



Socioecology of the Australian Tree Skink (*Egernia striolata*)

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Specialty section:

This article was submitted to
Social Evolution,
a section of the journal
Frontiers in Ecology and Evolution

Received: 08 June 2021

Accepted: 22 November 2021

Published: 10 December 2021

Citation:

Riley JL, Noble DWA, Stow AJ,
Bolton PE, While GM, Dennison S,
Byrne RW and Whiting MJ (2021)
Socioecology of the Australian Tree
Skink (*Egernia striolata*).
Front. Ecol. Evol. 9:722455.
doi: 10.3389/fevo.2021.722455

There is great diversity in social behavior across the animal kingdom. Understanding the factors responsible for this diversity can help inform theory about how sociality evolves and is maintained. The Australian Tree Skink (*Egernia striolata*) exhibits inter- and intra-population variability in sociality and is therefore a good system for informing models of social evolution. Here, we conducted a multi-year study of a Tree Skink population to describe intra-population variation in the social organization and mating system of this species. Skinks aggregated in small groups of 2–5 individuals, and these aggregations were typically associated with shared shelter sites (crevices and hollows within rocks and trees). Aggregations were typically made up of one or more adult females and, often, one male and/or juvenile(s). Social network and spatial overlap analyses showed that social associations were strongly biased toward kin. Tree skinks also exhibited high site fidelity regardless of age or sex. There were high levels of genetic monogamy observed with most females (87%) and males (68%) only breeding with a single partner. Our results indicate that Tree Skinks reside in small family groups and are monogamous, which corresponds with existing research across populations. Similar to previous work, our study area consisted of discrete habitat patches (i.e., rock outcrops, trees, or both), which likely limits offspring dispersal and promotes social tolerance between parents and their offspring. Our study clearly demonstrates that there is intra-population variability in Tree Skink social behavior, but it also provides evidence that there is a high degree of inter-population consistency in sociality across their geographic range. We also highlight promising possible avenues for future research, specifically discussing the importance of studying the nature and extent of Tree Skink parental care and quantifying the fitness outcomes of kin-based sociality in this species, which are topics that will further our understanding of the mechanisms underlying variation in vertebrate social behavior.

Keywords: lizard, mating system, monogamy, nuclear family, sociobiology, social organization, social structure, squamate reptile

INTRODUCTION

In a broad sense, animal sociality is the extent that conspecifics interact with one another and the complexity of these social interactions (i.e., the number of conspecifics in a social group, the nature of interactions, as well as their mating and care systems) (Kappeler, 2019). The extent of sociality itself varies considerably within and between individuals (i.e., social plasticity or competence as per Taborsky and Oliveira, 2012), among populations, and across taxa (Ward and Webster, 2016). There are many potential drivers of this social variation. For example, variation in resources (e.g., shelters, food, mates) may cause animals to group together for access (Graves and Duvall, 1995; Hatchwell and Komdeur, 2000). If, in turn, individuals residing in groups experience higher fitness, then selection favors sociality (Ward and Webster, 2016). Limited resources may also delay offspring dispersal from their natal social group, and association with their parents may offer protection, thus selecting for the formation of kin-based sociality and parental care (Halliwell et al., 2017). Ultimately, if we are to understand how the spectrum of animal sociality evolved, we need to connect the processes that underpin variation in social behavior at the level of the individual with patterns of social diversification we see at the population and species level. Further, understanding the factors that mediate this variation in sociality, as well as how this sets the stage for the evolutionary origins of sociality, are fundamental goals in animal behavior and evolutionary biology.

