

Isolation rearing does not constrain social plasticity in a family-living lizard

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1 Isolation rearing does not constrain social plasticity in a family-living lizard

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3 Julia L. Riley^{1*}, Côme Guidou¹, Caroline Fryns¹, Johann Mourier^{1,2}, Stephan T.

4 Leu^{1,3}, Daniel W.A. Noble⁴, Richard W. Byrne⁵, and Martin J. Whiting¹

5

6 ¹ Department of Biological Sciences, Macquarie University, Sydney, New South

7 Wales, Australia

8 ² CORAIL, EPHE, PSL Research University, UPVD, CNRS, USR 3278, CRIOBE,

9 66360 Perpignan, France

10 ³ School of Biological Sciences, Flinders University, Adelaide, South Australia,

11 Australia

12 ⁴ School of Biological, Earth, and Environmental Sciences, University of New South

13 Wales, Kensington, New South Wales, Australia

14 ⁵ School of Psychology and Neuroscience, University of St. Andrews, St. Andrews,

15 Fife, United Kingdom □

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17 *Corresponding author: julia.riley87@gmail.com

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3 **19 LAY SUMMARY**
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5 20 Loner lizards can become savvy socialites. An animal's social experience while
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7 21 growing up often influences how they interact socially, and it may also constrain their
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9 22 ability to adapt to dynamic social situations. Yet, we find that in the tree skink, a
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11 23 family-living lizard, social plasticity is not limited by their social experience during
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14 24 development. The tree skink has a variable social system, which may enable it to
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16 25 adapt to dynamic social situations.
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21 **27 TITLE**
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23 28 Isolation rearing does not constrain social plasticity in a family-living lizard
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27 **30 ABBREVIATED TITLE**
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29 31 Social plasticity is unaffected by early social experience
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33 **33 ABSTRACT**
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35 34 An animal's social environment can be both dynamic and complex. Thus, social
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37 35 species often garner fitness benefits through being plastic in their social behavior.
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39 36 Yet, social plasticity can be constrained by an individual's experience. We examined
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41 37 the influence of early social environment on social behavior in the tree skink (*Egernia*
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43 38 *striolata*), a family-living lizard. In the first phase of this study, we reared juveniles in
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45 39 two different social environments for 1.5 years: either in isolation or in unrelated
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47 40 pairs. We quantified each lizard's sociability at four-month intervals using a
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49 41 standardized laboratory assay, and found that isolated lizards were more sociable,
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51 42 spending the assay closer to an adult female, than socially-reared lizards. In the
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53 43 second phase of this study (at the end of 1.5 years), we released all lizards into a semi-
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3 44 natural environment, observed their associations, and used social network analysis to
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5 45 quantify social behavior. During the initial six weeks post-release, we detected no
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7 46 differences in social behavior between rearing treatments. However, during the
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9 47 following six months differences emerged. Isolated lizards were more homogeneous
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11 48 in the strength of their associations than socially-reared lizards. Also, at first, isolated
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13 49 lizards associated more strongly than socially-reared lizards. Over time, isolated
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15 50 lizard associations became weaker and involved fewer lizards. In contrast, the level
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17 51 and number of associations of socially-reared lizards were stable over time. Our
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19 52 findings suggest that early experience influences tree skink social behavior but does
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21 53 not constrain social plasticity: isolation rearing did not limit their ability to respond to
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23 54 a novel social environment.
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30 56 *Key words:* aggregation, developmental environment, plasticity, social competence,
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32 57 social network analysis, reptile
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3 59 **INTRODUCTION**
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5 60 Social associations are influenced by resource availability, predation risk, mating
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7 61 system, parental care, and an individual's age and experience (Schutz et al. 2007;
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9 62 Ward and Webster 2016). These factors can interact in complex ways resulting in a
10
11 63 dynamic social environment that is unpredictable, because it results from interactions
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13 64 between many individuals responding to inconstant environmental cues (Taborsky
14
15 65 and Oliveira 2012). A social-living individual needs to constantly adjust its behavior
16
17 66 in response to changes in their environment due to social and ecological factors, and
18
19 67 this ability impacts their fitness (social plasticity; Stacey and Bock 1978; Oliveira
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21 68 2012, Montiglio et al. 2017; Neelon and Höbel 2017). It is therefore expected that
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23 69 individuals of social species will be highly plastic in their social behavior and vary
24
25 70 their responses across social contexts to maximize individual fitness (termed 'social
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27 71 competence'; Taborsky and Oliveira 2012).
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32 The type and extent of social experience individuals are exposed to affects
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34 73 how they perceive, interpret, and act in social situations (Scott 1962; Taborsky and
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36 74 Oliveira 2012; Taborsky 2016; Bølting and von Engelhardt 2017). For example,
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38 75 isolation rearing negatively affects appropriate social behavior in mammals (Harlow
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40 76 et al. 1965; Toth et al. 2011), birds (Baron and Kish 1960), fishes (Hesse and
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42 77 Thünken 2014), and invertebrates (Liedtke and Scheider 2017; Schausberger 2017).
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45 78 To date, research investigating how early social experience affects social behavior has
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47 79 focused on obligate social animals with required parental care (e.g., mammals and
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49 80 birds; Baron and Kish 1960; Harlow et al. 1965; Mitchell et al. 1966; Varty et al.
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51 81 2000). For example, Harlow's research on rhesus macaques (*Macaca mulatta*) in the
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53 82 1960s often dominates our understanding of the impact social isolation can have on
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55 83 development, and may guide expectations that isolation severely negatively impacts
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3 84 an individual's behavioral development (Harlow et al. 1965; Mitchell et al. 1966).
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5 85 This focus has largely neglected the full spectrum of sociality, which includes species
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7 86 with only occasional interactions (e.g., interactions while defending territories or
8
9 87 during mating) or those that form seasonal aggregations (Ward and Webster 2016).
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11 88 Recently, however, studies have begun to investigate the impact of social
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13 89 environment on behavioral development in solitary spiders with a transient social life-
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15 90 stage (*Agelena labyrinthica*; Lesne et al. 2016), and in squamate species for which
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17 91 social organization has not been studied in detail (Ballen et al. 2014; Aubret et al.
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19 92 2016; Hoss et al. 2015).

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23 93 Squamate reptiles as a group have traditionally been viewed as relatively
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25 94 asocial (Doody et al. 2012). Yet, there is evidence that social environment can
26
27 95 influence reptile social behavior. For example, hatchling veiled chameleons
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29 96 (*Chameleo calyptratus*) reared in isolation are more submissive during conspecific
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31 97 interactions than socially-reared hatchlings (Ballen et al. 2014). Also, hatchling
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33 98 viperine water snakes (*Natrix maura*) incubated alone, versus in contact with other
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35 99 eggs, are less aggregative (Aubret et al. 2016), and depriving neonate cottonmouths
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37 100 (*Agkistrodon piscivorus*) of maternal attendance post-birth reduces their tendency to
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39 101 associate with conspecifics (Hoss et al. 2015). These studies suggest that the
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41 102 relationship between social experience and social competence found in other taxa
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43 103 might also apply to squamate reptiles; however limited research on this topic prevents
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45 104 us from making generalizations.

