

Social Environment Impacts Behavioural Development of a Family-Living Lizard

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Declaration

I certify that the work in this thesis entitled “Social Environment Impacts Behavioural Development of a Family-Living Lizard” has not been submitted for a degree nor has it been submitted as part of requirements for a degree to any other university or institution other than Macquarie University.

I also certify that the thesis is an original piece of research and it has been written by me. Any help and assistance that I have received in my research and the preparation of this thesis has been appropriately acknowledged.

In addition, I certify that all information sources and literature used are indicated in the thesis.

The research presented in this thesis was conducted in accordance with the Macquarie University Animal Ethics Committee under protocol numbers 2013/031 and 2013/039. Collection and research on wild lizards was licensed by the New South Wales National Parks and Wildlife Service, Office of Environment and Heritage (License # SL101264).

Julia Riley (Student ID: 43504213)

February 2017

List of Original Publications

This thesis is based on the following original publications, which are referred to in the text by Roman numerals. Original publications are reproduced with permission from their copyright holders where applicable.

- I **Riley JL**, Noble DWA, Byrne RW, Whiting MJ. 2017. Early social environment influences the behaviour of a family-living lizard. *Royal Society Open Science*, 4(5):161082, doi: <http://dx.doi.org/10.1098/rsos.161082>

- II **Riley JL**, Noble DWA, Byrne RW, Whiting MJ. 2017. Does social environment influence learning ability in a family-living lizard? *Animal Cognition*, 20(3):449-458, doi:10.1007/s10071-016-1068-0

- III **Riley JL**, Küchler A, Damasio T, Noble DWA, Byrne RW, Whiting MJ. A group-living lizard is resilient to isolation rearing. *In preparation*.

- IV **Riley JL**, Guidou C, Fryns C, Mourier J, Leu ST, Noble DWA, Byrne RW, Whiting MJ. Late bloomers: early experience impacts social behavior of a family-living lizard. *In preparation*.

Contributors and Division of Labour

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	I	II	III	IV
Conception and design	JR, RB, DN, MW	JR, RB, DN, MW	JR, RB, DN, MW	JR, RB, SL, DN, MW
Logistics and data collection	JR, DN	JR	JR, TD, AK	JR, CF, CG, SL
Statistical analysis	JR, DN	JR	JR	JR, JM
Writing the article	JR, RB, DN, MW	JR, RB, DN, MW	JR, RB, DN, MW	JR, RB, SL, DN, MW
Overall responsibility	JR	JR	JR	JR

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Thesis Summary

For group-living animals social experience during ontogeny is known to influence multiple facets of animal behaviour. Rearing social animals isolated from any conspecific contact can hinder development of behavioural traits, cognitive ability, and social competence. This thesis is an overview of how social environment effects behavioural development in a family-living lizard, *Egernia striolata*. I experimentally manipulated *E. striolata* early social environment, and raised skinks either in isolation or in pairs. I began by examining if social environment impacts development of skink behavioural traits across their first year of life. I found strong evidence that skink behavioural development was plastic depending on their social experience, and isolation itself did not hinder *E. striolata* behaviour in a similar manner as found in previous research. I then assessed how social isolation impacted skink cognitive ability. Contrary to previous research, I found no effect of social environment on individual learning ability in multiple cognitive tasks (e.g., spatial, motor and discrimination tasks). Additionally, juvenile tree skinks did not use social information from adults regardless of their early social environment. Finally, I studied if social environment affects skink social competence using repeated behavioural observations in a laboratory and semi-natural setting. I found that isolated skinks were initially more social than socially-raised skinks, but they decreased in their sociability over time once exposed to a social environment. This is evidence that *E. striolata* can flexibly alter their social behaviour in response to the environment they are exposed to, even after long-term social isolation. Overall, this thesis presents evidence that isolation rearing does not consistently result in negative impacts on behaviour across all social taxa, and instead, that *E. striolata* behavioural development responds flexibly, and potentially adaptively, to the social environment in which they are raised.

General introduction

We call a group of geese a gaggle, many toads a knot, and a faction of whales a pod. Our often silly and diverse nomenclature for groups of animals reflects human fascination with social taxa. Darwin himself recognized the challenges animal sociality presented to his theory of evolution within the *Origin of Species* (Darwin 1859). Since then, sociality has generated much scientific interest and discussion. For decades, scientists have been interested in the occurrence, causes, and consequences of sociality, and this research is a major aim within the field of animal behaviour (Ward and Webster 2016). Sociality is the degree to which individuals in a population aggregate together and interact (Gromov 2013; Hofmann 2014). Animals can be largely solitary and restrict their interactions with conspecifics to territory disputes and mating (Ward and Webster 2016). Alternatively, social aggregations of some species are limited to breeding events or overwintering periods (Graves and Duvall 1995). Other social animals live in stable kin-based cooperative groups, or complex eusocial societies (Nowak et al. 2010; Kappeler and van Schaik 2012). This diversity in animal sociality begs the question of why some species live in groups, while others primarily live alone? And, what are the determinants of a species' social system? Answering these questions can inform if there is a shared evolutionary pathway that all social animals may have experienced, and also add to our understanding of other evolutionary processes that are closely linked to a species' sociality like sexual selection (Emlen and Oring 1977; West-Eberhard 1979), kin selection (Hamilton 1964), cognition (Zuberbühler and Byrne 2006), and cooperation (Clutton-Brock 2002; Nowak 2006).

Occurrence and diversity of social taxa

Sociality is taxonomically widespread and has evolved independently numerous times. About 30% of mammal species exhibit obligate sociality (either living in social groups or socially monogamous; Lukas and Clutton-Brock 2013), many birds live in social groups (Cockburn 2006), and eusociality, although rare, has evolved in mole rats (*Heterocephalus glaber* and *Fukomys damarensis*; Jarvis 1981), ants, and termites (Chapman and Bourke 2001; Wilson and Hölldobler 2005; Nowak et al. 2010). Predominately, sociality has been studied in these taxa, but what about other life on our planet? Although traditionally viewed as relatively asocial, recent research has shown that squamate reptiles form stable aggregations, and can also reside in long-term family groups (Doody et al. 2012, Gardner et al. 2015). Amphibians are well known for their social systems that involve breeding aggregations, parental care, mating bonds, and territoriality (Wells 1977; Gergits and Jaeger 1990). Fish aggregate in shoals, and there is some evidence for kin association as well as parental care (Wisenden

1999; Ward and Hart 2003). Non-eusocial insects are also known for their social interactions, and capacity to form cooperative breeding associations (e.g., burying beetles, *Nicrophorus* spp.; Trumbo and Wilson 1993). Aquatic invertebrates, specifically cephalopods, can also be social although the nature of their conspecific interactions is not well documented (Ikeda 2009). Sociality is a trait that has evolved in many organisms, and surprisingly, even microbiologists find similarly complex social behaviour (e.g., cooperation, division of labour, recognition of kin, etc.) in microorganisms (e.g., bacteria, pathogens; as reviewed in Crespi 2001). Sociality is truly diverse and widespread throughout both invertebrates and vertebrates. Thus, it's reasonable to ask if there are unifying principles governing sociality across all these taxa?

Causes of the evolution of sociality

Animal aggregations are the first step in the evolution of complex sociality, and are thought to be initially caused by environmental constraints (While et al. 2009a; Nowak et al. 2010; Ward and Webster 2016). Animals are often forced to group together when required resources, like food, shelter or basking sites, overwintering habitat, oviposition or gestation sites, and mates, are constrained because of their limited availability, clumped spatial distribution, or seasonality (Graves and Duvall 1995; Hatchwell and Komdeur 2000). When these required resources are constrained, it is more costly for an individual to attempt to exclude conspecifics from this resource, and aggregations form (Graves and Duvall 1995). Research to determine the ecological factors that favour animal aggregations often refer to this theory as the “habitat heterogeneity hypothesis” and/or the “socioecological approach” (Lindenmayer and Fischer 2006; Morrison et al. 2006; Michael and Cunningham 2010; Gromov 2013). It has now been established that habitat heterogeneity and complexity, inclusive of spatial and temporal variability in habitat, can influence density and organization of individuals within a population (Lindenmayer and Fischer 2006; Morrison et al. 2006; Michael and Cunningham 2010). For example, aggregations of *Ameiva corax*, the Little Scrub Island lizard, are triggered by food resources (Eifler and Eifler 2014), and aggregations in eusocial insects were thought to have been first triggered through sharing a defensible nest (Nowak et al. 2010).

Although ecological factors appear to be a substantial driver triggering sociality, life history characteristics (e.g., life span, age at maturity, etc.) are also thought to make some species more predisposed to group-living than others (Covas and Griesser 2007; Blumstein 2008; Ward and Webster 2016). For example, the *Egernia* group of skinks is viviparous, typically long-lived, and late maturing (Chapple 2003). They can also be highly social. It's thought that their extreme dependence on crevice-sites for shelter, leads to high competition

for these resources in saturated habitats. Their reliance on this constrained resource combines with their life history characteristics (i.e., long life span and late age of sexual maturity) to select for stable, long-term pair bonds and juveniles delaying dispersal to remain with parents at natal sites (While et al. 2009a). In fact, a recent study found that the offspring of a social lizard (*Liopholis whitii*) reduced their dispersal within a experimentally-saturated environment (high conspecific density), which promoted formation of kin-based groups and increased juvenile survival (Halliwell et al. 2017). Thus, life-history traits can interact with ecological factors to favour formation of social groups (Duffield and Bull 2002).

Once animals are within aggregations, trade offs between fitness benefits and costs act to develop more complex forms of sociality (Ebensperger et al. 2012; Ward and Webster 2016). Costs to group-living include an increased conspicuousness to predators, and exposure to disease and parasites (Alexander 1974; Storz 1999; Lanham 2001; Chapple 2003; Clark et al. 2012; Ebensperger et al. 2012). In contrast, benefits that may promote maintenance of social groups include enhanced vigilance against predators and increased access to crucial resources (Lanham 2001; Chapple 2003; Clark et al. 2012; Ebensperger et al. 2012). Furthermore, if groups consist of kin, there may also be inclusive fitness benefits (Hamilton 1964). Kin selection and recognition may not only also serve to facilitate the maintenance of stable social systems (Hamilton 1964; Ho et al. 2013), but also could provide the basis for the evolution of complex social behaviour like cooperation and altruism (Clutton-Brock 2002; Cockburn 2006).

Consequences of sociality for individual behaviour

Why sociality evolved is an important research question. But, in order to truly understand the costs and benefits of social living, it is also crucial to understand how sociality impacts individual behaviour. Social factors across ontogeny significantly impact an individual's central nervous system and thus, an animal's physiology and behaviour (Laviola and Terranova 1998; Caldji et al. 2000; Daisley et al. 2005; Stamps and Groothuis 2010b). These resulting behavioural traits can then affect individual fitness (Ryan and Vandenberg 2002; Kaiser and Sachser 2005; Taborsky et al. 2012). Particular behavioural traits, like aggression, boldness, sociability, and activity level, relate to both an individual's fitness (Smith and Blumstein 2008) as well as their developmental environment (Stamps and Groothuis 2010a). For example, litter size and sex ratio affects behaviour of great tit nestlings (*Parus major*, Naguib et al. 2011), mice (*Mus musculus*, Laviola and Terranova 1998), and voles (*Lasiopodomys mandarinus*, Yu et al. 2013). Experiments in which social taxa are raised in isolation also demonstrate how social environment affects behavioural development (Cacioppo and Hawkley 2009). Obligately social mammals and birds that are raised in social

isolation tend exhibit lower activity, exploration, and boldness, but higher fear and aggression when compared with socially-raised conspecifics (Mitchell et al. 1966; Pryce et al. 2002; Schrijver et al. 2002; Rodel and Monclus 2011). These resulting differences in individual behavioural traits, can also affect other aspects of animal behaviour.

Social isolation has also been found to affect cognition. Cognition is the mechanism that animals use to acquire, process, and store information from their environment, and these mechanisms include memory, learning, perception, recognition, etc. (Shettleworth 2010).

Social animals raised in isolation generally have a reduced learning ability (Greenough et al. 1972; Morgan et al. 1975; Einon 1980; Juraska et al. 1984), yet in some studies have found variable/positive effects of isolation on learning (Wongwitdecha and Marsden 1996; Frisone et al. 2002; Goerlich et al. 2012). Overall, it is well established in mammals and birds with obligate sociality that early social environment affects individual learning ability.

Additionally, isolation rearing may affect an individual's ability to learn from others within its social group (aka. social learning; Hoppitt and Laland 2013). Social learning is thought to be a short-cut to learning, particularly when individual learning is costly, and allows individuals to adaptively alter behaviours including foraging, communication, habitat use, and motor abilities (Shettleworth 2010). Yet isolation rearing can reduce an individuals ability to associate with conspecifics, as well as hinder their understanding of social cues and behaviours (e.g., facial signalling, dominance hierarchies; Taborsky and Oliveira 2012). So, isolation rearing may also impact an individual's ability to process and use social information from conspecifics.

During development many social taxa acquire social skills that are required for perceiving, processing, interpreting, and reacting to social situations as adults. These social skills are often what social animals rely on to survive, successfully mate, and raise offspring. For example, rhesus monkeys (*Macaca mulatta*) raised in isolation were more submissive during conspecific interactions (Mason 1961a), avoided by other conspecifics within their social group (Mason 1961b), and even unable to effectively reproduce (Mason and Sponholz 1963). Also, in four species of endangered felids, hand-rearing negatively affects the number of offspring produced, an individual's parental care behaviour, and offspring mortality (Hampson and Schwitzer 2016). This relationship between isolation rearing and abnormal social behaviour has also been demonstrated in other many other mammals (Broom and Leaver 1978; Sachser and Lick 1991; Lukkes et al. 2009; Toth et al. 2011), birds (White et al. 2010; Ruploh et al. 2013; Bølting and Engelhardt 2017), and fish (Taborsky et al. 2012; Hesse and Thünken 2014). Recently, Ballen et al. (2014) found that hatchling veiled chameleons (*Chamaelo calyptratus*) that were raised in isolation were more submissive during interactions with another juvenile than hatchlings raised in groups. Also, hatchling

viperine water snakes (*Natrix maura*) that were incubated in their eggs alone, instead of in contact with other eggs, were less aggregative (Aubret et al. 2016), and neonate cottonmouths (*Agkistrodon piscivorus*) that were deprived maternal attendance post-birth were less affiliative (Hoss et al. 2015). Social isolation also affects social behaviour in a predatory mite, *Phytoseiulus persimilis*; isolated individuals had fewer social associations, as well as altered mating behaviour and cannibalism (Schausberger 2004; Schausberger et al. 2017). Thus, isolation affects development of social behaviour in many taxa.

Reptile sociality

The study of non-avian reptile social behaviour has been largely neglected, most likely due to the traditional view that they are ‘asocial’ creatures with a limited social repertoire (Brattstrom 1974; Doody et al. 2012; Burghardt 2013). In addition reptiles are generally cryptic, and as a result their social behaviour is not overt and can be challenging to study in the wild (Brattstrom 1974). Since the 2000s, scientific interest in reptile sociality has increased, and through long-term observational studies, molecular techniques, and experimental manipulations reptile associations have been uncovered (Gardner et al. 2001; Shah et al. 2003; Stow and Sunnucks 2004; Shine et al. 2005; Chapple and Keogh 2006; While et al. 2009b). Reptiles have variable mating systems, ranging from monogamy to polygynandry, and their social systems are equally as diverse (Uller and Olsson 2008, Whiting and While 2017). Sociality in reptiles varies from largely solitary species through to large stable family groups (Mouton and van Wyk 1997; Chapple 2003; Doody et al. 2012). Some large reptile aggregations are mainly to share required resources (e.g., overwintering sites, shelter during the night, etc.), and otherwise individuals do not associate (Graves and Duvall 1995, Mouton and van Wyk 1997; Schutz et al. 2007; Eifler and Eifler 2014). Other long-term associations occur independently of relatedness, for example eastern water dragons (*Intellagama lesueurii*) form social bonds independently of kinship (Strickland et al. 2014). Although, in many other reptiles, individuals recognize and preferentially aggregate with kin (e.g., diamondback terrapins, *Malaclemys terrapin*, Rife 2008; timber rattlesnakes, *Crotalus horridus*, Clark 2004). Parental care also exists in reptiles, though it is more rudimentary and facultative than in birds and mammals with obligate parental care (Doody et al. 2012). Generally, parental care is limited to: (1) to defence and brooding of eggs, such as thermogenesis of eggs in pythons (Harlow and Grigg 1984; Brashears and DeNardo 2003) or female skinks actively guarding their eggs from snakes (Huang 2006; Pike et al. 2016); (2) aid of offspring post-birth, like skinks assisting offspring out of their embryonic membranes (Chapple 2003) or monitors helping their hatchlings escape from termite mounds (Carter 1999); and (3) protection of offspring, such as female alligators defending their offspring

within rookeries (Webb et al. 1987) or tolerance of offspring within the parents' natal territory giving them access to resources and security from aggressive conspecifics (O'Connor and Shine 2004; Langkilde et al. 2007; Sinn et al. 2008). Reptiles also show complex social behaviour that match their diverse social systems, like social learning (Clark 2007; Wilkinson et al. 2010; Noble et al. 2014; Kis et al. 2015), communication between conspecifics (Burghardt 1977; Mason and Parker 2010), as well as individual (Carazo et al. 2008) and kin recognition (Bull et al. 1999; Bull et al. 2001; Clark 2004). Although reptile sociality already appears to be diverse, social aggregations have only been identified in a small proportion of species (Gardner et al. 2015); thus, numerous questions remain regarding reptile social behaviour, making it an exciting and rich field of study.

Highlighting our currently limited knowledge, kin-based sociality has currently only been identified in one higher-level group of reptiles: Scincoidea (Pyron et al. 2013; Gardner et al. 2015). Within this superfamily, kin-based sociality has only been documented within two of its four families (Xantusiidae and Scincidae; Whiting and While 2017). Within these families, species have been documented to live in kin groups with a socially and mostly monogamous parental unit (Chapple 2003; Davis et al. 2011). Group sizes can range from two individuals (e.g. *Xantusia vigilis*; Davis et al. 2011) to as many as 17 (e.g., *Egernia cunninghami* and *E. stokesii*; Gardner et al. 2001; Stow et al. 2001; Duffield and Bull 2002). Within these species, it is common for juveniles to delay dispersal, and remain with their parents for extended periods. These family-living species present a unique opportunity to study the causes and consequences of sociality (Whiting and While 2017) because their social behaviour is relatively simple and quantifiable. Also, there is enough variation in social strategies, both within and between species, to allow for meaningful comparisons. Furthermore, parental care is not required in these species, which allows social environment to be manipulated unlike in other animals where parental care is obligate (Whiting and While 2017). Overall, social reptiles are a promising model system for examining the evolution and consequences of sociality.

The *Egernia*-group as a model system

One radiation of scincid lizards from Australasia, the *Egernia* group, has a particularly high prevalence of family-living species. This group of lizards consists of seven genera (*Egernia*, *Liopholis*, *Lissoleps*, *Bellatoris*, *Cyclodomorphus*, *Tiliqua*, and *Corucia*), and is referred to as the *Egernia*-group because the former genus was recently split into multiple genera (Chapple 2003; Gardner et al. 2008; Pyron et al. 2013). Species within this group encompass the full spectrum of social organization; there are species that are mostly solitary (e.g. *Egernia coventryi*, Clemann et al. 2004; *Tiliqua adelaidensis*, Fenner and Bull 2011), while others

form long-term monogamous pairs (e.g., *Tiliqua rugosa*, Bull 2000) and stable kin groups (e.g., *Liopholis whitii*, Chapple and Keogh 2006; *Egernia striolata*, Duckett et al. 2012; *Egernia cunninghami*, Stow and Sunnucks 2004; *Egernia stokesii*, Gardner et al. 2006). For curious minds, a social group of *Egernia* skinks is termed a ‘fury’ (While et al. 2015). Within the *Egernia* group there is also intraspecific variation in social organisation – for example, *L. whitii* consistently varies in their social tendencies within populations (While et al. 2009b), and *E. striolata* social organization can differ among populations throughout their range (Bustard 1970; Bonnett 1999; Duckett et al. 2012). The inter- and intra-specific variation in *Egernia* group sociality is thought to be related to variation in ecological factors (Chapple 2003; Michael and Cunningham 2010; Halliwell et al. 2017) and particular life history characteristics (e.g., viviparity, long life span; Chapple 2003; While et al. 2009a). Reflecting the general literature on sociality, there are many benefits *Egernia* group spp. experience when living in groups: enhanced vigilance and protection from predation (Bull and Pamula 1998; Lanham and Bull 1999; Eifler 2001), parental defence of offspring (Masters and Shine 2002; O'Connor and Shine 2004; Langkilde et al. 2007; While et al. 2009a), and aggregations may also afford thermal benefits (Lanham 2001). But, family-living in this species may also come with costs, such as increased competition (O'Connor and Shine 2004; While and Wapstra 2008), and increased parasite transmission (Godfrey et al. 2006; Godfrey et al. 2009). The similarity of sociality within the *Egernia* group to other social taxa, the relative simplicity of their social interactions, and the diversity of *Egernia* spp. social systems makes it a desirable model system for sociality research.

My study species: the tree skink, *Egernia striolata*

My thesis explores how social environment can impact behavioural development using the family-living lizard, *Egernia striolata* (the tree skink). *Egernia striolata* is a medium-sized (18 - 22 cm in body length; Cogger 2014), viviparous skink that lives across central- and south-eastern Australia (Fig. 1). Females give birth to offspring from January to March each year, and litter size ranges from 2-6 offspring (Chapple 2003). The lifespan of *E. striolata* is unknown, but it is estimated to be about 5-10 years based on data from similar species (Cogger 2014). Juveniles reach sexual maturity in the wild at 2-3 years of age (Chapple 2003), but within captivity during my research *E. striolata* reached sexual maturity at 1.5 years of age (Riley unpubl. data). *E. striolata* inhabits cracks, hollow limbs, and bark of standing trees or fallen timber, or crevices in rock outcrops (Cogger 2014). Their behaviour is generally quite cryptic, and their colouration (grey to brown with white mottling; Fig. 1) affords them camouflage within their rock or tree crevices. *E. striolata* are omnivorous, sit-and-wait foragers (Reilly et al. 2007) that, in the wild, spend on average 98% of their time

stationary (95% *CI* = 96 to 100, *N* = 30 focal observations; Riley unpubl. data) and typically wait beside or within their crevices to capture passing insects. Although, for seasonal food items like flower nectar, tree skinks will actively forage, moving from their crevices to the ground to access this temporary food item (Riley personal observation). Yet, due to a lack of long-term demographic studies on this species, many aspects of its life history are still unknown. For example, the timing and rate of juvenile dispersal from their location of birth and parental social groups, as well as intra-specific signalling behaviour is still unknown. Also field investigations of this species' sociality has been largely anecdotal (Swanson 1976; Ehmann 1992) or occurred over the short-term (Bustard 1970; Bonnett 1999; Duckett et al. 2012), which, although limited, provides us a snapshot of this species' social organization.

Generally, *E. striolata* lives in kin-based social groups ranging in size from two to 10 individuals (Chapple 2003). These groups are thought to be formed by consecutive litters of offspring remaining with parents, which results in groups with stable mating pairs and variously aged juveniles (Chapple 2003). Yet, within populations, lizards vary in their social behaviour (Bonnett 1999; Duckett et al. 2012; Riley unpubl. data). *Egernia striolata* aggregation tendency is thought to depend on their age, sex, and relatedness (Bonnett 1999). Females tend to be more solitary than males, subadults are more likely to inhabit crevices with at least two other individuals, and individuals sharing crevices tend to be kin (Bonnett 1999; Duckett et al. 2012). Observations of *E. striolata* social systems within the same population (Pilliga region, New South Wales) also vary over time and space, which suggests that seasonality and environmental factors may also influence aggregation tendency of this species (Bustard 1970; Duckett et al. 2012).

Egernia striolata social structure also varies between populations throughout their range. Within arboreal populations, specifically forested habitats of the Pilliga region and the South-western slopes bioregion, New South Wales, skinks are mainly found in small groups (maximum of 3 individuals) and are often found alone (Bustard 1970; Cunningham et al. 2007). In other arboreal and in saxicolous populations, *E. striolata* predominately form social groups ranging in size from two to 10 individuals (Bonnett 1999; Michael and Cunningham 2010; Duckett et al. 2012). Although, these descriptions of *E. striolata* social systems suggest habitat plays a large role in promoting group formation, studies are not consistent in their findings. Some studies assert that *E. striolata* consistently associates, even when crevices are abundant (Bonnett 1999), while others have found that aggregation behaviour is dependent on habitat characteristics (Michael and Cunningham 2010). An alternative explanation for the inter-population variation in *E. striolata* social structure may be differences in study methodology (e.g., sampling intensity, seasonal timing).

Overall, variability in *E. striolata* aggregation tendency within and between populations ultimately means that each juvenile experiences a different social environment during development. Thus this species provides a unique opportunity to examine how early social environment affects behavioural development. My research will help us understand the ecological importance of behavioural development for this social lizard, give insights into the evolution of sociality, and afford us a glimpse into the social world of this skink. My thesis is structured into four separate but interrelated empirical chapters, and I provide a brief description of each study's aim below.

Thesis Aims

The main focus of my thesis is to strengthen the understanding of how social environment impacts behavioural development across social taxa, and the consequences of sociality for a family-living lizard. These goals will be accomplished by addressing the following four research foci (Fig. 2):

- I) Assess the influence of early social environment on individual behavioural traits;
- II) Examine the effect of social environment on individual learning ability;
- III) Determine if early social environment impacts social learning ability, and
- IV) Test if early social environment affects social competence using laboratory assays and social network analysis.

Chapter III, and IV are in preparation for publication, and have been formatted for potentially appropriate biological journals. Chapter I has been published in the journal *Royal Society Open Science*. Chapter II has been published in the journal *Animal Cognition*. Each empirical chapter is written and formatted as a stand-alone piece for publication, so there is some repetition among them in both experimental details and the data used. Each chapter addresses a different aspect of *E. striolata* behavioural development.



Figure 1. *Egernia striolata* group together within cracks in rocks and trees (top; photo credit James O’Hanlon). They inhabit both forest and rocky habitats (bottom left; two examples of *E. striolata* habitat) throughout eastern Australia (bottom right; range map adapted from Cogger 2014).

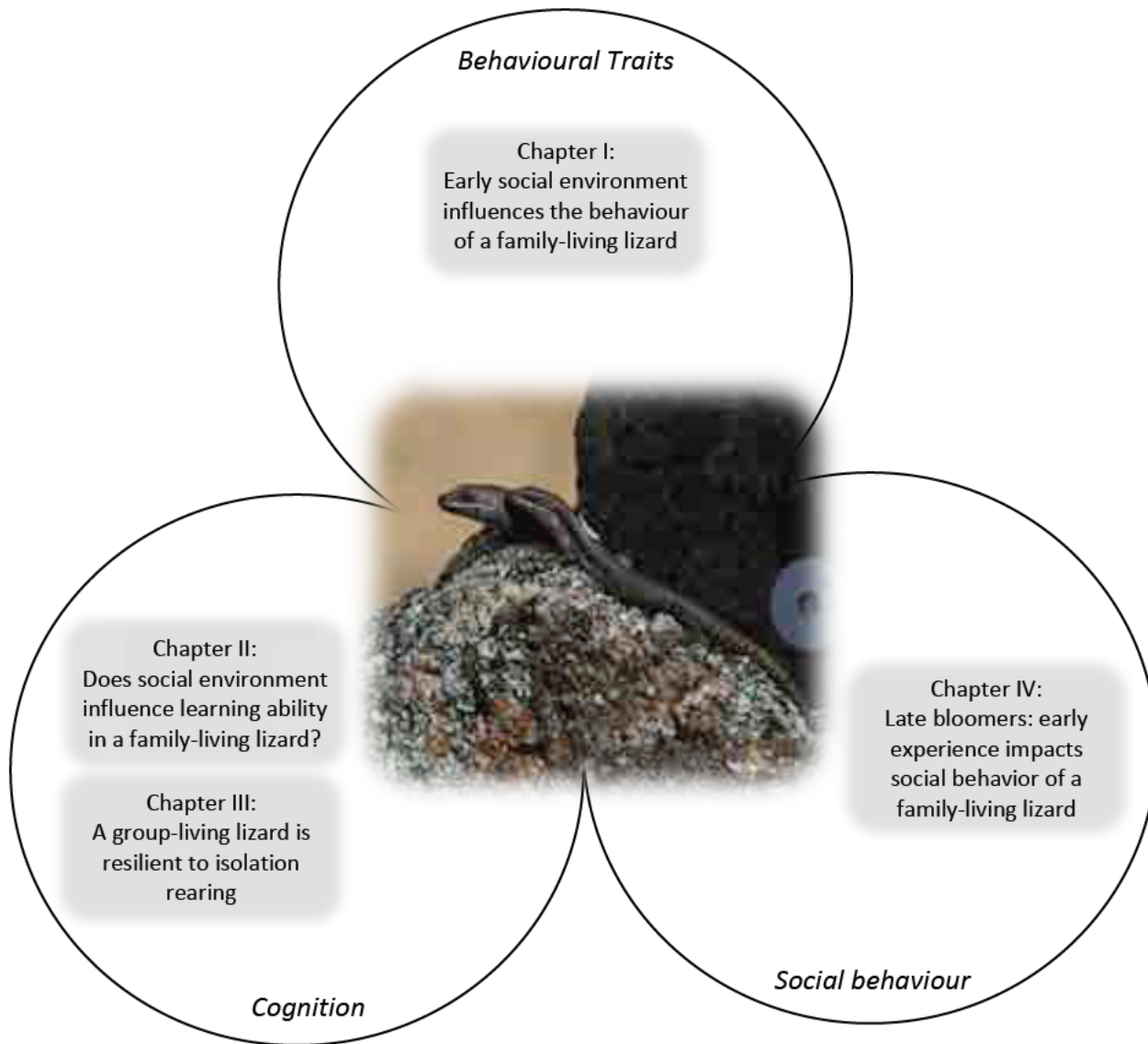


Figure 2. There are many facets of animal behaviour that are influenced by an individual's development. I focused on three aspects (general behavioural traits, cognition, and social tendencies) that affect an individuals' fitness.

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Chapter I

Early social environment influences the behaviour of a family-living lizard



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Early social environment influences the behaviour of a family-living lizard

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Early social environment can play a significant role in shaping behavioural development. For instance, in many social mammals and birds, isolation rearing results in individuals that are less exploratory, shyer, less social and more aggressive than individuals raised in groups. Moreover, dynamic aspects of social environments, such as the nature of relationships between individuals, can also impact the trajectory of development. We tested if being raised alone or socially affects behavioural development in the family-living tree skink, *Egernia striolata*. Juveniles were raised in two treatments: alone or in a pair. We assayed exploration, boldness, sociability and aggression repeatedly throughout each juvenile's first year of life, and also assessed social interactions between pairs to determine if juveniles formed dominant-subordinate relationships. We found that male and/or the larger skinks within social pairs were dominant. Developing within this social environment reduced skink growth, and subordinate skinks were more prone to tail loss. Thus, living with a conspecific was costly for *E. striolata*. The predicted negative effects of isolation failed to materialize. Nevertheless, there were significant differences in behavioural traits depending on the social environment (isolated, dominant or subordinate member of a pair). Isolated skinks were more social than subordinate skinks. Subordinate skinks also became more aggressive over time, whereas isolated and dominant skinks showed invariable aggression. Dominant skinks became bolder over time, whereas isolated and subordinate skinks were relatively stable in their boldness. In summary, our study is evidence that isolation rearing does not consistently affect behaviour across all social taxa. Our study also demonstrates that the social environment plays an important role in behavioural development of a family-living lizard.

