social organization, with lizard group size correlating with various attributes of the rock outcrops (Michael, *et al.*, 2010). In contrast, a study across seven populations of *E. stokesii* found strong conservatism in social group composition (Gardner, *et al.*, 2007). Furthermore, populations of *E. cunninghami* did not differ in social organization between a fragmented and non-fragmented habitat although there were differences in dispersal between the populations (Stow & Sunnucks, 2004). These results suggest that social organization in the *Egernia* group may be influenced by phylogenetic constraint (Gardner, *et al.*, 2007). Testing the relative roles of phylogenetic history and current ecology remains a major challenge for future research on lizard social organization (Gardner, *et al.*, 2016).

### 13.4.2 Biogeography

Species in the *Egernia* group are widespread across the entire range of the Australian continent and occupy a range of biomes (Chapple, 2003; Gardner, *et al.*, 2008). Chapple & Keogh (2004) showed that the *Liopholis* genus consists of two major clades that have undergone parallel adaptive radiations: those that are obligate burrowers in sandy deserts in the interior and those that are temperate-adapted rock-dwelling species. The arid zone *Liopholis* are the product of a single origin and subsequent radiation. More detailed biogeographic study of the remaining *Liopholis* will help clarify the role of history and the environment in generating the current distribution and diversity within the group. Interestingly, throughout these parallel adaptive radiations sociality has remained relatively conserved. In lizards more generally, species living in stable aggregations, which may include family groups, are distributed across all continents and a range of latitudes, suggesting that biogeography may not be as important as other factors.

### 13.4.3 Niches

Family-living lizards appear to occupy a relatively narrow and specialized habitat niche centered on a structural refuge consisting of either a rock crevice/outcrop, a burrow, or a refuge in a tree. Tree skinks (*E. striolata*) are slightly more general and will use both rock and upright or fallen trees. Likewise, many lizard species lacking kin-based sociality may occupy a similar niche, particularly on other continents. To properly understand the potential role of the niche, including all its dimensions, in influencing social organization and structure, we need to test for, and survey, a broader spectrum of species for sociality.

## 13.5 The Role of Evolutionary History in Shaping Sociality in Lizards

Given the enormous species richness of lizards, family living is extraordinarily rare overall (Table 13.1). Recent advances in our understanding of higher-level snake and lizard relationships (Wiens, *et al.*, 2012; Pyron, *et al.*, 2013) has helped depict an evolutionary picture of squamate reptile sociality. Based on extensive molecular sequencing, eight major groupings of squamates have been identified. Within these groups are a much larger number of lineages, each of which may include multiple families and subfamilies (Pyron, *et al.*, 2013). Interestingly, family living has been identified in only one of these major clades, the Scincoidea. Having said that, it is likely that family living will be documented in other clades in the future (Doody, *et al.*, 2013), such as the Iguania clade (e.g. Tropicuridae: *Liolaemus*, E. Santoyo-Brito & S. Fox, unpublished data) or even Gekkota (Diplodactylidae: *Hoplodactylus*, Barry, *et al.*, 2014), due to field observations of group age/sex composition suggesting family structure but for which relatedness has not yet been examined. There are four families within Scincoidea (Xantusiidae, Gerrhosauridae, Cordylidae and Scincidae), and each is

further divided into multiple subfamilies. The Cordylidae has numerous instances of species living in stable aggregations (Mouton, 2011). There is a distinct possibility that family living occurs in some of these species, but this remains to be confirmed by detailed genetic and population study. Similarly, the Gerrhosauridae are also known to aggregate, but family living has not been examined in this group. The observation that juveniles are frequently seen in association with adults is suggestive of family living (M. Whiting, *personal observations*). Finally, there is a single case of family living in the Xantusiidae, with the possibility of others (Davis, *et al.*, 2011).

The vast majority of instances of family living are all in the Scincidae and more specifically, in the *Egernia* group. The likely ancestor of the *Egernia* group is the prehensile-tailed skink *Corucia zebrata* from the Solomon Islands, from which it diverged about 25 ma (Skinner, *et al.*, 2011). *Corucia zebrata* does not live in family groups, although individuals nearest to one another are more closely related than expected by chance (Hagen, *et al.*, 2013). In contrast, family living is widespread across the *Egernia* group (Table 13.1). Evidence for family living has been produced in almost every study targeting sociality in this complex thus far, although this likely represents a bias towards species suspected of kin-based sociality based on observations of group living. Although the relationships among the *Egernia* group are mostly resolved (Gardner, *et al.*, 2008), a comprehensive phylogeny with greater population coverage is currently in preparation and will give a clearer perspective on the origins of kin-based sociality in the group. Furthermore, many of the gaps will likely be filled in the coming years now that sociality is receiving increased focus in this complex. Overall, family living has evolved only a few times independently in lizards.