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49 105 Recent evidence suggests that sociality in lizards and snakes is much more
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51 106 common and varied than previously believed (Whiting and While 2017). Phylogenetic
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53 107 analysis shows that stable aggregations have evolved multiple times in squamates,
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55 108 and of these aggregations a small proportion live in stable family groups (Gardner et
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3 109 al. 2015). The tree skink (*Egernia striolata*) aggregates within tree hollows or
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5 110 crevices, and cracks in rocks (Cogger 2014). This species can be found alone, or
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7 111 within groups consisting of adult pairs with or without offspring, or only of juveniles
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9 112 (Bonnett 1999; Duckett et al. 2012). Group size varies from 2-10 individuals, and
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11 113 there is within- and between-population variation in tree skink social behavior
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13 114 (Bustard 1970; Bonnett 1999; Duckett et al. 2012). This variation in group size and
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15 115 social behavior allows investigation of the influence of social environment on
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17 116 individual tree skink behavioral development and social behavior as adults, which we
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19 117 did in an experimental setting.
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23 118 We examined how the social environment during early life impacts tree skink
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25 119 social behavior. In the first phase of the study, we reared lizards within one of two
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27 120 social environments (isolation or within a pair) for 1.5 years, and quantified juvenile
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29 121 sociability with a laboratory assay. In the second phase, we released lizards into a
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31 122 semi-natural environment and recorded their association patterns over the short-
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33 123 (initial six weeks) and long-term (subsequent six months: weeks 7–34). We
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35 124 hypothesized that isolation rearing would reduce lizard social competence, and
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37 125 predicted that isolated lizards would avoid aggregating with conspecifics, as has been
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39 126 observed in other squamates, fishes, invertebrates, and mammals (Harlow et al. 1965;
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41 127 Aubret et al. 2016; Hesse and Thünken 2014; Schausberger 2017). An individual's
42
43 128 social competence is also reflected in its ability to change social behavior across
44
45 129 situations (Taborsky and Oliveira 2012). In this regard, the social environment during
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47 130 development can constrain an individual's behavioral plasticity (Harlow et al. 1965;
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49 131 Taborsky et al. 2012; Hesse and Thünken 2014). To investigate this we quantified
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51 132 consistency in an individual lizard's social behavior to examine plasticity in these
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3 133 traits, and whether consistency differed between rearing treatments and contexts
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5 134 (Aplin et al. 2015; Stamps 2015).
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10 136 **METHODS**

11 137 In this experiment, we used 66 tree skinks that were offspring from 35 females
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13 138 collected near Albury, New South Wales, Australia (35.98°S, 146.97°E). These
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15 139 offspring were from two, yearly cohorts (2014 and 2015; see supplementary materials
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17 140 for details on captive husbandry and housing). The data from the laboratory portion of
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19 141 this experiment has been previously published in Riley et al. (2017b) in which we
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21 142 quantified four behavioral traits (exploration, boldness, sociability, and aggression) of
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23 143 tree skinks throughout development. This current study aims to examine how social
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25 144 environment affects tree skink social behaviour. We re-analyzed the Riley et al.
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27 145 (2017b) sociability data (see Statistical Analyses section below) and changed our
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29 146 focus to comparing sociability between rearing treatments (isolation and social). This
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31 147 allowed us to interpret the adult social behavior of isolated and socially-reared tree
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33 148 skinks, that we quantified in semi-natural enclosures (the second and novel part of our
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35 149 study; see below), in relation to the treatment differences in sociability during the
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37 150 juvenile life-stage (Riley et al. 2017c).
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45 152 **Rearing treatment and laboratory sociability assays**

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47 153 After lizards were born (within a maximum of 12 hours) we separated them from their
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49 154 mothers and housed them individually (for dates of parturition see supplementary
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51 155 materials). After all juveniles were born each year, we conducted the first sociability
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53 156 assay (see below).
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3 157 After the first assay, we then randomly allocated juveniles into two social
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5 158 environments: isolated (housed alone; $N_{2014} = 14$ lizards and $N_{2015} = 16$ lizards), and
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7 159 social (two unrelated juveniles housed together; $N_{2014} = 14$ lizards within 7 pairs and
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9 160 $N_{2015} = 22$ lizards within 11 pairs). We split the number of offspring from each
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11 161 mother across treatments (see supplementary materials for details), but were unable to
12
13 162 sex juveniles prior to treatment allocation so we accounted for sex in our statistical
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15 163 analyses. Tree skink social groups often consist of parent(s) and offspring (Chapple
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17 164 2003), but we were unable to recreate this environment in captivity due to the risk of
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19 165 infanticide (Lanham and Bull 2000; Post 2000; O'Connor and Shine 2004; JL Riley,
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21 166 unpubl. data). The group size we used in our experiment is present in wild tree skink
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23 167 populations, because juvenile-only group size ranges from pairs to 4 individuals and
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25 168 juveniles are also observed on their own (Bonnett 1999; Michael and Cunningham
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27 169 2010; Duckett et al. 2012; JL Riley, unpubl. data).

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32 170 Once within their treatments, we assayed lizard sociability three more times:
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34 171 at ca. 5, 7, and 12 months of age (see supplementary materials for exact dates). We
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36 172 measured sociability within two batches due to space limitations of our experimental
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38 173 room (maximum of 24 lizards per batch ranging from 13 to 16 days apart; see
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40 174 supplementary materials for exact dates).

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43 175 During sociability assays we individually housed lizards in opaque, plastic
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45 176 arenas, which were separated into two compartments with a clear, Perspex[®] divider
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47 177 placed 11 cm from one end (Riley et al. 2017c; see supplementary materials for more
48
49 178 details). We first placed the focal juvenile within a shelter in the larger compartment
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51 179 and then placed an unrelated, adult female in the smaller compartment on the opposite
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53 180 side of the divider. Females were unrelated and unfamiliar to the focal lizard. We
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55 181 randomly paired females with each focal lizard, and ensured the female was different
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3 182 in each repetition of the assay (i.e., used only once/lizard). We then lifted the
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5 183 juvenile's shelter and remotely video-recorded the location of the juvenile in relation
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7 184 to the female for the next 5 h. From the video, at 10 min intervals over the full course
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9 185 of the trial, the juvenile was scored as being within one of four lateral quadrats (11 cm
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11 186 width) that sequentially reflected distances further away from the female. From these
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13 187 data, we calculated the weighted mean distance the juvenile was from the female
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15 188 across the whole trial, by multiplying the number of times in each quadrat (Q1, Q2,
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17 189 Q3, and Q4) by the mean distance the quadrat was away from the female's
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19 190 compartment (5.5 cm, 11 cm, 16.5 cm, and 22 cm, respectively) and dividing the
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21 191 product by the total number of observations ($N_{\text{obs}} = 30$). This weighted mean was
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23 192 used to quantify sociability across the first year of life; lower values reflect higher
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25 193 sociability. Due to issues with some videos (i.e., failure to record particular trials), 5
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27 194 juveniles were removed from this portion of our analysis: the final sample size of our
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29 195 laboratory sociability assay was 26 juveniles in 2014 (14 socially-reared and 12
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31 196 isolated), and 35 juveniles in 2015 (20 socially-reared and 15 isolated).
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198 **Spatial associations**