The majority of our insights into these processes are based on studies that have focused on a narrow range of species (e.g., group-living mammals like the African Striped Mouse, *Rhabdomys pumilio*, Mallarino et al., 2019; birds like the Acorn Woodpecker, *Melanerpes formicivorus*, Stacey and Ligon, 1987; and eusocial insects, Jeanson and Weidenmüller, 2014). As a result, research on social evolution has largely progressed within particular taxonomic silos (Elgar, 2015). In contrast, a range of other taxonomic groups have largely been ignored. This is particularly the case for reptiles (Bonnet et al., 2002; Rosenthal et al., 2017). The occurrence of conspecific aggregations has been investigated in less than 1% of all squamate reptiles (Gardner et al., 2016) with studies describing the composition, stability and genetic structure of social groups even rarer (i.e., testing for the presence of family-living; Whiting and While, 2017). One of the reasons for this is that reptile sociality tends to be less obvious than that observed in other social organisms. However, recent advances in spatial ecology and molecular techniques are providing new opportunities to study kin-based sociality in reptiles. While the Australian *Egernia*-group of skinks have been the “poster child” of family living in lizards (Chapple, 2003; While et al., 2015), it has also been identified in other lizards too (*Xantusia vigilis*: Davis et al., 2011; *Liolaemus leopardinus*: Brito, 2017). The sociality observed in these lizards is generally consistent with definitions of family-living; revolving around a stable association between parents(s) and their offspring after hatching or birth (Kramer and Meunier, 2019). In reptiles, kin associations can extend to other forms of aggregation too, like between juveniles (e.g., crèches in hatchling *Iguana iguana*, Burghardt et al., 1977) and between adults (e.g., the lizard

Intellagama lesueurii, Piza-Roca et al., 2019; and the snake *Crotalus horridus*, Clark et al., 2012), but due to the lack of basic information regarding reptile sociality, we have a poor understanding of how social behavior and sociality varies both within and among individuals and populations, respectively.

The Australian Tree Skink (*Egernia striolata*) is reported to be family-living across its range in south-eastern Australia (Bustard, 1970; Swanson, 1976; Ehmann, 1992; Bonnett, 1999; Derez, 2004; Michael et al., 2010; Duckett et al., 2012). However, Tree Skink sociality has been suggested to vary considerably both within and between populations, and, thus, sociality of this species has been described as facultative (Chapple, 2003; Riley, 2017; Whiting and While, 2017). For example, group composition of Tree Skinks varies across populations in New South Wales in association with key microhabitat features (e.g., number of crevices, crevice dimensions, and height of home sites) (Michael et al., 2010). This has led researchers to hypothesize that forested habitats that have an abundance of shelter sites (i.e., crevices and hollows) reduces aggregation tendency in this species, and saxicolous habitats that have limited shelter sites increases Tree Skink grouping behavior. However, other research has suggested that individuals associate independently of crevice site availability in both forest and rock habitats (Bonnett, 1999; Duckett et al., 2012). Yet, it is unclear where this inter-population variation in Tree Skink sociality arises from. Most of the previous studies on this species were anecdotal in nature and/or lacked detailed data relating to the complexity of this species' sociality within populations. Further, differences in study methodologies may also be the source of some of this variation (e.g., sampling intensity and method, differences in detectability between observers, and error rates of molecular data). An alternative explanation is that the inter-population variation in sociality that has been observed simply reflects a high degree of within and among individual variation in social behavior. This last hypothesis is what our study aims to investigate. Thus, to gain a comprehensive understanding of the complexity of Tree Skink sociality, we conducted a 2-year socioecological study of a Tree Skink population within a mixed habitat (i.e., rock outcrop and forest) that aimed to:

1. Describe Tree Skink habitat use and fidelity,
2. Quantify the demographics, size, and stability of aggregations (i.e., social organization as per Kappeler, 2019),
3. Test for sex-biased dispersal,
4. Describe the Tree Skink mating system through parentage assignment, and
5. Study the nature of Tree Skink social associations and test whether they are influenced by kinship (i.e., social structure as per Kappeler, 2019).