## II SOCIAL TRAITS

### 13.6 Traits of Social Species

Lizards with kin-based sociality tend to have numerous reproductive, life history, and social traits in common. Below we discuss the most important traits for understanding social evolution in lizards.

#### 13.6.1 Cognition and Communication

Lizards have been the subjects of considerable recent study with respect to learning ability. Not only are lizards capable of behavioral flexibility (Leal & Powell, 2012; Clark, *et al.*, 2014) but also social learning (Noble, *et al.*, 2014; Kis, *et al.*, 2014). The *Egernia* group may be an excellent model system with which to test social intelligence theory – the idea that social behavior sets the stage for increasingly complex cognition (Byrne & Bates, 2007) – because sociality is variable and they offer a unique phylogenetic control with closely related species varying in their degree of sociality.

Territorial lizards (particularly agamids and iguanids) are often conspicuously colored (males) and use dynamic visual signals to communicate at a distance (Ord &

Martins, 2006). This is consistent with a polygynous mating system. Conversely, the *Egernia* group and *Xantusia vigilis* lack obvious sex-based color differences and are not known for using conspicuous dynamic visual signals (Zweifel & Lowe, 1966; Chapple, 2003). This may be more in line with a monogamous mating system, although males do defend core areas. *Egernia*, and indeed many species of lizards, tongue-flick to acquire social information, which may be important for recognizing kin (Bull, *et al.*, 1999; Bull, *et al.*, 2001). This information can be obtained directly from the substrate or the animal itself. With the exception of color-based and dynamic visual signals, the mode of communication used by family-living lizards is therefore not unique compared to many less social and non-family living species.

### 13.6.2 Lifespan and Longevity

Kin-based sociality and/or monogamy in lizards are accompanied by increased longevity. The *Egernia* group are known to be long-lived, although data are limited to a relatively few long-term studies (Table 13.2). In the case of the monogamous sleepy lizard, individuals are able to live to be more than 50 years of age (C. Bull, *unpublished data*). Likewise, almost all the *Egernia* for which there are data are thought to live for more than 10 years. For example, *Egernia stokesii* live more than 25 years (Gardner, *et al.*, 2016), and a captive *Egernia cunninghami* is still alive after more than 50 years (P. Harlow, *unpublished data*). Finally, free-living desert night lizards, *X. vigilis*, can live at least 8 to 10 years and likely many more years than that based on undetectable growth in older individuals (Zweifel & Lowe, 1966; Davis, *et al.*, 2011). In contrast, a large proportion of lizards in less social species may only live 5 years or less, some are annual, and others only live for a few months (Pianka & Vitt, 2003; Karsten, *et al.*, 2008; Wilson, 2012;). Longevity is also accompanied by a suite of correlated life history traits including delayed maturity and high reproductive investment in relatively few offspring (Pianka & Vitt, 2003). As life history characteristics are less conserved in lizards than in birds, the *Egernia* group (and lizards in general) may provide an excellent model system for teasing apart the relative influence of habitat and life history traits – or their interaction – in promoting the evolution of family living (Chapple, 2003).

### 13.6.3 Fecundity

Fecundity (measured as relative clutch mass) can be correlated with and constrained by a range of factors including lifespan, body size, habitat use, and foraging mode (Huey & Pianka, 1981; Vitt, 1981; Pianka & Vitt, 2003; Uller & While, 2014). For example, females of many lizard species may have large clutch sizes and relative clutch mass, which in turn is linked to their ambush foraging strategy and even their diet (Vitt & Price, 1982). Conversely, the *Egernia* group all has relatively small litters of large offspring (mode: 1 to 4; range: 1 to 11) and in this sense, are more akin to traditional *K*-selected organisms. Furthermore, compared to many other lizard species, they are typically large-bodied, slow to mature (typically 2 to 3 years, but up to 5 years), skip

opportunities to reproduce (i.e. not reproduce every year), and invest more in individual offspring (Chapple, 2003, Table 13.2). *Xantusia vigilis* shows the same patterns of small litter size (1 to 2, very rarely 3), of proportionately large offspring, late maturity (2–3 years), and missed reproduction especially in years of low rainfall (Miller, 1951; Zweifel & Lowe, 1966). In general, the prediction that post-hatching parental care is more likely to be associated with high quality offspring is supported in family-living species although once again, it has a phylogenetic bias.