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41 199 We quantified lizard sociability within a semi-natural environment after they reached
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43 200 adulthood to assess long-term effects of rearing treatment on social associations. Tree
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45 201 skinks reach sexual maturity after ~1.5 years in captivity (JL Riley, unpubl. data). We
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47 202 used all 28 lizards reared in 2014 in this experiment (14 isolated and 14 socially-
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49 203 reared), and released them into a fenced outdoor enclosure with an area of 70 m² (10.5
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51 204 by 6.7 m) on 14 September 2015. A net surrounded the enclosure to exclude avian
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53 205 predators (Fig. S1).
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3 206 We provided 28 artificial crevices (hereafter refuges) inside the enclosure.
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5 207 This ensured that refuges were not a limited resource, thus allowing aggregation to
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7 208 depend on individual preference and not ecological factors (i.e., a limited resource).
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10 209 We placed two roofing tiles (each tile was 410 x 260 mm) on top of each other to
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12 210 form refuges (Fig. S1). These refuges were placed in four rows of seven 0.75 m apart
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14 211 and 1.25 m away from the perimeter (Fig. S1). Prior to release, we permanently
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16 212 marked all lizards with microchips (PIT tags) and visually numbered them with three
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18 213 circles of numbered cloth tape (Tesa[®], Hamburg, Germany; Fig. S1C; Olsson and
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20 214 Shine 2000; While et al. 2009a). The lizards were all released in the middle of the
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22 215 enclosure. If a lizard lost any marking tape, it was re-marked at the end of the day,
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24 216 after data collection, and immediately released back into its refuge of capture.
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27 217 We recorded lizard spatial positions within the enclosure over two time
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29 218 periods: the initial six weeks post-release (4x daily) and then the following six months
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31 219 (weeks 7- 34; twice weekly). Observers (CG and STL during the initial six weeks; CG
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33 220 and CF for the following six months) were blind to rearing treatment. Data collection
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35 221 took the same amount of time in both periods, on average 22 min (95% CI = 21, 23),
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37 222 which reflects similarity in sampling intensity and effort. Our sampling methods (see
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39 223 below) differed between six-week and six-month observations, and we quantified
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41 224 different social behaviors. Our short-term observations captured behavior across the
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43 225 daily activity period of lizards, whereas the long-term observations recorded which
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45 226 lizards were sharing refuges overnight and social associations before the start of daily
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47 227 activity.
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51 228 During the initial six weeks (14 September - 25 October 2015), we recorded
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53 229 lizard spatial position within the enclosure four times each day at 10:00, 12:00, 14:00
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55 230 and 16:00 h. We recorded locations for all lizards that we could visually observe (see
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3 231 Results for observation rates). First, we visually-scanned the entire enclosure from a
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5 232 raised tower (2.1 m tall), and then we slowly walked around the outside of the
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7 233 perimeter for a ground-level perspective thereby maximizing our ability to detect
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10 234 lizards. After the initial six weeks, we modified our protocol for the following six
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12 235 months (29 October 2015 to 29 April 2016) to focus on lizard social associations
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14 236 over-night (i.e., during shelter in refuges) rather than those during their daily activity
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16 237 period. We recorded lizard spatial positions every Monday and Friday, between
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18 238 07:00- 09:00 h, prior to the tree skink's activity period. At that time of day, lizards
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21 239 were still sheltering within refuges. During these observations we lifted each roofing
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23 240 tile, captured every lizard in the refuge to identify them from their PIT tag number
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25 241 using a PIT tag reader (lizards did not retain their identifying stickers during the six-
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27 242 month observations), and then placed them back at their site of capture. We also
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29 243 checked under water dishes and in the area between refuges for lizards. Each
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31 244 sampling period was started from a different location, and performed in a different
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33 245 pattern during each trial.
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38 247 **Statistical analyses**

39 248 *Analyses of laboratory sociability scores*

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43 249 We examined if tree skink sociability differed between rearing treatments, using a
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45 250 linear mixed effects model (LMM, *lmer* in the *lme4* R package; Bates et al. 2015; R
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47 251 Core Team 2016). In our model, we examined if the response variable, *sociability* (the
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49 252 weighted mean distance (mm) a lizard was located from an adult female during a
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51 253 trial), was affected by *rearing treatment* (isolated or social) while controlling for the
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53 254 additional fixed factors of *age* (continuous), *sex* (male or female), *cohort* (2014 or
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55 255 2015), *batch* (1 or 2), *body temperature* (continuous), and *body condition index*
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3 256 (continuous; residuals from a simple linear regression between log-transformed mass
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5 257 and snout-vent-length). Continuous fixed factors were z-transformed (mean centered
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7 258 and divided by standard deviation) before analysis, which standardizes the variables
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9
10 259 and facilitates interpretation of main effects in the presence of interactions (Schielezeth
11
12 260 2010). To control for dependencies within our data from sampling each lizard
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14 261 repeatedly we included a random intercept and slope for lizard identity across age. To
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16 262 control for repeated sampling of individuals from the same litter, we also included a
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18 263 random intercept for mother identity. We ensured that there were no influential
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20 264 outliers, no strong collinearity, and that the model assumptions of normality of
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22 265 residuals and heterogeneity of variance were met (as per Zurr et al. 2009; see
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24 266 supplementary materials for details).

27 267 We also examined the consistency of an individual's sociability and
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29 268 determined if this was affected by rearing treatment. To accomplish this we calculated
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31 269 adjusted repeatability ($R_{adj|age}$; Biro and Stamps 2015) for each treatment and the
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33 270 associated 95% confidence intervals by bootstrapping the data 1000 times with the
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35 271 *boot* function from the R package *boot* (Davison and Hinkley 1997; Canty and Ripley
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37 272 2017), while controlling for the same covariates that were within our LMMs
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39 273 (Nakagawa et al. 2010; Biro and Stamps 2015). We compared $R_{adj|age}$ between
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41 274 treatments by examining the overlap of each rearing treatment's 95% CIs.
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43 275 Repeatability ($R_{adj|age}$) theoretically ranges between 0 (individuals never express the
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45 276 same trait value over repeated measures) and 1 (individuals always express the same
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47 277 trait value over repeated measures; Nakagawa et al. 2010). Yet, in practice, the
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49 278 average repeatability observed in studies on animal behavior is 0.37 (Bell et al. 2009).
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56 280 *Social network analysis*
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3 281 Animal social network analysis is a powerful technique for quantifying association or
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5 282 interaction data (Farine and Whitehead 2015). We used social network analysis to
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7 283 quantify the associations we observed between lizards in the semi-natural enclosure.
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9 284 We considered lizards to be associating when they were at the same refuge within a
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11 285 sampling period (i.e., if 2+ lizards were located in/on the same refuge, they were
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13 286 defined as a group). Additionally, the refuges in our study were small (e.g., 410 x 260
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15 287 mm; approximately the size of two lizards), thus if lizards were sharing a refuge they
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17 288 would have been aware of each other. Association strength for each pair of lizards
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19 289 (dyad) was calculated using the half-weight association index (HWI). The HWI
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21 290 ranges between 0 (never observed in the same refuge) and 1 (always observed in the
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23 291 same refuge). It is a relative measure of association strength, which is most
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25 292 appropriately used when an entire population cannot be observed during each
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27 293 sampling period (Cairns and Schwager 1987), as is the case in our study (see Results
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29 294 for sampling rate).