To achieve these aims we conducted a mark-recapture study and collected data on individual social behavior and space use. We genotyped individuals at thousands of single nucleotide polymorphisms (SNPs) to characterize this species' mating system and dispersal patterns. In addition, we used this genotypic data, in combination with spatial overlap and social network analyses, to describe this species social behavior,

organization, and structure, as well as identify any kinship patterns guiding their sociality. Our integrative approach allowed increased accuracy and power in kin and parentage assignment (Foroughirad et al., 2019; Piza-Roca et al., 2019), as well as in quantification of the strength of social associations (Whitehead, 2008). We used these methods in combination with longitudinal field data to better understand the factors mediating variation in Tree Skink sociality at the individual level. Here we compare our findings with previous work to hypothesize about whether individual variation in social behavior may, when viewed at the population-level, result in intra-specific variation in social organization.

MATERIALS AND METHODS

All our methods were approved by the Macquarie University Animal Ethics Committee (ARA # 2013/039) and approved by the New South Wales National Parks and Wildlife Service, Office of Environment and Heritage (License # SL101264).

Study Species

The Tree Skink, *Egernia striolata*, is a medium-sized skink (180–220 mm in total adult body length) that is sexually monomorphic in coloration and morphology, except for slight sex-specific differences in head shape and size (i.e., males have larger heads; Duckett et al., 2012; Cogger, 2014). Females are viviparous and give birth to a litter of 1–6 offspring from January to March each year (Chapple, 2003). The Tree Skink lifespan is unknown, but is estimated to be between 10 and 20 years based on data from similar species (i.e., White's Skink, *Liopholis whitii*: G. White, pers. comm.). Tree skinks live in cracks, hollow limbs, beneath the bark of standing trees or fallen timber, and crevices in rock outcrops (Cogger, 2014). Individuals rely on these crevices as a “home-base” to forage, bask beside, and to take retreat. Tree Skinks are widely distributed, and can be found in dry sclerophyll forest, woodlands, and rock outcrops throughout central- and south-eastern Australia (inclusive of Queensland, New South Wales, and South Australia; **Figure 1**). For more details on the natural history of Tree Skinks refer to **Supplementary Materials**.

Mark-Recapture Surveys and Behavioral Observations

We conducted field surveys across the skink's active season (August to May) from December 2013 to March 2016. Our field site was 2.5 ha (250,000 m²) and consisted of isolated rock outcrops and trees within an agricultural field in Albury, NSW, Australia (−35.98°S, 146.97°E; **Supplementary Figure 1**). At this site, we numerically marked 40 trees and 126 rocks that were habitat for Tree Skinks and mapped their locations using a GPS to an error of ± 3 m (Garmin eTrex Legend HCx).

Field surveys were conducted in December 2013, May 2014, September/October 2014, November 2014, January 2015, March 2015, October 2015, December 2015, and March 2016. These field surveys spanned two Tree Skink active seasons (2014/15 and 2015/16), which is the period during the year these skinks are not dormant (i.e., the spring, summer, and fall). Methodology

was identical for all field surveys. First, all individuals in the population were captured using lassos, Elliott traps, and hand captures. Once captured, individuals were weighed (using a digital scale to 0.01 g) and measured (snout-vent and total length to 1 mm using a clear standard ruler). Sex was determined by eversion of the hemipenes. Skinks were identified as adults or juveniles using snout-vent length (SVL) as a guide. The cut-off used in our study to delineate adults was SVL > 80 mm, which is similar to cut-offs used in other studies of this species to delineate sexual maturity (Bonnett, 1999; Derezi, 2004). At each individual's first capture, it was permanently marked via subdermal insertion of a microchip (PIT-tag), or, if too small for insertion of a microchip (SVL < 60 mm), it was uniquely toe-clipped (Borges-Landaez and Shine, 2003). Tissue for genetic analysis was collected by trimming <5 mm of an individual's tail tip with scissors, which was then stored in 100% ethanol. This approach has a minimal impact because Tree Skinks regenerate their tails and tips naturally break off due to wear. Lastly, we temporarily marked all individuals with uniquely numbered cloth tape (Tesa®, Hamburg, Germany; Olsson and Shine, 2000) for visual identification from a distance. There is no evidence that visually marking lizards impacts their predation rate (Calderon-Chalco and Putman, 2019) or affects their natural behavior.