#### 13.6.4 Age at First Reproduction

In general, lizard reproduction has two extremes: fast maturing (often oviparous) species that mature rapidly and breed (and die) at a young age, and late maturing (often viviparous) species that mature slowly, breed later in life, and have better prospects for living much longer (Pianka & Vitt, 2003). Members of the *Egernia* group tend to be late maturing with variation in time to reach maturity between species related to body size such that small-medium sized species mature in 2 to 3 years, while larger species such as *E. cunninghami* may take at least five years (reviewed in Chapple, 2003).

#### 13.6.5 Dispersal

Delayed dispersal is a feature of all family-living lizards. Some species will disperse after their first year, while others may stay in a family group for 3 or more years (Gardner, *et al.*, 2001; O'Connor & Shine, 2003; Stow & Sunnucks, 2004; Davis, *et al.*, 2011). Ecological drivers of dispersal are largely unstudied, although *E. cunninghami* in deforested habitat had reduced dispersal ability (Stow, *et al.*, 2001). In *X. vigilis*, cross-fostering experiments show that juveniles placed with unrelated individuals were more likely to disperse and move greater distances than juveniles released with genetic relatives (i.e. mothers and siblings), suggesting kin presence itself can actively promote delayed dispersal (Davis, 2012). Clear dispersal patterns with regards to sex are yet to be documented, with some species exhibiting no sex bias in dispersal (Bull & Cooper, 1999; Gardner, *et al.*, 2012), others showing a male bias (Gardner, *et al.*, 2001, Stow, *et al.*, 2001), and still others showing evidence of both (Chapple & Keogh, 2005). It has been hypothesized that the predominant mating system of a population will dictate which sex disperses, with male-biased dispersal favored in polygynous mating systems (e.g. many mammal species) and female-biased or no sex-biased dispersal favored in monogamous mating systems (e.g. many bird species) (Greenwood, 1980; Perrin & Mazalov, 2000). Recent studies suggest that this relationship is more complex, and that social systems play a key role in dictating the intensity and direction of dispersal (Galliard, *et al.*, 2003; Lawson Handley & Perrin, 2007). Therefore, the within-population variation in both mating and social systems exhibited by *Egernia* group species may be responsible for the lack of a clear sex-biased dispersal pattern (e.g. Chapple & Keogh, 2005).



### 13.6.6 Other Traits: Reproductive Mode, Parental Care and Family-Living

All species that live in family groups are viviparous, a mode of reproduction present in only about 17 percent of squamates (Pyron & Burbrink, 2014). While there are numerous instances of parental care among oviparous species through brooding or nest protection (Somma, 2003), post-partum care is largely restricted to viviparous species (While, *et al.*, 2014a). The prolonged connection between parent and offspring, and their immediate contact following birth, may serve to reinforce a connection between mother and offspring (Davis, *et al.*, 2011), and set the stage for the emergence of family living. It is also possible that maternal manipulation of hormone delivery to offspring may be crucial to fostering parent-offspring social bonds, although this has not been investigated in squamate reptiles. This connection is likely fostered through chemical recognition because squamates are known for their acute chemosensory ability (Halpern, 1992). Furthermore, chemical cues play an important role in social behaviors including kin- and mother-offspring recognition (Main & Bull, 1996; O'Connor & Shine, 2006). Indeed, neonate rattlesnakes have been recorded to contact their mother using face-wiping and tongue-flicking at much higher frequencies following birth (Graves, *et al.*, 1987), and this might help imprint her chemical signature and facilitate maternal recognition. Ultimately, experimental testing of the role of viviparity in forging mother-offspring associations might be possible, particularly in populations of lizards that vary in reproductive mode.

## 13.7 Traits of Social Groups

Lizards that live in stable social groups tend to have high levels of genetic structure, delayed juvenile dispersal, and pair bonds that are stable across seasons. Nevertheless, there is considerable variation across species in the composition of groups and the form of their pair bond and mating system.