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34 295 We constructed six weekly networks and six monthly networks (i.e., one for
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36 296 each of the six weeks, and one for each of the next six months) that controlled for
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38 297 lizard space use (i.e., the function included refuge number, which reflects lizard
39
40 298 location, during construction of the group-by-individual matrix; Farine 2013) to
41
42 299 ensure the associations we were describing were based on social, and not abiotic,
43
44 300 biotic, or spatial factors (Fig. 1). The edge weights in these networks were the HWI
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46 301 association strength (described above), resulting in weighted, undirected networks in
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48 302 which individuals (nodes) were connected if $HWI > 0$. Network construction and
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50 303 analysis were performed using the *asnipe* R package (Farine 2013).

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54 304 For each network (6 weekly and 6 monthly networks), we calculated three
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56 305 network metrics that quantified individual social behavior: binary degree, weighted
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3 306 degree, and the coefficient of variation (CV) of edge weights. Binary degree is the
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5 307 number of lizards the focal lizard was observed sharing a refuge with, and weighted
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7 308 degree (also termed “strength”; Whitehead 2008) is the sum of edge weights (dyadic
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10 309 HWIs) of the focal lizard (Whitehead 2008). These metrics both reflect the sociability
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12 310 of an individual and are complementary; an individual can have high numbers of
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14 311 associates with weak associations (high binary degree and low weighted degree) or, in
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16 312 contrast, a low number of strong associations (low binary degree and high weighted
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18 313 degree). The CV of edge weights is a measure of social heterogeneity (also termed
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20 314 “social differentiation” and the “clustering coefficient”; Whitehead 2008) of a focal
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22 315 lizard and quantifies variability of an individual’s relationships (Leu et al. 2016).
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24 316 High values of social heterogeneity means that relationships are variable, and that the
25
26 317 focal lizard is mainly associating strongly (i.e., preferentially) and/or weakly (i.e.,
27
28 318 avoiding) with conspecifics (Farine and Whitehead 2015). In contrast, low values of
29
30 319 social heterogeneity means that relationships are more homogeneous, and that focal
31
32 320 lizards are associating relatively evenly with conspecifics (Farine and Whitehead
33
34 321 2015).

322 323 *Temporal aspects of social relationships*

324 We used separate LMMs to determine if the observed network metrics (binary degree,
325 weighted degree, and CV of edge weights) differed between rearing treatments across
326 each time period (six weeks or six months). All LMMs included the fixed factors of
327 *time period* (week or month, respectively), *rearing treatment* (isolated or social), *sex*
328 (male or female), as well as interactions between *time period and sex* and *time period*
329 *and treatment*. If interactions were not significant (according to P_{rand} , see below) they
330 were removed and the models re-fitted. Models also included the random intercept

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3 331 and slope of lizard identity across time, and the random intercept of mother identity.
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5 332 Our observed network metric dataset was explored prior to statistical analyses to
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7 333 investigate normality, the presence of outliers, and collinearity. Additionally, the
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10 334 assumptions of normality of residuals and heterogeneity of variance were verified for
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12 335 all LMMs analyzing observed data (Zuur et al. 2009; see supplementary materials for
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14 336 details). Binary and weighted degree were $\log(x+1)$ transformed to normalize the
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16 337 data. We also wanted to examine the consistency of social metrics for each rearing
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18 338 treatment, and calculated treatment-specific $R_{adj}|time$ (weeks or months; Biro and
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20 339 Stamps 2015) using the same protocol as described above.

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23 340 Hypothesis testing for data generated from social networks is based on null
24
25 341 models constructed with data from random permutations (Farine and Whitehead
26
27 342 2015). This is necessary because of non-independence of the data from social
28
29 343 networks. Permutations were done using our group-by-individual matrix by randomly
30
31 344 swapping individuals between groups, while controlling for location because original
32
33 345 network construction already accounted for this (Farine 2013). These permutations
34
35 346 were done separately for each weekly/monthly network. Importantly, this permutation
36
37 347 technique retains the structure of our observed dataset: it maintains the same number
38
39 348 of dyads observed, number of times an individual is sighted, and number of
40
41 349 individuals recorded during each sampling period as our observed data (Whitehead
42
43 350 2008; Croft et al. 2009; Farine and Whitehead 2015). During the first six weeks, one
44
45 351 lizard (female, socially-reared) died of natural causes, and during our six-month
46
47 352 observations, predators unexpectedly infiltrated the enclosure resulting in the removal
48
49 353 of five lizards (3 isolated males, 1 isolated female, 1 socially-reared male) during the
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51 354 third month, and one lizard (socially-reared female) during the fifth month due to
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53 355 predation and/or injury. Our permutation technique took this into consideration.
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3 356 From the randomized data, we then reconstructed the networks, derived the
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5 357 same three social metrics, and conducted the same LMMs and calculations of
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7 358 $R_{adj|time}$ as we did for the observed data. Randomizations were repeated 10,000
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9 359 times, and P values (P_{rand}) for each effect were calculated by comparing model
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11 360 coefficients from the observed data to the distribution of model coefficients based on
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13 361 the randomized data (Aplin et al. 2015; Farine and Whitehead 2015; Leu et al. 2016).
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15 362 We considered effects to be significant if observed values fell outside the 95% range
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17 363 of the random coefficient distributions. We compared $R_{adj|time}$ between treatments by
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19 364 examining overlap of each rearing treatment's 95% CIs. We assessed if observed
20
21 365 $R_{adj|time}$ differed from what you would expect by chance alone by examining overlap
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23 366 between 95% CIs for observed $R_{adj|time}$ estimates and the 95% range of the random
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25 367 $R_{adj|time}$ estimates.
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32 **RESULTS**

33 **Laboratory-based sociability assays**

34
35 370 Socially-reared lizards were located further from an adult female, exhibiting lower
36
37 371 sociability, than isolated lizards (Table 1). Distance from an adult female decreased as
38
39 372 lizards aged, reflecting increasing sociability, for both isolated and socially-reared
40
41 373 lizards as they aged (Table 1). There were no batch, cohort, or sex effects on the
42
43 374 distance lizards were located from an adult female, and this distance was also not
44
45 375 related to body temperature or body condition (Table 1). $R_{adj|age}$ of sociability was
46
47 376 moderate (isolated: $R_{adj|age} = 0.427$, 95% CI = 0.216 to 0.637; social: $R_{adj|age} =$
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49 377 0.304, 95% CI = 0.000 to 0.665), and did not differ between rearing treatments (Fig.
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51 378 2A).
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381 **Social relationships in a semi-natural environment**

382 During the initial six weeks post-release, all 28 lizards were observed at least once
383 during 168 sampling periods (6 weeks x 7 days x 4 observations per day; total
384 observations of lizards = 2061). Each sampling period 48% (95% CI = 44, 52) of the
385 lizards were observed; but each week, across 28 sampling periods, 98% (95% CI =
386 95, 100) of the lizards were observed. In the following six months, all 27 lizards were
387 observed at least once during a total of 52 sampling periods (28 weeks x 2
388 observations per week; total observations = 985). Within each sampling period during
389 these six months, 98% (95% CI = 97, 100) of the lizards were observed.