Within each active season (2014/15 and 2015/16), the mark-recapture surveys as described above were conducted four times for 7–10 days each, and then were followed by visual observations of the skinks to collect spatial and behavioral data for 7–10 days. During the observation period, we walked around the survey site, visually locating skinks from a distance with binoculars. We then recorded the spatial location of the individual (rock or tree number) and whether individuals were aggregating with a conspecific or not. We also noted the nature of these aggregations—if individuals were situated on the same rock/tree, within two body lengths (~40 cm) of one another, sharing a crevice, in visual contact (i.e., within each other's line of sight), and/or in physical contact. Tree Skinks live in near-permanent association with crevices in rock outcrops as well as cracks, hollow limbs, or spaces beneath the bark of standing trees or fallen timber (Cogger, 2014). These crevices and hollows are the anchor to their social aggregations (Bustard, 1970; While et al., 2015). This means that skinks which share the same rock or tree, in most cases, form a social group (Bonnett, 1999; Duckett et al., 2012). We recorded this spatial and behavioral data a maximum of twice per day with 4 h separating observation periods (i.e., morning and afternoon observations). Across this study we captured and observed 203 individuals, which is 85% of the estimated population size (240 ± 42.2 SE; refer to **Supplementary Materials** for details). The population consisted of 17% juveniles, and the sex ratio was female-skewed (**Supplementary Table 1**). In the 2014/15 active season we recorded 1,308 observations of 139 individuals. In the 2015/16 active season, we recorded 2,285 observations of 127 individuals.

Analyzing Tree Skink Sociality

We analyzed the spatial and behavioral observational data collected over 2 study years ($n = 3,593$ observations of skinks) and brought multiple lines of evidence together to describe the nature



FIGURE 1 | Tree Skinks (*Egernia striolata*) aggregate within crevices and hollows in rocks and trees (top; photo credit James O'Hanlon). They inhabit both forest and rocky habitats (bottom left; two examples of Tree Skink habitat photographed by Julia Riley) within their range in eastern Australia (bottom right; range map adapted from Cogger, 2014).

of Tree Skink aggregations and social associations. Specifically, we (1) summarized aggregation size, composition, and stability across active seasons, (2) calculated the spatial overlap between skinks in our population as a proxy for social associations (as per Bull and Baghurst, 1998; Osterwalder et al., 2004; While et al., 2009a; Qi et al., 2012; Strickland et al., 2014), and (3) quantified social associations between individuals using social network analyses which allowed for a finer scale understanding of the nature of social interactions between individuals (as per Leu et al., 2016; Piza-Roca et al., 2019). Below we detail each of these components.

Size, Composition, and Stability of Social Groups

We considered skinks to be aggregating if individuals were on the same rock or tree during one of the twice-daily observation periods (similar to the definition used in Bonnett, 1999; Duckett et al., 2012). This definition was also used in our social network

analyses (see section “Social Network Analysis”). Tree skinks use multiple lines of communication (i.e., visual, tactile, olfactory) to guide their social interactions (Fox et al., 2003; Baeckens and Whiting, 2021). Olfactory cues from scat-piling may influence individual habitat use and avoidance/preference for rocks/trees inhabited by a particular set of conspecifics on the landscape (Bull et al., 1999, 2000). Our definition (i.e., shared rock/tree use) of aggregations was therefore inclusive of all possible means of communication guiding Tree Skink social behavior. Based on our knowledge of the natural-history of this species as well as our field observations, it was clear that if skinks were on the same rock or tree they were aware of each other. Further, for reptiles like *E. striolata*, with cryptic social behavior and where social interactions are concentrated around a shared resource, definitions like ours for aggregations have been highly reliable at documenting social systems (Doody et al., 2013; Farine, 2015; Whiting and While, 2017).