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1. Introduction

Conditions during ontogeny affect many aspects of juvenile development. For example, poor nutrition [1] and parasite exposure [2] affect morphological and behavioural development of juveniles and can have long-lasting impacts on individual fitness. The social environment also influences behavioural development, especially in animals with complex social structure. Perhaps the simplest and clearest demonstration of the relationship between social environment and behavioural development comes from experiments that raise social animals in isolation [3,4]. Mammals and birds raised in isolation show decreased activity, exploration, boldness and sociability, but increased fear and aggression [5–8]. These effects on behaviour can be long-lasting, and significantly reduce individual fitness because of abnormal behaviour [5,8]. However, the relationship between social environment and development has predominately been studied in overtly social taxa, specifically mammals and birds. Little is known about the developmental impacts of social environment in less-studied social taxa, like insects, fishes, amphibians, and reptiles.

The limited literature examining how social environment impacts reptile development indicates trends similar to studies on birds and mammals. For example, hatchling veiled chameleons (*Chamaeleo calyptratus*) raised in isolation are more submissive during social interactions and had lower performance in a foraging task [9], which suggests decreases in sociability and boldness. Similarly, water snakes (*Natrix maura*) that were incubated alone were less social than snakes that were incubated in contact with other eggs [10]. Such similarity between studies across social taxa suggests isolation rearing may consistently affect behavioural development across species. However, none of these studies on reptilian behaviour examined the temporal stability of effects produced by social isolation, which limits our understanding of whether such effects are long-lasting or are variable over time. It is also important to realize that the impact of social environment on development is not always as simple as just the presence/absence of conspecifics [11,12]. A social environment is dynamic, and interactions between all individuals within a social group contribute to an individual's experience and development.

Dominant–subordinate relationships often form between individuals in social groups [13]. An individual's social rank, and the social interactions it experiences as a result of this rank, can affect its behaviour and fitness [14–16]. Dominance hierarchies, which are often size-based, can form among juveniles if they are raised together, and especially if that litter or clutch is born or hatched asynchronously. Asynchronous birth or hatching describes the time span between the birth of the first and last offspring within a litter or clutch [17], and is widespread across many animals (e.g. insects [18], sharks [19], amphibians [20], reptiles [21], and birds [15]). An asynchronously produced juvenile's social rank has been found to affect their individual growth rate, survival, and behaviour [15,16]. For example, the order of hatching in some nidicolous birds leads to siblicide of younger hatchlings by older clutch mates [22]. If social experience due to differences in social rank affects juvenile development, then the resulting divergence in sibling phenotype and behaviour may promote variable life-history strategies that could ensure survival of at least one offspring if faced with an unpredictable environment.

We examined whether social environment affects behavioural development in a social lizard, the tree skink (*Egernia striolata*). Females have asynchronously born litters ranging in size from one to four juveniles ([23], J.L. Riley 2015, unpublished data), and wild populations aggregate in social groups made up of either mating adult pairs, parents with offspring, or just juveniles [24,25]. In the laboratory, we reared juveniles in isolation or with another conspecific (a social environment). We examined the dynamics within the social environment to determine if pairs were forming dominant–subordinate relationships. Also, we quantified four behavioural traits (exploration, boldness, sociability, and aggression; table 1) of juveniles across their first year of life. We asked four questions:

- (1) Are tree skink behavioural traits correlated?
- (2) Does social environment impact individual phenotype?
- (3) Does social environment affect behavioural development?
 - a. We predicted that isolation would impact behavioural development similarly to how it has in other social taxa; isolated skinks would be less social, exploratory, and bold, as well as more aggressive compared with socially reared lizards.
 - b. We predicted evidence of a dominant–subordinate relationship between socially reared pairs, and also expected that these social interactions would influence individual phenotype and behaviour.
- (4) Does social environment influence temporal consistency of behavioural traits?

2. Material and methods

We collected gravid tree skinks from Albury, New South Wales (35.98° S, 146.97° E) in January 2014 and 2015, and monitored their parturition at Macquarie University. In our study, tree skink litter size ranged from one to four juveniles (mean = 2.25, 95% CI: 2.04 to 2.47). Tree skinks give birth to a litter, within captivity, over a mean of 1.6 days (95% CI: 1.45 to 1.75, $N = 55$; JL Riley 2015, unpublished data) and each juvenile within a litter was born within a mean of 0.77 days (95% CI: 0.70 to 0.84; JL Riley 2015, unpublished data) of each other. We sampled 28 juveniles in 2014 and 38 juveniles in 2015 (see the electronic supplementary materials for more details on our study species, captive husbandry, and measurements recorded).

2.1. Behavioural trait assays

After all juveniles within a cohort were born, we carried out an initial 'baseline' assay. We then randomly allocated juveniles into two treatments: isolated and social. The isolated treatment housed lizards alone ($N_{2014} = 14$ lizards, $N_{2015} = 16$ lizards), while the social treatment housed two unrelated juveniles together ($N_{2014} = 14$ lizards within 7 pairs, $N_{2015} = 22$ lizards within 11 pairs). Both treatments were representative of wild social rearing environments because juveniles have been observed both alone and in pairs [24,25], JL Riley 2016, unpublished data), although most commonly, social groups consist of parent(s) and one to three offspring [23]. Including parents in our social treatment was not feasible because adult *Egernia* spp. can be highly aggressive towards juveniles [26,27] and infanticide can occur [26,28,29]. Once within their treatments, we assayed behavioural traits three more times: around five months of age, seven months of age and 12 months of age (see the electronic supplementary material for exact dates).

Each assay period was 12 days in duration, and consisted of eight 'trait assays' and four 'break days' (electronic supplementary material, figure S1). Owing to the size of our experimental room, we had to measure juvenile behaviour within two batches (maximum of 24 per batch; see the electronic supplementary materials for details on batch allocation and sample sizes). During assays, skinks were individually housed in rectangular arenas (690 mm W × 470 mm L × 455 mm H), and assays were remotely video recorded (see the electronic supplementary materials for details). Each assay aimed to categorize one of four behavioural traits: exploration, boldness, sociability, and aggression (table 1).

2.2. Exploration assays

To categorize exploratory behaviour, we introduced skinks into a novel environment (e.g. akin to an open-field test). We repeated this procedure on two subsequent days (electronic supplementary material, figure S1). The first arena had a sand substrate, two black refuge boxes (120 mm W × 175 mm L × 38 mm H) with one entrance on the inner side placed at each end of the arena, and four white clay tiles (47 mm W × 47 mm L × 4 mm H) placed in the middle of the arena (electronic supplementary material, figure S2). The second arena had a grid-paper substrate and two black refuge boxes (same dimensions and orientation as above; electronic supplementary material, figure S2). At the beginning of each trial, we introduced the lizard into the arena within a central, containment refuge. The skink acclimated within this refuge for 5 min. The trial started when we lifted the central refuge, and then the trial ran for 30 min (electronic supplementary material, video S1).

From video recordings, we scored: (i) time spent moving (s) and (ii) number of times they entered a refuge. These two measures were combined using a principal component analysis (PCA). Our PCA used the correlation matrix because our variables were on different scales and this approach standardizes the data [30]. The PCA was performed using the *princomp* function in R v 3.0.3 [31]. These two behaviours were highly correlated and positively loaded on a single component (electronic supplementary material, table S1). We used the first principal component (PC1) in further analyses as our 'exploratory score'; as the value increases, it reflects more exploratory behaviour (table 1).

2.3. Boldness assays

We categorized skink boldness with three predator-response assays that occurred on consecutive days (electronic supplementary material, figure S1). For our boldness assays, we positioned the heat lamp directly over one of the lateral refuges, which resulted in a 'hot' refuge (electronic supplementary material, figure S2). We placed an ice pack beneath the other refuge, under the arena, resulting in a

Table 1. Behavioural traits we quantified and their descriptions within the context of our study. We also detail how the behavioural traits were measured, and what the resulting response variable was for our statistical analyses.

behavioural trait	description	quantification	behavioural variable
exploration	<ul style="list-style-type: none"> — how a skink assesses and searches a novel environment — varies from sedentary to exploratory 	<ul style="list-style-type: none"> — from videos we scored: <ol style="list-style-type: none"> (1) time spent moving within a novel environment (s) (2) number of times entered refuges within a novel environment — conducted a PCA with the two variables to combine them into an exploratory score — scored the latency to return to basking (s) after a 'predator' chase 	<ul style="list-style-type: none"> — exploratory score (PCI) — as the value increases, the skinks are more exploratory
boldness	<ul style="list-style-type: none"> — how a skink reacts to a risky situation — varies from brave (risky) to shy (safe) 	<ul style="list-style-type: none"> — scored how far away (mm) the focal skink was from a conspecific every 10 min during the 5 h assay — then, calculated the weighted average distance each focal skink was from the conspecific across the whole trial — from an interaction with a replica, scored: <ol style="list-style-type: none"> (1) number of mouth gapes (2) number of bites (3) latency to retreat (s) — conducted a PCA with the three variables to combine them into an aggression score 	<ul style="list-style-type: none"> — latency to return to bask (s) — as the value increases, skinks are less bold — sociality score — lower values reflect more aggressive behaviour, and higher values reflect avoidance
sociability	<ul style="list-style-type: none"> — how a skink aggregates with conspecifics — varies from solitary (avoidance) to social (aggregative) 		
aggression	<ul style="list-style-type: none"> — how a skink reacts in a defensive scenario — varies from a fight (aggressive) to flight (passive) response 		<ul style="list-style-type: none"> — aggression score (PCI) — lower values indicate a higher aggressive response from the skink (i.e. more bites, more gapes, longer latency to retreat)

'cold' refuge with temperatures outside the skink's optimal range (electronic supplementary material, figure S2). After set-up, we left the skink for 1 h to ensure it was either on top of, or within the 'hot' refuge. Then, we simulated a predatory attack by 'chasing' the skink away with a gloved hand from the 'hot' refuge until it entered the 'cold' refuge at the opposite end of the arena [32]. We then recorded the skink's behaviour for 45 min after it entered the 'cold' refuge (electronic supplementary material, video S1). We scored the time (s) it took the skink to return to the 'hot' refuge. If the skink did not return, we assigned it a value of 2700 s. We used the latency to return to the 'hot' refuge as our quantification of boldness; lower values indicate bolder behaviour (table 1).

2.4. Social assays

Our social assay began by placing the skink into the central refuge. We then inserted a clear, Perspex[®] divider 110 mm from the front of the arena (electronic supplementary material, figure S2). An unrelated female was randomly assigned to each juvenile, and placed on the opposite side of the Perspex to that of the juvenile. The refuge was lifted, and we recorded the juvenile and female for 5 h (electronic supplementary material, video S1).

From the video, at 10 min intervals over 5 h, the juvenile was scored as being in one of four lateral quadrats (110 mm width) in relation to the female (electronic supplementary material, figure S2). We calculated the weighted average distance the juvenile was from the conspecific across the entire trial by multiplying the number of times in each quadrat (Q1, Q2, Q3 and Q4) by the average distance the quadrat was away from the female (55 mm, 110 mm, 165 mm and 220 mm, respectively) and dividing the product by the number of observations ($N_{obs} = 30$). The distance the juvenile was located from the conspecific during the trial was used as a 'sociality score' in further analyses; lower values were reflective of the juvenile being closer to the adult conspecific (table 1).

2.5. Aggression assays

Our aggression assay was based on the methods outlined by Sinn *et al.* [27] and was repeated on two consecutive days (electronic supplementary material, figure S1). The arena was set up with the heat lamp pointed at one end of the bin, and the refuge at the opposite side (electronic supplementary material, figure S2). After set-up, we allowed 1 h for the skink to begin to bask beneath the heat lamp. The aggression assay began when a researcher approached the bin, and then waited within view of the skink for 30 s. After this, the researcher touched the nose of the basking skink with a soft Plasticine replica of a juvenile tree skink attached to the end of a stick. The skink was tapped on the nose every 12 s over a maximum of 2 min (i.e. maximum of 10 taps). The assay ended once the skink retreated into the refuge (electronic supplementary material, video S1). The replica skink was size-matched to the average snout-vent length (SVL) and total length of experimental skinks at each assay time period (i.e. the replica grew in size at the same rate as the juveniles).

We scored: (i) number of times a skink gaped and/or (ii) bit the replica, and (iii) the time (s) until the skink took refuge within the hide. If the skink did not take refuge within the hide, it was assigned a time of 120 s. These three measures were combined using a PCA using their correlation matrix [30]. These behaviours were highly intercorrelated and all negatively loaded on a single component (electronic supplementary material, table S1). We used the first principal component (PC1) in further analyses as our 'aggression score': lower values indicate greater aggression (table 1).

2.6. Social dynamics within socially reared pairs

We quantified social dynamics between socially reared pairs to determine if they were forming dominant-subordinate relationships. After all behavioural assays were completed for the 2014 cohort, we observed the social pair interacting during reintroduction into their mutual captive housing tub (for housing details, see the electronic supplementary materials) after being separated for 18 days for a learning experiment [33]. We observed skinks after this period of separation (18 days) because we assumed they would have to re-establish their dominance-subordinate relationship upon reintroduction. We recorded the social pair interacting for 15 min [25]. Before observations, we marked each individual with numbered cloth tape (Tesa[®], Germany) to allow identification. From recordings, we counted the following behaviours for each individual:

- (1) 'Bite': the focal skink grasps another with its jaws [3]

- (2) 'Nip': the focal skink grasps another with its jaws and then releases immediately, less than 1 s later [3]
- (3) 'Chase': the focal skink follows another fleeing skink [2]
- (4) 'Lie-on': the focal skink lies on another such that some part of its head or body is on top of the other skink [1]
- (5) 'Move-over': the focal skink moves over the top of another skink [1]
- (6) 'Flee': the focal skink moves away from another chasing skink [-2]
- (7) 'Move-away': the focal skink moves away from another skink [-1]

To quantify the role each individual played in the interaction, we multiplied the number of times each of the behaviours occurred by its weight (in curly brackets above), and summed to create an aggression score [9,26]. Weights for behavioural scores were guided by Ballen *et al.* [9] and Langkilde *et al.* [34]. Submissive behaviours (6 and 7) had negative weights, so they reduced the aggression score of the individual.

We compared aggression scores of social pairs to determine if individuals were dominant or subordinate. Six of seven social pairs differed in their aggression score: all individuals that were categorized as dominant (higher aggression score) were larger (SVL) than the subordinate (lower aggression score) individual (two sample *t*-test: $t_{12} = 2.55$, $p = 0.03$). Of these pairs, three of six contained both males and females, and all of the males were categorized as 'dominant'. As these trends were consistent across pairs, we categorized all socially reared skinks as dominant if they had a larger SVL, and/or were the only male within their social pair. Herein, we refer to individuals from the social environment simply as 'dominant' or 'subordinate'.

2.7. Statistical analyses

Prior to conducting analyses, we explored the data following Zuur *et al.* [35] (see the electronic supplementary material). We used a Bayesian analysis framework with a Markov chain Monte Carlo (MCMC) sampling approach to fit all our models. To fit our models (see specific details below), MCMC was applied using the *MCMCglmm* R package [36]. We used a burn-in of 150 000 iterations, a thinning rate of 1350, and 1 500 000 iterations for each posterior distribution. Uniform priors were used for the regression, and inverse Wishart priors for variance parameters ($V = 1$, $nu = 0.002$ [36]). Continuous covariates in all models were mean-centred prior to analysis. We visually inspected all trace plots from our models to ensure chains were well mixed. Autocorrelation of the chains of both fixed and random effects was assessed to ensure levels were low (lag < 0.1) using the *autocorr* function, and we also performed Geweke and Heidelberg autocorrelation diagnostics (from the R package *coda* [37]). Model assumptions of normality of residuals and homogeneity of variance were verified ([35]; see the electronic supplementary materials). In our results, we present pooled posterior modes and 95% credible intervals. Parameter estimates were considered significant when the credible intervals did not include 0, and the *p*MCMC values calculated by *MCMCglmm* were less than 0.05 [36]. When we predicted fitted lines from the models for visualizations, we set the continuous fixed factors to the mean and the factorial fixed factors to the intercept-level values.

2.7.1. Are behavioural traits correlated?

To evaluate whether there were correlations between our four behavioural traits, we used a multi-response linear mixed-effects model [38,39]. Our model included random intercepts for each behavioural trait, and a random intercept and slope for juvenile identity across age (details in the electronic supplementary materials about model variable selection). We assumed a multivariate normal distribution with a variance-covariance structure specifying the within- and between-individual variance and covariances among behaviours [36,38]. We used a temporally comparable subset of data for this model: data from the first replication of a behavioural trait (i.e. explore A, bold A and aggression A; see the electronic supplementary material, figure S1) at 5, 7 and 12 months of age ($N_{obs} = 153$, $N_{juv} = 51$).

2.7.2. Does social experience impact individual phenotype?

We compared the number of lizards that partially or fully autotomized their tails at least once with a Fischer's exact test. Then, we examined whether skink (i) SVL (mm) and (ii) relative tail length (RTL = tail length/SVL) differed among isolated, dominant and subordinate skinks. RTL was used as a proxy for the frequency of tail autotomy experienced by each individual—we expected that tail length

decreases in relation to the number of times it is autotomized [40]. We fitted identical Gaussian linear mixed-effects models (LMMs) for each response variable. Fixed factors were *social experience* (categorical with three levels), *age* (days; continuous), *cohort* (categorical with two levels), and an *interaction between social experience and age*. To incorporate the dependency among observations of the same individual, we included a random intercept and slope for juvenile identity across age; and to incorporate the dependency among observations of lizards from the same litter, we included a random intercept for mother identity. We also included a random intercept for housing tub to incorporate dependency among observations of lizards from the same captive environment. The model with RTL as the response variable only included data from the 2015 cohort. We calculated contrasts between dominant and subordinate skinks by comparing posterior distributions from model estimates.

2.7.3. Does social experience affect behavioural development?

We separately performed four identical Gaussian LMMs for each behavioural trait to assess how they were affected by skink *social experience* (categorical with three levels). Models also included the fixed factors of *age* (continuous), *batch* (categorical with two levels), *cohort* (categorical with two levels), *body temperature* (continuous), and *sex* (categorical with two levels) [39,41]. We also included a random intercept and slope for juvenile identity across age, and random intercepts for mother identity and housing tub. We also included an *interaction between social experience and age*, but if the interaction was not significant, we removed and refitted the model. Our boldness variable (latency to return to bask, *s*) was log-transformed to normalize the data, and we used a rank transformation to normalize our aggression score [42]. Also, for the model with aggression as the response variable, we included data from only time periods 1–3 (electronic supplementary material, figure S1).

2.7.4. Does social experience influence consistency of behavioural traits?

Repeatability, in general, refers to the extent to which individual differences in traits are maintained over time [38,41,43], and, in the case of this study, quantifies consistency of our four behavioural traits. To calculate repeatability for each behavioural trait, we calculated adjusted repeatability from the above models examining how behavioural traits differed between social experiences (i.e. *R*_{time} from Biro and Stamps [41], but in our case the time variable was skink age). For comparison, we also modelled each behavioural trait with LMMs that only contained an intercept and the random factors of juvenile identity, mother identity and housing tub (electronic supplementary material, table S2). From these models, we calculated LMM-based repeatability that did not consider additional explanatory factors (adapted *R*_M [38,39,43]). Finally, we subset the data by social experience and reran the original models (fixed and random factors varied as appropriate depending on the subset of data; electronic supplementary material, tables S3–S5). We then calculated adjusted repeatability from those models [41], and compared it between social experience qualitatively.

3. Results

3.1. Are behavioural traits correlated?

Aggression and exploration were significantly negatively correlated ($\rho_{\text{exploration, aggression}} = -0.668$, 95% CI = -1.000 to -0.068) at the between-individual level; which means that free skinks that had a higher exploration score (representing more explorative behaviours; see figure 1a) would have a lower aggression score (representing more aggressive behaviours; see figure 1d). All other between- and within-individual covariances and correlations were not significant (table 2).

3.2. Does social experience impact individual phenotype?

Isolated skinks were significantly larger in SVL than subordinate skinks (table 3; figure 2a). SVL did not differ between isolated and dominant skinks, or subordinate and dominant skinks ($\beta_{\text{DomSub}} = 0.966$, 95% CI = -0.369 to 2.547 ; table 3 and figure 2a). Isolated skink growth rate was significantly faster than subordinate skinks, and marginally faster ($p_{\text{MCMC}} = 0.086$) than dominant skinks (table 3 and figure 2a). Growth rate was not different between dominant and subordinate skinks ($\beta_{\text{DomSub}} = 0.727$, 95% CI = -0.180 to 1.819).

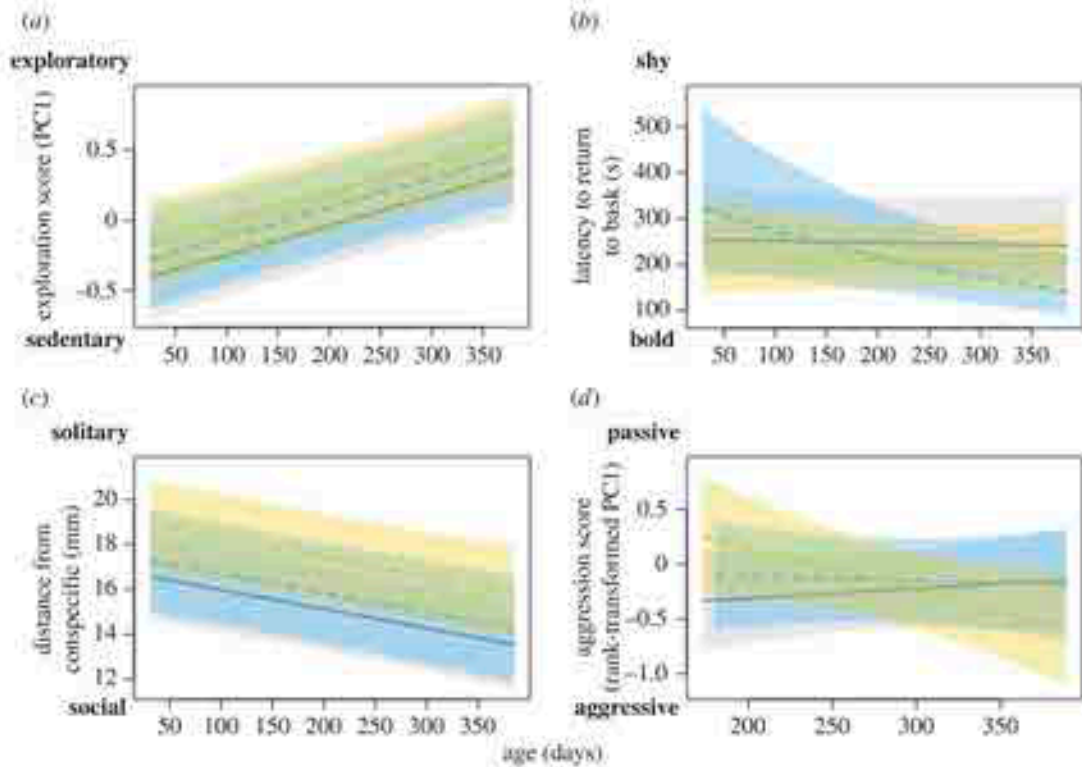


Figure 1. Tree skink social experience (isolated: grey polygon with solid line, dominant: blue polygon with dashed line, and subordinate: yellow polygon with dashed line) affects behavioural traits differently. (a) Exploration did not differ between social experiences. (b) Dominant skinks increased in their boldness (i.e. the inverse of latency; table 1) as they aged, whereas isolated and subordinate skinks maintained their level of boldness over time. (c) Subordinate skinks were less sociable than isolated skinks, but there was no difference in sociability between subordinate and dominant skinks, nor dominant and isolated skinks. (d) Subordinate skinks increased in aggression (i.e. the inverse of our aggression score; table 1) as they aged, and this change in aggression was different from that of isolated skinks but not different from that of dominant skinks. Aggression was also not different between dominant and isolated skinks. Shaded polygons around predicted fitted means are 95% predicted credible intervals.

Table 2. Variance (dark grey shaded), covariance (white background) and correlation (light grey shaded) estimates between the four behavioural traits for (a) between- and (b) within-individual error with associated 95% credibility intervals (in brackets) testing for correlation between behavioural traits in *Egernia striolata*. We bolded variables if the 95% credible intervals did not include 0 to indicate their significance.

	exploration	boldness	sociability	aggression
(a) between-individual variances, covariances, correlations and their associated 95% credibility intervals				
exploration	0.355 (0.026, 0.387)	-0.062 (-0.229, 0.067)	0.236 (-0.382, 0.945)	-0.078 (-0.248, 0.004)
boldness	-0.462 (-0.941, 0.316)	0.398 (0.057, 0.418)	0.390 (-0.317, 0.965)	0.079 (-0.030, 0.234)
sociability	0.515 (-0.262, 0.851)	0.354 (-0.282, 0.778)	6.270 (2.615, 10.150)	-0.173 (-0.692, 0.534)
aggression	-0.668 (-1.000, -0.068)	0.704 (-0.038, 0.986)	-0.168 (-0.667, 0.466)	0.116 (0.053, 0.377)
(b) within-individual variances, covariances, correlations and their associated 95% credibility intervals				
exploration	0.962 (0.723, 1.210)	0.036 (-0.137, 0.199)	0.270 (-0.250, 0.788)	0.089 (-0.083, 0.241)
boldness	0.056 (-0.149, 0.233)	0.750 (0.566, 1.005)	0.026 (-0.386, 0.650)	0.014 (-0.097, 0.191)
sociability	0.083 (-0.095, 0.289)	0.011 (-0.149, 0.270)	7.111 (5.598, 9.774)	0.151 (-0.265, 0.714)
aggression	0.073 (-0.103, 0.273)	0.016 (-0.136, 0.226)	-0.129 (-0.314, 0.281)	0.760 (0.618, 1.020)

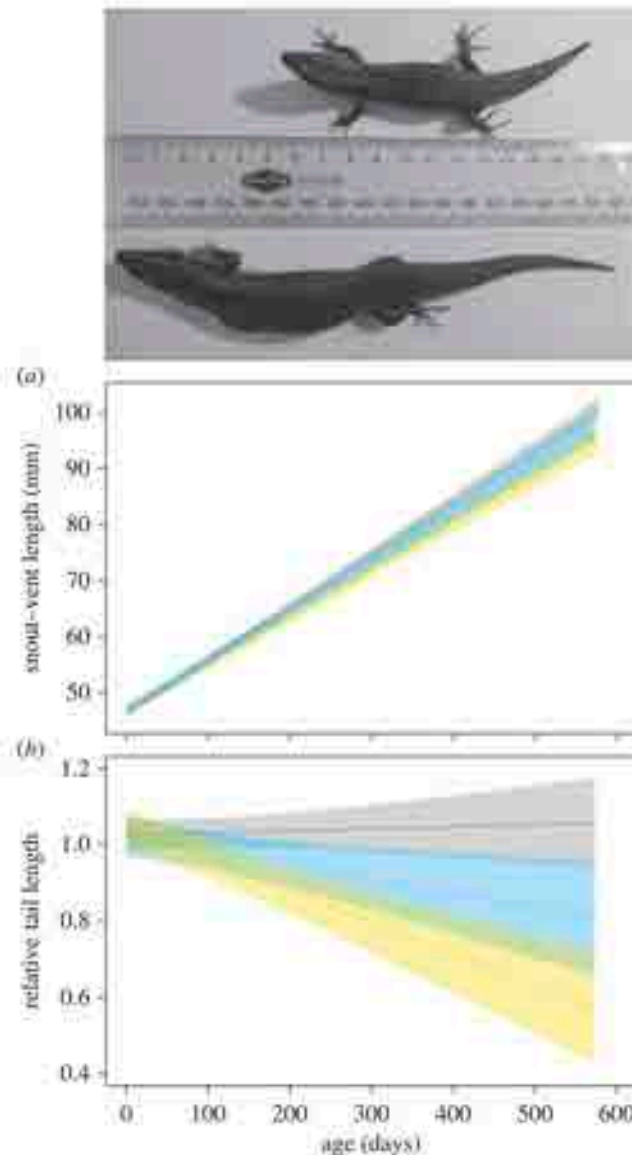


Figure 2. (a) Subordinate tree skinks (yellow polygon and dashed line) had smaller snout–vent lengths than isolated skinks. Isolated skinks (grey polygon and solid line) increased in SVL faster than dominant (blue polygon and dashed line) and subordinate skinks. (b) RTL, as well as the rate of change in RTL, differed between all social experiences (photograph shows difference in size found within a social pair). Shaded polygons around predicted probabilities are 95% predicted credible intervals.

Fifty-five percent (6/11) of dominant skinks and 73% (8/11) of subordinate skinks partially or fully autotomized their tails at least once. By contrast, no isolated skinks (0/16) autotomized their tails (Fisher's exact test, $p < 0.001$). The rate of change in RTL over time was significantly different among all social environments (isolated, dominant, and subordinate), which means RTL of isolated skinks grew at almost an equivalent rate to their SVL, but tails of subordinate skinks grew the slowest probably because of multiple instances of caudal autotomy ($\beta_{\text{DomSub}} = 0.067$, 95% CI = 0.009 to 0.144; table 3 and figure 2b).

3.3. Does social experience affect behavioural development?

Skink exploration did not differ among social experience ($\beta_{\text{DomSub}} = -0.154$, 95% CI = -0.434 to 0.204), nor did it change differently among social experiences as skinks aged (table 4 and figure 1a).

Boldness did not differ among social experiences ($\beta_{\text{DomSub}} = -0.093$, 95% CI = -0.337 to 0.263). However, as dominant skinks aged, they became bolder. This was significantly different from isolated

Table 3. Outcomes of linear mixed-effects models testing if SVL and RTL were affected by age (mean-centred), social experience (isolated, ISO; dominant, DOM; and subordinate, SUB), and the interaction between age \times social experience. Cohort (2014 and 2015) was also included in the model examining SVL, but not the model examining RTL, (as indicated with 'n/a'). The models also included the random effects of juvenile identity, mother identity, and housing tub.

fixed effects	SVL (mm)				RTL					
	$N_{\text{obs}} = 903$, $N_{\text{juv}} = 66$, $N_{\text{DOM}} = 35$, $N_{\text{SUB}} = 48$	β	2.5%	97.5%	p_{MCMC}	$N_{\text{obs}} = 432$, $N_{\text{juv}} = 37$, $N_{\text{DOM}} = 20$, $N_{\text{SUB}} = 27$	β	2.5%	97.5%	p_{MCMC}
intercept (ISO and 2014)		69.868	68.892	70.954	<0.001 ^a		1.053	0.986	1.086	<0.001 ^a
age		15.813	15.086	16.284	<0.001 ^a		0.004	-0.029	0.046	0.580
social experience: DOM		-1.138	-2.473	0.411	0.138		-0.091	-0.170	-0.018	0.008 ^a
social experience: SUB		-2.295	-3.700	-0.846	0.004 ^a		-0.187	-0.251	-0.101	<0.001 ^a
cohort		1.964	0.800	2.593	0.002 ^a		n/a	n/a	n/a	n/a
age \times social experience: DOM		-0.767	-1.718	0.170	0.086 ^b		-0.078	-0.135	-0.013	0.020 ^a
age \times social experience: SUB		-1.506	-2.526	-0.241	0.002 ^a		-0.169	-0.212	-0.092	<0.001 ^a
random effects	σ^2	2.5%	97.5%							
juvenile identity	11.224	7.488	17.727	0.079	0.010	0.036				
mother identity	0.003	0.000	0.947	0.001	0.000	0.004				
housing tub	0.003	0.000	0.978	0.001	0.000	0.003				
residual	12.206	10.640	12.991	0.011	0.010	0.013				

^aIndicates significant variables.

^bIndicated marginally significant variables.

skinks that were stable in their boldness over ontogeny, and marginally different from subordinate skinks that were also stable in their boldness ($\beta_{\text{DOMSub}} = -0.238$, 95% CI = -0.440 to 0.009; table 4 and figure 1b).