390 During both time periods, mean group size was two (six week: standard
391 deviation = 0.28, range = 2 - 8; six month: standard deviation = 0.28, range = 2 - 4;
392 Fig. 1). However, individuals were also frequently observed alone (Fig. 1). Lizards
393 were observed alone in a refuge 80.4% (1340/1667) of the time during the initial six
394 weeks, and 77.3% (612/792) of the time during the next six months. Thus, our
395 network metrics and model parameter estimates that quantify social associations are
396 lower than would be expected in a species that constantly associates with other
397 individuals (Table 2).

398

399 **Temporal Variation in Social Relationships**

400 *Initial six weeks*

401 Network metrics (binary degree, weighted degree, and CV of edge weights) did not
402 differ between rearing treatments during this period (Table 2A). Sex did not affect
403 binary degree or CV of edge weights, but female lizards initially had stronger
404 associations (higher weighted degree) than males and decreased in the strength of
405 their social associations (weighted degree) more quickly over time than males (Table

1
2
3 406 2A). In general, the number and strength of associations (binary and weighted degree)
4
5 407 decreased over time, whereas social heterogeneity (CV of edge weights) increased
6
7 408 over time (Table 1A; Fig 2).

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9 409 $R_{adj|week}$ of our three social metrics were low for both rearing treatments.
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11 410 $R_{adj|week}$ did not differ between rearing treatments, and was not different from what
12
13 411 we would expect by chance alone (95% CIs from both the observed and random
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15 412 $R_{adj|week}$ overlap). Non-significance was likely due to large variation in our observed
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17 413 $R_{adj|week}$ estimates (Fig. 2B).

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22 415 **Subsequent six months**

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24 416 Initially, isolated lizards had stronger associations (higher weighted degree) than
25
26 417 socially-reared lizards (Table 2B). Over time, isolated lizards decreased in their
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28 418 number of associates (binary degree) and their associations became weaker (weighted
29
30 419 degree). In contrast, socially-reared lizards were constant in their number of
31
32 420 associates and level of associations (binary and weighted degree) over time (Table
33
34 421 2B). Social heterogeneity (CV of edge weights) was significantly lower in isolated
35
36 422 than socially-reared lizards, and social heterogeneity decreased over time in both
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38 423 rearing treatments (Table 2B; Fig. 1). None of the network metrics were affected by
39
40 424 sex (Table 2B; Fig. 1).

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43 425 $R_{adj|month}$ did not significantly differ between rearing treatments, because
44
45 426 95% CIs overlapped (Fig. 2C). $R_{adj|month}$ of binary degree, weighted degree, and CV
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47 427 of edge weights ranged between moderate to high for both rearing treatments (Fig.
48
49 428 2C). Our observed $R_{adj|month}$ did not significantly differ from what was expected by
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51 429 chance alone (95% CIs from both the observed and random $R_{adj|month}$ overlap; Fig.
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53 430 2C).

431

432 **DISCUSSION**

433 We generally found a positive relationship between isolation rearing and social
434 associations in tree skinks, in contrast to our prediction. During the juvenile life-stage,
435 isolated lizards spent laboratory trials closer to an unrelated adult female than
436 socially-reared lizards. After lizards reached adulthood we released them into a semi-
437 natural enclosure, and, after the first six weeks post-release, we found isolated lizards
438 initially associated more strongly with others than socially-reared lizards (weighted
439 degree). Isolated lizards were also more homogeneous in their social associations than
440 socially-reared lizards (i.e., lower CV of edge weights). Interestingly, over the six
441 month period, isolated lizards gradually began to associate with fewer lizards, more
442 weakly (i.e., decreased in binary and weighted degree), whereas socially-reared
443 lizards were stable in associations over time. This suggests that individuals reared in
444 isolation were able to respond flexibly to their new social environment. In further
445 support of this conclusion, our repeatability ($R_{adj|time}$) estimates for isolated lizards'
446 social behavior were low to moderate. However, repeatability did not differ between
447 rearing treatments, nor from what is expected by chance alone. This suggests that tree
448 skink social behavior is impacted by isolation rearing, and also that, regardless of
449 isolation rearing, tree skinks maintain plasticity in social behavior.

450

451 **Sociability during the juvenile life-stage**

452 Isolation rearing increased juvenile affiliation with an adult female. This finding was
453 the opposite of what we had hypothesized: that isolation would result in individuals
454 that avoid social situations and/or exhibit costly social behavior (e.g., high aggression;
455 Harlow et al. 1965; Mitchell et al. 1966; Hesse and Thünken 2014; Leidtke and