### 13.7.1 Genetic Relatedness

*Egernia* group species are characterized by social groups with long-term stability, high levels of genetic monogamy, and delayed juvenile dispersal. As such, they are characterized by strong genetic structure (Gardner, *et al.*, 2001; Chapple & Keogh, 2005; McAlpin, *et al.*, 2011; While, *et al.*, 2014b). Indeed, in all species studied to date, within-group relatedness is significantly greater than between-group relatedness (e.g. Stow & Sunnucks, 2004; Fuller, *et al.*, 2005). This results primarily from delayed juvenile dispersal (often multiple cohorts), which leads to high levels of relatedness between adults and offspring within a social group (see also Davis, *et al.*, 2011 for similar patterns in *Xantusia*). However, in species that live in extended families, there is also evidence of either retention of offspring in the social group into adulthood or preferential association with kin. For example, in large social groups of *E. stokesii*, within group relatedness between adult females was extremely high (0.25 less than  $r$

less than 0.55), strongly suggesting the possibility that these groups comprise mothers and their adult daughters (Gardner, *et al.*, 2001).

One of the major challenges associated with increased genetic structure in social groups is the risk of inbreeding depression. Species in the *Egernia* group exhibit a number of mechanisms to deal with this. First, recognition of kin, by both parents and offspring, has been documented in several species (Bull, *et al.*, 1994; Main & Bull, 1996; Bull, *et al.*, 1999, 2001; O'Connor & Shine, 2006). However, the mechanism of kin recognition may differ among species (O'Connor & Shine, 2006). Second, there is strong evidence of non-random mate choice with respect to relatedness (Bull & Cooper, 1999; Gardner, *et al.*, 2001; Chapple & Keogh, 2005; While, *et al.*, 2014b). In some species, this occurs at the social pair level, with pairs less related to one another than expected by chance (Bull & Cooper, 1999; Gardner, *et al.*, 2001; Chapple & Keogh, 2005). In other species, pairs are more related to one another than expected by chance, but females choose extra-pair partners who are significantly less related (While, *et al.*, 2014b). As a consequence, extra-pair offspring have significantly higher genetic heterozygosity compared to their half-siblings (While, *et al.*, 2014b). Taken together, these results suggest considerable plasticity within the genus with respect to mate choice, which has implications for the genetic structure within social groups.

### 13.7.2 Group Structure, Breeding Structure and Sex Ratio

Species in the *Egernia* group are characterized primarily by long-term stable adult pair-bonds and delayed juvenile dispersal resulting in the formation of small family groups consisting of adults and their offspring (Chapple, 2003). However, despite the fact that these broad traits are relatively consistent across the *Egernia* group, there is considerable variation in group size and composition both within and among species. There are four main categories of group organization that have been identified within the *Egernia* group: (1) species that are largely solitary (e.g. *Tiliqua adelaidensis*, Schofield, *et al.*, 2014; *Liopholis inornata*, Daniel, 1998; *Lissolepis coventryi*, Taylor, 1995); (2) species in which adults pair-bond during the breeding season (e.g. *T. rugosa*, Bull, 2000); (3) species which live in small family groups (e.g. *L. whitii*, *E. saxatilis*, O'Connor & Shine, 2003); and (4) species which live in large stable extended family groups (e.g. *E. cunninghami*, Stow & Sunnucks, 2004; *E. stokesii*, Gardner, *et al.*, 2001). Each of these categories of group organization differ in both the nature and formation of adult pair bonds as well as extent of delayed juvenile dispersal.

As mentioned previously, the best example of consistent, potentially life-long pair bonds is the sleepy lizard, *T. rugosa*. Such extended long-term monogamy within an entire activity season has since been shown to form the basis for social organization within most species in the *Egernia* group. Specifically, species that live in small family groups tend to be characterized by long-term socially monogamous pair bonds (e.g. *L. whitii*, *E. saxatilis*, *L. kintorei*). However, in all of these species, polygynous social groups where some males form pair bonds with multiple females (typically 2 to 5 females) are also common, albeit often at a lower frequency than monogamous pair

bonds. For example, 30 percent of social groups in *Egernia whitii* are characterized by a single male sharing his crevice site with up to three females (While, *et al.*, 2009b).

In other species, variation in social organization includes not only monogamous and polygynous social groups, but also aggregations containing multiple adults of both sexes. These social groups typically contain one unrelated breeding pair as well as several adult offspring of the breeding pair. Perhaps the best example of this is *E. stokesii*, where up to 11 adults (both males and females; up to 17 individuals total, including offspring) can co-occur in a stable social aggregation sharing a single crevice site (Gardner, *et al.*, 2002; Gardner, *et al.*, 2001; Duffield & Bull, 2002). Other species, such as *E. cunninghami*, *E. mcphoei* and *E. striolata* also live in large communal groups containing multiple adults (Stow, *et al.*, 2001; Chapple, 2003; Stow & Sunnucks, 2004).