Subordinate skinks were less social than isolated skinks, but did not differ in sociability from dominant skinks ($\beta_{\text{DOMSub}} = -1.348$, 95% CI = -3.877 to 0.434; table 4). Isolated and dominant lizards did not differ in their sociability (table 4 and figure 1c). Sociability did not change differently among social experiences as skinks aged (table 4).

Aggression did not differ among social experiences ($\beta_{\text{DOMSub}} = 0.112$, 95% CI = -0.342 to 0.429; table 4). However, subordinate skink aggression increased with age, and this was significantly different from isolated skink aggression, which slightly decreased as they aged (table 4). Change in aggression over ontogeny did not significantly differ between dominant and subordinate, or dominant and isolated, skinks ($\beta_{\text{DOMSub}} = 0.156$, 95% CI = -0.062 to 0.537; table 4 and figure 1d).

3.4. Does social experience influence consistency of behavioural traits?

Repeatability, calculated from intercept-only models (R_{AG} ; electronic supplementary material, table S2), was lower than the adjusted repeatability calculated from full models ($R_{\text{ADJ|age}}$) that also considered covariates (table 4). $R_{\text{ADJ|age}}$ for exploration, boldness, aggression and sociability scores was low (table 4). Between social experiences $R_{\text{ADJ|age}}$ varied from low (e.g. subordinate skink exploration $R_{\text{ADJ|age}} = 0.004$, 95% CI = 0.001, 0.161) to high (e.g. dominant skink sociability $R_{\text{ADJ|age}} = 0.622$, 95% CI = 0.189, 0.886), although, due to the overlap of 95% credibility intervals, there was no significant differences in $R_{\text{ADJ|age}}$ among social experiences (figure 3).

4. Discussion

4.1. Are behavioural traits correlated?

Juvenile tree skinks that were more explorative than others also tended to be more aggressive towards a size-matched conspecific, regardless of social experience. These were the only two of the four behavioural traits we quantified that were correlated. Correlation between behavioural traits interests behavioural ecologists because it may suggest that correlated traits are selected upon simultaneously and may not be free to evolve independently [39,44]. In animal personality research, a correlation between two or more behavioural traits across multiple observations is termed a 'behavioural syndrome' [45,46]. Our findings

Table 4. Outcomes of linear mixed-effects models examining if behavioural traits of *Egernia striolata* differed among social experiences (ISO, isolated; DOM, dominant; SUB, subordinate). These models also included the fixed factors of age, batch (1 or 2), cohort (2014 and 2015), body temperature, and sex (male or female), as well as the random effects of juvenile identity, mother identity, and housing tub. All continuous variables were mean-centred. The social experience \times age interaction effect was included if it was significant, but if it was removed from the model due to non-significance then it is indicated with an 'n/a'.

fixed effects	exploration						boldness						sociability						aggression					
	$N_{\text{obs}} = 496, N_{\text{age}} = 62, N_{\text{batch}} = 35, N_{\text{cohort}} = 46$						$N_{\text{obs}} = 672, N_{\text{age}} = 56, N_{\text{batch}} = 31, N_{\text{cohort}} = 44$						$N_{\text{obs}} = 244, N_{\text{age}} = 61, N_{\text{batch}} = 31, N_{\text{cohort}} = 45$						$N_{\text{obs}} = 300, N_{\text{age}} = 50, N_{\text{batch}} = 30, N_{\text{cohort}} = 29$					
	β	2.5%	97.5%	pMCMC	β	2.5%	97.5%	pMCMC	β	2.5%	97.5%	pMCMC	β	2.5%	97.5%	pMCMC	β	2.5%	97.5%	pMCMC				
intercept (ISO, 1, FEMALE, and 2014)	-0.001	-0.281	0.270	0.916	5.537	5.201	5.843	<0.001*	15.004	13.028	16.716	<0.001*	-0.188	-0.548	0.158	0.178								
age	0.266	0.133	0.377	<0.001*	-0.026	-0.136	0.302	0.776	-0.883	-1.318	-0.508	<0.001*	0.093	-0.105	0.249	0.542								
social experience: DOM	0.141	-0.133	0.387	0.346	-0.259	-0.509	0.120	0.218	0.681	-0.889	2.614	0.430	0.060	-0.220	0.427	0.616								
social experience: SUB	0.302	-0.071	0.548	0.138	-0.138	-0.484	0.173	0.298	2.086	0.440	4.157	0.016*	0.131	-0.379	0.393	0.842								
batch: 2	0.241	0.082	0.449	0.012*	-0.212	-0.357	-0.054	0.004*	-0.661	-1.501	0.196	0.302	-0.190	-0.466	0.038	0.096								
cohort: 2015	-0.459	-0.743	-0.187	<0.001*	0.596	0.237	0.898	<0.001*	-0.777	-2.624	1.068	0.576	0.530	0.147	0.811	0.010*								
body temperature	0.192	0.091	0.272	<0.001*	-0.131	-0.258	-0.054	<0.001*	0.267	-0.345	0.633	0.282	0.071	-0.036	0.211	0.196								
sex: MALE	0.246	-0.100	0.468	0.362	-0.014	-0.308	0.293	0.972	1.364	-0.676	3.021	0.270	0.105	-0.282	0.427	0.588								
age \times social experience: DOM	n/a	n/a	n/a	n/a	-0.250	-0.409	-0.013	0.022*	n/a	n/a	n/a	n/a	n/a	-0.084	-0.364	0.175	0.536							
age \times social experience: SUB	n/a	n/a	n/a	n/a	-0.053	-0.201	0.193	0.942	n/a	n/a	n/a	n/a	n/a	-0.245	-0.598	-0.029	0.034*							
random effects	σ^2	2.5%	97.5%	σ^2	2.5%	97.5%	σ^2	2.5%	97.5%	σ^2	2.5%	97.5%	σ^2	2.5%	97.5%	σ^2	2.5%	97.5%	σ^2	2.5%	97.5%			
juvenile identity	0.005	0.001	0.245	0.003	0.003	0.001	0.148	0.078	0.003	9.226	0.001	0.225	0.005	0.001	0.225	0.005	0.001	0.225	0.005	0.001	0.225			
mother identity	0.001	0.000	0.098	0.002	0.002	0.000	0.121	0.042	0.000	8.619	0.001	0.078	0.001	0.000	0.078	0.001	0.000	0.078	0.001	0.000	0.078			
housing tub	0.002	0.000	0.109	0.131	0.001	0.231	0.014	0.014	0.000	5.126	0.002	0.179	0.002	0.000	0.179	0.002	0.000	0.179	0.002	0.000	0.179			
residual	0.907	0.777	1.006	0.820	0.709	0.893	7.688	5.954	10.311	0.819	0.665	0.968	0.819	0.665	0.968	0.819	0.665	0.968	0.819	0.665	0.968			
repeatability	R^2	2.5%	97.5%	R^2	2.5%	97.5%	R^2	2.5%	97.5%	R^2	2.5%	97.5%	R^2	2.5%	97.5%	R^2	2.5%	97.5%	R^2	2.5%	97.5%			
R^2 from intercept-only model	0.002	0.000	0.056	0.001	0.000	0.082	0.001	0.000	0.451	0.001	0.451	0.003	0.001	0.451	0.003	0.001	0.451	0.003	0.001	0.451	0.003	0.001	0.451	
R^2 from full model	0.013	0.002	0.206	0.003	0.001	0.134	0.004	0.000	0.505	0.004	0.505	0.004	0.001	0.505	0.004	0.001	0.505	0.004	0.001	0.505	0.004	0.001	0.505	

Indicates significant variables.

*Indicates significant variables.

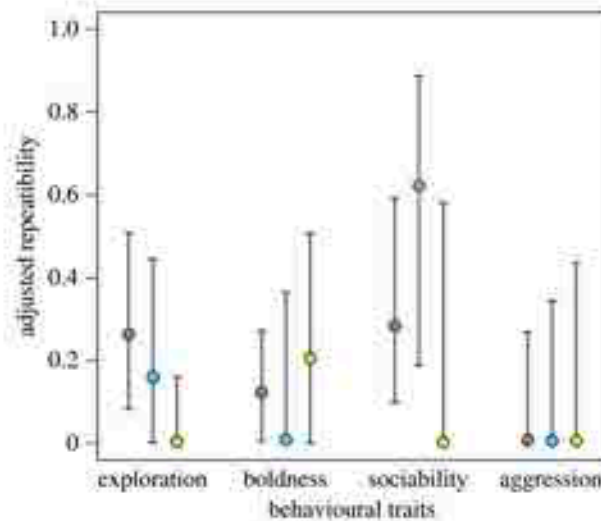


Figure 3. Adjusted repeatability ($R_{A01|age}$) varies among social experiences of tree skinks (isolated, grey circle; dominant, blue circle; subordinate, yellow circle) depending on the behavioural trait. $R_{A01|age}$ of exploration and boldness was low for all social experiences, and $R_{A01|age}$ of aggression was no different from 0 for all social experiences. By contrast, $R_{A01|age}$ of sociability was moderate for dominant skinks, low for subordinate skinks, and no different from 0 for isolated skinks. Differences between social experiences are not significant because of the large overlap of 95% credibility intervals.

agree with the bulk of current findings about correlations between behavioural traits, which typically show that more exploratory individuals are also more aggressive (e.g. shy–bold, reactive–proactive continuum of traits [45,47–49]). We currently do not know much about the ecology and life history of tree skink juveniles in the wild, and thus how covariance of these two traits may benefit an individual is unknown. However, in a closely related skink, White's skink (*Liopholis whitii*), juveniles' dispersal from their natal group is thought to vary depending on the degree of relatedness to their social father [50]. Juveniles that are from extra-pair matings, and are thus not related to the male within the social group, have a larger home range that only overlaps with their mother and siblings [50]. So, in the case of these more dispersive and more exploratory juveniles, it may pay to be more aggressive in encounters with size-matched siblings to gain resources like maternal access, food, and shelter space that are more limited to them. Alternatively, the correlation may simply be explained by this species' ecology. Tree skinks live in a constrained habitat (i.e. crevices), and within this habitat the likelihood of encountering conspecifics is high. Perhaps tree skinks that are more exploratory inhabit a larger home range, and thus are also more aggressive, so they can defend their territory from other conspecifics. Overall, more research is needed to understand the fitness benefits of trait covariance in this social lizard species.

4.2. Does social experience impact individual phenotype?

Individual social experience across ontogeny impacted morphological development in tree skinks. Our socially reared pairs formed dominant–subordinate relationships wherein skinks that were larger and/or male were consistently dominant in their pairings. While we standardized resources between social and isolated treatments, growth rate of socially reared skinks was slower than in isolated skinks. This may have been the result of resource competition (e.g. for food or basking locations, or increased activity and energy waste from social interactions) between pairs that was a product of the dominant–subordinate relationship, as has been shown in other lizard species. For example, Stamps [51] found that juvenile bronze anoles (*Anolis aeneus*) with high territory overlap experienced reduced growth rate due to increased food competition. The hypothesis that socially reared pairs were competitive and aggressive towards each other is also supported by the fact that the majority (73%) of subordinate skinks autotomized their tails at least once, and the RTL of subordinate skinks decreased sharply over time instead of remaining stable. Tail loss is also a consequence of juvenile aggression in other *Egernia* spp. (e.g. the black rock skink, *E. saxatilis* [26]), suggesting that the social environment may be more costly for juveniles than previously thought. There are substantial costs of tail autotomy (e.g. reduced motor ability, energetic costs, indirect effects on communication, reduced survival and fecundity [40,52]), and

impacts are more extreme for juveniles than adults because they need to allocate energy towards both tail regeneration and somatic growth [40]. The physical impacts on development we observed within the social treatment indicate that the social environment is costly, especially for subordinate (smaller in size and/or female) skinks.

4.3. Does social experience affect behavioural development?

Contrary to our prediction, isolation rearing did not affect behavioural development in ways expected from the literature. We expected that isolated skinks would be less exploratory, less bold, less social and more aggressive than socially reared conspecifics. Instead, isolated skinks were more social than subordinate skinks, opposite to our prediction. Also, isolated skinks remained consistently bold and aggressive, whereas we predicted a change in both these traits. Thus, being raised in isolation did affect behavioural development in tree skinks, yet not in the way previously observed in other taxa [3,9, 53–55]. In most mammals and birds, isolation rearing greatly hinders individual development and fitness. Although we did not measure fitness consequences of the behavioural differences we found for isolated tree skinks, the behavioural changes we observed (higher sociability) may not have significant negative impacts on individual fitness. This finding has important implications for reptile conservation and management projects, as well as ethical considerations. It is important to consider each target animal's sociality in any research and management project; however, our findings suggest that isolation rearing does not consistently, negatively impact behaviour across all social taxa. In wild populations of tree skinks and other *Egernia* group species, developing in isolation is an option [24,25]: for example, in White's skink growing up in isolation and/or with reduced social contact often occurs for a proportion of offspring in each litter (e.g. juveniles unrelated to the social father; [56]). Since variable social exposure occurs over development in these social lizards, they may be predisposed to cope well with isolation rearing. From this hypothesis, we would predict that a mammal or bird with a similar social structure and ecological constraints as the tree skink would show the same, unexpected, reaction to social isolation.

As expected, with dominant-subordinate relationships within socially raised pairs, behavioural development differed between these social experiences. Dominant skinks increased in boldness as they aged, which was significantly different from isolated skinks and marginally different from subordinate skinks that remained stable in their boldness over time. Perhaps, as they repeatedly 'won' in social interactions and/or recognized they were the larger skink within their environment, they were more inclined to exhibit risky behaviour [42]. Subordinate skinks were the least social and increased in aggression over time, yet these trends were only significantly different from isolated skinks, not from dominant skinks. This lack of significance, despite a clear trend, was probably due to large variation in skink behaviour. After aggressive encounters with their social partner, subordinate skinks may have tended to avoid social interactions and learnt to react aggressively to conspecifics over time. Our experiment differs from natural conditions because social groups lacked the presence of parent(s) [23] and lizards were restricted within their housing tubs; however, this restriction of space may not be so different from natural conditions because tree skink social groups are always constrained by restricted resources (i.e. crevices and hollows [23,57]). Our findings demonstrate that behavioural development is affected by social feedback experienced during the juvenile life stage. This may help explain why asynchronous birth that generates social rivalries within litters, a common phenomenon across multiple taxa, might be an adaptive strategy.

Many *Egernia* group species, including tree skinks, give birth over several days or weeks [21,58–60]. Research on White's skink has shown that embryo development prior to birth is synchronous and that females retain offspring to delay births over time [21], suggesting this may be an adaptive behaviour. Within litters that are born asynchronously, a size-based dominance hierarchy forms, and the youngest and smallest offspring exhibit reduced growth rates and increased mortality because of competition and aggression from siblings [15,16,22]. In our study, the difference in age between social pairs (range from 1 to 18 days) is an analogous comparison to juveniles within an asynchronously born litter. We examined if the difference in age between social pairs was related to the difference in their aggression scores, and found that social pairs that were more different in age tended to also exhibit a larger difference in aggression (see the electronic supplementary material, figure S3). This relationship was not significant, probably because of our limited sample size, but the trend suggests that competitive asymmetries are more pronounced in juvenile social pairings that are more different in age. Thus, in our study, older lizards had a head start on growth and were able to more easily dominate younger individuals, which is exactly what occurs in litters born asynchronously [16,17,22]. We found that subordinate lizards were less social and became more aggressive over time. These behavioural traits might be linked to a higher rate of dispersal away from social groups. Our evidence

that social rank within a social group impacts development provides support for the hypothesis that asynchronous birth may be beneficial because it promotes divergence in offspring traits, and potentially life-history strategies, which could ensure survival of at least one offspring if faced with an unpredictable environment. These insights from our laboratory experiment provide promising avenues for future research directly testing the adaptive value of asynchronous birth of *Egernia* group species in the wild.

4.4. Does social experience influence consistency of behavioural traits?

Our adjusted repeatability scores were very low for all four behavioural traits. Also consistency in behavioural traits did not differ between lizards within different social environments, and was highly variable between individuals. Thus, tree skink behavioural traits were not temporally consistent over their first year of life, nor can they be classified as 'personality' traits as they can be referred to in animal behaviour [46,61]. Contrasting with our results, in a study that assayed adult tree skink behavioural traits twice over 12 days, there was high to medium repeatability in exploration, boldness and aggression, but no repeatability in sociability and activity [39]. There is a disparity in the scale of time that behavioural traits were examined between these two studies (behaviour is more likely to be consistent over 12 days than 1 year), but perhaps juveniles undergoing development are generally more variable in behaviour because they are more sensitive to change than during adulthood. Currently, there are only a few studies that examine the development of personality traits, yet they consistently have demonstrated that personality (or behavioural) traits are less temporally stable in juveniles when compared with adults [62–64]; our findings corroborate this trend.

5. Conclusion

In summary, we found evidence that the social environment (isolation, dominant member of a pair and subordinate member of a pair) impacts behavioural development in tree skinks. To the best of our knowledge, this is the first time social environment has been shown to play an important role in the behavioural development of a reptile, an under-studied taxon in regard to social behaviour [65]. Many environmental factors (e.g. predation pressure, incubation temperature, nutrition; [62,66–68]) impact behavioural development and cause behavioural divergence. Our study highlights that both lack of social interaction and the nature of social interactions are other factors that can potentially drive change and divergence across behavioural development. Our study also helps to inform an often-overlooked area of personality research: how behavioural traits may change over the course of development. Specifically, our results corroborate previous work that found that juvenile personality is not temporally stable.

Overall, our study provides evidence that isolation rearing does not consistently impact behaviour across all social taxa. Tree skinks cope well in isolation rearing, perhaps due to existing social variation within wild rearing conditions. Other social species, with a similarly varied social structure, may also exhibit this coping ability for isolation rearing. A more thorough understanding of behavioural development across all social taxa might also be gained from our evidence that suggests that social rank within a group of conspecifics could influence behavioural divergence in an adaptive manner when growing up in a variable environment.

Ethics. Experimental protocols were approved by the Macquarie University Animal Ethics Committee (ARA no. 2013/039). Our research on skinks was approved by the New South Wales National Parks and Wildlife Service, Office of Environment and Heritage (License no. SL101264).

Data accessibility. All data and R code for analyses used in this study can be accessed from the Bitbucket repository: https://julia_riley@bitbucket.org/julia_riley/e-striolata-personality.git.

Authors' contributions. J.L.R. coordinated the study, collected experimental data, scored behaviours and completed statistical analyses. D.W.A.N. assisted with statistical analyses. J.L.R., D.W.A.N., R.W.B. and M.J.W. designed the study and prepared the manuscript. All authors approved the final publication.

Competing interests. We have no competing interests.

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Supplementary Materials

Material and methods

Study species

Tree skinks are a medium-sized, viviparous skink found across southeastern Australia [1]. This skink typically resides within cracks or hollows within trees and rocks [1] and exhibits variable social organization both within and between populations. Within a population, individuals can either be found alone or in groups of variable size (2-10 skinks; [2,3]). Across the tree skink's range, different social systems have been described between populations. In some arboreal populations, tree skinks have been found in small groups (maximum of 3 individuals) and are often found alone [2,4]. In other arboreal and in saxicolous populations, tree skinks were often observed in large social groups (< 10 lizards) of closely related individuals [3,5-8].

Field collection and captive housing

Gravid female tree skinks were collected from Albury, New South Wales (35.98°S, 146.97°E) in January 2014 (N = 15) and 2015 (N = 20), and maintained at Macquarie University until parturition. Parturition occurred in 2014 from 10 February to 12 March, and in 2015 from 17 January to 10 February. The females were kept in a climate-controlled room (maintained at 24°C) within opaque plastic tubs (350 mm W x 487 mm L x 260 mm H). These tubs were lined with newspaper, and contained tree bark, a water dish, and a refuge (120 mm W x 175 mm L x 38 mm H). Each lizard's tub was lit by a UV lamp, and had under-cage heating wire limited to one side of the tub to allow thermoregulation. All housing tubs were cleaned once weekly. Lizards were fed 3 adult crickets dusted with calcium and vitamins twice a week, and puréed fruit (1.25 ml of Heinz® baby food: apple and mango, apple, and pear) once weekly.

During parturition, we checked the females twice a day to see if they had given birth. Offspring were separated from females immediately post-parturition, and housed separately until all females had given birth. Before separation, we measured each juvenile's snout-vent length (mm, SVL: the distance between the tip of the snout and the posterior edge of the cloaca), total length (mm), and tail length (mm) with a standard ruler to the nearest 1 mm. We also recorded mass with a digital scale (SP6001, Scout Pro, Ohaus, Pine Brook NJ, USA) to

the nearest 0.01 g, and marked each juvenile with a unique toe-clip [9]. We re-measured each skink monthly throughout their first year of life and at a maximum of a week prior to each behavioural assay. During each measurement period, we also noted if lizards had complete or damaged tails (i.e., were their tails autotomized). We calculated relative tail length ($RTL = \text{tail length}/SVL$), and used this in our analyses as a proxy for the frequency of tail autotomy in each individual; if a lizard underwent multiple instances of tail autotomy their RTL would be lower and would decrease over time instead of remaining stable (around 1; [10]). The offspring were housed within smaller opaque plastic tubs than the females (85 mm W x 140 mm L x 60 mm H). All other housing criteria were the same, except they were fed nymph crickets instead of adult crickets. In 2014, a total of 28 juveniles were included in our experiments, and in 2015 a total of 38 juveniles were sampled. During winter months (June to August), lizards were maintained at a reduced temperature (18°C).

Timing and sample sizes of behavioural assays

Baseline behavioural assays occurred from 23 March to 14 April 2014, and 15 April to 9 May 2015. We repeated the behavioural assays three more times within each year: (1) ca. 5 months of age (23 August to 18 September 2014, and 19 September to 7 October 2015), (2) ca. 7 months of age (29 October to 21 November 2014, and 3 to 26 November 2015), and (3) ca. 12 months of age (31 January to 23 February 2015, and 18 January to 10 February 2016).

Due to the size of our experimental room, we had to measure juvenile behaviour within two batches (maximum of 24 per batch). Juveniles were approximately equally, randomly allocated to a batch for each assay period. In the 2014 cohort ($N=28$), 12 skinks were in batch 1 and 16 skinks were in batch 2 lizards during the baseline trials. At 5 and 7 months of age, 18 and 10 skinks were in batch 1 and 2, respectively. At 12 months of age, 15 and 13 skinks were batch 1 and 2, respectively. In the 2015 cohort ($N=38$), 19 skinks were in both batch 1 and 2 during the baseline assays. At 5 months of age, 22 and 16 skinks were in batch 1 and 2, respectively. At 7 and 12 months of age, 18 and 20 skinks were in batch 1 and 2, respectively.

Experimental housing and data collection

During behavioural assays, all lizards were housed in 100 L opaque plastic arenas (690 mm W x 470 mm L x 455 mm H) within a climate-controlled room. Each arena was warmed on one side with a heat lamp, and contained a refuge and a water dish except during assays. Lizards were fed as usual (see above) but only after assay completion each day. Immediately after assays finished each day, body temperature of each lizard was measured using an infrared thermometer (accuracy of 1.5°C, model # RIT310, Ryobi, Techtronic Industries

Australia Pty Ltd, Doncaster, Victoria). We recorded behavioural assays using a mounted security camera system (CCTV security systems, Melbourne, Victoria), and behaviour was scored from these videos. Videos were scored blind to social treatment, and were scored by the same person (JLR) to avoid inter-observer bias.

Additional information about statistical analyses

Initially, in our univariate LMMs to assess differences in behavioural traits, we included *body condition index* (residuals from a simple linear regression between log-transformed mass and SVL) as a covariate, but it was not significant in any model. So, we removed it in order to implement the simplest model with the most power in our analyses.

In the multivariate LMM to assess correlations between all four behavioural traits, we considered if maternal effects should also be included in the model. The deviance information criterion (DIC) value for the model without mother identity (*DIC* 1279.647) was not very different with mother identity included (*DIC* = 1279.443). So, we opted to use the simplest model, as maternal effects did not appear to explain a substantial amount of variation.

Results

Data exploration and model validation

During data exploration for all models, we did not find any unexplainable outliers, and no strong collinearity was found between predictor variables. We did remove missing values where applicable, thus there are a variable number of observations and individuals within each model (sample sizes are provided in all tables).

Mixing of our chains was good in the two models that examined the response variables of SVL and RTL, as well as all three models that examined behavioural traits. Visual inspection of residual plots for each model did not reveal any obvious deviations from homoscedasticity or normality of residuals.

Relationships between covariates and behavioural traits

The fixed effects (age, batch, cohort, body temperature, and sex) each differently influenced behavioural traits (table 2). Sex was not significantly related to any behavioural trait.

Individuals spent more time exploring as they aged, exploration was positively related to body temperature, skinks from our second batch were more exploratory, and skinks from the 2015 cohort were less exploratory (table 2). Skinks increased in boldness (a lower latency to return to bask) as they aged and increased in body temperature, as well skinks from the 2015 cohort were less bold (table 2). As lizards aged they situated themselves, on average, closer to

conspecific adults (higher sociability; table 2). Lizards from our 2015 cohort had a higher aggression score than lizards from our 2014 cohort (table 2).

Relationship between difference in age and aggression score between social pairs

We examined if absolute difference in aggression score was related to the absolute difference in age (days) between social pairs using a simple linear regression (function *lm* from the *base* R package; [11]). We found that as age difference increased, so did the difference in aggression score ($t_{1,5} = 1.914$, $P = 0.114$, $R^2 = 0.308$; Fig. S3). However this relationship was not significant, probably because of our small sample size ($N = 7$).

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Supplemental Tables

Table S1. Component loadings from our principal component analysis (PCA) for the behaviours scored from our *E. striolata* exploration and aggression assays. The PCA for the exploration assay consisted of two behaviours (time spent moving in a novel environment, and number of times a skink entered two refuges within the new environment). The PCA for the aggression assay consisted of three behaviours (latency to retreat into a refuge after being repeatedly touched by a replica lizard, number of times the lizard gaped, and number of times it bit the replica). These traits were measured for 66 skinks (within two cohorts; $N_{2014} = 28$, $N_{2015} = 38$) eight times (two times during four time-periods within each skinks' first year of life; $N_{\text{obs}} = 792$).

Behaviour	Component one loadings
Exploration	
Time spent moving (sec)	0.707
Number of times entered refuges	0.707
Aggression	
Latency to retreat into the refuge (sec)	-0.651
Number of gapes	-0.429
Number of bites	-0.657

Table S2. Outcomes of intercept-only linear mixed-effect models used for estimating repeatability (adapted R_M from Nakagawa and Schielzeth 2010) of behavioural traits in *Egermia striolata*. The model also included the random effects of juvenile and mother identity. Significant parameters in each model are indicated asterix (*) to the right of the 95% credibility intervals and the $pMCMC$ values.

	Exploration $N_{obs} = 496, N_{juv} = 62, N_{mom} = 35$				Boldness $N_{obs} = 672, N_{juv} = 56, N_{mom} = 31$				Sociability $N_{obs} = 244, N_{juv} = 61, N_{mom} = 31$				Aggression $N_{obs} = 300, N_{juv} = 50, N_{mom} = 30$					
Fixed effects	β	2.5%	97.5%	$pMCMC$														
Intercept	0.017	-0.146	0.151	0.988	5.674	5.495	5.858	<0.001	*	15.380	14.559	16.168	<0.001	*	-0.033	-0.156	0.145	0.982
Random effects	σ^2	2.5%	97.5%															
Juvenile identity	0.001	0.000	0.103		0.101	0.031	0.265			5.867	1.616	8.979			0.104	0.000	0.210	
Mom's identity	0.057	0.001	0.205		0.138	0.000	0.272			0.016	0.000	4.786			0.001	0.000	0.095	
Residual	1.035	0.925	1.206		0.879	0.766	0.960			9.719	7.975	11.985			0.833	0.683	0.979	
Repeatability	R	2.5%	97.5%															
R_M	0.001	0.000	0.087		0.098	0.030	0.238			0.305	0.121	0.504			0.003	0.000	0.581	

Table S3. Results of linear mixed-effect models that only examined data for isolated skinks used for estimating repeatability (adapted $R_{adj|time}$ from Biro and Stamps 2015) of behavioural traits. These models also include the fixed factors of age, batch (1 or 2), cohort (2014 and 2015), body temperature, and sex (M: male or F: female), and the random effect of juvenile identity. All continuous variables were mean centred. We highlighted important variables in each model with an asterix (*) to the right of the 95% credibility intervals and the $pMCMC$ values.

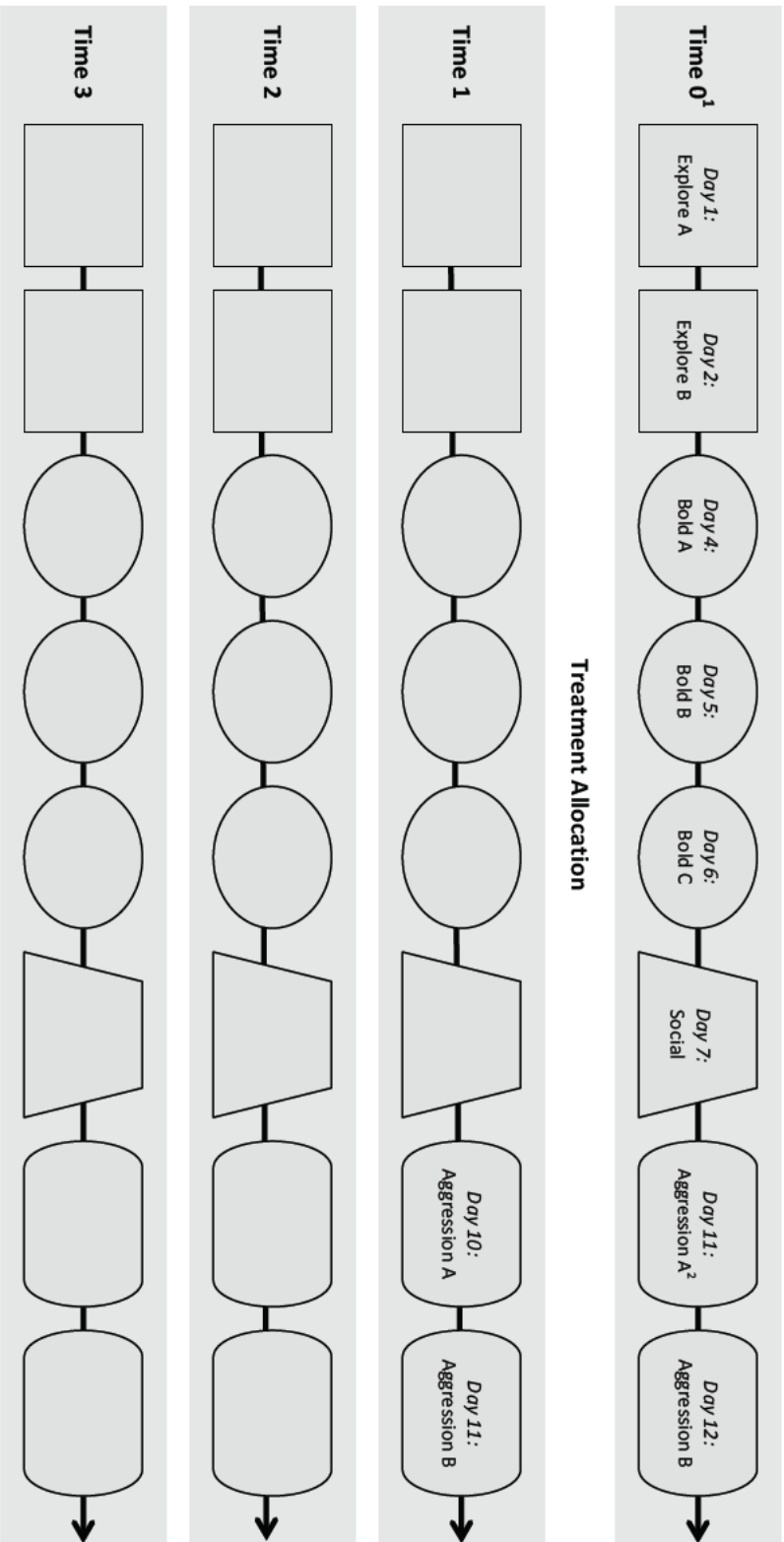
Fixed effects	Exploration $N_{obs} = 224, N_{juv} = 28, N_{mom} = 28$				Boldness $N_{obs} = 312, N_{juv} = 26, N_{mom} = 26$				Sociability $N_{obs} = 108, N_{juv} = 27, N_{mom} = 27$				Aggression $N_{obs} = 132, N_{juv} = 22, N_{mom} = 22$			
	β	2.5%	97.5%	$pMCMC$												
Intercept (1, 2014, F)	0.019	-0.263	0.411	0.790	5.601	5.262	5.991	<0.001	14.822	12.358	16.722	<0.001	0.090	-0.440	0.437	0.922
Age	0.259	0.101	0.385	0.002	0.005	-0.130	0.119	0.894	-1.024	-1.731	-0.492	<0.001	0.133	-0.117	0.290	0.368
Batch: 2	0.331	-0.002	0.555	0.034	-0.281	-0.497	-0.015	0.030	-0.142	-1.336	1.079	0.822	-0.301	-0.727	0.165	0.216
Cohort: 2015	-0.445	-0.924	-0.132	0.024	0.428	0.087	0.846	0.028	0.089	-2.231	2.299	0.976	0.210	-0.247	0.653	0.382
Body temperature	0.118	0.041	0.305	0.012	-0.108	-0.212	-0.008	0.040	0.302	-0.378	0.753	0.534	0.015	-0.168	0.232	0.640
Sex: M	0.030	-0.289	0.389	0.582	0.029	-0.398	0.365	0.938	0.459	-1.969	2.411	0.850	-0.014	-0.540	0.353	0.694
Random effects																
Juvenile identity	σ^2	2.5%	97.5%													
Mom's identity	0.281	0.020	0.647		0.077	0.004	0.299		3.258	0.623	10.263		0.008	0.001	0.340	
Residual	--	--	--		--	--	--		--	--	--		--	--	--	
	0.755	0.651	0.961		0.837	0.689	0.974		7.377	5.717	11.268		0.982	0.676	1.209	
Repeatability																
R	2.5%	97.5%														
Rad age	0.264	0.083	0.508		0.123	0.006	0.272		0.284	0.099	0.591		0.008	0.001	0.269	

Table S4. Outcomes of linear mixed-effect models that only examined data for dominant skinks used for estimating repeatability (adapted R_{adj} from Biro and Stamps 2015) of behavioural traits. These models also include the fixed factors of age, batch (1 or 2), cohort (2014 and 2015), body temperature, and sex (M: male or F: female), and the random effects of juvenile and mother identity. All continuous variables were mean centred. We highlighted important variables in each model with an asterix (*) to the right of the 95% credibility intervals and the $pMCMC$ values.