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3 456 Schneider 2017; Schausberger 2017). Our prediction was based predominately on
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5 457 studies of species that have obligate parental care like mammals and birds (Harlow et
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7 458 al. 1965; Baron and Kish 1960), where socially manipulating these species during
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9 459 development results in costly physiological (e.g., abnormal levels of sex and stress
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11 460 hormones; Kaiser and Sachser 2005; Bötting and von Engelhardt 2017) and
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13 461 behavioral changes that reduce fitness (e.g., avoidance of conspecifics, inappropriate
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15 462 mating behavior; Harlow 1965; Yu et al. 2013; Hampson and Schiwitzer 2016). Tree
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17 463 skinks' rudimentary parental care and facultative social system differs from that of
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19 464 mammals and birds. Therefore, we need to consider how our findings may influence
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21 465 tree skink fitness, while considering their social system.
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25 466 Social associations, including affiliative ones, are not always beneficial, and
26
27 467 can be costly and even fatal in some cases. For example, yellow-bellied marmots
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29 468 (*Marmota flaviventris*) that are more affiliative are more likely to die during
30
31 469 hibernation, potentially because hibernating in close proximity to other individuals
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33 470 may disrupt required thermoregulation (Yang et al. 2017). Although we did not
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35 471 directly quantify the fitness consequences of the altered social behavior we observed
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37 472 in isolation-reared tree skinks, we interpret our findings based on our knowledge of
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39 473 *Egernia*-group social systems (While et al. 2015; Whiting and While 2017). In the
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41 474 wild, unrelated adult *Egernia* spp. pose a direct mortality threat to juveniles; they are
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43 475 often highly aggressive and infanticide can occur (*E. stokesii*, Lanham and Bull 2000;
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45 476 *E. hosmeri*, Post 2000; *E. saxatilis*; O'Connor and Shine 2004; *Liopholis whitii*, Sinn
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47 477 et al. 2008; While and Wapstra 2008). In a previous study, we quantified the nature of
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49 478 the interactions that occurred between individuals that were reared in pairs (Riley et
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51 479 al. 2017c). These individuals were also used in this experiment. We found that
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53 480 socially-reared lizards experienced aggressive interactions within their social pair
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3 481 (Riley et al. 2017c), which impacted their growth rate and behavioral development.
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5 482 These aggressive interactions between juveniles may have exposed socially-reared
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7 483 lizards to a learning experience that facilitated anticipation of potentially dangerous
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9 484 interactions with conspecifics. Within our laboratory sociability assay, avoiding the
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11 485 unfamiliar, unrelated adult, as socially-reared lizards did, may be the most beneficial
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13 486 behavior to exhibit. In contrast, isolation rearing resulted in socially naïve lizards with
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15 487 greater affiliation towards unfamiliar, adult females; we hypothesize that this is a
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17 488 costly and maladaptive behavioral response.
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21 489 Further research is needed to examine this hypothesis, as well as the fitness
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23 490 and developmental implications (i.e., reproductive success, survival, and neurological
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25 491 consequences) of social rearing environment in tree skinks, and other facultatively
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27 492 social animals. Many facets of development in obligate social species are affected by
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29 493 social rearing environment, which has long-term fitness implications (Mason and
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31 494 Sponholz 1963; Hampson and Schwitzer 2016). Yet, as we show in this study, the
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33 495 impact of social environment on development of facultative social species is not
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35 496 always consistent with findings in obligate social species. For example, the cognitive
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37 497 ability of obligate social species is often hindered by isolation rearing (e.g., primates,
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39 498 Harlow et al. 1965; rats, Amitai et al. 2014). In contrast, tree skink cognitive ability
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41 499 was unaffected by social rearing environment (i.e., spatial learning ability; Riley et al.
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43 500 2017b). This lack of consistency in the relationship between social rearing
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45 501 environment, development, and long-term fitness across species differing in sociality,
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47 502 suggests each social system has unique set of selective pressures, and underscores the
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49 503 need for further research.
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56 505 **Adult social associations**
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3 506 During the initial six weeks after release into our semi-natural enclosure, we did not
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5 507 detect a difference in social behavior between rearing treatments. Lizards may have
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7 508 been habituating to, and exploring, their novel environment, as well as establishing
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9 509 social structure during this period. Our finding that number and strength of
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11 510 associations (binary and weighted degree) decreased, and social heterogeneity (CV of
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13 511 edge weights) increased over this six-week period supports the hypothesis that lizards
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15 512 were establishing social structure. Consequently, all individuals, independent of the
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17 513 experimental treatment, may have interacted with more conspecifics, and also more
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19 514 frequently, than in a population with an established social structure. Conversely, the
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21 515 social behavior we recorded over the following six months (i.e., lizards sharing
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23 516 refuges overnight) may more clearly reflect this lizard's social preferences than social
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25 517 associations during their daily activity period. During the day, lizard interactions are
26
27 518 likely to be influenced by their activity (e.g., encounters with individuals at refuges
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29 519 during foraging or other movements), and may also include social interactions that are
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31 520 short and/or agonistic instead of affiliative. Previous studies have also found that
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33 521 crevice-sharing behavior directly reflects tree skink social associations (Bonnett 1999;
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35 522 Chapple 2003; Duckett et al. 2012), and because refuges were not limited within our
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37 523 enclosure sharing a refuge overnight can be expected to reflect an individual's social
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39 524 preference.

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41 525 We found evidence that rearing treatment affected crevice-sharing behavior
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43 526 over the following six months. Isolated lizards were more homogeneous in their social
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45 527 associations, and all lizards, regardless of rearing treatment, became more
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47 528 homogeneous in their social associations over time. At the beginning of the six-month
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49 529 period, isolated lizards associated more strongly with others, in congruence with our
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51 530 laboratory behavioral assays. But, over time, isolated lizard associations weakened
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3 531 and were with fewer lizards, whereas socially-reared lizard associations were similar
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5 532 in number and frequency over time. Abnormal social rearing environments (e.g.,
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7 533 isolation, hand-rearing in captivity, etc.) have been shown to constrain social
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10 534 plasticity in a number of species (Baron and Kish 1960; Tardif et al. 1984; Taborsky
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12 535 et al. 2012; Hesse and Thünken 2014), leading to negative fitness consequences like
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14 536 reduced survival of offspring in two species of Callitrichidae (Tardif et al. 1984), as
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16 537 well as reduced longevity, offspring production, and increased infant mortality in
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18 538 some hand-reared species of endangered felids (Hampson and Schiwitzer 2016). Yet,
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21 539 in tree skinks, isolation did not constrain flexibility in their social behavior. Isolated
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23 540 lizards, after having experienced a competitive and potentially aggressive social
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25 541 environment, were able to change their crevice-sharing behavior to reflect that of
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27 542 socially-reared lizards. Retaining the ability to plastically respond to changing social
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29
30 543 contexts may be beneficial for this facultatively social lizard.

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32 544 Animal behavior has the potential to significantly contribute to conservation
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34 545 biology (Sutherland 1998; Buchholz 2007; Caro 2007). Our study highlights the
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36 546 importance of considering each target species' social system when rearing animals in
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38 547 captivity. In the case of tree skinks, isolation rearing impacted social behavior, but
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40 548 individuals reared in isolation had the highest growth rates (Riley et al 2017b). Thus,
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43 549 isolation rearing optimizes morphological development but impacts behavioral
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45 550 development. Yet, isolation rearing does not constrain social plasticity. Thus, in the
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47 551 case of tree skinks, a captive-rearing program could benefit from isolation rearing if
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49 552 paired with a 'soft-release' or 'exposure period' that exposes individual to natural
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51
52 553 social contexts that could normalize an individual's social behaviour prior to release.
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54 554 Conservation programs for Caribbean rock iguanas (*Cyclura* sp.) have utilized this
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56 555 approach: exposing captive-reared juveniles to natural predators and social situations
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3 556 within a controlled environment prior to release (Alberts 2007). Overall, knowledge
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5 557 of a target species' social system, and how social rearing environment impacts
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7 558 behavior and fitness, can directly benefit conservation.
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11 560 **Consistency in social phenotypes**

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14 561 Consistency in behavioral traits over time is the antithesis to plasticity. If behavioral
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16 562 traits are consistent across time (i.e., personality; Stamps 2015) it suggests that certain
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18 563 traits are steadily selected for over others. In a dynamic social environment, it is
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20
21 564 theorized that plasticity in social traits is adaptive (Taborsky and Oliveira 2012). Our
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23 565 findings support this hypothesis, as consistency in the social behaviors we measured
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25 566 was generally not significantly different than what we would expect from chance
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27 567 alone. The exception to this was under laboratory conditions, where tree skinks were
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29
30 568 within stable social environments for 1.5 years (either social or isolated), and
31
32 569 consistency of isolated lizard sociability was moderately repeatable ($R_{adj|age} =$
33
34 570 0.427). In comparison, sociability of socially-reared lizards was not significantly
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36 571 repeatable over the same time frame. When lizards were released into the much more
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38 572 dynamic environment of a large semi-natural enclosure, consistency in social
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41 573 behavior was lower and did not increase significantly over the following six months.