We found that in 1007/3593 (28%) of behavioral observations individual Tree Skinks were aggregating with at least one conspecific. In total, we observed 438 aggregations (≥ 2 individuals on the same rock or tree) across our study's two active seasons. Of these 438 aggregations, we found that 190 were unique (i.e., each group consisted of a distinct set of individuals). We then calculated size and categorized the demographic composition for each of these unique aggregations. We also assessed whether there was stability in these unique aggregations across our study by categorizing whether they were observed (or not) in both active seasons. This summary was used to give an indication of this species' social organization and its variability at our study site.

Habitat Use and Spatial Overlap

To analyze Tree Skink habitat use and site fidelity, we used data from skinks with >10 spatial observations ($n = 132$). To summarize habitat use at our study site, we counted the number of times these skinks were observed on rocks vs. trees. To categorize this species' site fidelity we also counted the number of times skinks were observed at each tree/rock location (see **Supplementary Materials** for more details).

As mentioned above, spatial overlap between skinks also gives an indication of their social associations. Therefore, to calculate spatial overlap between skinks at our study site, we first calculated the home range for each skink. We followed Smith (1995) and Qi et al. (2012) to determine the minimum number of spatial observations needed for home range estimation by regressing individual home range area (see details on estimation below) by the number of times sighted. We started by including all individuals that had at least 6 observations and found there was not a statistically significant relationship between home range size and the number of observations [$R^2 = 0.01$, $F_{(1,148)} = 1.65$, $p = 0.20$]. We also determined that Tree Skink home and core range overlap was highly correlated between study years (see **Supplementary Materials**). Thus, in our analysis of spatial overlap, we included skinks that had 6 or more spatial observations recorded for them over our 2 field seasons. The dataset included 4,830 spatial observations of 146 tree skinks. The number of locations varied between individuals from a minimum of 5 to a maximum of 106 (mean = 32.2, standard deviation = 22.42, median = 28). This and all analyses carried out in this study, unless stated otherwise, were completed in R version 3.4.4 (R Core Team, 2018). We estimated home ranges using bivariate normal kernel analysis with a reference bandwidth smoothing parameter (using the R package "adehabitatHR" and the function "kernelUD"; Calenge, 2011). We calculated home range area using 95% isopleths, and core area using 50% isopleths using the function "getverticeshr" (While et al., 2009b; Calenge, 2011). Although 95% isopleths reflect the area in which Tree Skinks carry out all their activities (i.e., foraging, dispersal, thermoregulation, etc.), it is hypothesized that the core area estimated using 50% isopleths reflects where most social behavior occurs for saxicolous reptiles (While et al., 2009b). Spatial overlap was calculated as the area (m^2) each skink overlapped another's home- and core-range.

Social Network Analysis

To quantify social associations between skinks within our population we used social network analysis. We restricted our analyses to data collected during the observation periods (a total of 3,593 observations of 167 skinks across 2 study years), excluding data generated during the mark-recapture surveys because physically capturing skinks likely altered their natural social behavior. Social network construction and analysis was performed using the "asnipe" R package (Farine, 2013). We combined observational data across all study periods because social associations were highly correlated across active seasons (see **Supplementary Materials**). For our social network analyses, we defined social associations as we did in see section "Size, Composition, and Stability of Social Groups": individuals were associating if they were on the same rock or tree during one of the twice-daily observation periods. Association strength for each pair of skinks (dyad) was calculated using the half-weight association index (HWI). The HWI ranges between 0 (never observed on the same rock or tree) and 1 (always observed on the same rock or tree). HWI is typically used when an entire population cannot be observed during each sampling period (Cairns and Schwager, 1987), as is the case in our study. We constructed a social network with edge weights that were association strength values. This resulted in a weighted, undirected social network in which individuals were connected with $HWI > 0$ (**Figure 2**). This social network (i.e., a matrix