	Exploration				Boldness				Sociability				Aggression					
	$N_{obs} = 144, N_{juv} = 18, N_{mom} = 15$				$N_{obs} = 180, N_{juv} = 15, N_{mom} = 12$				$N_{obs} = 72, N_{juv} = 18, N_{mom} = 15$				$N_{obs} = 96, N_{juv} = 15, N_{mom} = 14$					
Fixed effects	β	2.5%	97.5%	pMCMC														
Intercept (1, 2014, F)	-0.041	-0.552	0.365	0.706	4.864	4.044	5.396	<0.001	*	16.617	13.798	20.844	<0.001	*	-0.314	-0.886	0.119	0.164
Age	0.124	-0.055	0.334	0.142	-0.273	-0.416	-0.090	0.006	*	-0.918	-1.544	0.403	0.150		0.015	-0.259	0.154	0.844
Batch: 2	0.425	0.117	0.773	0.016	-0.170	-0.496	0.087	0.176		-1.055	-2.705	0.352	0.104		-0.163	-0.576	0.244	0.366
Cohort: 2015	-0.623	-1.034	-0.116	0.020	1.049	0.578	1.841	<0.001	*	-2.945	-6.165	0.835	0.150		0.758	0.150	1.232	0.012
Body temperature	0.261	0.115	0.450	<0.001	-0.204	-0.333	-0.029	0.032	*	0.560	-0.353	1.271	0.212		-0.030	-0.246	0.161	0.748
Sex: MALE	0.712	0.005	0.998	0.036	0.174	-0.321	0.602	0.446		1.674	-2.208	3.856	0.466		0.263	-0.186	0.737	0.318
Random effects	σ^2	2.5%	97.5%															
Juvenile identity	0.026	0.002	0.700		0.011	0.001	0.482			8.895	0.116	39.688			0.007	0.001	0.345	
Mom's identity	0.003	0.000	0.170		0.003	0.000	0.270			0.059	0.000	14.588			0.003	0.000	0.276	
Residual	0.835	0.636	1.106		0.816	0.669	1.032			8.921	4.885	11.985			0.704	0.476	0.914	
Repeatability	R	2.5%	97.5%															
Rad age	0.161	0.002	0.445		0.009	0.001	0.365			0.622	0.189	0.886			0.007	0.001	0.345	

Table S5. Outcomes of linear mixed-effect models that only examined data for subordinate skinks used for estimating repeatability (adapted R_{adj} time from Biro and Stamps 2015) of behavioural traits. These models also include the fixed factors of age, batch (1 or 2), cohort (2014 and 2015), body temperature, and sex (M: male and F: female), as well as the random effects of juvenile and mother identity. All continuous variables were mean centred. We highlighted important variables in each model with an asterix (*), and marginally important variables with a tilde (~) to the right of the 95% credibility intervals and the $pMCMC$ values.

Exploration					Boldness					Sociability					Aggression				
$N_{obs} = 128, N_{juv} = 16, N_{mom} = 14$					$N_{obs} = 180, N_{juv} = 15, N_{mom} = 14$					$N_{obs} = 64, N_{juv} = 16, N_{mom} = 14$					$N_{obs} = 72, N_{juv} = 12, N_{mom} = 11$				
Fixed effects	β	2.5%	97.5%	pMCMC															
Intercept (1, 2014, F)	0.442	0.095	0.859	0.028	*	5.226	4.574	5.640	<0.001	*	16.627	14.223	18.318	<0.001	*	-0.492	-0.974	0.144	0.146
Age	0.286	0.079	0.493	0.016	*	0.042	-0.161	0.179	0.976		-0.777	-1.739	-0.058	0.038	*	-0.240	-0.564	-0.043	0.040
Batch: 2	-0.098	-0.497	0.284	0.590		-0.014	-0.327	0.267	0.878		-0.658	-2.114	1.138	0.588		0.098	-0.572	0.423	0.738
Cohort : 2015	-0.567	-0.965	-0.054	0.018	*	0.762	0.200	1.448	0.016	*	-0.456	-2.282	2.907	0.842		0.577	0.047	1.354	0.034
Body temperature	0.136	-0.046	0.307	0.168		-0.100	-0.227	0.018	0.094	~	0.044	-0.733	0.689	0.974		0.224	0.045	0.516	0.040
Sex: M	--	--	--	--		--	--	--	--		--	--	--	--		--	--	--	--
Random effects					σ^2	2.5%	97.5%												
Juvenile identity	0.011	0.001	0.211																
Mom's identity	0.002	0.000	0.108																
Residual	1.066	0.815	1.386																
Repeatability					R	2.5%	97.5%												
R _{adj} age	0.004	0.001	0.161																
					0.207	0.001	0.506												
					0.003	0.000	0.581												
					0.007	0.001	0.436												



¹Within each time period, the tree skinks were randomly separated into two experimental batches due to space constraints within our experimental rooms.

²Tree skinks from the 2014 cohort did not undergo the assays: Aggression A, and Aggression B.

Figure S1. Sequence of behavioural trait assays the 2014 (N = 28) and 2015 (N = 38) cohorts of tree skinks underwent to categorize their personality traits. The type of behavioural trait assay is represented with a different *shape*, and sequence is noted within the shape. At each time period (Time 0, 1, 2, and 3), we first categorized their exploratory behaviour with two repeated assays (represented by *rectangles*), boldness with three repeated assays (*circles*), sociality with one assay (*quadrilateral*), and aggression with two repeated assays (*rectangle with rounded ends*). The timing of aggression assays changed between Time 0 and Time 1, 2, and 3: from day 11 and 12, to day 10 and 11.

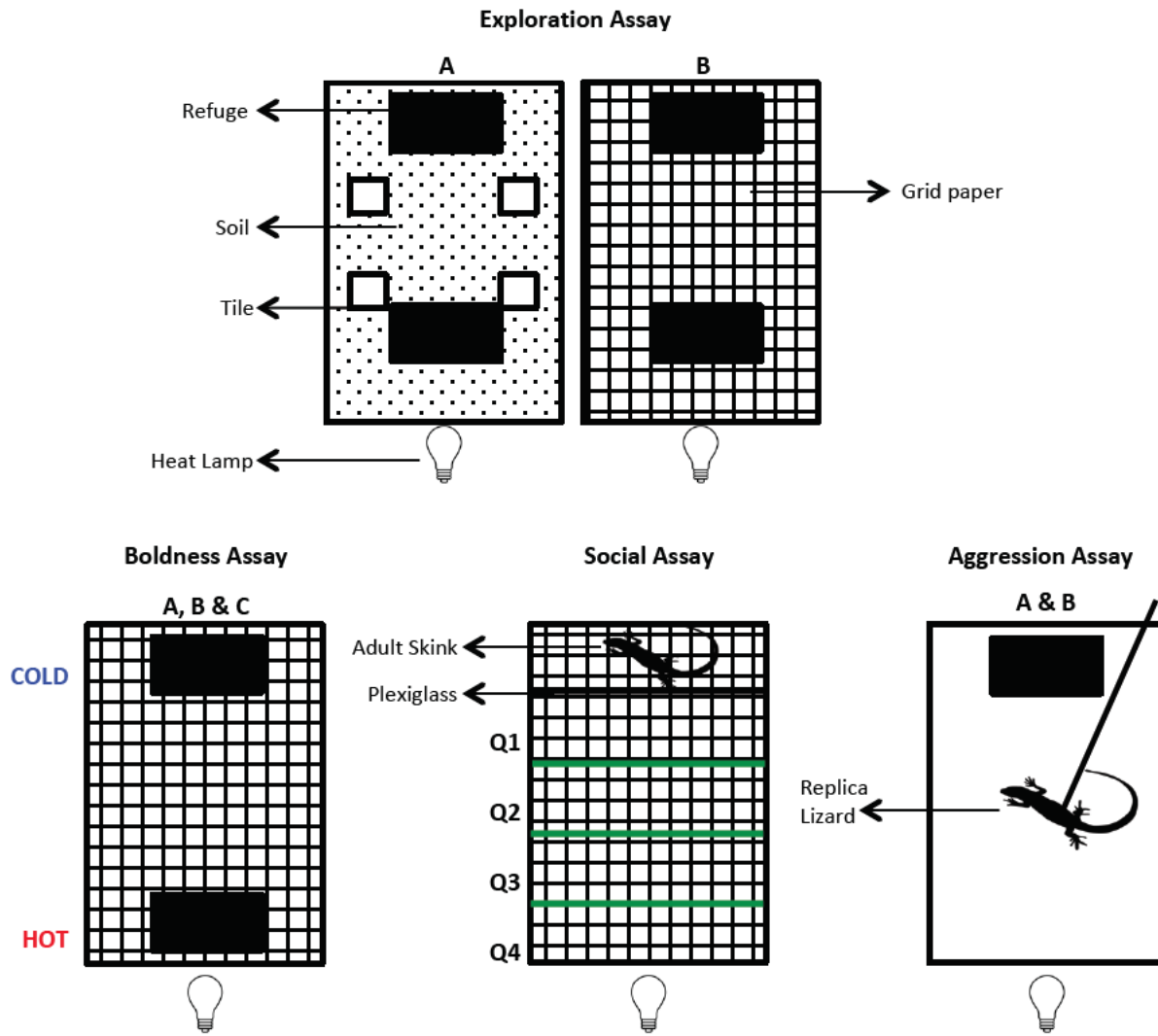


Figure S2. Experimental arena set-ups for our behavioural trait assays.

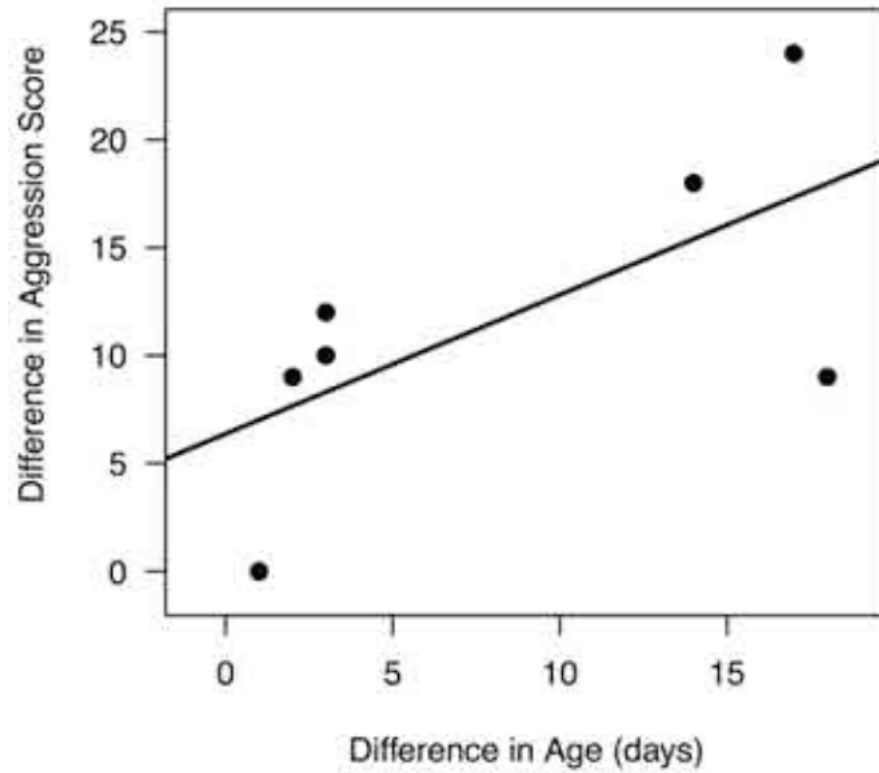


Figure S3. Socially-reared skink pairs ($N = 7$) that were more different in age (e.g., one individual born early in the season, and the other born late in the season) tended to also have a larger difference in aggression score (e.g., one very aggressive skink, and one very submissive skink). However, probably because of our small sample size, this relationship was not significant ($t_{1,5} = 1.914$, $P = 0.114$, $R^2 = 0.308$).

Chapter II

Does social environment influence learning ability in a family-living lizard?



Julia L. Riley, Daniel W.A. Noble, Richard W. Byrne, and Martin J. Whiting

The following manuscript has been published in the journal *Animal Cognition*. It is presented as published within the journal. This article's supplemental video can be found via the link in Appendix 1.

Pages 55-64 of this thesis have been removed as they contain published material under copyright. Removed contents published as:

Riley, J.L., Noble, D.W.A., Byrne, R.W. et al. (2017) Does social environment influence learning ability in a family-living lizard?. *Animal Cognition*, vol. 20, no. 3, pp. 449–458 . <https://doi.org/10.1007/s10071-016-1068-0>

Does social environment influence learning ability in a family-living lizard?

Animal Cognition

Julia L. Riley, Daniel W.A. Noble, Richard W. Byrne, and Martin J. Whiting

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Supplementary Materials

Behavioural scoring agreement

JLR initially scored task success for the first stage of the task and the full task, latency to complete the task, and number of errors during each trial in May 2016. After 7 months had passed, JLR re-scored the same behaviours for a random selection of 10% of our videos ($N = 86$), while being blind to the original scores, to assess agreement. We assessed score agreement using Cohen's Kappa (using the function *cohen.kappa* from the R package *psych* in R v 3.0.3; Kaufman and Rosenthal 2009; R Core Team 2016). Cohen's Kappa agreement scores are considered "excellent" when $k \geq 0.75$ (Kaufman and Rosenthal 2009). Scores of task success for the first stage of the task and the full task agreed 100% of the time ($k = 1$ for both the first stage and the full task). Score agreements for both latency ($k = 1$, 95% $CI = 0.99-1$) and number of errors ($k = 0.99$, 95% $CI = 0.98-1$) were also high. Our assessment suggests that our behavioural scoring was accurate to quantify tree skink behaviours.

References

- Kaufman AB, Rosenthal R (2009) Can you believe my eyes? The importance of interobserver reliability statistics in observations of animal behaviour. *Anim Behav* 78:1487-1491.
doi: 10.1016/j.anbehav.2009.09.014
- R Core Team (2016) A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria, URL <https://www.R-project.org/>.

Table S1. Tally of correct (1) and incorrect (0) choices for the first stage (3 ladder choice) of the spatial learning task. The learning criterion (5/6 correct choices) is outlined for each lizard. The trial at which each lizard ‘learns’ the task is bolded and italicized. The trials that we used to assess robustness of our learning criterion are shaded in grey. Lizard treatment (I = isolated, S = social), number of trials taken to learn the task, each lizard’s learning categorization (learner = Y, non-learner = N), tally of correct/incorrect trials for the assessment of the learning criterion, and binomial probability of each assessment of the learning criterion are also specified.

Lizard	Treatment	T1	T2	T3	T4	T5	T6	T7	T8	T9	T10	T11	T12	T13	T14	T15	T16	T17	T18	T19	T20	T21	T22	T23	T24	T25	T26	T27	T28	T29	T30	Number of trials to learn	Learning	Tally of correct choices	Binomial probability		
B0053	I	1	0	0	1	0	0	1	0	1	1	0	0	1	0	1	0	1	1	1	0	1	1	1	1	1	1	0	0	0	1	25	Y	3/6	0.22		
B0025	S	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	9	Y	21/22	<0.001		
B0062	S	1	0	0	0	1	0	1	0	1	0	0	1	0	0	1	1	0	1	1	1	0	1	1	1	1	0	0	1	1	1	1	24	Y	5/7	0.04	
B0130	S	0	1	0	0	1	1	0	1	0	0	0	0	1	1	0	0	0	1	0	1	0	0	1	1	1	1	1	1	1	1	29	Y				
B0010	S	0	0	0	0	0	0	0	1	1	1	0	0	1	1	1	0	1	1	1	1	0	0	1	1	1	1	1	1	1	1	1	28	Y			
B0102	S	0	1	1	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	0	0	1	1	1	1	1	1	1	1	1	1	14	Y	12/17	0.002	
B0120	I	0	1	1	0	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	13	Y	17/18	<0.001	
B0020	S	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	10	Y	21/21	<0.001	
B0123	S	0	0	0	0	0	0	1	1	0	0	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	16	Y	13/15	<0.001	
B0133	I	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	16	Y	12/15	<0.001	
B0201	I	0	1	1	1	1	0	1	1	1	1	1	0	1	1	1	1	1	1	1	0	1	1	1	1	0	1	1	1	1	1	1	7	Y	18/24	<0.001	
B0152	S	0	0	0	0	0	0	1	1	0	1	1	0	0	1	1	0	0	1	1	0	1	1	1	1	0	0	1	1	1	1	1	0	N			
B0033	I	0	0	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	8	Y	19/23	<0.001	
B0050	I	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	8	Y	22/23	<0.001	
B0115	S	0	1	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	12	Y	18/19	0.001	
B0205	S	0	0	0	0	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	0	0	1	1	1	1	1	1	1	1	1	1	15	Y	10/16	0.01	
B0112	I	0	0	0	0	0	0	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	13	Y	15/18	<0.001	
B0202	I	0	0	1	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	19	Y	9/12	0.003	
B0125	I	1	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	11	Y	20/20	<0.001	
B0003	I	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	10	N			
B0150	I	0	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	10	Y	20/21	<0.001
B0111	I	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	6	Y	21/25	<0.001	
B0113	I	0	1	1	1	1	0	0	0	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	23	Y	3/8	0.27	
B0210	I	1	0	0	0	1	0	0	0	0	0	1	1	1	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	20	Y	9/11	0.001	
B0151	S	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	6	Y	24/25	<0.001	
B0131	S	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	6	Y	22/25	<0.001	
B0122	S	0	0	0	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	9	Y	19/22	<0.001	
B0001	S	0	1	0	1	0	0	0	0	0	0	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	0	0	0	1	1	N			

Table S2. Tally of correct (1) and incorrect (0) choices for the full spatial learning task (3 ladder choice followed by a 2 ladder choice). The learning criterion (5/6 correct choices) is outlined for each lizard. The trial at which each lizard ‘learnt’ the task is bolded and italicized. The trials that we used to assess robustness of our learning criterion are shaded in grey. Lizard treatment (I = isolated, S = social), number of trials taken to learn the task, each lizard’s learning categorization (learner = Y, non-learner = N), tally of correct/incorrect trials for the assessment of the learning criterion, and binomial probability of each assessment of learning criterion are also specified.

Lizard	Treatment	T1	T2	T3	T4	T5	T6	T7	T8	T9	T10	T11	T12	T13	T14	T15	T16	T17	T18	T19	T20	T21	T22	T23	T24	T25	T26	T27	T28	T29	T30	Number of trials to learn	Learning	Tally of correct choices	Binomial probability	
B0053	I	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	1	1	2	1	0	0	0	1	1	1	1	1	0	1	1	19	Y	8/12	<0.001
B0025	I	0	0	0	1	0	0	1	1	1	1	0	0	0	1	1	1	1	1	1	0	1	1	1	0	1	1	1	1	1	1	9	Y	17/22	<0.001	
B0002	S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	29	N			
B0130	S	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	29	Y		
B0010	S	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	28	N		
B0102	S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	20	Y	8/11	<0.001	
B0120	I	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	10	Y	21/21	<0.001	
B0020	S	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	16	Y	12/15	<0.001	
B0123	S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	19	Y	9/12	<0.001	
B0133	I	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	N			
B0201	S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	20	N			
B0152	S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	13	Y	4/11	0.07	
B0033	I	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	13	Y	11/18	<0.001	
B0050	I	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	12	Y	12/19	<0.001	
B0115	S	0	0	1	1	0	0	0	1	1	1	1	0	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	14	Y	6/13	0.01
B0205	S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	19	Y	7/10	<0.001	
B0112	I	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	N			
B0202	I	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	N			
B0125	I	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	N		
B0003	I	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	10	Y	17/21	<0.001
B0150	I	0	0	0	1	1	1	1	0	0	1	0	0	0	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	17	Y	6/14	0.01
B0111	I	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	N			
B0210	I	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	19	Y	9/12	<0.001	
B0151	S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	13	Y	15/18	<0.001	
B0131	S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	13	Y	17/18	<0.001	
B0122	S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9	Y	19/22	<0.001	
B0053	I	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	19	Y	8/12	<0.001	

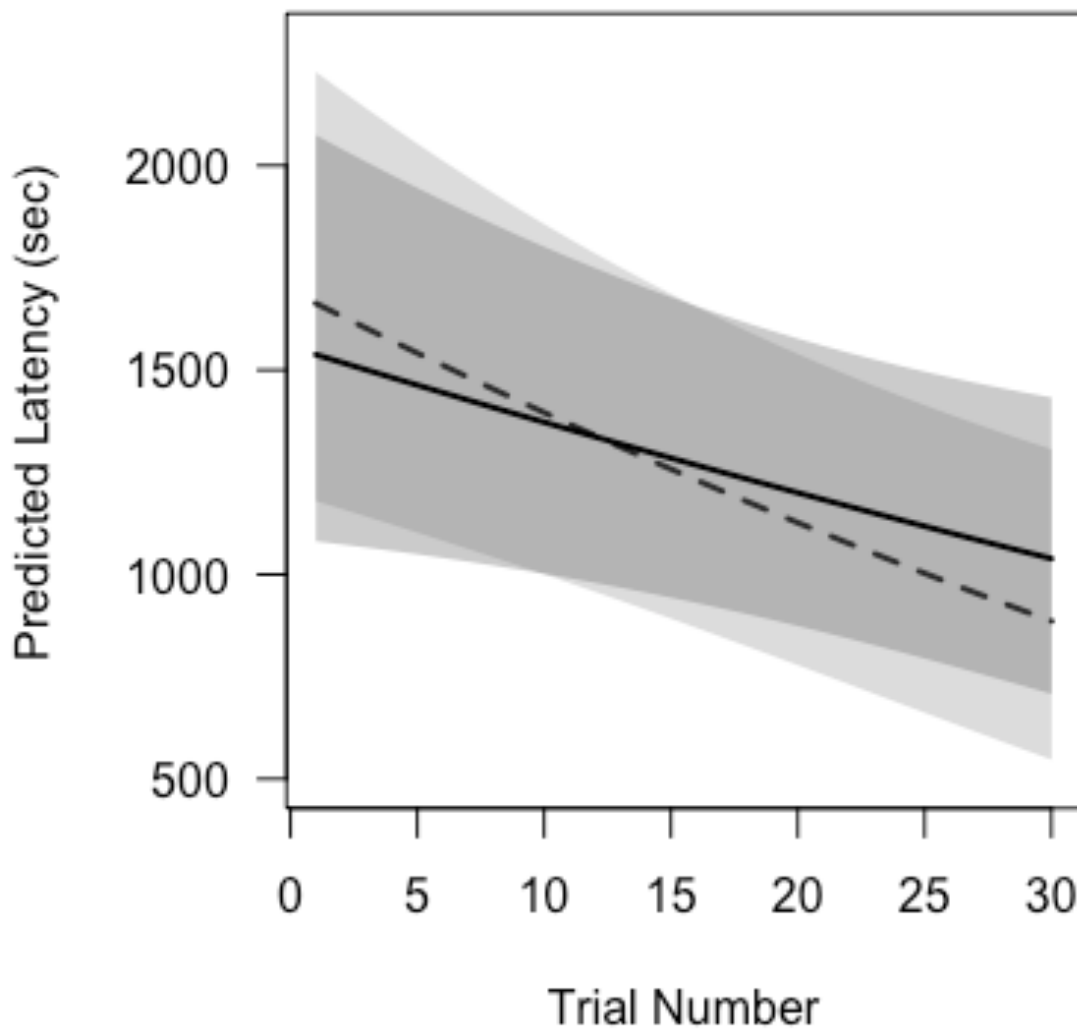


Fig. S1 Predicted latency until successful completion of the task (s) during each trial did not differ between rearing treatments (social: light grey shading and dashed line; isolated: dark grey shading and solid line) for the full spatial learning task. Latency did decrease over time, which indicates tree skinks were learning the task. The darkest shade of grey is where the 95% predicted credible intervals, which are represented by shaded polygons around predicted latencies, overlap.

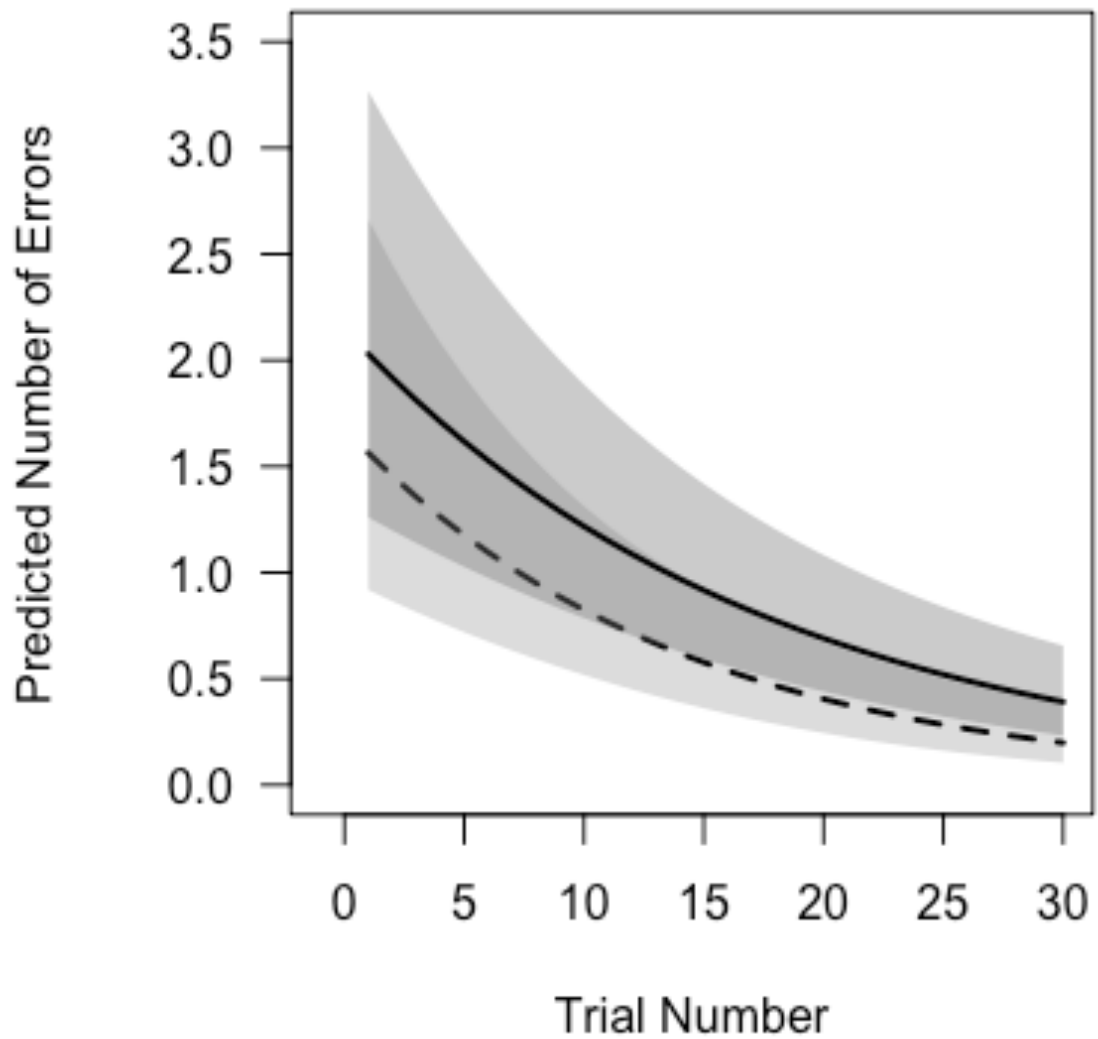


Fig. S2 Predicted number of errors during each trial did not differ between rearing treatments (social: light grey shading and dashed line; isolated: dark grey shading and solid line) for the full spatial learning task. The number of errors did decrease over time, which indicates skinks were learning the task. The darkest shade of grey is where the 95% predicted credible intervals, which are represented by shaded polygons around predicted number of errors, overlap.

Chapter III

A group-living lizard is resilient to isolation rearing



Julia L. Riley, Anna Küchler, Théo Damasio, Daniel W.A. Noble, Richard W. Byrne, and
Martin J. Whiting

The following manuscript is being prepared for publication. It follows the format of the journal *Biology Letters*. Tables and then figures follow this manuscript's references. This article's supplemental video can be found via the link in Appendix 1.

ABSTRACT

The social environment during development can affect learning; for example, raising a social mammal in isolation hinders their learning ability. However, we know little about how the social environment impacts learning in less-studied social taxa, like group-living lizards. We reared tree skinks (*Egernia striolata*) in two treatments, either with a conspecific or in isolation. We used a three-step foraging task (motor, discrimination, and reversal) to assess learning ability. Skinks performed tasks under two learning treatments: either after demonstration (social learning), or without social information (individual learning). The majority of skinks learnt our motor (91%) and discrimination tasks (100%), and a third learnt our reversal task (34%). Contrary to our predictions, and the majority of previous literature, we detected no negative effect of rearing treatment on learning in any task. We also did not find any evidence that tree skinks used social information. Our surprising findings are likely due to this lizard's variable social system, and we suggest that birds and mammals with facultative sociality may also be resilient to isolation rearing.