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43 574 Consistency in social behavior did not differ between rearing treatments. As
44
45 575 socially-reared lizards were always exposed to a social environment in our study, we
46
47 576 expected their social behavior to be more consistent than isolated lizards (even though
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49
50 577 there was a change from laboratory to semi-natural conditions for this treatment). In
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52 578 contrast, isolated lizards changed from no social contact during development to a
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54 579 social environment during adulthood. With such a substantial change, we expected
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56 580 isolated lizards to be variable in their social behavior, but only if their behavioral
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3 581 plasticity was not constrained by their development. As both rearing treatments
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5 582 showed similar consistency in behavior, we interpret this finding as evidence that
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7 583 isolation rearing did not impact an individual's natural social plasticity.
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10 584 The tree skinks' facultative and variable social system may select for social
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12 585 plasticity. In wild tree skink populations, and those of other *Egernia*-group spp.,
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14 586 developing with limited social contact may occur for a proportion of each litter
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16 587 (Bonnett 1999; While et al. 2009b). For example, in White's skink (*Liopholis whitii*) a
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18 588 closely-related *Egernia*-group skink, the degree of social contact during development
19
20 589 varies depending how related a juvenile is to their social father (While et al. 2009b).
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22 590 Furthermore, tree skinks are long-lived and the social system of this species may be
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24 591 influenced by seasonality and environmental factors (Michael and Cunningham 2010;
25
26 592 Duckett et al. 2012). It is likely that throughout a lizard's lifetime it could experience
27
28 593 a diversity of social situations ranging from near-isolation to family-living, thus
29
30 594 plasticity in social behavior would be adaptive. Such variability contrasts with the
31
32 595 more stable social environment of obligate social animals with parental care, which is
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34 596 the basis of the majority of research on this subject (Harlow et al. 1965; Baron and
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36 597 Kish 1960; Varty et al. 2000; Yu et al. 2013). The facultative kin-based sociality of
37
38 598 tree skinks, in relation to obligate sociality, best explains our contrasting results and
39
40 599 the degree to which these lizards are able to adjust to a novel social environment.
41
42 600 Though wild social groupings of tree skinks can differ from what we were examined
43
44 601 in our experiment - groups can consist of parent(s) and offspring, and social groups
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46 602 can be larger (i.e., up to 10 individuals in some cases; Chapple 2003). Thus, our
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48 603 understanding of social plasticity, and social environment's impact on tree skink
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50 604 behavioral development, could benefit from further laboratory- and field-based
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52 605 investigations on how parents, kin, and larger group sizes affect social behavior.
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5 607 **Conclusion**

6
7 608 Isolation rearing impacted tree skink social behavior. Isolated, juvenile tree skinks
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9 609 spent laboratory trials closer to an unrelated, adult female. Reflecting the trend we
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11 610 observed in the lab, isolated skinks associated more strongly with conspecifics at the
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13 611 beginning of the six-month monitoring period within a semi-natural environment.
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15 612 Also, isolated skinks were more homogeneous in the strength of their associations
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17 613 than socially-reared skinks. These findings suggest that isolation rearing resulted in
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19 614 naïve juveniles that were more likely to associate with unfamiliar conspecifics, which
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21 615 could be potentially costly within the tree skink's social system (i.e., a higher chance
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23 616 of infanticide/aggressive encounters).

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25 617 Although isolation rearing affected social behavior, it did not constrain social
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27 618 plasticity. Isolated lizards gradually decreased the strength and number of associations
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29 619 with conspecifics over the six-month monitoring period in the semi-natural
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31 620 environment. We hypothesize that the tree skink's facultative social system selects for
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33 621 plasticity in social behavior, which allows individuals to respond to the variable social
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35 622 contexts they are faced with throughout their lives. Overall, our study demonstrates
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37 623 that the impact social rearing environment has on social behavior may depend on a
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39 624 species' social system, and this finding may have important implications for
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41 625 conservation programs.

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49 627 **SUPPLEMENTARY MATERIAL**

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51 628 Supplementary information on our study methodology, and one additional figure can
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53 629 be found online.

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4

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12
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18 638 **ETHICS STATEMENT**
19

20 639 All protocols in this study were approved by the Macquarie University Animal Ethics
21
22 640 Committee (ARA # 2013/039) and work on lizards was approved by the New South
23
24 641 Wales National Parks and Wildlife Service, Office of Environment and Heritage
25
26 642 (License # SL101264).
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30
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32

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52 653 Data accessibility: Analyses reported in this article can be reproduced using the data
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54 654 and R code provided by Riley et al. (2017a).
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FIGURE CAPTIONS

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840

841 **Figure 1.** Weighted social networks across our six week (top) and six month

842 observations (bottom). We aggregated the association data for each week or month,

843 respectively, and constructed six weighted, undirected networks for each time period.

844 These social networks reflect the association matrices used in our analyses. Node size

845 reflects weighted degree of each individual. If lizards were removed from the social

846 network during a time period (e.g., due to death or injury), nodes are replaced with a

847 grey “X”.

848

849 **Figure 2.** Adjusted repeatability ($R_{adj|time}$) and 95% confidence intervals for isolated

850 (black circle and lines) and socially-reared (grey circle and black lines) lizards for (A)

851 laboratory sociability scores, and the three individual network metrics: binary degree,

852 weighted degree, and coefficient of variation across the (B) initial six weeks and (C)

853 subsequent six months. $R_{adj|time}$ was not significantly different between rearing

854 treatments, because 95% CIs for both rearing treatments (black error bars)

855 overlapped. Grey bars show the 95% range of the $R_{adj|time}$ estimates calculated from

856 10,000 data randomizations controlling for location. Our observed $R_{adj|time}$ was not

857 different than what you would expect from chance alone, because the 95% range of

858 the random $R_{adj|time}$ estimates (grey bars) overlapped with 95% CIs for observed

859 $R_{adj|time}$ estimates (black error bars) in all cases.

860

TABLES AND TABLE LEGENDS

Table 1. Effects of rearing treatment (ISOLATED or SOCIAL) and age on lizard sociability ($N_{obs} = 244$, $N_{juv} = 61$, $N_{mom} = 35$) that was quantified using a laboratory behavioral assay. 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			
Maternal 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. Coefficients and 95% confidence intervals (italics in brackets) are presented for both observed and randomized data sets. P_{rand} is also presented, which is the comparison between the coefficients from observed data to the distribution of model coefficients from the randomized data. Effects are considered significant if observed coefficient values are outside the 95% range of random coefficient distributions; we have bolded these significant effects.