Although long-term data are only available for a small number of species, these monogamous, polygynous, and polygynandrous pair bonds exhibit surprising stability across seasons. For example, sleepy lizard pair bonds appear to be life-long (Leu, *et al.*, 2015). Similarly, *L. whitii* pairs exhibit considerable stability across years with some pairs together for 10 years (G. While, *unpublished data*; see also Chapple & Keogh, 2006; While, *et al.*, 2009b), constituting the majority of those adults' reproductive lifespan (up to 13 years; G. While, *unpublished data*). Studies over several breeding seasons have confirmed strong social stability between years in *E. cunninghami* (Stow & Sunnucks, 2004) and *E. saxatilis* (O'Connor & Shine, 2003). Unsurprisingly, separation by choice (i.e. not mortality) is extremely rare in these systems. In *L. whitii*, while there are moderate levels of unplanned separation (i.e. mortality of approximately 40 percent) only 15 percent of pairs across 8 years ended in separation by choice (G. While, *unpublished data*), which suggests a remarkable level of pair fidelity.

Delayed offspring dispersal and prolonged parent-offspring association are also key features of the *Egernia* group, but they vary considerably both within and among species. At a broad level, parent-offspring association in the *Egernia* group ranges from species that do not exhibit any parental tolerance of offspring (e.g. *L. inornata*, Daniel, 1998; *T. rugosa*, Bull & Baghurst, 1998) to those that predominantly tolerate a single offspring or cohort of offspring (e.g. *L. whitii*, Chapple & Keogh, 2006; While, *et al.*, 2009a; *Liopholis slateri*, Fenner, *et al.*, 2012), to species that tolerate multiple cohorts of offspring resulting in the formation of multigenerational family groups (e.g. *E. cunninghami*, Stow, *et al.*, 2001; *E. saxatilis*, O'Connor & Shine, 2003; *E. stokesii*, Gardner, *et al.*, 2012). This variation in tolerance of offspring tends to be closely related to variation in social organization such that larger adult social groups appear to have greater tolerance of offspring (e.g. multigenerational family groups). However, this is not always the case, as predominantly solitary species such as *T. adelaidensis*, exhibit some, albeit low levels, of maternal care despite the complete lack of adult group structure (Schofield, *et al.*, 2014).

Similar to species in the *Egernia* group, social organization in *Xantusia vigilis* is also characterized by long-term male-female pair bonds and delayed juvenile dispersal. However, these groups are a little different because they are seasonal, reforming each

winter after more solitary behavior in the summer. The specific composition of social groups also varies among individuals within a population. For example, group size varies from between 2 to 18 individuals, with social organization including both nuclear families and extended family groups (Davis, *et al.*, 2011). Social groups also show moderate stability with 29 percent of groups stable across consecutive years, with stability being higher for nuclear family groups than for extended family groups (Davis, *et al.*, 2011). However, at least four breeding pairs and their multiple cohorts of offspring formed “dynasties”, re-aggregating in the same groups underneath the same logs every winter for up to 4 years (Davis, *et al.*, 2011).

Unlike obligate cooperatively breeding and eusocial species, the social groups in the *Egernia* group do not display high reproductive skew. In general, sex ratios are relatively even within groups and all females and most males in a population have the opportunity to breed (While, *et al.*, 2011), although reproduction opportunities in *X. vigilis* seem to favor social over solitary males (Davis, *et al.*, 2012). However, there is still considerable variation in breeding structure within and among populations, which has the potential to place strong selective pressure on the stability of social systems within the group.

Social groups are characterized by relatively high levels of genetic monogamy. As with many other socially monogamous systems, while genetic monogamy is the rule, species in the *Egernia* group also exhibit some level of extra-pair mating. Levels of extra-pair paternity differ considerably both within and among populations. For example, in *E. cunninghami*, only 2.6 percent of litters have extra-pair offspring (Stow & Sunnucks, 2004). Levels of extra-pair paternity are low for other species including 12 to 26 percent in *L. whitii* (Chapple & Keogh, 2005; While, *et al.*, 2009b), 20 percent in *E. saxatilis* (O'Connor & Shine, 2003), 25 percent in *E. stokesii* (Gardner, *et al.*, 2001), and 19 percent in *T. rugosa* (Bull, *et al.*, 1998). In contrast, less social and non-family living species appear to have higher levels of genetic polyandry. In *T. adelaidensis*, 75 percent of offspring within litters are the result of multiple mating (Schofield, *et al.*, 2014). These patterns of predominant social and genetic monogamy with moderate levels of extra-pair paternity closely mirror those observed for many other family-living species (Griffith, *et al.*, 2002; Cornwallis, *et al.*, 2010; Lukas & Clutton-Brock, 2012).