1. BACKGROUND

Learning ability is predicted to impact survival; for instance, spatial learning ability may benefit foraging and predator avoidance, and innovation may enhance survival in novel environments [1]. While learning ability can be important for individual fitness, many factors affect its manifestation including the developmental environment [2].

Social factors during ontogeny substantially impact physiological, behavioural, and cognitive development. This relationship was first demonstrated in 1965 when research established that socially-isolated juvenile rhesus macaques (*Macaca mulatta*) had impaired learning abilities [3]. Subsequently, many studies have also found a negative relationship between isolation rearing and learning in mammals and birds with obligate sociality [2]. Isolation rearing can reduce an individual's ability to interact with others by hindering their comprehension of social cues and behaviour [3,4]. Social interactions can be a source of information that enhances learning (*aka*, social learning [5,6]). Thus, isolation rearing may impact both individual and social learning ability.

Wild *Egernia striolata* (tree skinks) are found alone or in groups of variable size (2-10 skinks) mainly consisting of kin [7]. Furthermore, their social rearing environment impacts morphological and behavioural development [8]. Their facultative sociality and developmental plasticity makes *E. striolata* a good model for studying whether the social environment affects learning ability, and an individual's capacity to use social information. We presented skinks from two rearing treatments (social or isolated) with three learning tasks under two learning treatments (social or individual learning). We hypothesized that isolation

rearing would hinder cognitive development and reduce the likelihood of using social information. We predicted: **1)** isolated skinks would be less likely and take longer to learn compared to socially-reared skinks; and **2)** that isolated skinks would be less likely to use social information compared to socially-reared skinks.

2. METHODS

We used 32 *E. striolata* that were offspring from 19 females collected near Albury, New South Wales (35.98°S, 146.97°E; see supplementary materials for details about husbandry and measurements). We randomly allocated juveniles into two rearing treatments: isolated (housed alone; N = 16), or social (housed in unrelated pairs; N = 16 within 8 pairs). Skinks resided within rearing treatments for approximately 1.5 years before this experiment. During development, both treatments had limited visual exposure to adult conspecifics during a separate study (details in supplementary materials).

During the experiment, we housed skinks in opaque plastic tubs split in half by a fixed, transparent Perspex[®] divider covered by a removable opaque wooden cover (details in supplementary materials). Skinks acclimated to the arena for 48 hours before experiments.

Social learning experiment

Our experiment was modified from Noble et al. [6] by altering the food reward from mealworms to 1.25 ml of puréed fruit (Heinz[®] baby food: apple, and pear). The experiment consisted of motor, discrimination, and reversal foraging tasks. There were two learning treatments: social learning, where lizards observed a conspecific demonstrator executing the task correctly, and individual learning, where lizards simply observed a non-demonstrating conspecific. We allocated an equal number of isolated and socially-reared skinks to each learning treatment (Table S1). We randomly paired an unrelated, adult female skink with each experimental lizard for a total of 16 ‘demonstrators’ and 16 ‘non-demonstrating’ conspecifics. Demonstrators performed tasks correctly in all trials, which ensured that experimental lizards received correct social information.

During all tasks, the cover was removed to provide an unobstructed view. After 20 min of viewing the conspecific, the cover was replaced and the lizard attempted each task for 1 hour. Trials were recorded for behavioural scoring. We conducted two trials each weekday, in the morning (0900-1130 h) and the afternoon (1330-1600 h).

(a) Motor task (lid removal)

This task required lizards (N = 32; Table 1) to remove an opaque, yellow lid from a dish to gain a food reward (Video S1). Lizards were given 24 trials to complete this task, and were

classified as learners if they performed 5/6 trials correctly (Table S2). Twenty-nine skinks (91%) learnt this task, and moved on to the discrimination task.

(b) Discrimination task

This task required skinks (Table 1) to associate a blue lid with a reward, when presented with two dishes on a wooden block (blue vs. white lid, Video S1). The colours blue and white were chosen as the targets, because tree skinks have an equal preference for each colour (Whiting et al. 2017 unpubl. data). To control for chemical cues, we placed pureed fruit in both dishes but the reward under the white lid was inaccessible (Fig. S1). We randomly counter-balanced the blue lid's location across rearing and learning treatments. Skinks were given this task for 24 trials, and were classified as learners if they performed 7/8 trials correctly (Table S3). All skinks (100%) learnt this task, and moved on to the reversal task.

(c) Reversal of discrimination task (hereafter, reversal)

This task was identical to the discrimination task with two exceptions: 1) skinks needed to associate the white lid with a reward instead of the blue lid (Video S1), and 2) skinks were given this task for 34 trials as it was more difficult. Ten skinks (34%) met the reversal task's learning criterion (7/8 trials correct; Table S4).

Behavioural Scoring

From video recordings, we ensured that experimental lizards were viewing demonstrator lizards, as well as scored successful task performance during each trial (either removing the yellow, or correctly coloured lid). Behavioural scores from different observers were highly congruent (see supplementary materials).

Statistical Analysis

We tested for effects of rearing treatment, learning treatment, and trial number, while accounting for dependences in our data, using generalized linear mixed effect models. We also tested the robustness of our learning criteria for all tasks, and found they were sufficient. See supplementary materials for more analysis details.

3. RESULTS

(a) Motor task

Rearing treatment did not affect whether a skink learnt this task ($z = -0.60$, $p = 0.55$; Table 1). Isolated skinks learnt the motor task in 3 fewer trials than socially-reared skinks ($z = -2.09$, $p = 0.04$), but the confidence intervals of the rearing treatment unconditional means overlapped

(e.g., a non-significant effect; Table 2). The probability of removing the lid during a trial was only 9% higher for isolated skinks ($z = 1.73$, $p = 0.08$), and the confidence intervals of unconditional means overlapped (Table 2).

Learning treatment did not affect whether a skink learnt this task ($z = -0.60$, $p = 0.55$), the number of trials to learn the task ($z = -0.15$, $p = 0.88$; Table 1), or the probability of removing the lid during a trial ($z = 0.86$, $p = 0.39$).

Across trials, the probability of removing the lid increased as trials progressed ($z = 6.95$, $p < 0.01$; Fig. 1A).

(b) Discrimination task

We did not analyse the probability of learning this task because all lizards were successful. Neither rearing nor learning treatment affected the number of trials to learn the discrimination task (rearing treatment: $z = -0.38$, $p = 0.70$; learning treatment: $z = 0.28$, $p = 0.78$; Table 1), or the probability of making a correct choice (rearing treatment: $z = -1.01$, $p = 0.31$; learning treatment: $z = -0.62$, $p = 0.53$). Across trials, the probability of removing the lid increased as trials progressed ($z = 3.67$, $p < 0.01$; Fig. 1B).

(c) Reversal task

Neither rearing nor learning treatment affected whether a skink learnt the task (rearing treatment: $z = 0.84$, $p = 0.40$; learning treatment: $z = 0.16$, $p = 0.88$), the number of trials to learn the task (rearing treatment: $z = 0.14$, $p = 0.89$; learning treatment: $z = 0.06$, $p = 0.95$; Table 1), or the probability of making a correct choice (rearing treatment: $z = 0.32$, $p = 0.75$; learning treatment: $z = -0.22$, $p = 0.83$). Across trials, the probability of removing the lid increased as trials progressed ($z = 5.29$, $p < 0.01$; Fig. 1C).

4. DISCUSSION

Our hypothesis that isolation would hinder cognitive development in *E. striolata* was not supported; we found no effect of rearing treatment on *E. striolata* performance for any of our three cognitive tasks. Our results contrast with the negative effects of isolation rearing on cognitive ability that has been found previously. Potentially, alternative cognitive tasks may have revealed an effect of rearing treatment [2,3]; but we also failed to find any impact of rearing environment on *E. striolata* individual learning of a vertical, spatial maze [9]. The social system of *E. striolata* is variable [7], and the facultative nature of their sociality and parental care may select for resilience to the effects of social isolation during development. Conversely, in obligate social mammals and birds with parental care, the requirements of social exposure for behavioural development may be more fixed. Perhaps, a mammal or bird

with facultative sociality (e.g., the African striped mouse; [10]) would show the same, unexpected, relationship between isolation and learning ability.

An alternative hypothesis is that the presence or absence of parents and/or siblings during development may differently affect *E. striolata* cognition. Our rearing treatments did not include parents or siblings due to logistical constraints (see supplementary materials) so these effects were not quantified. Offspring of *Egernia* spp. benefit from the presence of parents by gaining protection, enhanced thermoregulation, and increased access to prey [11,12]. Litters of *E. whitii* form size-based dominance hierarchies in which competition reduces growth and increases mortality in the youngest siblings [13]; so the social environment is costly for some. Benefits and costs of living with kin still need to be considered in the cognitive development of *E. striolata*.

Contrary to our predictions, we also found no evidence that sub-adult *E. striolata* used social information. Social learning propensity may develop as individuals age [5], or may not be present at particular life-stages [6]. In the context of our study, sub-adults may avoid unfamiliar adults because they can be lethally aggressive [7,11]. Thus, we are hesitant to conclude this group-living lizard cannot use social information, and instead posit that sub-adults avoid using social information from unfamiliar, potentially aggressive, adults. Future research, focusing on social learning between individuals matched in age or between individuals within the same social group (i.e., familiar and/or related) may still find evidence that *E. striolata* learns socially.

In summary, we did not find that isolation rearing hindered *E. striolata* learning ability. Our study is an initial examination of how social environment impacts individual and social learning in a taxonomic group (squamate reptiles) underappreciated for its degree of sociality, and our results contrast with the majority of findings in obligately social mammals and birds. Our unexpected findings may stem from this species' variable social system, and suggests that other facultatively social taxa may also be resilient to isolation rearing.

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Table 1. Sample sizes (N), number of skinks that learnt each task, and the average number of trials it took to learn all tasks (with 95% *CI*s calculated from raw data) for each rearing and learning treatment.

Rearing Treatment	Learning Treatment	(a) Motor Task		(b) Discrimination Task		(c) Reversal Task				
		<i>N</i>	Number of Learners	Number of Trials Taken to Learn	<i>N</i>	Number of Learners	Number of Trials Taken to Learn			
Social	Social	8	7	12 (9 to 15)	7	7	10 (7 to 13)	7	1	30
Social	Individual	8	8	13 (9 to 17)	8	8	12 (7 to 16)	8	3	22 (14 to 31)
Isolated	Social	8	7	10 (4 to 15)	7	7	12 (9 to 14)	7	2	24 (14 to 33)
Isolated	Individual	8	7	9 (5 to 13)	7	7	9 (7 to 11)	7	4	28 (17 to 38)

Table 2. *Unconditional means and 95% CIs for each rearing and learning treatment.*

(a) Motor Task			(b) Discrimination Task			(c) Reversal Task		
Probability of Learning the Task	Number Trials Taken to Learn	Probability of Trial Success	Number Trials Taken to Learn	Probability of Trial Success	Probability of Learning the Task	Number Trials Taken to Learn	Probability of Trial Success	
Rearing Treatment								
Social	0.94 (0.67, 0.99)	12.32 (9.84, 15.42)	0.84 (0.68, 0.93)	10.73 (8.95, 12.87)	0.90 (0.85, 0.94)	0.21 (0.03, 0.68)	24.30 (19.69, 29.99)	0.39 (0.30, 0.48)
Isolated	0.88 (0.61, 0.97)	9.18 (7.29, 11.55)	0.93 (0.84, 0.97)	10.24 (8.55, 12.27)	0.87 (0.81, 0.92)	0.41 (0.15, 0.73)	24.80 (20.98, 29.31)	0.41 (0.32, 0.50)
Learning Treatment								
Social	0.88 (0.61, 0.97)	10.58 (8.43, 13.28)	0.91 (0.80, 0.96)	10.68 (8.85, 12.88)	0.88 (0.82, 0.92)	0.31 (0.09, 0.69)	24.70 (20.53, 29.72)	0.40 (0.32, 0.49)
Individual	0.94 (0.67, 0.99)	10.79 (8.70, 13.38)	0.87 (0.73, 0.94)	10.32 (8.68, 12.28)	0.90 (0.84, 0.93)	0.28 (0.06, 0.70)	24.50 (20.35, 29.50)	0.39 (0.30, 0.48)

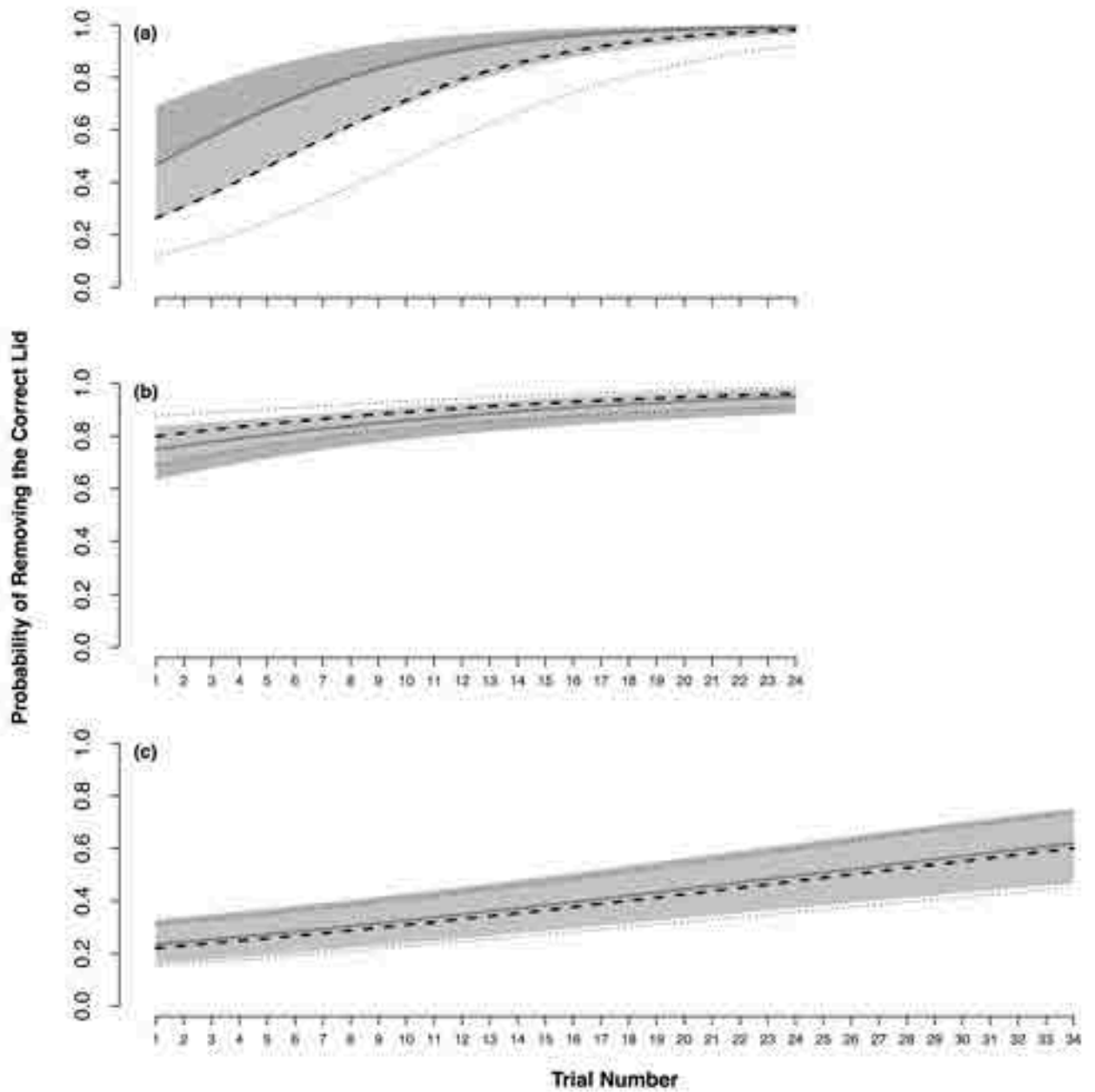


Figure 1. Probability of removing the correct lid during each trial of the (a) motor, (b) discrimination, and (c) reversal task for isolated skinks (grey 95% CI polygon and solid fitted line) and socially-reared skinks (black dotted 95% CI lines and dashed fitted line).

Supplementary Materials

METHODS

**Please note that to make the methods as clear as possible, we have repeated some information from the main text.*

Field collection, captive housing, and rearing treatment considerations

In January 2015, we collected 19 gravid female *E. striolata* from near Albury, New South Wales (35.98°S, 146.97°E). We maintained these skinks at Macquarie University during parturition (from 17 January to 10 February 2016) in a climate-controlled room (maintained at 24°C) within opaque plastic tubs (350 mm W x 487 mm L x 260 mm H). We lined these tubs with newspaper, and placed tree bark, a water dish, and a refuge (120 mm W x 175 mm L x 38 mm H) in each. A UV lamp lighted each skink's tub, and each tub had under-cage heating wire restricted to one side. We cleaned tubs once weekly. We fed skinks 3 adult crickets dusted with calcium and vitamins twice a week, and puréed fruit (1.25 ml of Heinz® fruit baby food: mango, apple, and pear) once weekly.

During parturition, we checked females twice a day to see if they had given birth. Less than a maximum of 12 h after birth, we measured each juvenile's snout-vent length (mm, SVL: the distance between the tip of the snout and the posterior edge of the cloaca), total length (mm), and tail length (mm) with a clear standard ruler to the nearest 1 mm. We also recorded mass with a digital scale (SP6001, Scout Pro, Ohaus, Pine Brooks NJ, USA) to the nearest 0.01 g, and marked each juvenile with a unique toe-clip [1].

After all juveniles were born, measured, and uniquely marked, we randomly allocated juveniles into their two rearing treatments: either isolated or social. Juvenile social groupings of similar sizes have been reported for wild populations of *E. striolata* ([2,3], Riley unpubl. data). These juvenile-only groups vary in size, ranging from pairs to 4 individuals, and juveniles are also observed on their own [2-4]. However, social groups do most commonly consist of parent(s) and offspring [5]. Including parents in our social treatments was not logistically feasible because adult *Egernia* are known to be highly aggressive towards juveniles and infanticide has been reported in multiple *Egernia* group spp. [6-8]. There are even instances, within captivity, where females eat their own offspring (*E. stokesii* [6]; *E. striolata*, Riley pers. obs. 2015). Thus, due to these ethical and logistical considerations, our

study was restricted to social groups consisting of juveniles. Kin recognition in *E. striolata* is based on both familiarity and the degree of relatedness [9], and in other *Egernia* spp. familiarity is also known to play a large role in determination of social groups (*Tiliqua rugosa*, [10]; *E. stokesii* [11]). The mechanism of kin recognition remains unknown in this species, and may either be based on phenotypic matching or on signals learnt from being in proximity to their natal, family social group [9]. Thus, although unrelated juveniles were paired within our social rearing treatment, these individuals lacked exposure to related skinks and thus, we expect that the social pair within our study would determine their social group based on proximity and familiarity (similarly to what may happen via crevice-sharing in the wild [9]). During development, we observed similar social interactions within our social pairs as have been observed in litters of closely-related *Egernia* spp. in previous studies (*E. saxatilis* [8]; *E. whitii* [12]). Thus, the social rearing environment within our study was comparable to the potential social developmental environments within a wild population of *E. striolata*.

Juveniles were housed within smaller opaque plastic tubs than the females (85 mm W x 140 mm L x 60 mm H), either alone if in the isolated treatment or with their social pair. All other housing criteria were the same, except they were fed nymph crickets instead of adult crickets. During the winter (June to August), we maintained skinks at a reduced temperature (18°C). A total of 32 juveniles were included in our social learning experiment. Across their development, all individuals from both treatments were visually exposed to adult conspecifics while quantifying their sociability in a separate study [13]. This sociability assay exposed each juvenile to four unrelated, adult, female conspecifics during four behavioural trait assays that were 5 h in length, and which occurred at ca. 5, 7, 9, and 12 months of age [13]. During this assay, the juveniles could not smell or touch the adult female because they were separated via a fixed transparent Perspex[®] divider [13]. Thus all skinks within this study were habituated to visually encountering a variety of adult tree skinks prior to their exposure to them in this study. Prior to this experiment, we re-measured each skink's morphometrics and recorded their sexes on 12 August 2016, which was 3 days before our learning experiment.

Housing and husbandry during the experiment

During social learning experiments, we housed juveniles in newspaper-lined, opaque plastic tubs (390 mm W x 580 mm L x 390 mm H) divided in half by a fixed transparent Perspex[®] divider covered by a removable opaque wooden cover. This allowed us to keep skinks physically separated while also controlling when they viewed each other. The tubs contained

a water dish and a refuge (120 mm W x 175 mm L x 38 mm H), which were removed during tasks to provide an unobstructed view of the “demonstrator” or “non-demonstrating” conspecific. A 100 W heat lamp was directed at the refuge, which allowed skinks to thermoregulate and illuminated each arena. We fed skinks 3 crickets (adults for adult skinks and nymphs for juveniles) dusted with calcium and vitamins once a week after assays were completed. Other than that, the only food the skinks received was the food reward (1.25 ml of puréed fruit; Heinz® apple and pear) that was offered twice daily, and eaten only if the trial was completed successfully. Prior to trials commencing, we gave skinks 48 hours to acclimate to the novel experimental arena.

Inter-observer reliability assessment

JLR and AK scored task success (removing the dish lid) from motor task videos, and JLR, AK and TD scored task success (removing the correctly coloured lid colour) in discrimination and reversal tasks. Inter-observer reliability statistics were run from data for 21% of the trials for the motor task, as well as the discrimination and reversal task combined using Cohen’s Kappa (using the function *cohen.kappa* from the R package *psych* in R v 3.0.3 [14,15]). For the motor task, inter-observer agreement scores were high ($k = 0.96$). For the discrimination and reversal tasks, inter-observer agreement scores were also high (comparison between all 3 observers ranged from $k = 0.98$ to 1). These Cohen’s Kappa agreement scores are considered “excellent” ($k \geq 0.75$ [14]).

Statistical analyses

Prior to conducting analyses, we explored the data to ensure it fitted the assumptions of our analyses (e.g., no influential outliers, etc. [16]). To fit all our generalized linear mixed effect models (GLMMs) we used the function *glmer* in the *lme4* R package [17]. For all models, we opted to use the simplest possible model to avoid over-parameterization and issues with model convergence. So we included the two fixed factors of rearing and learning treatment in all models, and in models that examined the temporal nature of the data (e.g., learning curves) we also included the fixed factor of trial number. As well, we first considered if interactions between *trial number* x *rearing and learning treatment* were significant; if not, they were removed and we re-fitted the model. Other potentially confounding factors (e.g., skink sex or size) were experimentally balanced across rearing and learning treatments to minimize any impact on the data. Also, we have previously shown that sex does not significantly affect learning in *E. striolata* [18]. For all models, α was set at 0.05. When we predicted fitted lines from the models for visualization, we set the factorial fixed factors to intercept-level values.

Data from motor, discrimination and reversal tasks were analysed separately, but the variables included in each of the models were consistent (see Tables S5, S6, and S7 for finalized models):

- (1) This binomial GLMM examined if the *probability of learning a task* (learner = 1, non-learner = 0) was influenced by the *rearing treatment* (isolated or social) or *learning treatment* (social or individual). We accounted for dependency between observations of multiple skinks from each clutch by including a random intercept for *mother identity*. We also included a random intercept for *housing tub* to incorporate dependency among observations of lizards from the same captive environment (e.g., social pairings). Binomial denominator was 1 throughout. It was not possible to analyse the probability of learning the discrimination task because all lizards were successful, so we only performed this analysis for the motor and reversal task.
- (2) This Poisson GLMM examined if the *number of trials taken to learn the task* was influenced by the *rearing treatment* (isolated or social) or *learning treatment* (social or individual). This model also included the random intercepts of *mother identity* and *housing tub*.
- (3) This binomial GLMM examined if *probability of task success during each trial* (either removing the lid or correctly choosing lid colour = 1) was influenced by *trial number* (aka. time), *rearing treatment* (isolated or social) or *learning treatment* (social or individual). This model also included the random intercepts of *mother identity* and *housing tub*, as well as a random intercept and slope for juvenile identity across trial number to incorporate the dependency among repeated observations of the same individual. If their effect was significant, we also included the additional fixed effects of interactions between *trial number* x *rearing treatment* and *trial number* x *learning treatment*. Binomial denominator was 1 throughout.

Given the difficulty in obtaining large samples sizes across our treatments due to logistical constraints, we also calculated unconditional means and corresponding 95% *CI*s (corrected for non-independence) using the function *Effect* in the R package *effect* [19,20].

Unconditional means of all response variables in each task (probability to learn, number of trials until learnt a task, and probability of task success) were calculated for each rearing and learning treatment. We compared unconditional means between rearing treatments (socially-raised vs. isolated) and learning treatments (social vs. individual) using their 95% *CI*s to

judge significance (e.g., 95% *CIs* that encompass both treatment means indicate no significant difference between groups). Assessment of unconditional means and the magnitude of their differences (i.e., effects) places more emphasis on biological significance, rather than just statistical significance (which can be affected by sample size) of differences between our treatments [21,22].

Assessment of learning criteria

We assessed the robustness of our learning criteria by tallying the number of correct/incorrect choices from the last trial in the learning criterion to the skink's last trial (e.g., if a skink performed 5/6 trials correctly during the motor task we started the tally at the 6th trial [18,23,24]; Table S2, S3 and S4). We used the subset of skinks that had six or more trials after the trial in which they learnt for this assessment. We tested whether this tally of correct/incorrect choices was significant according to an exact binomial choice test [23,25]. For the motor, discrimination, and reversal tasks respectively, 25/27 (93%), 25/28 (89%), and 4/7 (57%) of skinks performed the task correctly significantly more than expected by chance after meeting learning criteria. Our sample size of skinks that met the learning criterion for the reversal task was low, thus it is difficult to judge if our learning criterion was robust for that task. Although, a less stringent reversal task's learning criterion (5/6) has previously been found to be robust by Kar (unpubl. data 2016). Yet, for the motor and discrimination tasks, our assessment suggests our learning criterion was sufficient in categorizing individuals that learnt from those that did not.

RESULTS

Data exploration & model validation

During data exploration for all models, we did not find any unexplainable or influential outliers. We did remove missing values where applicable, thus there are a variable number of observations and individuals within each model (sample sizes are provided in all results tables; Table S5, S6, S7).

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TABLES

Table S1. Each experimental lizard's (N = 32) rearing treatment (I = isolated, S = social), learning treatment (SL = social, IL = individual), the identity of their mother (PIT-tag number), housing tub number (a shared tub number indicates social pairs), sex (M = male, F = female), snout-vent-length (SVL, mm), and mass (g).

Skink	Rearing Treatment	Learning Treatment	Mother Identity	Housing Tub	Sex	SVL (mm)	Mass (g)
B1122	I	IL	1468494	S19	F	102	22.7
B1121	I	IL	1468537	S28	F	94	19.0
B1110	I	IL	1468538	S29	M	95	21.5
B1022	I	IL	1468544	S30	M	91	20.7
B1011	I	IL	1469229	S33	F	91	16.7
B0323	I	IL	1468506	S22	F	95	20.5
B1010	I	IL	1468549	S31	M	93	21.2
B0230	I	IL	1468460	S16	F	97	21.9
B0212	I	SL	1468504	S21	F	99	24.5
B0220	I	SL	1468529	S26	M	100	22.7
B0302	I	SL	1468480	S17	F	95	20.7
B0322	I	SL	1468515	S24	F	96	22.3
B0331	I	SL	1468532	S27	M	95	21.9
B0333	I	SL	1468532	S25	F	98	23.7
B1000	I	SL	1468509	S23	F	98	22.7
B1031	I	SL	1468510	S32	F	97	21.7
B1012	S	IL	1468476	P24	F	76	10.8
B0303	S	IL	1468506	P16	M	90	19.6
B0320	S	IL	1468515	P18	F	92	17.9
B0330	S	IL	1468532	P19	F	76	10.3
B0332	S	IL	1468516	P18	F	92	20.1
B0213	S	IL	1468529	P19	F	99	24.1
B0214	S	IL	1468529	P20	M	96	23.8
B0223	S	IL	1468460	P13	F	90	15.7
B0200	S	SL	1468515	P17	M	90	19.1
B0203	S	SL	1468506	P12	F	90	18.9
B0221	S	SL	1468460	P11	F	92	19.7
B0222	S	SL	1468460	P12	M	90	18.8
B1001	S	SL	1468509	P17	F	99	20.6
B1002	S	SL	1468549	P21	F	98	22.7
B1030	S	SL	1468491	P25	F	88	17.5
B1032	S	SL	1468502	P25	F	93	20.6

Table S2. Tally of correct (1) and incorrect (0) task performance for our motor task. The learning criterion (5/6 correct choices) is outlined for each skink. The trial at which each skink met our learning criterion for the motor task is bolded and italicized. The trials that we used to assess robustness of our learning criterion are shaded in grey. Skink rearing treatment (I = isolated, S = social), learning treatment (SL = social, IL = individual), number of trials taken to meet learning criterion, each skink's learning categorization (learner = Y, non-learner = N), tally of correct/incorrect trials for the assessment of learning criterion, and binomial probability of each assessment of learning criterion are also specified.

Skink	Rearing Treatment	Learning Treatment	T1	T2	T3	T4	T5	T6	T7	T8	T9	T10	T11	T12	T13	T14	T15	T16	T17	T18	T19	T20	T21	T22	T23	T24	Number of Trials until Learnt	Learner	Tally of Correct Choices	Binomial Probability	
B0200	S	SL	1	0	1	0	1	0	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	12	Y	13/13	<0.001	
B1122	I	IL	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	6	Y	18/19	<0.001	
B0203	S	SL	1	1	0	0	1	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	14	Y	11/11	<0.001	
B1121	I	IL	1	1	1	0	0	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	11	Y	14/14	<0.001	
B0212	I	SL	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	6	Y	19/19	<0.001		
B1110	I	IL	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	6	Y	19/19	<0.001		
B0220	I	SL	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	6	Y	19/19	<0.001		
B1022	I	IL	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	6	Y	18/19	<0.001		
B0221	S	SL	0	1	0	0	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	10	Y	15/15	<0.001		
B1012	S	IL	0	0	0	0	0	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	14	Y	10/11	0.005		
B0222	S	SL	0	0	0	0	0	0	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	15	Y	10/10	0.001		
B1011	I	IL	0	0	0	1	0	0	1	0	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	19	Y	4/6	0.234		
B0302	I	SL	0	1	0	1	0	1	0	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	1	8	N	16/17	<0.001	
B0303	S	IL	1	0	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	11	Y	14/14	<0.001		
B0322	I	SL	0	0	1	0	0	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	7	Y	17/18	<0.001		
B0320	S	IL	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	11	Y	14/14	<0.001		
B0331	I	SL	1	1	1	0	0	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	8	Y	15/17	0.001		
B0323	I	IL	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	6	Y	18/19	<0.001		
B0333	I	SL	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	13	Y	11/12	0.003		
B0330	S	IL	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	6	Y	19/19	<0.001		
B1000	I	SL	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	18	Y	4/7	0.273		
B0332	S	IL	0	0	0	1	0	1	0	1	1	1	1	0	0	1	1	0	0	1	0	1	1	1	0	0	7	N	18/18	<0.001	
B1001	S	SL	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	10	Y	11/15	0.042		
B1010	I	IL	0	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	13	Y	11/12	0.003		
B1002	S	SL	0	0	1	0	0	1	1	1	0	1	1	1	1	1	0	0	1	0	1	1	1	1	1	6	Y	19/19	<0.001		
B0213	S	IL	0	1	0	0	0	0	0	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	10	Y	14/15	<0.001		
B1030	S	SL	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	22	Y				
B0214	I	IL	0	1	0	0	0	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	20	Y			
B1031	I	SL	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	1	1	1	1	1	1	17	Y			
B0223	S	IL	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1	1	1	1	1	1	1	1	N			
B1032	S	SL	1	0	1	0	1	1	1	1	0	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	17	Y	8/8	0.004
B0230	I	IL	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	1	0	1	1	1	1	1	1	N			

Table S3. Tally of correct (1) and incorrect (0) choices for our discrimination task. The learning criterion (7/8 correct choices) is outlined for each skink. The trial at which each skink met our learning criterion for the discrimination task is bolded and italicized. The trials that we used to assess robustness of our learning criterion are shaded in grey. Skink rearing treatment (I = isolated, S = social), learning treatment (SL = social, IL = individual), number of trials taken to meet learning criterion, each skink's learning categorization (learner = Y, non-learner = N), tally of correct/incorrect trials for the assessment of learning criterion, and binomial probability of each assessment of learning criterion are also specified.