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

	Binary Degree			Weighted Degree			Coefficient of Variation		
	β_{obs}	β_{rand}	P_{rand}	β_{obs}	β_{rand}	P_{rand}	β_{obs}	β_{rand}	P_{rand}
Intercept (FEMALE, SOCIAL)	1.682 <i>(1.406, 1.958)</i>	1.775 <i>(1.639, 1.918)</i>	0.901	0.671 <i>(0.543, 0.799)</i>	0.376 <i>(0.337, 0.426)</i>	< 0.001	215.194 <i>(153.606, 276.782)</i>	221.103 <i>(191.002, 250.109)</i>	0.652
Week	-0.010 <i>(-0.151, -0.042)</i>	-0.059 <i>(-0.085, -0.038)</i>	0.002	-0.083 <i>(-0.112, -0.056)</i>	-0.050 <i>(-0.061, -0.041)</i>	< 0.001	22.942 <i>(7.457, 38.428)</i>	6.010 <i>(-0.362, 13.146)</i>	< 0.001
Sex: MALE	-0.087 <i>(-0.348, 0.174)</i>	0.043 <i>(-0.077, 0.155)</i>	0.230	-0.133 <i>(-0.322, 0.056)</i>	-0.022 <i>(-0.114, -0.065)</i>	0.006	15.793 <i>(-29.213, 60.799)</i>	4.227 <i>(-24.644, 31.422)</i>	0.323
Social Treatment: ISOLATED	-0.012 <i>(-0.233, 0.210)</i>	0.034 <i>(-0.081, 0.136)</i>	0.869	-0.010 <i>(-0.092, 0.072)</i>	0.003 <i>(-0.017, 0.021)</i>	0.357	-19.010 <i>(-63.555, 25.535)</i>	-10.786 <i>(-38.004, 18.176)</i>	0.310
Week*Sex	---	---	---	0.024 <i>(-0.024, 0.072)</i>	0.007 <i>(-0.013, 0.028)</i>	0.039	---	---	---
Week*Social Treatment	---	---	---	---	---	---	---	---	---

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

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

	Binary Degree			Weighted Degree			Coefficient of Variation		
	β_{obs}	β_{rand}	P_{rand}	β_{obs}	β_{rand}	P_{rand}	β_{obs}	β_{rand}	P_{rand}
Intercept (FEMALE, SOCIAL)	0.953 <i>(0.601, 1.304)</i>	1.938 <i>(1.781, 2.090)</i>	1.000	0.307 <i>(0.186, 0.428)</i>	0.210 <i>(0.173, 0.250)</i>	< 0.001	369.011 <i>(274.825, 463.197)</i>	222.483 <i>(193.372, 256.836)</i>	< 0.001
Month	-0.035 <i>(-0.139, 0.068)</i>	-0.105 <i>(-0.140, -0.066)</i>	1.000	-0.011 <i>(-0.041, 0.019)</i>	-0.012 <i>(-0.021, -0.004)</i>	0.552	-19.566 <i>(-40.925, 1.793)</i>	6.066 <i>(-1.644, 13.775)</i>	< 0.001
Sex: MALE	-0.028 <i>(-0.304, 0.248)</i>	0.033 <i>(-0.097, 0.156)</i>	0.679	-0.032 <i>(-0.144, 0.079)</i>	-0.006 <i>(-0.041, 0.031)</i>	0.095	-11.264 <i>(-101.847, 79.319)</i>	7.526 <i>(-21.646, 35.802)</i>	0.502
Social Treatment: ISOLATED	0.486 <i>(0.017, 0.955)</i>	-0.284 <i>(-0.534, 0.024)</i>	0.067	0.155 <i>(-0.009, 0.319)</i>	-0.030 <i>(-0.039, 0.108)</i>	< 0.001	-50.382 <i>(-137.910, 37.147)</i>	-12.225 <i>(-40.907, 17.167)</i>	0.002
Month*Sex	---	---	---	---	---	---	---	---	---
Month*Social Treatment	-0.144 <i>(-0.288, -0.000)</i>	0.091 <i>(0.029, 0.148)</i>	0.039	-0.044 <i>(-0.086, -0.002)</i>	-0.015 <i>(-0.031, -0.000)</i>	< 0.001	---	---	---

association strength and coefficient of variation. If interactions were not significant (according to P_{rand}), they were removed and the models re-fitted.

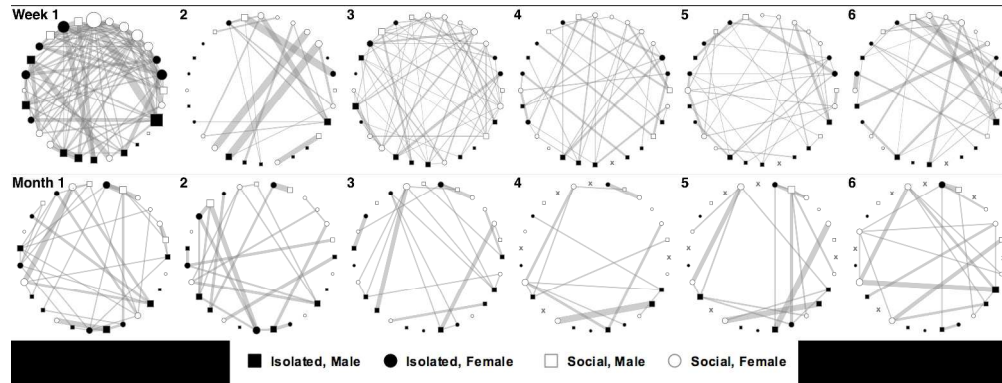


Figure 1

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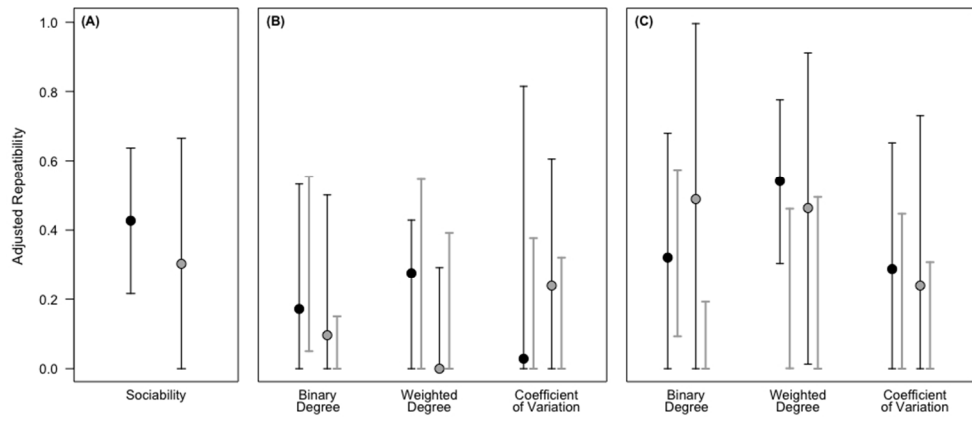


Figure 2

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Review Only