### III SOCIAL SYNTHESIS

Group living brings individuals into close contact and invariably, reproductive or resource-based conflict. Consequently, groups may vary in their stability depending on the environmental and social factors that influence fitness. Lizards have been identified as a useful model for understanding the transition to “complex” sociality because some species delay dispersal and have elementary parental care coupled with monogamy and family living. Surprisingly, sociality has only evolved within one major squamate lineage (Scincoidea, *sensu* Pyron, *et al.*, 2013) although future work could reveal additional instances.

## 13.8 A Summary of Lizard Sociality

Within lizards, various forms of territoriality have evolved many times over among all the major lizard radiations (Stamps, 1977) and in snakes (Webb, *et al.*, 2015). Polygyny is a general feature of these systems, although males may also defend territories in monogamous species (Chapple, 2003; While, *et al.*, 2009a). In territorial systems, males and females are likely to form social bonds, as are females that share space (Strickland, *et al.*, 2014). These non-kin based social bonds are therefore likely to be the most common form of social structure in lizards, although most studies do not quantify these bonds directly (but see Strickland, *et al.*, 2014). Instead, social structure is inferred by examining patterns of spatial overlap. Typically, we learn that males maintain exclusive space overlapping multiple females while females commonly overlap each other in space. These social bonds are likely to be relatively stable over time because males of many different species have high site fidelity and typically return to the same territories every breeding season. Unfortunately, most studies of lizard sexual selection do not focus on social relationships *per se*, but instead, on reproductive and sometimes morph-specific tactics. Likewise, parent–offspring associations, a hallmark of sociality, could be far more common than we realize because so little attention has been directed towards this possibility. Finally, many species over-winter communally in hibernacula for which they have strong fidelity. We know little about the potential social bonds that might form between potential mates in these systems, particularly since hibernation precedes mating (Graves & Duvall, 1995; Schuett, *et al.*, 2016).

Parental care through association between mother and offspring is also likely to be far more common than thus far documented because these links can be cryptic. Unlike in mammals and birds, there is little or only subtle direct interaction between parents and offspring in lizards. For example, many researchers may not know the relatedness of juveniles and adults in the field unless mothers are brought into captivity to give birth before being released back into the wild. We believe that this factor alone has likely resulted in a disconnect between researchers of social behavior in lizards and the possibility of parental care. Thus far, almost all known instances of mother-offspring association are in viviparous species, including a substantial number of rattlesnake species (Greene, *et al.*, 2002; Schuett, *et al.*, 2016). This parent–offspring association may result in direct protection against predators or infanticide, particularly from unrelated adults (O'Connor & Shine, 2004). This obvious fitness advantage has likely resulted in its independent evolution many times across the entire phylogeny of squamate reptiles.

There is only a single well-documented case of long-term monogamy in a lizard in which there is no parental care. Unlike lizards that live in family groups, the sleepy lizard, *Tiliqua rugosa*, lives in relatively homogenous habitat and is wide-ranging. Their pair bonds are remarkably stable (current record: more than 27 years) and one advantage of long-term monogamy appears to be effective coordination of reproduction between paired males and females (Leu, *et al.*, 2015).

The pinnacle of sociality in lizards is kin-based family living in the *Egernia* group of lizards and the North American xantusiid: *Xantusia vigilis*. These few instances of