Skink	Rearing Treatment	Learning Treatment	T1	T2	T3	T4	T5	T6	T7	T8	T9	T10	T11	T12	T13	T14	T15	T16	T17	T18	T19	T20	T21	T22	T23	T24	Number of Trials until Learnt	Learner	Tally of Correct Choices	Binomial Probability
B0200	S	SL	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	8	Y	16/17	<0.001
B1122	I	IL	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	9	Y	17/17	<0.001
B0203	S	SL	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	9	Y	15/16	<0.001
B1121	I	IL	0	0	0	1	1	1	0	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	14	Y	11/11	<0.001
B0212	I	SL	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	9	Y	15/16	<0.001
B1110	I	IL	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	8	Y	16/17	<0.001
B0220	I	SL	0	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	14	Y	11/11	<0.001
B1022	I	IL	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	8	Y	16/17	<0.001
B0221	S	SL	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	8	Y	16/17	<0.001
B1012	S	IL	0	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	8	Y	16/16	<0.001
B0222	S	SL	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	8	Y	15/17	0.001
B1011	I	IL	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	8	Y	15/17	0.001
B0903	I	IL	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	8	Y	16/17	<0.001
B0322	I	SL	1	1	0	1	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	15	Y	9/10	0.010
B0320	S	IL	1	1	1	1	0	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	24	Y		
B0331	I	SL	1	1	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	13	Y	11/12	0.003
B0323	I	IL	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	9	Y	11/16	0.067
B0333	I	SL	0	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	14	Y	9/11	0.027
B0330	S	IL	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	9	Y	15/16	<0.001
B1000	I	SL	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	10	Y	12/15	0.014
B0332	S	IL	0	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	9	Y	16/16	<0.001
B1010	I	IL	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	8	Y	10/17	0.148
B1002	S	SL	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	8	Y	17/17	<0.001
B0213	S	IL	1	1	1	1	0	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	14	Y	11/11	<0.001
B1030	S	SL	0	1	1	1	0	1	0	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	17	Y	6/8	0.309
B0214	S	IL	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	12	Y	11/13	0.010
B1031	I	IL	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	8	Y	12/17	0.047
B0223	S	IL	0	1	1	1	0	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	9	Y	16/16	<0.001
B1032	S	SL	0	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	13	Y	10/12	0.016

Table S4. Tally of correct (1) and incorrect (0) choices for our reversal task. The learning criterion (7/8 or 8/10 correct choices) is outlined for each skink. The trial at which each skink met learning criterion for the reversal task is bolded and italicized. The trials that we used to assess robustness of our learning criterion are shaded in grey. Skink rearing treatment (I = isolated, S = social), learning treatment (SL = social, IL = individual), number of trials taken to meet learning criterion, each skink's learning categorization (learner = Y, non-learner = N), tally of correct/incorrect trials for the assessment of learning criterion, and binomial probability of each assessment of learning criterion are also specified.

[illegible]

Table S5. Outcomes of mixed effect models that examined the effect of a skink's rearing treatment (ISOLATED or SOCIAL) and learning treatment (social learning; SL or individual learning; IL) on (1) the probability of learning the motor task, (2) number of trials until learnt the motor task, and (3) probability of removing the lid during each trial. Our third model also included the additional fixed factors of trial number, and interactions between trial number x rearing and learning treatment; if a fixed factor was not included in a model it is indicated with 'na'. If models initially included a fixed factor, but it was removed from the final full model due to non-significance it is indicated with '—'. Parameter estimates for binomial models are on the *log odds* link scale, and Poisson models are on the *log* link scale. Significance is indicated using an asterix (*), and marginal significance is indicated using a tilde (~) to the right of the *P*-value.

Fixed Effects	Probability of Learning $N_{ind} = 32, N_{mom} = 19, N_{ub} = 27$					Number of Trials until Learnt $N_{ind} = 29, N_{mom} = 19, N_{ub} = 27$					Probability of Removing the Lid $N_{obs} = 768, N_{ind} = 32, N_{mom} = 19, N_{ub} = 27$				
	β	SE	z-value	P		β	SE	z-value	P		β	SE	z-value	P	
Intercept (SOCIAL, IL, F)	3.158	1.343	2.351	0.019	*	2.521	0.125	20.117	<0.001	*	-1.239	0.506	-2.451	0.014	*
Trial Number	na	na	na	na		na	na	na	na		0.215	0.031	6.954	<0.001	*
Rearing Treatment (ISOLATED)	-0.771	1.287	-0.599	0.549		-0.295	0.141	-2.094	0.036	*	0.898	0.518	1.733	0.083	~
Learning Treatment (SL)	-0.771	1.287	-0.599	0.549		-0.020	0.130	-0.153	0.879		0.449	0.519	0.864	0.387	
Trial Number * Rearing Treatment	na	na	na	na		na	na	na	na		—	—	—	—	
Trial Number * Learning Treatment	na	na	na	na		na	na	na	na		—	—	—	—	

Table S6. Outcomes of mixed effect models that examined the effect of a skink's rearing treatment (ISOLATED or SOCIAL) and learning treatment (social learning; SL or individual learning; IL) on (1) number of trials until learnt the discrimination task and (2) probability of a correct choice during each trial. Our second also included the additional fixed factors of trial number, and interactions between trial number x rearing and learning treatment; if a fixed factor was not included in a model it is indicated with 'na'. If models initially included a fixed factor, but it was removed from the final full model due to non-significance it is indicated with '—'. Parameter estimates for binomial models are on the *log odds* link scale, and Poisson models are on the *log* link scale. Significance is indicated using an asterix (*), and marginal significance is indicated using a tilde (~) to the right of the *P*-value.

<i>Fixed effects</i>	Number of Trials until Learnt <i>N_{ind} = 29, N_{mom} = 19, N_{tub} = 25</i>				Probability of Making Correct Choice <i>N_{obs} = 696, N_{ind} = 29, N_{mom} = 19, N_{tub} = 25</i>			
	β	<i>SE</i>	<i>z-value</i>	<i>P</i>	β	<i>SE</i>	<i>z-value</i>	<i>P</i>
Intercept (SOCIAL, IL)	2.357	0.105	22.530	<0.001 *	1.300	0.305	4.264	<0.001 *
Trial Number	na	na	na	na	0.080	0.022	3.672	<0.001 *
Rearing Treatment (ISOLATED)	-0.047	0.122	-0.382	0.702	-0.290	0.286	-1.013	0.311
Learning Treatment (SL)	0.034	0.121	0.277	0.781	-0.177	0.284	-0.623	0.534
Trial Number * Rearing Treatment	na	na	na	na	—	—	—	—
Trial Number * Learning Treatment	na	na	na	na	—	—	—	—

Table S7. Outcomes of mixed effect models that examined the effect of a skink's rearing treatment (ISOLATED or SOCIAL) and learning treatment (social learning; SL or individual learning; IL) on (1) the probability of learning the reversal task, (2) number of trials until learnt the reversal task, and (3) probability of a correct choice during each trial. Our third model also included the additional fixed factors of trial number, and interactions between trial number x rearing and learning treatment; if a fixed factor was not included in a model it is indicated with 'na'. If models initially included a fixed factor, but it was removed from the final full model due to non-significance it is indicated with '—'. Parameter estimates for binomial models are on the *log odds* link scale, and Poisson models are on the *log* link scale. Significance is indicated using an asterix (*), and marginal significance is indicated using a tilde (~) to the right of the *P*-value.

	Probability of being a Learner <i>N_{ind}</i> = 29, <i>N_{mon}</i> = 19, <i>N_{ub}</i> = 25					Number of Trials until Learnt <i>N_{ind}</i> = 29, <i>N_{mon}</i> = 19, <i>N_{ub}</i> = 25					Probability of Making Correct Choice <i>N_{obs}</i> = 986, <i>N_{ind}</i> = 29, <i>N_{mon}</i> = 19, <i>N_{ub}</i> = 25				
	<i>β</i>	<i>SE</i>	<i>z-value</i>	<i>P</i>		<i>β</i>	<i>SE</i>	<i>z-value</i>	<i>P</i>		<i>β</i>	<i>SE</i>	<i>z-value</i>	<i>P</i>	
<i>Fixed effects</i>															
Intercept (SOCIAL, IL)	-1.391	1.210	-1.149	0.250		3.186	0.107	29.658	<0.001	*	-1.313	0.238	-5.512	<0.001	*
Trial Number	na	na	na	na		na	na	na	na		0.051	0.010	5.294	<0.001	*
Rearing Treatment (ISOLATED)	0.944	1.130	0.835	0.404		0.020	0.143	0.143	0.887		0.081	0.255	0.317	0.751	
Learning Treatment (SL)	0.158	1.009	0.157	0.876		0.008	0.140	0.058	0.954		-0.055	0.254	-0.218	0.827	
Trial Number * Rearing Treatment	na	na	na	na		na	na	na	na		—	—	—	—	
Trial Number * Learning Treatment	na	na	na	na		na	na	na	na		—	—	—	—	

FIGURE



Figure S1. The set-up for our discrimination and reversal task: two dishes were placed on a wooden block. One dish had a white lid, and the other a blue lid. During the discrimination task the food reward was under the blue lid, and during the reversal task the food reward was under the white lid. Under the incorrect lid, the food was made inaccessible by plastic mesh.

Chapter IV

Late bloomers: early experience impacts social behavior of a family-living lizard



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ABSTRACT

An animal's social environment can be both dynamic and complex. Thus, social species often garner fitness benefits through plasticity in their social behavior. Yet, behavioral plasticity can be constrained by an individual's social experience. We examined the influence of early social environment on social behavior in the tree skink (*Egernia striolata*), a family-living lizard. In the first phase of this study, we reared juveniles in two different social environments for 1.5 years: either in isolation or in unrelated pairs. We quantified each lizard's sociability at four-month intervals using a standardized laboratory assay, and found that isolated lizards were more sociable than socially-reared lizards. In the second phase of this study (at the end of 1.5 years), we released all lizards into a semi-natural environment, observed their associations, and used social network analysis to quantify social behavior. During the initial six weeks post-release, we detected no differences in social behavior between rearing treatments. However, during the following six months differences emerged. At first, isolated lizards associated more strongly with more lizards than socially-reared lizards. Yet, over time isolated lizard associations became weaker and with fewer lizards, potentially converging with the level and number of associations of socially-reared lizards that were stable over time. Isolated lizards were also less variable in the strength of their associations than socially-reared lizards. Our findings suggest that social experience influences *E. striolata* social behavior, but does not constrain social plasticity: isolation rearing did not affect their ability to respond to a novel social environment.

INTRODUCTION

Social associations are influenced by resource availability, predation risk, mating systems, parental care, and an individual's age and experience (Schutz et al. 2007; Ward and Webster 2016). Factors that affect social behavior can be complex, particularly in dynamic social systems. Thus, it is expected that individuals of social species will be highly plastic in their social behavior and vary their responses across social contexts to maximize individual fitness [termed 'social competence' (Taborsky and Oliveira 2012)]. Nevertheless, an individual's social competence can be constrained by personality (Aplin et al. 2013), inheritance (Ilany and Akcay 2016), or the social environment experienced during development (Scott 1962; Bekoff 1972; Kaiser and Sachser 2005). These constraints limit an individual's social repertoire, and can negatively impact their survival and reproductive success.

The type and extent of social experience during early life often affects how individuals perceive, process, interpret, and act in social situations as adults (Kaiser and Sachser 2005; Taborsky and Oliveira 2012). For example, isolation rearing negatively affects appropriate social behavior in mammals (Sachser and Lick 1991; Kaiser and Sachser 2005; Toth et al.

2011), birds (Baron and Kish 1960; Lauay et al. 2004; White et al. 2010; Ruploh et al. 2013; Boogert et al. 2014), and fishes (Taborsky et al. 2012; Hesse and Thünken 2014). To date, most work investigating how early social experience affects social behavior has focused on obligate social animals with required parental care. This focus neglects the large spectrum of sociality, which includes species with only occasional interactions (e.g., interactions while defending territories or during mating) or those that form seasonal aggregations (Ward and Webster 2016).

Squamate reptiles as a group have traditionally been viewed as relatively asocial (Doody et al. 2012). However, recent evidence suggests that sociality is much more common and varied than previously believed (Whiting and While 2017). Phylogenetic analysis shows that stable aggregations have evolved multiple times in squamates, and of these aggregations a small proportion live in stable family groups (Gardner et al. 2015). *Egernia striolata* (the tree skink) aggregates within tree hollows or crevices, and cracks in rocks (Cogger 2014). This species can be found alone, or within groups consisting of adult pairs with or without offspring, or only of juveniles (Bonnett 1999; Duckett et al. 2012). Group size varies from 2-10 individuals, and there is within- and between-population variation in *E. striolata* social behavior (Bustard 1970; Bonnett 1999; Duckett et al. 2012). Perhaps, social environment affects *E. striolata* behavioral development, and is a source of this intra- and inter-population variation. There is evidence from other squamate reptiles that social environment can influence social behavior. For example, hatchling veiled chameleons (*Chameleo calyptratus*) reared in isolation are more submissive during conspecific interactions than socially-reared hatchlings (Ballen et al. 2014). Also, hatchling viperine water snakes (*Natrix maura*) incubated alone, instead of in contact with other eggs, are less aggregative (Aubret et al. 2016), and depriving neonate cottonmouths (*Agkistrodon piscivorus*) of maternal attendance post-birth reduces their tendency to associate with conspecifics (Hoss et al. 2015). These initial studies suggest that the relationship between social experience and social competence found in mammals, birds, and fishes might also apply to squamate reptiles, however the currently limited research on this topic in reptiles prevents us from making generalizations.

We examined how the social environment during early life impacts *E. striolata* social behavior. In the first phase of the study, we reared lizards within one of two social environments (isolation or within a pair) for 1.5 years, and quantified juvenile sociability with a laboratory assay. In the second phase, we released lizards into a semi-natural environment and recorded their association patterns over the short- (initial six weeks) and long-term (subsequent six months: weeks 7 -34). We hypothesized that isolation rearing would reduce lizard social competence, and predicted that isolated lizards would avoid aggregating with conspecifics, as has been observed in other squamates, birds, mammals, and fishes (Harlow et

al. 1965; Aubret et al. 2016; Hesse and Thünken 2014; Bölting and von Engelhardt 2017). An individual's social competence is also reflected in its ability to change social behavior across situations (Taborsky and Oliveira 2012). In this regard, isolation rearing can constrain an individual's behavioral plasticity (Kaiser and Sachser 2005, Taborsky et al. 2012). Consequently, we also quantified consistency in an individual lizard's social behavior to examine plasticity in these traits, and whether consistency differed between rearing treatments (Aplin et al. 2015; Stamps 2015).

METHODS

In this experiment, we used 66 *E. striolata* that were offspring from 35 females collected near Albury, New South Wales (35.98°S, 146.97°E). These offspring were from two, yearly cohorts (2014 and 2015; see supplementary materials for details on captive husbandry and monitoring).

Rearing treatment and laboratory sociability assays

After lizards were born (within a maximum of 12 hours) we separated them from their mothers and housed them individually (for dates of parturition see supplementary materials). After all juveniles were born each year, we conducted the first sociability assay (see below).

We then randomly allocated juveniles into two social environments: isolated (housed alone; $N_{2014} = 14$ lizards and $N_{2015} = 16$ lizards), and social (two unrelated juveniles housed together; $N_{2014} = 14$ lizards within 7 pairs and $N_{2015} = 22$ lizards within 11 pairs). Juvenile social groupings of similar sizes have been reported for wild populations of *E. striolata* (Bonnett 1999; Duckett et al. 2012; JL Riley, unpubl. data). These juvenile-only groups vary in size, ranging from pairs to 4 individuals, and juveniles are also observed on their own (Bonnett 1999; Michael and Cunningham 2010; Duckett et al. 2012). However social groups often consist of parent(s) and offspring (Chapple 2003), but we were unable to recreate this environment in captivity due to a risk of infanticide (Lanham and Bull 2000; Post 2000; O'Connor and Shine 2004; JL Riley, unpubl. data).

Once within their treatments, we assayed lizard sociability three more times: at ca. 5, 7, and 12 months of age (see supplementary materials for exact dates). We had to measure sociability within two batches due to space limitations of our experimental room (maximum of 24 lizards per batch; see supplementary materials).

During sociability assays we individually housed lizards in opaque, plastic arenas, which were separated into two compartments with a clear, Perspex® divider placed 11 cm from one end (Riley et al. 2017; see supplementary materials for more details). We first placed the focal juvenile within a shelter in the larger compartment and then placed an

unrelated, adult female in the smaller compartment on the opposite side of the divider. Females were randomly paired with each focal juvenile, but were different in each repetition of the assay (i.e., used only once/juvenile). We then lifted the juvenile's shelter and remotely video-recorded the location of the juvenile in relation to the female for the next 5 h. From the video, at 10 min intervals over the full course of the trial, the juvenile was scored as being within one of four lateral quadrats (11 cm width) that sequentially reflected distances further away from the female. From these data, we calculated the weighted mean distance the juvenile was from the female across the whole trial, by multiplying the number of times in each quadrat (Q1, Q2, Q3, and Q4) by the mean distance the quadrat was away from the female's compartment (5.5 cm, 11 cm, 16.5 cm, and 22 cm, respectively) and dividing the product by the total number of observations ($N_{\text{obs}} = 30$). This weighted mean was used to quantify sociability across the first year of life; lower values reflect higher sociability.

Spatial associations

We quantified lizard sociability within a semi-natural environment after they reached adulthood to assess long-term effects of rearing treatment on social associations. *Egernia striolata* reaches sexual maturity after ~1.5 years in captivity (JL Riley, unpubl. data). We used all 28 lizards reared in 2014 in this experiment (14 isolated and 14 socially-reared), and released them into a fenced outdoor enclosure with an area of 70 m² (10.5 by 6.7 m) on 14 September 2015. A net surrounded the enclosure to exclude avian predators (Fig. S1).

We provided 28 artificial crevices (hereafter refuges) inside the enclosure. This ensured that refuges were not a limited resource, thus allowing aggregation to depend on individual preference and not ecological factors (i.e., a limited resource). We placed two roofing tiles (each tile was 410 x 260 mm) on top of each other to form refuges (Fig. S1). These refuges were placed in four rows of seven 0.75 m apart and 1.25 m away from the perimeter (Fig. S1). Prior to release, on 11 September 2015, we permanently marked all lizards with microchips (PIT tags) and visually numbered them with three circles of numbered cloth tape (Tesa[®], Hamburg, Germany; Fig. S1C; Olsson and Shine 2000; While et al. 2009a). The lizards were all released in the middle of the enclosure. If a lizard lost any marking tape, it was re-marked at the end of the day, after data collection, and quickly released back at its location of capture.

We recorded lizard spatial positions within the enclosure over two time periods: the initial six weeks post-release (4x daily) and then the following six months (weeks 7- 34; twice weekly). Observers (CG and STL during the initial six weeks; CG and CF for the following six months) were blind to rearing treatment. Data collection took the same amount of time in both periods, on average 22 min (95% CI = 21, 23), which reflects similarity in sampling

intensity and effort. Our sampling methods (see below) differed between six-week and six-month observations, and we quantified different social behaviors. Our short-term observations captured behavior across the daily activity period of lizards, whereas the long-term observations recorded which lizards were sharing refuges overnight and social associations before the start of daily activity .

During the initial six weeks (14 September - 25 October 2015), we recorded each lizard's spatial position within the enclosure four times each day at 10:00, 12:00, 14:00 and 16:00. First, we scanned the entire enclosure from a raised tower (2.1 m tall), and then we walked around the outside of the perimeter for a ground-level perspective thereby maximizing our ability to detect lizards. After the initial six weeks, we changed to a new sampling protocol for the following six months (29 October 2015 to 29 April 2016). We recorded lizard spatial positions every Monday and Friday, between 07:00 - 09:00 h, prior to husbandry (see supplemental materials). During these observations we lifted each roofing tile, captured every lizard in the refuge in order to identify them from their PIT tag number (lizards did not retain their identifying stickers during the 6 month observations), and then placed them back at their site of capture. We also checked under water dishes and in the area between refuges for lizards. Each sampling period was started from a different location, and performed in different pattern during each trial.

Statistical analyses

Analyses of laboratory sociability scores

We examined if *E. striolata* sociability differed between rearing treatments, using a linear mixed effects model (LMM, *lmer* in the *lme4* R package; Bates et al. 2015; R Core Team 2016). In our model, we examined if the response variable, *sociability* (the mean distance (mm) a lizard was located from an adult female during a trial), was affected by *rearing treatment* (isolated or social) while controlling for the additional fixed factors of *age* (continuous), *sex* (male or female), *cohort* (2014 or 2015), *batch* (1 or 2), *body temperature* (continuous), and *body condition index* (continuous; residuals from a simple linear regression between log-transformed mass and SVL). Continuous fixed factors were mean centered before analysis. To control for dependencies within our data from sampling each lizard repeatedly and sampling individuals from the same litter, we included a random intercept and slope for lizard identity across age, as well as a random intercept for mother identity. We ensured that there were no influential outliers, no strong collinearity, and that the model assumptions of normality of residuals and heterogeneity of variance were met.

We also examined the consistency of an individual's sociability and determined if this was affected by rearing treatment. To accomplish this we calculated adjusted repeatability

(R_{adj}/age ; Biro and Stamps 2015) for each treatment and the associated 95% confidence intervals by bootstrapping the data 1000 times with the *boot* function from the R package *boot* (Davison and Hinkley 1997; Canty and Ripley 2017), while controlling for the same covariates that were within our LMMs (Nakagawa et al. 2010; Biro and Stamps 2015). We compared R_{adj}/age between treatments by examining overlap of each rearing treatment's 95% CIs.

Social network analysis

Animal social network analysis is a powerful technique for quantifying association or interaction data (Farine and Whitehead 2015). We used social network analysis to quantify the associations we observed between lizards in the semi-natural enclosure. We considered lizards to be associating when they were at the same refuge within a sampling period (e.g., if 2+ lizards were located in/on the same refuge, they were defined as a group). Additionally, the refuges in our study were small (e.g., 410 x 260 mm; approximately the size of two lizards), thus if lizards were sharing a refuge they would have been aware of each other. Association strength for each pair of lizards (dyad) was calculated using the half-weight association index (HWI). The HWI ranges between 0 (never observed in the same refuge) and 1 (always observed in the same refuge). It is a relative measure of association strength, which is most appropriately used when an entire population cannot be observed during each sampling period (Cairns and Schwager 1987), as is the case in our study (see Results for sampling rate).

We constructed six weekly networks, and six monthly networks that controlled for lizard space use (i.e., the function included refuge number, which reflects lizard location, during construction of the group-by-individual matrix; Farine 2013) to ensure the associations we were describing were based on social, and not abiotic, biotic, or spatial factors (Fig. 1). The edge weights in these networks were the HWI association strength (described above), resulting in weighted undirected networks in which individuals (nodes) were connected if $HWI > 0$. Network construction and analysis were performed using the *asnipe* R package (Farine 2013).

For each network (6 for each week and 6 for each month), we calculated three network metrics that quantified individual social behavior: binary degree, weighted degree, and the coefficient of variation (CV) of edge weights. Binary degree is the number of lizards the focal lizard was observed sharing a refuge with, and weighted degree [also termed “strength” (Whitehead 2008)] is the sum of edge weights (dyadic HWIs) of the focal lizard (Whitehead 2008). These metrics both reflect the sociability of an individual and are complementary; an individual can have a high numbers of associates with weak associations (high binary degree

and low weighted degree) or, in contrast, a low number of strong associations (low binary degree and high weighted degree). The CV of edge weights is a measure of social heterogeneity [also termed “social differentiation” and the “clustering coefficient” (Whitehead 2008)] of a focal lizard and quantifies variability of an individual’s relationships (Leu et al. 2016). High values of social heterogeneity means that relationships are variable, and that the focal lizard is mainly associating strongly (i.e., preferentially) and/or weakly (i.e., avoiding) with conspecifics (Farine and Whitehead 2015). In contrast, low values of social heterogeneity means that relationships are more homogenous, and that focal lizards are associating relatively evenly with conspecifics (Farine and Whitehead 2015).

Temporal aspects of social relationships

We used separate LMMs to determine if the observed network metrics (binary degree, weighted degree, and CV of edge weights) differed between rearing treatments across each time period (six weeks or six months). All LMMs included the fixed factors of *time period* (week or month, respectively), *rearing treatment* (isolated or social), *sex* (male or female), as well as interactions between *time period and sex* and *time period and treatment*. If interactions were not significant (according to P_{rand} , see below) they were removed and the models re-fitted. Models also included the random intercept and slope of lizard identity across time, and the random intercept of mother identity. Binary and weighted degree were $\log(x+1)$ transformed to normalize the data. We also wanted to examine the consistency of social metrics for each rearing treatment, and calculated treatment-specific $R_{adj}/time$ (weeks or months; Biro and Stamps 2015) using the same protocol as described above.

Hypothesis testing for data generated from social networks is based on null models constructed with data from random permutations (Farine and Whitehead 2015). This is necessary because of non-independence of the data from social networks. Permutations were done using our group-by-individual matrix by randomly swapping individuals between groups, while controlling for location because original network construction already accounted for this (Farine 2013). These permutations were done separately for each weekly/monthly network. Importantly, this permutation technique retains the structure of our observed dataset: it maintains the same number of dyads observed, number of times an individual is sighted, and number of individuals recorded during each sampling period as our observed data (Whitehead 2008; Croft et al. 2009; Farine and Whitehead 2015). During the first six weeks, one lizard (female, socially-reared) died of natural causes, and, during our six-month observations, predators unexpectedly infiltrated the enclosure resulting in the removal of five lizards (3 isolated males, 1 isolated female, 1 socially-reared male) during the third

month, and one lizard (socially-reared female) during the fifth month due to predation and/or injury. Our permutation technique took this into consideration.

From the randomized data, we then reconstructed the networks, derived the same three social metrics, and conducted the same LMMs and calculations of $R_{adj}/time$ as we did for the observed data. Randomizations were repeated 10,000 times, and P values (P_{rand}) for each effect were calculated by comparing model coefficients from the observed data to the distribution of model coefficients based on the randomized data (Aplin et al. 2015; Farine and Whitehead 2015; Leu et al. 2016). We considered effects to be significant if observed values fell outside the 95% range of the random coefficient distributions. We compared $R_{adj}/time$ between treatments by examining overlap of each rearing treatment's 95% CI s. We assessed if observed $R_{adj}/time$ differed from what you would expect by chance alone by examining overlap between 95% CI s for observed $R_{adj}/time$ estimates and the 95% range of the random $R_{adj}/time$ estimates.

RESULTS

Laboratory-based sociality assays

Socially-reared lizards were located further from an adult female, exhibiting lower sociability, than isolated lizards (Table 1). Distance from an adult female decreased, reflecting increasing sociability, for both isolated and socially-reared lizards as they aged (Table 1). There were no batch, cohort, or sex effects on the distance lizards were located from an adult female, and this distance was also not related to body temperature or body condition (Table 1). R_{adj}/age of sociability was moderate (isolated: $R_{adj}/age = 0.427$, 95% $CI = 0.216$ to 0.637 ; social: $R_{adj}/age = 0.304$, 95% $CI = 0.000$ to 0.665), and did not differ between rearing treatments (Fig. 2A).

Social relationships in a semi-natural environment

During the initial six weeks post-release, all 28 lizards were observed during 168 sampling periods (6 weeks x 7 days x 4 observations per day; total observations of lizards = 2061). Each sampling period 48% (95% $CI = 44, 52$) of the lizards were observed. But each week, across 28 sampling periods, 98% (95% $CI = 95, 100$) of the lizards were observed. In the following six months, all 27 lizards were observed during a total of 52 sampling periods (28 weeks x 2 observations per week; total observations = 985). Within each sampling period during these six months, 98% (95% $CI = 97, 100$) of the lizards were observed.

During both time periods, mean group size was two (six week: standard error = 0.03, range = 2 - 8; six month: standard error = 0.02, range = 2 - 4). However, individuals were also frequently observed alone. Lizards were observed alone in a refuge 80.4% (1340/1667) of the time during the initial six weeks, and 77.3% (612/792) of the time during the next six months.

Thus, our network metrics and model parameter estimates that quantify social associations are lower than what you might find in a species that constantly associates with other individuals (Table 2).

Temporal Variation in Social Relationships

Initial six weeks

Network metrics (binary degree, weighted degree, and CV of edge weights) did not differ between rearing treatments during this period (Table 2A). Sex did not affect binary degree or CV of edge weights, but female lizards initially had stronger associations (higher weighted degree) than males and decreased in the strength of their social associations (weighted degree) more quickly over time than males (Table 2A). In general, the number and strength of associations (binary and weighted degree) decreased over time, whereas social heterogeneity (CV of edge weights) increased over time (Table 1A; Fig 2).

$R_{adj}/week$ of our three social metrics were low to moderate for both rearing treatments. $R_{adj}/week$ did not differ between rearing treatments, and was not different from what we would expect by chance alone (95% CIs from both the observed and random $R_{adj}/week$ overlap). Non-significance was likely due to large variation in our observed $R_{adj}/week$ estimates (Fig. 2B).

Subsequent six months

Initially, isolated lizards had stronger associations (higher weighted degree) with more lizards (higher binary degree, marginally significant $p = 0.07$) than socially-reared lizards (Table 2B; Fig. 1). Over time, isolated lizards decreased in their number of associates (binary degree) and their associations became weaker (weighted degree). In contrast, socially-reared lizards were constant in their number associates and level of associations (binary and weighted degree) over time (Table 2B; Fig. 1). Social heterogeneity (CV of edge weights) was significantly lower in isolated than socially-reared lizards, and social heterogeneity decreased over time in both rearing treatments (Table 2B; Fig. 1). None of the network metrics were affected by sex (Table 2B).

$R_{adj}/month$ did not significantly differ between rearing treatments, because 95% CIs overlapped (Fig. 2C). $R_{adj}/month$ of binary degree, weighted degree, and CV of edge weights was moderate for both rearing treatments (Fig. 2C). Our observed $R_{adj}/month$ did not significantly differ from what was expected by chance alone (95% CIs from both the observed and random $R_{adj}/month$ overlap; Fig. 2C).

DISCUSSION

We generally found positive relationships between isolation rearing and social associations in *E. striolata*, in contrast to our predictions. During the juvenile life-stage, isolated lizards spent laboratory trials closer to an unrelated adult female than socially-reared lizards. After lizards reached adulthood we released them into a semi-natural enclosure, and, after the first six weeks post-release, we found isolated lizards initially associated more strongly with more lizards than socially-reared lizards (i.e., higher binary and weighted degree). Isolated lizards were also more homogenous in their social associations than socially-reared lizards (i.e., lower CV of edge weights). Interestingly, over the six month period, isolated lizards gradually began to associate with fewer lizards, more weakly (e.g., decreased in binary and weighted degree) whereas socially-reared lizards were stable in associations over time. This suggests that *E. striolata* individuals reared in isolation were able to respond flexibly to their social environment. In further support of this conclusion, our repeatability ($R_{adj/time}$) estimates were low to moderate, and they did not differ between rearing treatments nor from what is expected by chance alone. This suggests that *E. striolata*, regardless of rearing treatment, is plastic in its social behavior.

Sociability during the juvenile life-stage

Isolation rearing increased juvenile affiliations with adult females. This finding was the opposite of what we had hypothesized: that isolation would result in individuals that avoid social situations and/or exhibit costly social behavior (e.g., high aggression; Mitchell et al. 1966; Kaiser and Sachser 2005). Our prediction was based predominately on studies about species that have obligate parental care (Mitchell et al. 1966; Kaiser and Sachser 2005), where socially isolating these species during development results in costly physiological (e.g., abnormal levels of sex and stress hormones; Kaiser and Sachser 2005; Bötting and von Engelhardt 2017) and behavioral changes that reduce fitness (e.g., avoidance of conspecifics, inappropriate mating behavior; Harlow 1965; Buchholz 2007; Rilling and Young 2014). The rudimentary parental care and the facultative social system of *E. striolata* differs from that of obligate social animals. Therefore, we need to consider how our findings may influence fitness in *E. striolata*, while considering their social system.

Social associations, even affiliative ones, are not always beneficial, and can even be quite costly and even fatal in some cases. For example, yellow bellied marmots (*Marmota flaviventris*) that are more affiliative are more likely to die during hibernation, potentially because hibernating in close proximity to other individuals may disrupt required thermoregulation (Yang et al. 2017). In the case of juvenile *E. striolata*, social interactions with unfamiliar adults are potentially costly. In the wild, unrelated adult *Egernia* spp. pose a

direct mortality threat to juveniles; they are often highly aggressive and infanticide can occur (*E. stokesii*, Lanham and Bull 2000; *E. hosmeri*, Post 2000; *E. saxatilis*; O'Connor and Shine 2004; *Liopholis whitii*, Sinn et al. 2008; While and Wapstra 2008). Within our experiment socially-reared lizards experienced aggressive interactions within their social pair (Riley et al. 2017); these encounters may have exposed juveniles to a learning experience that may have better prepared individuals for potentially dangerous interactions with conspecific adults. Avoiding an unfamiliar, unrelated adult, as socially-reared lizards did, may be the most beneficial behavior to exhibit in this social situation. In contrast, isolation rearing resulted in socially naïve lizards with greater affiliation towards unfamiliar, adult females; this is likely a costly and maladaptive behavioral response.

Adult social associations

During the initial six weeks after release into our semi-natural enclosure, we did not detect a difference in social behavior between rearing treatments. Lizards may have been habituating to, and exploring, their novel environment during this short time period. Conversely, the social behavior we recorded over the following six months (i.e., lizards sharing refuges over night) may more clearly reflect stable social bonds and this lizard's social preferences, than social associations during their daily activity period. During the day, lizard interactions are likely influenced by their activity (e.g., random encounters with individuals at refuges during foraging or other movements), and may also include social interactions that are short and/or agonistic instead of affiliative. Previous studies have also found that crevice-sharing behavior directly reflects social associations in *E. striolata* (Bonnett 1999; Chapple 2003; Duckett et al. 2012), and because refuges were not limited within our enclosures sharing a refuge overnight likely reflects an individual's social preference.

We did find evidence that rearing treatment affected crevice-sharing behavior over the following six months. Isolated lizards were more homogenous in their social associations, and all lizards, regardless of rearing treatment, became more homogenous in their social associations over time. At the beginning of the six month period, isolated lizards associated more strongly with more lizards, in congruence with our laboratory behavioral assays. But, over time, isolated lizard associations weakened and were with fewer lizards, whereas socially-reared lizard associations were similar in number and frequency over time. Isolation rearing has previously been shown to constrain social plasticity in a number of species (White et al. 2010; Taborsky et al. 2012; Ruploh et al. 2013), leading to negative fitness consequences (Taborsky and Oliveira 2012). Yet, in *E. striolata*, isolation did not constrain flexibility in their social behavior. Isolated lizards, after having experienced a competitive and potentially aggressive social environment (Riley et al. 2017), were able to change their

crevice-sharing behavior in line with socially-reared lizards. Retaining the ability to plastically respond to changing social contexts may be beneficial for this facultatively social lizard.

Animal behavior is purported to have great potential to significantly contribute to conservation biology (Sutherland 1998; Buchholz 2007; Caro 2007). Our finding that early social environment may not limit behavioral plasticity has important implications for wildlife management and conservation projects. It highlights the importance of considering each target species' social system independently when rearing social animals in captivity. In some cases, the social environment may be - surprisingly - more costly than being reared in isolation, or species could be highly plastic and thrive whatever their social situation. Overall, knowledge of a target species' social system, and how early social environment can impact their behavior and fitness, would directly benefit conservation.

Consistency in social phenotypes

Consistency in behavioral traits over time is the antithesis to plasticity. If behavioral traits are temporally consistent (i.e., personality; Stamps 2015) it suggests that certain traits are regularly selected for over others. In a complex and ever-changing social environment, it is theorized that plasticity in traits is adaptive (Taborsky and Oliveira 2012). Our findings support this hypothesis, as consistency in the social behaviors we measured was only low or moderate over time. In the lab, where *E. striolata* were within stable social environments for 1.5 years (either social or isolated), consistency of behavioral traits was moderate. In comparison, when lizards were released into the enclosure, a much more dynamic environment, consistency in social behavior was lower and did not increase significantly over the following six months.

Consistency in social behavior also did not differ between rearing treatments. As socially-reared lizards were always exposed to a social environment in our study, we expected their social behavior to be more consistent than isolated lizards (even though there was a change from lab to semi-natural conditions for this treatment). In contrast, isolated lizards changed from no social contact during development to a social situation during adulthood. This is a substantial change, so we expected isolated lizards to be variable in their social behavior, but only if their behavioral plasticity was not constrained by their development. As both rearing treatments showed similar consistency in behavior, we interpret this finding as evidence that isolation rearing did not impact an individual's natural social plasticity.

The facultative and variable nature of *E. striolata*'s social system may select for behavioral plasticity. In wild populations of *E. striolata*, and other *Egernia* group spp., developing with limited social contact may occur for a proportion of each litter (Bonnett

1999; While et al. 2009b). For example, in White's skink (*Liopholis whitii*) a closely-related *Egernia*-group skink, the degree of social contact during development is thought to vary depending on the degree to which a juvenile is related to their social father (While et al. 2009b). Furthermore, *E. striolata* is long-lived and the social system of this species may be influenced by seasonality and environmental factors (Michael and Cunningham 2010; Duckett et al. 2012). It is likely that throughout a lizard's lifetime it could experience a range of social situations ranging from near-isolation to family-living, thus plasticity in social behavior would be adaptive. This differs from the social environment within obligate social animals with parental care, which is the basis of the majority of research on this subject (Kaiser and Sachser 2005; Toth et al. 2011). The facultative kin-based sociality of tree skinks, in relation to obligate sociality, best explains our contrasting results and the degree to which these lizards are able to adjust to a novel social environment.

Conclusion

Isolation rearing resulted in naïve juveniles that were more likely to associate with unfamiliar conspecifics regardless of the potential costs. Although isolation rearing affected social behavior, it did not constrain social plasticity. We hypothesize that natural variation in the social system of *E. striolata* selects for plasticity in social behavior, which allows them to respond to the variable social contexts they are faced with throughout their lives. Overall, our study demonstrates that the impact early social environment has on social behavior may depend on a species' social system and this finding has important implications for conservation programs.

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Table 1. Effects of rearing treatment (ISOLATED or SOCIAL) and age on lizard sociability ($N_{obs} = 244$, $N_{juv} = 61$, $N_{mom} = 35$). Significant coefficients are bolded.

Fixed effects	<i>B</i>	<i>SE</i>	<i>t-value</i>	<i>P</i>
Intercept (SOCIAL, 1, 2014, and FEMALE)	16.636	0.769	21.645	<0.001
Age	-0.939	0.229	-4.099	<0.001
Rearing treatment (ISOLATED)	-1.459	0.727	-2.007	0.045
Batch (2)	-0.521	0.402	-1.297	0.195
Cohort (2015)	-0.769	0.833	-0.923	0.356
Body temperature	0.307	0.194	1.581	0.114
Body condition index	0.374	0.203	1.837	0.066
Sex (MALE)	0.188	0.798	0.236	0.813
Random effects	σ^2			
Juvenile identity	5.237			
Mom's identity	1.573			
Residual	6.792			

The LMM formula in R was `lmer(sociability ~ age + social_treat + batch + cohort + body_temp + body_cond + (1+age|liz_id) + (1|mom_id))`. The interaction between age and rearing treatment was not significant, so it was removed and the model re-fit.

Table 2. Effects of sex (MALE or FEMALE), rearing treatment (ISOLATED or SOCIAL), and time (either week or month) on individual network metrics. Significant coefficients are bolded.

(A) Short-term data (6 weeks; $N_{obs} = 168$, $N_{juv} = 28$, $N_{mom} = 15$)

	Binary Degree			Weighted Degree			Coefficient of Variation		
	β	P_{rand}	95% CI_{rand}	β	P_{rand}	95% CI_{rand}	β	P_{rand}	95% CI_{rand}
Intercept (FEMALE, SOCIAL)	1.682	0.901	(1.639, 1.918)	0.671	< 0.001	(0.337, 0.426)	215.194	0.652	(191.002, 215.194)
Week	-0.010	0.002	(-0.085, -0.038)	-0.083	< 0.001	(-0.061, -0.041)	22.942	< 0.001	(-0.362, 13.146)
Sex: MALE	-0.087	0.230	(-0.077, 0.155)	-0.133	0.006	(-0.114, -0.065)	15.793	0.323	(-24.644, 31.422)
Social Treatment: ISOLATED	-0.012	0.869	(-0.081, 0.136)	-0.010	0.357	(-0.017, 0.021)	-19.010	0.310	(-38.004, 18.176)
Week*Sex	---	---	---	0.024	0.039	(-0.013, 0.028)	---	---	---
Week*Social Treatment	---	---	---	---	---	---	---	---	---

(B) Long-term data (6 months; $N_{obs} = 162$, $N_{juv} = 27$, $N_{mom} = 15$)

	Binary Degree			Weighted Degree			Coefficient of Variation		
	β	P_{rand}	95% CI_{rand}	β	P_{rand}	95% CI_{rand}	β	P_{rand}	95% CI_{rand}
Intercept (FEMALE, SOCIAL)	0.953	1.000	(1.781, 2.090)	0.307	< 0.001	(0.173, 0.250)	369.011	< 0.001	(193.372, 256.836)
Month	-0.035	1.000	(-0.140, -0.066)	-0.011	0.552	(-0.021, -0.004)	-19.566	< 0.001	(-1.644, -13.775)
Sex: MALE	-0.028	0.679	(-0.097, 0.156)	-0.032	0.095	(-0.041, 0.031)	-11.264	0.502	(-21.646, 35.802)
Social Treatment: ISOLATED	0.486	0.067	(-0.534, 0.028)	0.155	< 0.001	(-0.039, 0.108)	-50.382	0.002	(-21.464, 35.802)
Month*Sex	---	---	---	---	---	---	---	---	---
Month*Social Treatment	-0.144	0.039	(0.029, 0.148)	-0.044	< 0.001	(-0.031, -0.000)	---	---	---

The LMM formula in R was `lmer(binary_degree ~ week + sex + social_treat + sex:week + social_treat:week + (1+week|liz_id) + (1|mom_id))`, and respectively for association strength and coefficient of variation. If interactions were not significant (according to P_{rand}), they were removed and the models re-fitted.

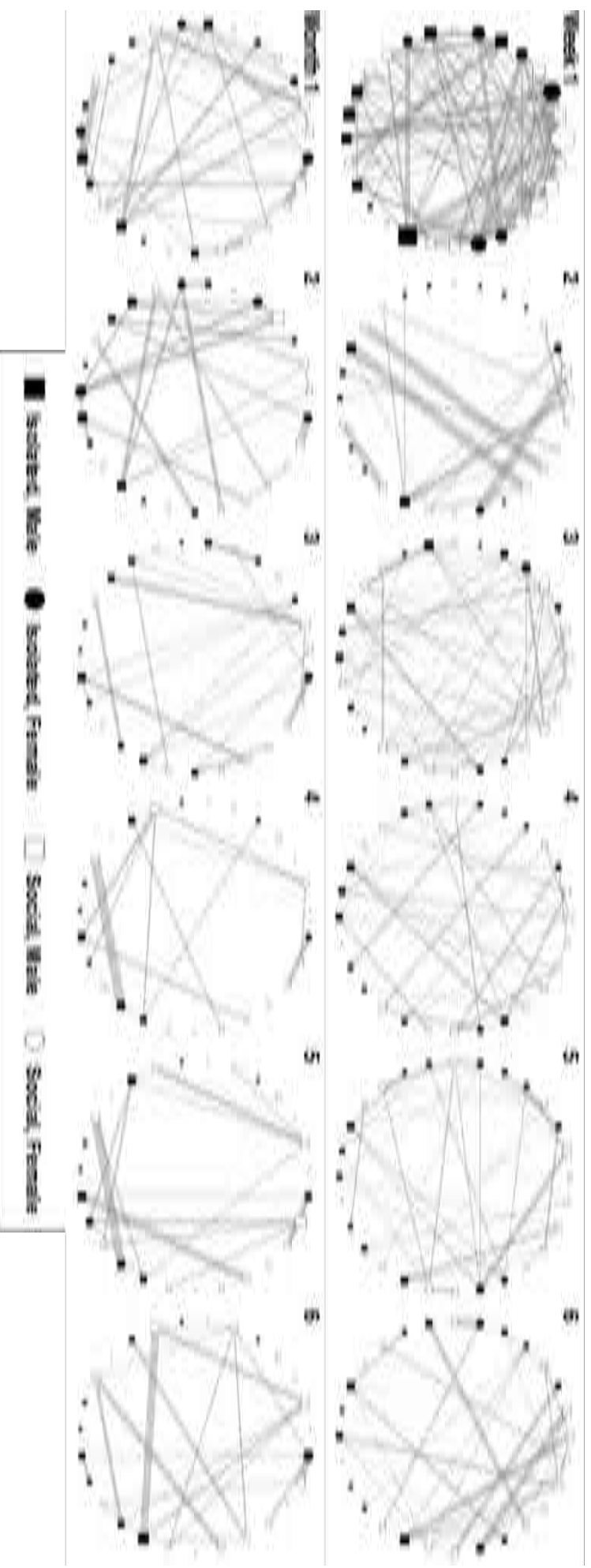


Figure 1. Weighted social networks across our six week (top) and six month observations (bottom). We aggregated the association data for each week or month, respectively, and constructed six weighted, undirected networks for each time period. These social networks reflect the association matrices used in our analyses. Node size reflects weighted degree of each individual. If lizards were removed from the social network during a time period (e.g., due to death or injury), nodes are replaced with a grey “X”.

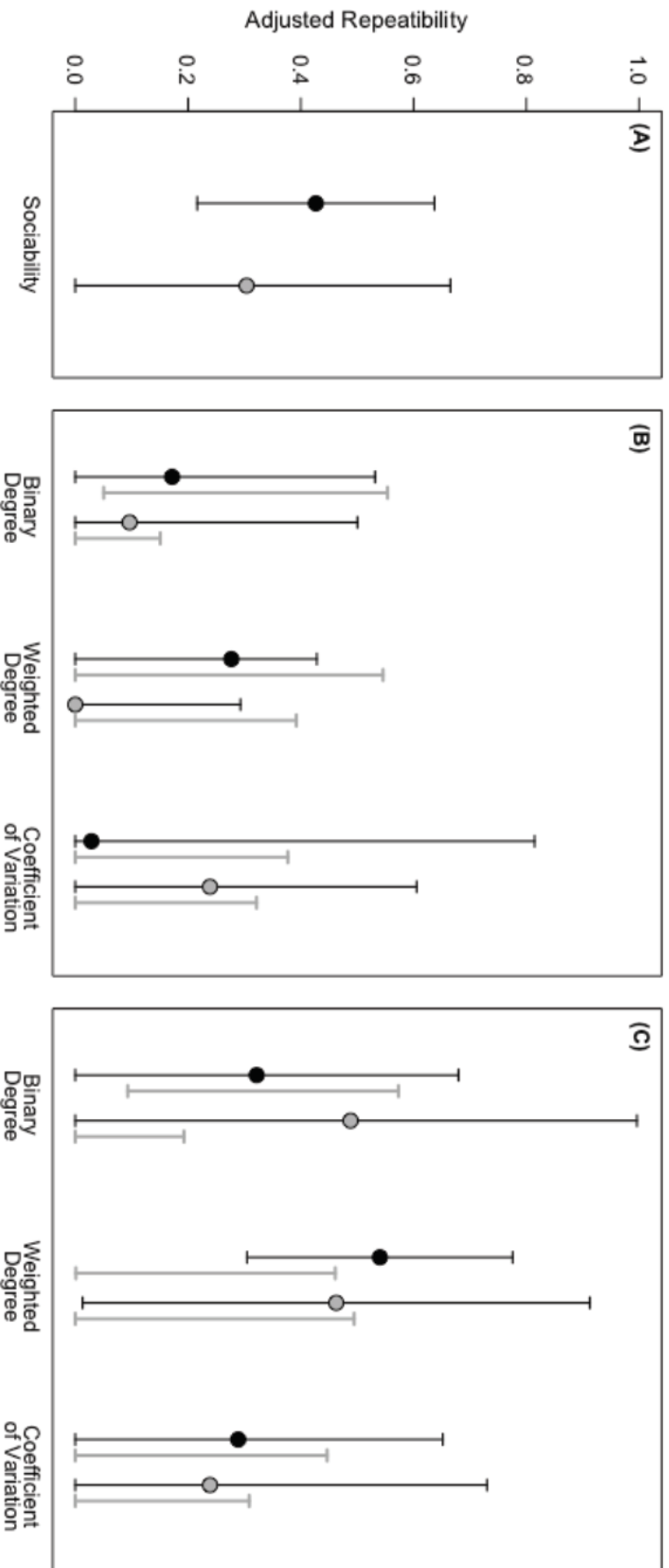


Figure 2. Adjusted repeatability ($R_{adj|time}$) and 95% confidence intervals for isolated ($N_{liz} = 14$: black circle and lines) and socially-reared ($N_{liz} = 14$: grey circle and black lines) lizards for (A) laboratory sociability scores, and the three individual network metrics: binary degree, weighted degree, and coefficient of variation across the (B) initial six weeks and (C) subsequent six months. $R_{adj|time}$ was not significantly different between rearing treatments, because 95% CIs for both rearing treatments (black error bars) overlapped. Grey bars show the 95% range of the $R_{adj|time}$ estimates calculated from 10,000 data randomizations controlling for location. Our observed $R_{adj|time}$ was not different than what you would expect from chance alone, because the 95% range of the random $R_{adj|time}$ estimates (grey bars) overlapped with 95% CIs for observed $R_{adj|time}$ estimates (black error bars) in all cases.

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Supplementary Materials

METHODS

**Please note that to make the methods as clear as possible, we have repeated some information from the main text.*

Field collection and captive housing

Near Albury, NSW we captured gravid female *E. striolata* by hand, noosing or Eliot trap in January 2014 (N = 15) and 2015 (N = 20), and then transported them by vehicle to Macquarie University. We monitored female parturition from 10 February to 12 March 2014, and from 17 January to 10 February 2015. During parturition, we kept females in a climate-controlled room (24°C) within opaque plastic tubs (350 mm W x 487 mm L x 260 mm H). Each tub was lined with newspaper, and contained tree bark, a water dish, and a shelter (120 mm W x 175 mm L x 38 mm H). Under each tub we provided under-cage heating wire, and lit the tub with a UV lamp. We cleaned housing tubs once weekly. We fed female lizards 3 adult crickets dusted with calcium and vitamin powder twice a week, and puréed fruit (1.25 ml of Heinz® baby food: mango, apple, or pear) once weekly.

We checked if females gave birth twice daily. Immediately after offspring were found, we measured their snout-vent-length (mm, SVL: the distance between the tip of the snout and the posterior edge of the cloaca), total length (mm), and tail length (mm) with a standard ruler to the nearest 1 mm. We also measured juvenile mass with a digital scale (SP6001, Scout Pro, Ohaus, Pine Brooks NJ, USA) to the nearest 0.01 g, and uniquely marked each juvenile with a toe-clip. Juveniles were housed within their rearing treatments in smaller opaque plastic tubs than the females' (85 mm W x 140 mm L x 60 mm H). All other housing criteria were the same as the females, except juveniles were fed nymph crickets instead of adult crickets. In total, 28 juveniles born in 2014 and 38 juveniles born in 2015 were included in our experiment. During each Australian winter (from June to August 2014 and 2015), juveniles were maintained at a reduced temperature (18°C).

Timing and sample sizes of sociability assays

We measured juvenile sociability within two batches due to limitations of our experimental room (maximum of 24 lizards per batch), and we randomly allocated individuals to each batch approximately equally. In the 2014 cohort ($N = 28$), 12 lizards were in batch 1 and 16 lizards were in batch 2 during the initial trials. At 5 and 7 months of age, 18 and 10 lizards were in batch 1 and 2, respectively. At 12 months of age, 15 and 13 lizards were in batch 1 and 2, respectively. In the 2015 cohort ($N = 38$), 19 lizards were in both batch 1 and 2 during the baseline assays. At 5 months of age, 22 and 16 lizards were in batch 1 and 2, respectively. At 7 and 12 months of age, 18 and 20 lizards were in batch 1 and 2, respectively.

Our initial sociability assays occurred on 31 March and 14 April in 2014, and 21 April and 5 May in 2015. We repeated the sociability assay three more times within each year: (1) ca. 5 months of age (29 August and 14 September in 2014, and 20 September and 3 October in 2015), (2) ca. 7 months of age (4 and 17 November 2014, 9 and 22 November 2015), and (3) ca. 12 months of age (6 and 19 February 2015, 24 January and 6 February in 2016).

Sociability assay housing and data collection

Sociability assays were part of a more encompassing series of behavioral trait assays; the results of which have been previously reported (Riley et al. 2017). During the sociability assays, lizards were housed in opaque plastic arenas (690 mm W x 470 mm L x 455 mm H) within a climate-controlled room (24°C). Each arena was warmed on one side with a heat lamp, and contained a shelter and a water dish except during assays. Lizards were fed as usual (see above) but only after assay completion each day. A maximum of a week before each sociability assay we re-measured each lizard (SVL, mass, and total length). Using the measurements for each time period, we calculated a body condition index using residuals from a simple linear regression between log-transformed mass and SVL. Immediately after assays finished each day, body temperature of each lizard was measured using an infrared thermometer (accuracy of 1.5°C, model # RIT310, Ryobi, Techtronic Industries Australia Pty Ltd, Doncaster, Victoria). We recorded the assay using a mounted security camera system (CCTV security systems, Melbourne, VIC), and behavior was scored from these videos. Videos were scored blind to rearing treatment by JLR. We restricted video scoring to one person to avoid inter-observer bias.

Husbandry within the semi-natural enclosure

During the first six weeks, we provided lizards with water on Mondays, Wednesdays, and Fridays by misting the enclosure heavily. During following six months, lizards were provided

water *ad libitum* from four water dishes placed symmetrically within the enclosure (Fig. S1); in each water dish, two roofing tiles were placed to allow access to the water and prevent drowning. We fed lizards throughout the experiment on Mondays, Wednesdays, and Fridays by placing puréed fruit (1.25 ml of Heinz® baby food: mango, apple, and pear) on a dish and putting one dish on top of each refuge to ensure food resources were evenly distributed.

References

Riley JL, Noble DWA, Byrne RW, Whiting MJ. 2017. Early environment influences the behaviour of a family-living lizard. *R Soc Open Sci.* 4:161082.

Supplemental Figures

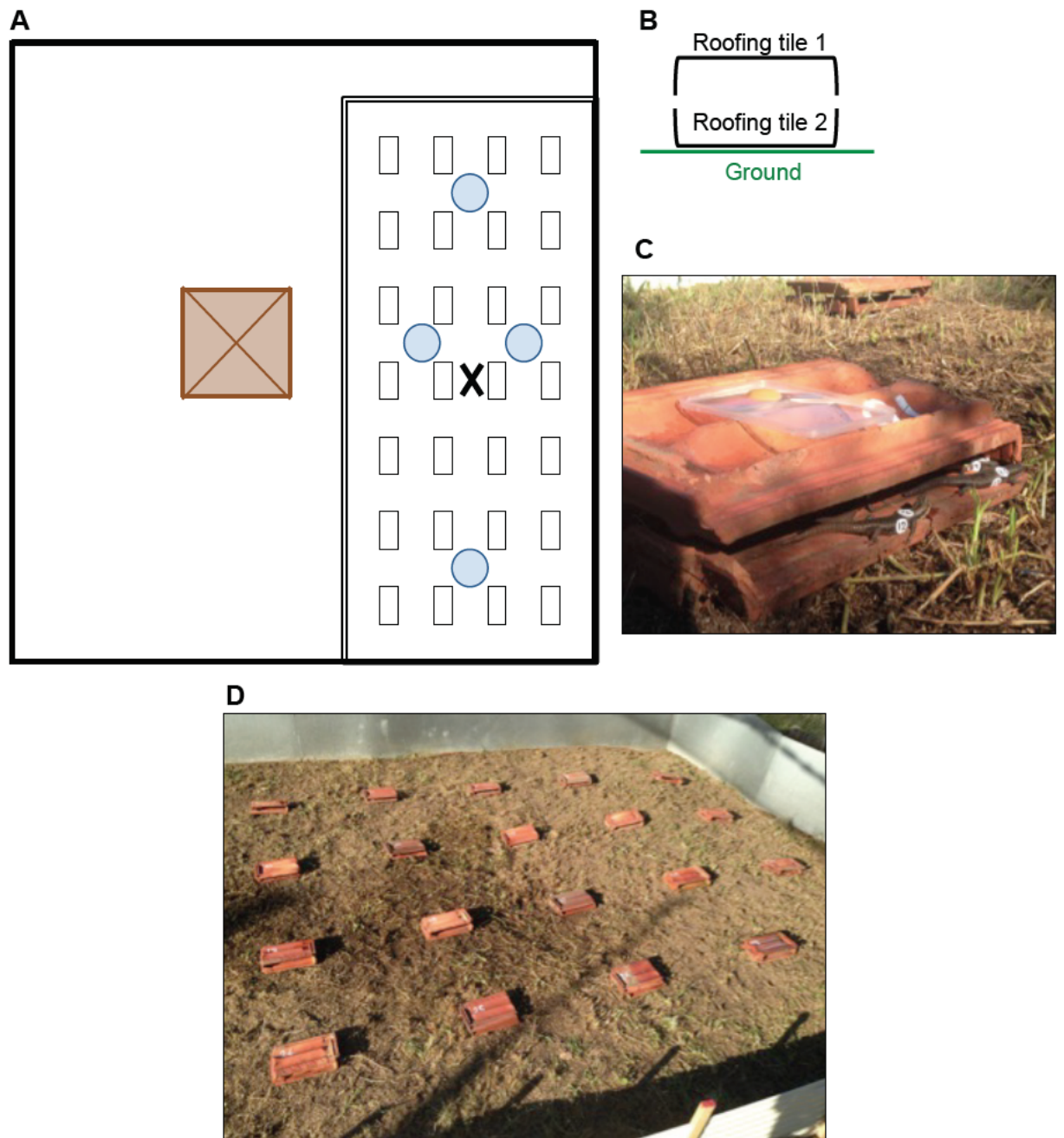


Figure S1. Schematic diagram (A) and photo (D) of the outdoor enclosure wherein 28 *E. striolata* were released (in the middle at 'X'); we observed the lizards in their refuges (small rectangles) from an observation tower (brown square) and outside of the enclosure fence (plastic represented as the double line, and metal as the thick line). Water dishes (blue circles) were added to the enclosure on 26 October 2015. Each refuge consisted of a single crevice made from two tiles (B and C).

General Conclusions

The research within this thesis has focused on understanding how early social environment impacts behavioural development in a family-living lizard, and specifically examined behavioural traits, cognitive ability, and social behaviour. Overall, this research expands our knowledge of the consequences of sociality into squamate reptiles, and brings to light more questions about how sociality may impact the lives of under-studied social species.

Social system and behavioural development

A major finding of my thesis is that social isolation does not broadly hinder *E. striolata* behavioural development. This finding was contrary to my expectations that were informed by previous literature about the link between rearing environment and behaviour. The focus of prior research has been on obligate social taxa (e.g., mammals and birds with obligate sociality and required parental care; Pryce et al. 2002; Kaiser and Sachser 2005; Goerlich et al. 2012); and the consensus within this literature is that social species require a ‘suitable development history’ to generate normal behaviour (e.g., access to parental care, interactions with conspecifics). Interestingly the limited studies examining this in squamate reptiles have found that social isolation affected behaviour by reducing social tendencies (*Chamaeleo calyptrotus*, Ballen et al. 2014; *Agkistrodon piscivorus*, Hoss et al. 2015; *Natrix maura*, Aubret et al. 2016). Their findings agree with the previous literature concerning obligately social animals, yet these squamates are considered to be mainly solitary and offspring do not require parental care. Thus, my conflicting findings instantly presented me with another question - why? I hypothesize that a species’ social system determines the impact early social environment has on behavioural development. In the case of my research, the facultative social system of *E. striolata* appears to select for behavioural flexibility across an individual’s lifetime. Also, the precocial nature of *E. striolata* offspring may favour behavioural flexibility, because developing in isolation is an option (Bonnett 1999; Duckett et al. 2012) and it would be maladaptive to have this state generate negative or abnormal behaviour. Some literature already supports these ideas. For example, the social performance of precocial labyrinth spiderlings (*Agelena labyrinthica*), a solitary species, were not affected by isolation rearing (Lesne et al. 2016). Yet, as stated above, the current findings in other precocial squamates found a negative influence of social isolation on social behaviour (Ballen et al. 2014; Hoss et al. 2015; Aubret et al. 2016). In a facultatively social mammal, the striped mouse (*Rhabdomys pumilio*), experimental manipulations of developmental environment (i.e., weaning period, parental care) resulted in increased occurrence of abnormal behaviours (e.g., stereotypical behaviours like bar-biting, self-removal of hair), which have the potential to

reduce individual fitness (Jones et al. 2010). Thus, results from current studies are not consistent across social taxa, or social systems, and my research adds to that inconsistency. More research is required spanning the spectrum of social taxa, to truly understand the consequences of sociality on behavioural development.

Ecological Implications

Since the 2000s, research on the *Egernia* group of skinks has greatly advanced our understanding of social living in reptiles, as well as the early evolution of sociality (Chapple 2003; Whiting and While 2017). Yet, when I began my thesis there was little known about the behavioural consequence of sociality in the *Egernia* group, and generally in reptiles. Consequently, much of my thesis research has been experimental in nature, and involved creating two extremes on the natural spectrum of social experience (Bonnett 1999; Duckett et al. 2012). Experiments are a rigorous way of testing cause-and-effect relationships providing any manipulations are within the range of social experience that occurs in the wild. Even still the results may not be directly applicable to wild populations. Thus, field studies are essential to further our knowledge on the behavioural consequences of sociality, and how these consequences may affect survival and reproductive success of individuals.