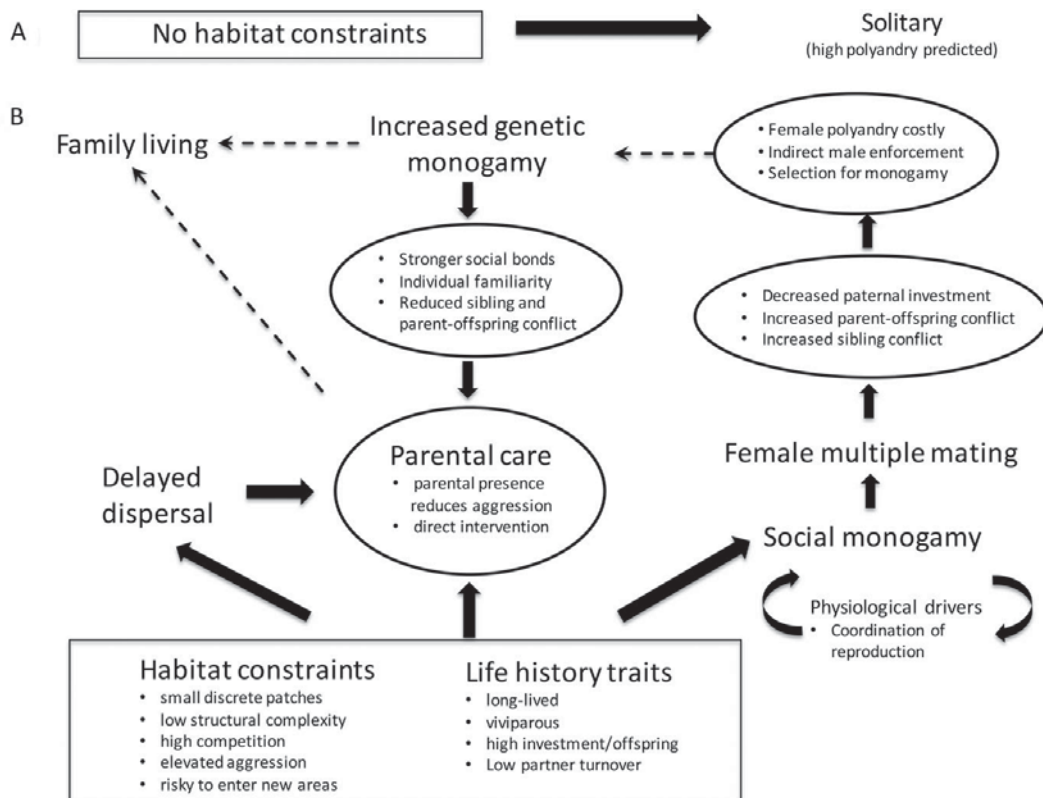
family living are all from a single major radiation of lizards (Scincoidea) in which long-term stable group living has been documented in multiple genera. It is highly likely that future genetic and field studies will uncover more instances of family living, such as in the African Cordylidae or the South American tropidurid genus *Liolaemus*. In the former systems, parental units are mostly monogamous although multiple mating does occur (Uller & Olsson, 2008; Wapstra & Olsson, 2014). One or more generations of kin delay dispersal, and males appear more likely to disperse than females, although this is not always clear and data are needed from additional species. Post-hatching parental care is primarily in the form of parent–offspring associations, although cases of direct parental care have been reported (While, *et al.*, 2014a).

An hypothesis for the evolution of kin-based sociality in lizards that has received empirical support is that family living is best explained as an interaction between indirect male enforcement of female fidelity and kin-based benefits through protection against predation or infanticide (While, *et al.*, 2009a). Kin benefits and enforcement of female fidelity are intimately linked because any offspring sired by the non-resident male will be forced to a restricted area of the parental home range and potentially pay a fitness cost through aggressive interactions from the resident male, reduced food acquisition, growth rates, and/or future survival (While, *et al.*, 2009a). Furthermore, while we know very little about parental care in the majority of species, juveniles are more likely to be attacked by adults other than their parents, particularly when their parents are not around, in at least the two species in which this has been studied (O'Connor & Shine, 2004; While, *et al.*, 2009a). The family-living species of the *Egernia* group frequently occur in patchy habitat where high density can limit dispersal opportunity and where venturing away from protection can be very risky. This helps set the stage for group stability and reinforcement of parent–offspring and sibling–sibling bonds and parental care, particularly in a group that is long-lived and in some species, slow to mature, relative to most other species of lizards (Figure 13.3). Increased pair stability and low female polyandry across years will increase the average relatedness of offspring within and among cohorts, which reduces competition and could lead to the evolution of larger social colonies as found in some species of *Egernia* (e.g. *Egernia stokesii*, Gardner, *et al.*, 2001).

### 13.9 Comparative Perspectives on Lizard Sociality

Lizards, and to a lesser degree snakes, exhibit a wide range of life history strategies, social organization, social structure, and mating systems (Stamps, 1977; Pianka & Vitt, 2003; Vitt, *et al.*, 2003). Sociality in lizards overlaps most with fishes, birds, and mammals, but bears little resemblance to the eusocial insects. Lizards fundamentally differ from these groups in that parental care is uncommon and when it occurs, is largely cryptic (except egg brooding) and typically involves tolerance of offspring (and therefore access to key resources) and protection against infanticide although direct protection of offspring is possible (While, *et al.*, 2014a). Furthermore, unlike birds and mammals, lizards do not provision their young and therefore, do not breed