Many of my findings suggest that early social environment could impact individual behavioural traits that are important for fitness and may influence *E. striolata* ecology. For example, within my socially-reared pairs, dominance hierarchies formed. This reflects the relationships that form within *Egernia* group litters, because many species have asynchronous birth that can generate size-based dominance hierarchies (e.g., *Liopholis whitii*, Chapple 2003; While and Wapstra 2008; While and Wapstra 2009). I found that subordinate lizards within social pairs were less social and more aggressive than isolated skinks (Chapter I). This raises the question of whether these behavioural traits also encourage these individuals to disperse away from their natal social group and be less associative throughout their lives? How does this affect individual fitness? These differences in behaviour that my thesis uncovered via lab experimentation are informative. Yet, we also have to understand how these behaviours affect *E. striolata* fitness to truly comprehend the consequences of developmental environment for this species' ecology.

Evolutionary Implications

Recently, interest in individual differences in behavioural plasticity has surged within the field of animal behaviour through examination of animal personality, behavioural syndromes, and reaction norms (Stamps 2015). Temporal consistency in behavioural traits (i.e., personality; Stamps 2015) suggests there is regular selection for certain traits over others. My

thesis findings were that consistency of *E. striolata* behavioural traits (Chapter I) and association tendency (Chapter IV) was low to moderate in all lizards. One reason for this lack of consistency in tree skink behaviours is that behavioural traits may be less temporally stable in developing juveniles than in adults. Only a few studies have currently examined the development of personality traits, and they agree with our findings: that juvenile behavioural traits are not consistent across development (*Pogona vitticeps*, Siviter 2016; *Gallus gallus*, Favati 2016). More research is needed to understand how behavioural traits may change over the course of development.

An alternative explanation for the lack of consistency in juvenile tree skink behaviour is that selection may favour behavioural plasticity when an animal's environment is complex and dynamic (Taborsky and Oliveira 2012; Adriaenssens and Johnsson 2013; Biro and Stamps 2015). Facultative sociality, which typically creates a highly dynamic, variable, and context-dependent environment, may promote behavioural plasticity. Findings from my thesis support this hypothesis: consistency of *E. striolata* behavioural traits (Chapter I) and association tendency (Chapter IV) was low to moderate in all lizards. Yet, results from other studies focused on facultative social species are not consistent. For example White's skinks, another facultatively social *Egernia* group skink, also showed limited consistency in some behaviours (i.e., sociability and activity) and moderate repeatability in others (i.e., exploration, boldness, aggression; McEvoy et al. 2015). Whereas striped mice, a facultatively social mammal, maintained consistency in their behavioural traits even when switching social tactics (Yuen et al. 2015). More research is needed to determine if facultative sociality promotes behavioural plasticity, and the *Egernia* group would be a suitable model system this hypothesis because it contains closely-related species that vary from stable social systems (solitary and long-term family groups) to facultative sociality (Whiting and While 2017). Furthermore, multiple species of the *Egernia* group live in similar habitats across Australia, and experience similar selective pressures (e.g., diet, life-history, and predators; Chapple 2003). So, one could truly concentrate on teasing apart how an animal's social system may select for consistency in behavioural traits.

Implications for Conservation

Unfortunately reptiles are a globally imperilled taxon, with almost one in every five species facing extinction (Böhm et al. 2013). Many conservation initiatives breed and raise reptiles in captivity, often with the goal of reintroducing them back into the wild (Burke 1991; Dodd Jr and Seigel 1991; Connolly and Cree 2008; Burke 2015). Yet a limitation for these programs is a lack of knowledge about how sociality (both the social system and parental care) impacts reptile development, because rearing conditions have the potential of long-lasting effects on

behaviour and fitness (Beck and Power 1988; Lindburg and Snyder 1994; Hampson and Schwitzer 2016). My thesis highlights the importance of considering each target species' social system independently when planning a captive rearing program. In my facultative social species, rearing within a social pair was costly for the subordinate lizard (Chapter I), which could reduce the productivity of a rearing program. Furthermore, isolation rearing, although initially impacting social behaviour, did not constrain an individual's ability to change their social behaviour when faced with a new social situation (Chapter IV). So, in the case of my study species', a rearing program may benefit from including a 'soft-release' or 'exposure period' that introduces individuals to natural social contexts, because it may serve to normalize an individual's behaviour. Conservation programs for iguanas have utilized this approach: exposing captive-reared juveniles to natural predators and social situations within a controlled environment prior to release (Alberts 2007). An increased understanding of the relationships between social environment and reptile behaviour is also important for ethical considerations about how best to house reptiles within zoos and aquaria (Burghardt and Layne 1995). In this Anthropocene epoch, where more species are at risk each year (Barnosky 2011) and conservation projects are increasing *ex situ* efforts to protect them, we need to understand the relationship between social environment and behaviour across a greater diversity of social taxa.

Future research directions

There are a number of research directions that still need examination to fully understand and interpret the findings uncovered in this thesis. Below is a brief list of topics that warrant further investigation.

- 1) *Fitness consequences of social situations and behavioural traits* – The findings of my thesis would greatly benefit from understanding the costs and benefits of a variety of social situations *E. striolata* are exposed to (e.g., dynamics within litters, impact of associating with parents, interactions between unrelated conspecifics and juveniles, etc.). Furthermore, understanding how behavioural traits are linked to individual fitness within this species is critical to fully understand the impacts of early social environment.
- 2) *Stress, social environment, and behavioural development* - Costly social environments can increase individual stress, and this, in turn, may be a mechanism behind behavioural changes (Pryce et al. 2002). Understanding the link between physiological stress, social environment, and behaviour would help understanding the mechanism behind my thesis results. Physiological stress during development influences animal social networks

(Boogert et al. 2014), behavioural traits (Barnard et al. 1993; Kaiser and Sachser 2005; Naguib et al. 2011), and learning ability (Burghardt 2013; Crino et al. 2014).

Quantifying glucocorticoids levels, a product that is produced during activation of the hypothalamic-pituitary-adrenal axis after encountering a stressor (Sapolsky 2000; Moore and Jessop 2003), is one of the most commonly-used indicators for physiological stress. The main glucocorticoid measured in reptiles is corticosterone (Moore and Jessop 2003), and chronically-elevated levels of corticosterone can decrease individual growth rate, reproductive success, and survival (Morici et al. 1997; Moore and Jessop 2003). Field studies could assess *E. striolata* stress levels, and relate them to their social network position to identify particular aspects of *E. striolata* sociality that may be costly. Also, laboratory experiments that either - (1) manipulate developmental social environment, measure stress, and behavioural traits; or (2) alter lizard stress levels and then quantify behavioural traits - could elucidate if physiological stress is the mechanism behind behavioural change.

- 3) *Consequences of sociality across the Egernia group* – The *Egernia* group of lizards contains species across the full spectrum of sociality. My thesis was restricted to assessing the behavioural consequences of social developmental environment in *E. striolata*, a facultatively, social species. Social developmental environment may affect species with a different social system in another way. This unique model system allows a rigorous framework to investigate this.
- 4) *Kin and Parental influence on behavioural development* – I was logistically unable to consider parental or kin effects on behavioural development within my thesis, but the most common social group of wild *E. striolata* is parents with offspring (Bonnett 1999; Duckett et al. 2012). Including parents in our social treatments was not logistically feasible because adult *Egernia* sp. are known to be highly aggressive towards juveniles and infanticide has been reported in multiple species (Lanham and Bull 2000; Post 2000; O'Connor and Shine 2004). There are also instances where captive females eat their own offspring (*E. stokesii*, Lanham and Bull 2000; *E. striolata*, Riley pers. obs. 2015) and young lizards have fewer options for escape in a captive environment. Thus, due to these ethical and logistical considerations, our study was restricted to social groups consisting of juveniles. Another experimental limitation of our research was that the social rearing treatment within our study consisted of two unrelated juveniles, which potentially contrasts with social groups of *E. striolata* within the wild because they typically consist of kin (Bonnett 1999; Duckett et al. 2012). This assumption may have been incorrect, yet during development, we observed similar social interactions within our social pairs as have been observed in litters of closely-related *Egernia* spp. in

previous studies (*E. saxatilis*, O'Connor and Shine 2004; *E. whitii*, While and Wapstra 2008) so I assert that the social rearing environment within our study was comparable to that within wild populations of *E. striolata*. That being said, studies that investigate the influence of kin or parental effects on *E. striolata* behavioural development may find results that differ from this research. Future studies could be undertaken in the laboratory, but another potential follow-up experiment could examine behavioural differences between wild individuals that vary in their social behaviour (e.g., spend more or less of their time in social groups).

Juvenile *Egernia* group spp. benefit from the presence of their parents by gaining protection from predators and unfamiliar conspecifics, and increased access to resources (e.g., thermoregulation, prey, crevice sites; O'Connor and Shine 2004; Langkilde et al. 2007; Sinn et al. 2008). Thus, one may also expect there could be parental effects on offspring behavioural traits, social tendencies, as well as individual and social learning ability. There may also be benefits from associating with kin (e.g., siblings or aunts) across development (Hamilton 1964). In mammals and birds with obligate sociality, parental care (e.g., weaning date, grooming, food provisioning) often greatly affects behavioural development (Kaiser and Sachser 2005; Rilling and Young 2014). Thus, it is important to investigate the effects the presence of parents and kin may have on the behavioural development of tree skinks, other *Egernia* group spp, and other reptiles wherein this relationship has yet to be investigated.

5) *Asynchronous birth and divergence of behavioural traits* – Asynchronous birth is found in numerous animals, including the *Egernia* group (Chapple 2003; While and Wapstra 2008). As it has evolved independently in multiple taxa, asynchronous birth is thought to be adaptive. Within asynchronously born litters, dominance hierarchies commonly form and an individual's rank within the litter affects juvenile growth rate, survival, and behaviour (Hahn 1981; While and Wapstra 2008; Mainwaring and Hartley 2013). Thus, this size-hierarchy, because it can affect parental and offspring fitness, is the basis of many of the hypotheses aimed at explaining birth asynchrony (e.g., sibling rivalry hypothesis, Hahn 1981; insurance hypothesis, Forbes et al. 1997; dietary diversity hypothesis, Magrath 1989; peak load reduction hypothesis, Hébert and McNeil 1999, etc.). To date, none of these numerous hypotheses have found unequivocal support. The *Egernia* group provides an ideal model system for investigating the adaptive nature of asynchronous birth, because lizards can be manipulated in experiments and behaviours are easily quantifiable.

6) *Impact of individual behaviour on social associations and social systems* – It would be interesting to assess how individual behavioural traits may influence individual- and

population-level variation in social associations. Our understanding of the social system of *E. striolata* is derived from mainly anecdotal and short-term observations (Bustard 1970; Swanson 1976; Ehmann 1992; Duckett et al. 2012). Long-term population monitoring could give us insights into the stability of tree skink social groups, as well as consistency in individual social behaviours in the wild. Additionally, if paired with behavioural assays in the field, it could be a valuable long-term snapshot into the social system of *E. striolata*, and the factors, particularly behavioural traits, that may influence it.

Conclusion

For many reptiles, social behaviour begins as an embryo (Doody et al. 2012; Ferrara et al. 2013), continues throughout their life, and is likely a major determinant of individual fitness (Graves and Duvall 1995; Fox et al. 2003; Burghardt 2013). We need to embrace recent research that demonstrates the diversity of reptile sociality head-on, and realise how our current lack of knowledge about reptilian social systems limits their conservation, influences interpretations of reptile research, and impacts our scientific biases (Shine and Bonnet 2000). As I commenced this thesis, there was not much known about the behavioural consequences of sociality in *E. striolata*, and generally in reptiles. My research has shown that a tree skink's social environment during development affects aspects of their behavioural development. My findings are also evidence that isolation rearing does not consistently result in negative impacts on behaviour across all social taxa, and instead, that *E. striolata* behavioural development responds flexibly, and potentially adaptively, to the social environment in which they are raised. We need to target our efforts to address our lack of knowledge about reptile sociality, and embrace the great potential reptiles have as model systems for increasing our knowledge of the occurrence, causes, and consequences of sociality across taxa. My thesis addressed a wide range of questions about how early social environment impacts behavioural development in the family-living tree skink, *Egernia striolata*. It also generated novel directions for future research that hold great potential for advancing the study of sociality within the field of animal behaviour.

Photo credit: Mitchell Francis



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CHAPTER I

Video S1. Behavioural assay procedures. Videos are sped up 2x to increase the pace of lizard behaviours for viewing and edited to highlight the important behaviours scored in our study. Currently accessible here: <https://youtu.be/JIJbnu6mhOc>

CHAPTER II

Supplementary video 1. Correct demonstration of our spatial learning task for *Egernia striolata*. Currently accessible here: <https://youtu.be/-jrQpk7KiH0>

CHAPTER III

Video S1. *E. striolata* attempting the (a) instrumental, (b) association and (c) reversal task. On the left are juveniles that are attempting the task after viewing a demonstrator performing the same task correctly (social learning treatment), and on the right are juveniles attempting the task after simply viewing an adult female (individual learning treatment). Both juveniles perform the instrumental (removing the yellow lid off the dish to access food), and the association task (accessing food from under the blue lid) correctly. Only the juvenile on the left performs the reversal task correctly (accessing food from under the white lid). Videos are sped up 4x, and edited to contain the successful task performance. Currently accessible here: <https://youtu.be/qS5juqqHiew>

Conference presentations

- **Riley JL**, Guidou C, Fryns C, Mourier J, Leu S, Noble D, Bryne R, Whiting M. Late bloomers: early experience impacts tree skink social behaviour. Australian Society of Herpetologists, Fairbridge, Western Australia, Australia, July 20-23rd 2017.
- **Riley JL**, Noble DWA, Byrne RW, Whiting MJ. Does social environment affect behavioural development in a social lizard? The 8th World Congress of Herpetology, Tonglu, China, August 15 – 21st 2016.
- **Riley JL**, Noble DWA, Byrne RW, Whiting MJ. Does social environment affect behavioural development in a social lizard? The 43rd Annual Conference of the Australasian Society for the Study of Animal Behaviour (ASSAB), Katoomba, New South Wales, July 5-8th 2016. *Awarded best student talk*.
- **Riley JL**, Noble DWA, Byrne RW, Whiting MJ. Skinks and ladders: does social environment impact lizard learning? Australian Society of Herpetologists, Launceston, Tasmania, Australia, February 15-19th 2015. *Honourable mention in best student talk competition*.
- **Riley JL**, Noble DWA, Byrne RW, Whiting MJ. Early social environment affects development of behavioural traits in a lizard. Behaviour 2015, Cairns, Queensland, Australia, August 9-15th 2015.
- **Riley JL**, Noble DWA, Whiting MJ. The buddy system: effect of social environment on development of behavioural traits in lizards. Australian Society of Herpetologists, Elidon, Victoria, Australia, January 21-24th 2015.

Other presentations

- **Riley, JL**, Noble DWA, Byrne RW, Whiting MJ. Tree Skink (*Egernia striolata*) sociality (2013-2015). *Egernia* Workshop, Hobart, Tasmania, Australia, February 14th 2015.

Media appearances

- Interview on ABC Melbourne, Saturday Breakfasts (7 Jan 2017) with Jacinta Parsons
- Interview on ABC Mornings (4 Jan 2017) with Mark Fennell
Link: <http://whitinglab.com/?p=5085>
- Featured in a mini-documentary by In-situ Science: “Lizard Societies”
Link: <https://insituscience.com/2016/06/10/lizard-societies-julia-riley-from-macquarie-university/>

Appendix 3: Articles unrelated to my thesis published during my candidature

Peer-reviewed publications

Riley JL, Baxter-Gilbert JH, Litzgus JD. 2017. A comparison of three external transmitter attachment methods for snakes. *Wildlife Soc Bull.* doi:10.1002/wsb.748

Davy CM, Mastromonaco GF, Riley JL, Baxter-Gilbert JH, Mayberry HW, Willis CKR. 2016. Physiological carry-over effects in bats exposed to an emerging pathogen implicate an overlooked potential driver of the extinction vortex. *Conserv Biol.* doi:10.1111/cobi.12841

Riley JL, Baxter-Gilbert JH, Guiglielmo CG, Litzgus JD. 2016. Scanning snakes to measure condition: a validation of quantitative magnetic resonance. *J Herpetol.* 50:627-632.

Baxter-Gilbert JH, Riley JL, Neufeld C, Lesbarrères D, Litzgus JD. 2015. Road mortality responsible for billions for pollinating insect deaths annually. *J Insect Conserv.* 19:1029-1035.

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Riley JL, Freedberg S, Litzgus JD. 2014. Incubation temperature in the wild influences hatchling phenotype of two freshwater turtle species. *Evol Ecol Res.* 16:397-416.

Riley JL, Tattersall G, Litzgus JD. 2014. Potential sources of intra-population variation in the overwintering strategy of painted turtle (*Chrysemys picta*) hatchlings. *J Exp Biol.* 217:4174-4183.

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Baxter-Gilbert JH, Riley JL, Lesbarrères D, Litzgus JD. 2014. A novel technique to measure chronic levels of corticosterone in turtles living around a major roadway. *Conserv Physiol.* 2:1-9.

Riley JL, Litzgus JD. 2014. Cues used by predators to detect freshwater turtle nests persist late into incubation. *Can Field Nat.* 128:179-188.

Natural history notes

Baxter-Gilbert JH, Riley JL. 2015. *Intellagama lesuerii lesuerii* (Eastern Water Dragon) Trifid Tail. *Herpetol Rev.* 46:433-434.

Baxter-Gilbert JH, Riley JL, Moldowan PD, Litzgus JD. 2015. *Sistrurus catenatus catenatus* (Eastern Massasauga Rattlesnake) and *Nerodia sipedon sipedon* (Northern Watersnake) Gut Contents and Foreign Object. *Herpetol Rev.* 46:107.

Appendix 4: Animal ethics approvals and scientific license



ANIMAL RESEARCH AUTHORITY (ARA)

AEC Reference No.: 2013/031

Date of Expiry: 17 October 2014

Full Approval Duration: 18 October 2013 to 17 October 2016 (36 Months)

This ARA remains in force until the Date of Expiry (unless suspended, cancelled or surrendered) and will only be renewed upon receipt of a satisfactory Progress Report before expiry (see Approval email for submission details).

Principal Investigator:
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Associate Investigators:
Daniel Noble 0430 290 053

In case of emergency, please contact:
the Principal Investigator / Associate Investigator named above
Animal Welfare Officer - 9850 7758 / 0439 497 383, or Manager, Fauna Park - 9850 4109 / 0425 213 420

The above-named are authorised by MACQUARIE UNIVERSITY ANIMAL ETHICS COMMITTEE to conduct the following research:

Title of the project: Evolution of social learning in a model lizard system

Purpose: 4 - Research: Human or Animal Biology

Aims: To uncover the possible early evolution and complex relationship between cognition and sociality by integrating cognitive ability, and lizards' social system within a multi-species evolutionary framework

Surgical Procedures category: 1 - Observation involving Minor Interference

All procedures must be performed as per the AEC-approved protocol, unless stated otherwise by the AEC and/or AWO.

Maximum numbers approved (for the Full Approval Duration):

Species	Strain	Age	Total	Source
27 - Lizards	Liopholis inornata	Adult/sub-adults	400	Wild
27 - Lizards	Liopholis inornata	Adult/sub-adults (retained for social learning exp.)	48 (A subset of the above 400)	Wild
27 - Lizards	Liopholis	Adult/sub-adults	400	Wild
27 - Lizards	Liopholis	Adult/sub-adults (retained for social learning exp.)	48 (A subset of the above 400)	Wild
27 - Lizards	Bellatorias major	Adult/sub-adults	400	Wild
27 - Lizards	Bellatorias major	Adult/sub-adults (retained for social learning exp.)	48 (A subset of the above 400)	Wild
27 - Lizards	Egernia saxatilis	Adult/sub-adults	400	Wild
27 - Lizards	Egernia saxatilis	Adult/sub-adults (retained for social learning exp.)	48 (A subset of the above 400)	Wild
27 - Lizards	Egernia striolata	Adult/sub-adults	400	Wild
27 - Lizards	Egernia striolata	Adult/sub-adults (retained for social learning exp.)	96 (A subset of the above 400)	Wild
27 - Lizards	Lissolepis luctuosa	Adult/sub-adults	400	Wild
27 - Lizards	Lissolepis luctuosa	Adult/sub-adults (retained for social learning exp.)	48 (A subset of the above 400)	Wild
27 - Lizards	Egernia kingii	Adult/sub-adults	400	Wild
27 - Lizards	Egernia kingii	Adult/sub-adults (retained for social learning exp.)	48 (A subset of the above 400)	Wild
TOTAL			2,800	

Location of research:

Location	Full street address
Fauna Park	209 Culloden Road, Macquarie University, NSW 2109
Field sites for animal collection	List to be submitted

Amendments approved by the AEC since initial approval: N/A

Conditions of Approval: N/A

Being animal research carried out in accordance with the Code of Practice for a recognised research purpose and in connection with animals (other than exempt animals) that have been obtained from the holder of an animal suppliers licence.

Professor Mark Connor (Chair, Animal Ethics Committee)

Approval Date: 17 October 2013

Adapted from Form C (issued under part IV of the Animal Research Act, 1985)

ANIMAL RESEARCH AUTHORITY (ARA)

AEC Reference No.: 2013/039

Date of Expiry: 9 December 2014

Full Approval Duration: 10 December 2013 to 9 December 2016 (36 Months)

This ARA remains in force until the Date of Expiry (unless suspended, cancelled or surrendered) and will only be renewed upon receipt of a satisfactory Progress Report before expiry (see Approval email for submission details).

Principal Investigator:
Dr Martin Whiting
Biological Sciences
Macquarie University, NSW 2109
martin.whiting@mq.edu.au
0402 752 229

Associate Investigators:
Daniel Noble 0430290053

In case of emergency, please contact:

the Principal Investigator / Associate Investigator named above

Animal Welfare Officer - 9850 7758 / 0439 497 383, or Manager, Fauna Park - 9850 4109 / 0425 213 420

The above-named are authorised by MACQUARIE UNIVERSITY ANIMAL ETHICS COMMITTEE to conduct the following research:

Title of the project: Kin recognition and influence of social environment on sociality and cognition in the lizard *Egernia striolata*

Purpose: 4 - Research: Human or Animal Biology

Aims: 1. To test for kin selection and phenotype matching, a key tenet of sociality, in *E. striolata*;
2. To understand the role of the social environment in the development of social cognition.

Surgical Procedures category: 3 - Minor Conscious Intervention

All procedures must be performed as per the AEC-approved protocol, unless stated otherwise by the AEC and/or AWO.

Maximum numbers approved (for the Full Approval Duration):

Species	Strain	Age/Sex	Total	Supplier/Source
27	<i>Egernia striolata</i>	Adult Females (A subset of 96 individuals from ARA 2013/031)	42	Wild
27	<i>Egernia striolata</i>	Offspring	168 - 320	Captive born
		TOTAL	362	

Location of research:

Location	Full street address
Fauna Park	209 Culloden Rd, Macquarie University, NSW 2109
Field sites for animal collection	Little Para River – North of Para Wirra recreation park, Birds Australia Gluepot Reserve, Mt Remarkable National Park – especially Mambray Creek Area, SA

Amendments approved by the AEC since initial approval: N/A

Conditions of Approval: N/A

Being animal research carried out in accordance with the Code of Practice for a recognised research purpose and in connection with animals (other than exempt animals) that have been obtained from the holder of an animal suppliers licence.

Professor Mark Connor (Chair, Animal Ethics Committee)

Approval Date: 5 December 2013



SCIENTIFIC LICENCE

NATIONAL PARKS & WILDLIFE ACT, 1974
Section 132c

Name and postal address of principal licensee

Dr Martin Whiting
Macquarie University
209 Culloden Rd
MARSFIELD NSW 2122

Nominated premises (where appropriate)

Your licence number is: SL101264

This licence is valid from: 18 November 2013

This licence will expire on: 30 September 2016

Additional authorisations:

Project Title: Evolution of social learning and sociality in a model lizard system

This licence authorises the following activities: Harm, trap, capture, measure, collect tissue samples from, mark, hold up to 96 individuals for captive trials, release, euthanase *Egernia striolata*.

This licence authorises the principal licensee and any associates named in **Attachment A** to conduct those activities authorised above, to those species, communities or materials listed in **Attachment B**, at the locations specified in **Attachment C** of this licence.

This licence also authorises the principal licensee to import or export those species, or materials listed in **Attachment B** interstate as provided under s126 of the *National Parks and Wildlife Act 1974* (NPW Act) and to conduct research on park under clause 23 of the *National Parks and Wildlife Regulation 2009* (NPW Reg), where this forms part of a project approved by a delegated officer of OEH.

This licence is issued subject to the provisions of NPW Act, NPW Reg, the general conditions listed below, any special conditions as may be notified in writing to the licensee by the Director General of the Department of Premier and Cabinet ("Director General") or a 'delegated officer' of OEH ("delegated officer") and the OEH "Scientific Licensing" policy.

Signature of Delegated Officer

Date: 18 November 2013

Signature of Principal Licensee*

Date:...

* This licence is not valid unless it is signed by the principal licensee. By signing this licence the licensee agrees that they have read, understood and agree to comply with all of the conditions listed on the licence.

LICENCE CONDITIONS

Specific

- a) Work on NPWS estate may only be undertaken with the prior written approval of the relevant local area office.
- b) The licensee must comply with any restrictions or limitations imposed by the area office.
- c) Fauna must be managed in accordance with a current animal care and ethics approval.
- d) Spread collection sites out over as wide an area as possible.
- e) A maximum of 96 individuals may be taken into captivity.
- f) Only animals that have been in captivity for less than three months, have been kept in quarantine conditions and are given a health check by a veterinarian may be released under this licence.
- g) Should an animal be suitable for release in accordance with condition (f), the release must be at the site from which they were originally captured.
- h) The licensee must contact the WLMU to discuss alternative disposal methods if required.

General

1. Only the person/s named on the licence, or authorised to operate under the terms and conditions of the licence, may undertake the work. This licence is not transferable except with written confirmation from Wildlife Licensing & Management Unit ("WLMU").
2. The principal licensee may vary the associated parties authorised during the term of the licence only by maintaining a signed and dated register of the associates. A copy of the register must be provided to WLMU at renewal or on request by an authorised officer.
3. The licensee must carry this licence at all times whilst work is being undertaken in the field. Where multiple parties are listed, photocopies will suffice provided some other proof of identity can be provided e.g. Driver's licence.
4. The licensee must provide other parties authorised to conduct the specified activities with a copy of this licence.
5. The licensee must obtain the permission of the owner, manager or occupier of lands upon which research is conducted (for persons working on NPWS lands see also conditions 18-20).
6. Specimens or samples taken under this licence must not be sold, bartered, given, lent or promised to others without the prior written approval of the Director General or delegate.
7. Collections or research shall, as far as is possible, be carried out away from the view of the public.
8. The licensee shall indemnify and keep indemnified, so far as the law allows, Her Majesty Queen Elizabeth II, the Minister administering the National Parks and Wildlife Act 1974, the Government of New South Wales, the Director General of the Department of Premier and Cabinet, and the National Parks and Wildlife Service and its servants, agents or contractors (herein jointly and severally referred to as "OEH"), FROM AND AGAINST all lawful suits, claims, demands, proceedings, costs, (including solicitor - client costs) and expenses of any nature whatsoever which the OEH may suffer or incur in connection with loss of life, personal injury or damage to property from an occurrence in connection with any land, premises, vehicle or other mode of conveyance or other item under the care, control or management of the OEH, and arising either directly or indirectly from any negligent or wrongful act or omission of the licensee in the course of an operation or activities pursuant to the licence or otherwise.

Reporting requirements

9. The licensee undertaking survey, research or other biodiversity assessment works must provide a full report of the work carried out under this licence in the standard OEH excel format available at <http://www.environment.nsw.gov.au/resources/nature/scientificLicenceDataSheet.xls>
10. The licensee must ensure that data submitted to OEH in the above format is accurate to **not less than 100m** (without suitable justification).
11. The licensee must submit reports online using a secure login acquired from OEH Wildlife Data Unit. Contact atlas@environment.nsw.gov.au for account details and guidelines.
12. Licensees undertaking work that cannot be supplied in the above format must provide a report to the OEH specifying:
 - a. Title of the project
 - b. A precise description of the locality including geographic coordinates where practical
 - c. Results of the project
13. The licensee may also be required to complete a metadata proforma for works on NPWS estate.
14. Licensees undertaking permanent/semi-permanent marking, banding or tagging must provide marking details (e.g. tag number, date, location, species) to OEH with any renewal application.
15. The licensee must provide a copy of any final report and/or any scientific papers relating to this work to the Director General (marked "attention Wildlife Licensing & Management Unit") when the study is completed.

Additional reporting requirements for consultants

16. Licences issued to consultants and consulting companies for survey and assessment purposes are required to provide a list of the sites where work was conducted and a list of the reports produced. A copy of these reports may be requested.
17. Reports in accordance with licence conditions 9. to 16. must be provided annually, from the "valid from" date of the licence.

Projects undertaken on NPWS managed land

18. The licensee may only undertake works in NPWS managed lands with the prior written approval of the relevant Area Manager and comply with any imposed restrictions or conditions.
19. The licensee must maintain regular contact with the NPWS Area office throughout the project as park management activities and other events may affect access to research locations. Access to reserves may be restricted during management activities or other while the reserve is closed for other reasons.
20. The licensee must only use vehicles on public roads unless otherwise approved by an authorised officer.

It is an offence under the *National Parks & Wildlife Regulation 2009* to breach any of the conditions of this licence, issue any false receipt, make a false entry in any record, or otherwise keep a false record or provide false or misleading records or information (Maximum Penalty \$3300).

Records, notifications and inquiries should be directed to:

Wildlife Licensing and Management Unit
Office of Environment and Heritage
PO Box 1967
Hurstville NSW 1481

Phone: 02 9585 6406
Fax: 02 9585 6401
Email: wildlife.licensing@environment.nsw.gov.au

Additional Information for licence holders

It is the licence holder's responsibility to ensure they are familiar with any other relevant statutory or regulatory provisions relevant to this licence such as the *National Parks and Wildlife Regulation 2009* particularly with respect to activities undertaken on NPWS managed lands, the *Firearms Act 1999*, any local council, building and health requirements and codes of practice under the *Prevention of Cruelty to Animals Act 1979* as well as specific requirements under the *Animal Research Act 1985*. On the expiration of your permit the onus is on you to renew. While OEHL forwards renewal notices to permit holders, it will not be responsible for the non-receipt of such a notice.

It is the licensee's responsibility to inform themselves of any likely hazards and ensure that appropriate risk management and emergency procedures are developed and in place for works undertaken on NPWS managed lands. The risk management and emergency procedures will also extend to cover OEHL staff and any other third parties which may be impacted by the licensee's works. OEHL accepts no responsibility for any event which results in the licensee suffering any loss. The licensee will be held liable for any damages resulting from their works which have impacted on OEHL staff or any other third party.

Attachment A

Other parties

In addition to the principal licensee identified above, the following parties are also authorised under this licence:

Title	Name
Mr	Daniel Noble
Dr	Geoff White



**Office of
Environment & Heritage**
NSW National Parks & Wildlife Service



NATIONAL PARKS & WILDLIFE ACT, 1974
SECTION 132c

Attachment B

Licence Class

Class Name	Class Start Date
Research	18/11/2013

Focus of work

This project authorises the licensee to Harm, Pick, collect or otherwise interact with the following species, communities or materials as described on this licence in the listed quantities:

Species Type	Family	Genus	Species	Subspecies	Species Code	Common Name	Target Parts	Units	Qty
FA	Scincidae	Egernia	striolata		2429	TREE-CREVICE SKINK	Individuals		400



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Attachment C

Project location

This project is authorised in the following areas:

NPWS Estate

Tenure Type	Branch	Region	Area	Park	Karst Area
NPWS Estate	Western	Northern Plains	Baradine	Pilliga Nature Reserve	

Other

Tenure Type	State Forests	CMA Region	LGA	Lot Sec DP	Marine Park	Other Location
Other						Outcrops in private land surrounding Wagga Wagga, Albury, Cowra Region, Lachlan catchment



**Office of
Environment & Heritage**
NSW National Parks & Wildlife Service

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