**Figure 13.3** A graphical model for the evolution and maintenance of sociality in lizards based upon our knowledge of multiple species from the *Egernia* group and adapted and expanded from While, *et al.* (2009a). (A) When habitat availability is not constrained or discrete at a fine scale, species are predicted to be more solitary and to mate multiply. We have not depicted this graphically, but these species would have roughly opposite life history traits compared to more social species (i.e. oviparous, low investment/offspring, comparatively reduced longevity). (B) When habitat is discrete or patchy, species are more likely to form aggregations. Many species occur on discrete habitat patches such as trees and rocks and are dependent on refuges. Habitat availability is variable in the wild, but in cases where higher quality patches are limited, there may be greater competition for resources and more frequent contact with conspecifics. Dispersal under these conditions can be costly because unfamiliar juveniles (i.e. non-kin) are frequently attacked by adults and therefore, there is a risk of infanticide. Evidence for heightened aggression against non-kin has been found in *Egernia saxatilis* (O'Connor & Shine, 2004) and *Liopholis whitii* (While, *et al.*, 2009a). Delayed dispersal also sets the stage for the formation and strengthening of parent-offspring bonds, regardless of whether kin recognition is genetic or based on familiarity/phenotype matching. Furthermore, the stage is set for parental care either by simple association with a parent (thereby deterring attacks from unrelated adults) or through direct protection. Finally, male parental tolerance of related offspring helps promote female fidelity because unrelated offspring are excluded from the male's territory thereby potentially imposing a fitness cost on the mother. Life history traits also set the stage for sociality. Lizard species with kin-based sociality are all viviparous, often slow to mature, invest relatively heavily in offspring production, and are long-lived. Monogamy likely initially evolved as a consequence of limited habitat availability (i.e. saturation) interacting with life history and resulting in low mate availability and/or breeder turnover. Under these circumstances, it would pay to remain with the same mate, and monogamy may have been preceded by simple mate guarding of females by males. This scenario could result in a feedback loop where monogamy is reinforced through better coordination of breeding (Leu, *et al.*, 2015) and/or reduced promiscuity by females through indirect costs to her offspring.

cooperatively. Lizard family groups typically contain a long-term monogamous parental unit that is also territorial, similar to that found in certain mammals (e.g. numerous species of small African antelope, Skinner & Chimimba, 2006), and may contain multiple generations of offspring. In mammals, social monogamy is derived from an ancestral state in which females were solitary and males attempted to overlap the ranges of multiple females. This ancestral state is similar to many polygynous systems in lizards where territorial males control resources that encompass the home ranges of multiple females. However, the transition to kin-based sociality in lizards has likely followed a different path to that of mammals. In mammals, transitions to social monogamy are a consequence of intolerance among breeding females coupled with intense competition for resources and low population density. Mating systems and monogamy in particular, are frequently linked to parental care in birds (Cornwallis, *et al.*, 2010) and mammals (Lukas & Clutton-Brock, 2012) and this also appears to be the case in lizards.

### 13.10 Concluding Remarks

A suite of traits and abiotic factors correlate with kin-based sociality in lizards. These include use of a discrete habitat patch or refuge (e.g. rocks or trees) or in the case of some sand-living lizard species, a burrow complex. Males defend a core area such as a crevice, tree hollow, or burrow. All lizards that live in stable family groups have a viviparous reproductive mode, many are omnivorous or herbivorous, are generally long-lived, and they may have delayed maturity. These traits in combination appear to be an important precursor for kin-based sociality (Figure 13.3), although any inferences we make must be tempered by the phylogenetic bias represented by this clade. If future genetic testing reveals more instances of kin-based sociality across the lizard phylogeny then this bias will be reduced and the importance of habitat and life history traits will be amplified.

Many of the arguments that we make 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 birds, mammals, and insects (Hughes, *et al.*, 2008; Cornwallis, *et al.*, 2010; Lukas & Clutton-Brock, 2012). Recent research has suggested that to truly understand the conditions under which group formation and social life initially emerged and evolved, we need to move away from systems in which sociality is derived, and in which individuals exhibit obligate or permanent forms of group living (Smiseth, *et al.*, 2003; Falk, *et al.*, 2014). Instead, we should focus on identifying the nature of social behavior and organization in species that exhibit facultative and/or temporary forms of social grouping. To this end, lizards, and the *Egernia* group in particular, offer an outstanding model system. In only a few other systems is there the combination of relatively simply ancestral forms of parental care and social behavior coupled with both within- and among-species diversity in social complexity (see also Chapters 8 and 9). Taken collectively, this is a system that could inform on the basic triggers required to transition to kin-based family living and

relatively complex sociality. There is a rich potential for new discovery and we anticipate that lizards will feature more prominently in the social behavior literature in the future.

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