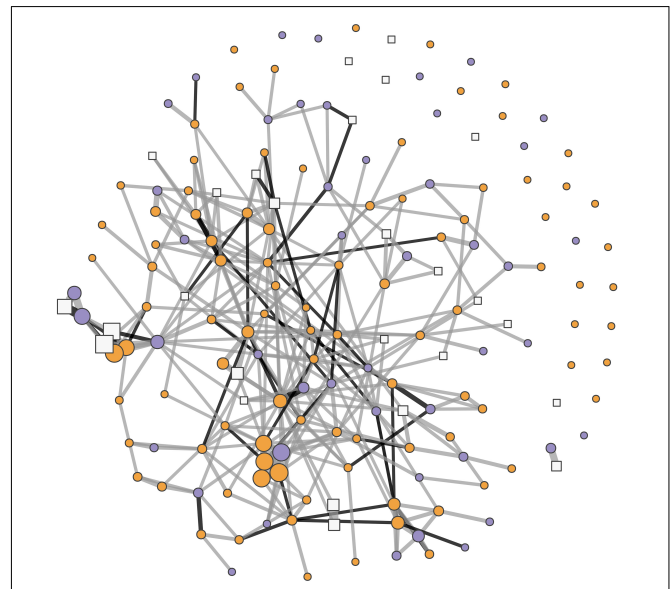


FIGURE 2 | A social network depicting all the (overall) social associations between Tree Skinks (*Egernia striolata*) in our Albury, NSW population over two active seasons (2014–2016). Adults are represented with circles (orange are female, and purple are male), and juveniles are represented with white squares. The size of nodes reflects an individual's weighted degree (i.e., the strength of their social associations or HWI). The thickness of connecting lines (edges) correspond to the HWI values (i.e., the strength of associations between skinks). Genetic relatedness estimates of more than 0.125, representative of at least first cousins, are depicted with black lines (edges), and all other lines are gray.

containing all pairwise HWI reflecting Tree Skink association strength) was then used in downstream analyses. This overall social network contained social associations that occur both randomly and non-randomly (Whitehead, 2008). To determine if associations were significantly different from random, we identified a dyad as having a preferred association when their HWI was twice the mean, including all zeros (Gero et al., 2005). In our study, this means that dyads with an HWI > 0.004 were identified as preferred. This value was chosen because it is approximately twice the expected value if associations were completely random. The network of preferred social associations was also used in downstream analysis, to investigate if non-random associations between skinks were directed to related individuals.

From the overall social network, we summarized three network metrics that quantify an individual's social behavior: binary degree, weighted degree, and the coefficient of variation (CV) of edge weights. Binary degree is a tally of skinks the focal individuals were observed associating with. Weighted degree (also called "strength"; Whitehead, 2008) is the sum of edge weights (i.e., the dyadic HWIs) of the focal skink (Whitehead, 2008). Both binary and weighted degree reflects the sociability of an individual. The CV of edge weights (similar to "social differentiation" or "clustering coefficient"; Whitehead, 2008) of a focal skink quantifies variability of an individual's associations. High CV values suggests that the focal skink's associations are variable; in contrast, low CV values means that focal skink's associations with conspecifics are relatively homogeneous (Riley et al., 2018b). We used three separate linear models to test if these network metrics differed between adult female, adult male, and juvenile skinks (details in **Supplementary Materials**).

Molecular Analyses to Estimate Genetic Relatedness

We used molecular analyses to quantify the genetic relatedness between individuals within our population. DNA was extracted from tissue samples using GenCatchTM Blood and Tissue Genomic Mini Prep Kits (Epoch Life Science, Inc., Sugarland, Texas), followed by genotyping of SNPs by Diversity Arrays Technology Pty Ltd. (Canberra, Australia). The resulting SNP dataset was filtered to ensure it consisted of loci that were physically unlinked and conformed to the expectations of HWE (more details in **Supplementary Information** and Riley et al., 2021). Our final filtered dataset consisted of 2,105 SNPs. We used the program COANCESTRY (Wang, 2011) to estimate relatedness between individual Tree Skinks. Through data simulation (see **Supplementary Materials**) we determined the dyadic likelihood relatedness estimator (Milligan, 2003) was the most appropriate for our data, and we used it to calculate pairwise relatedness values (R). This resulted in a matrix of pairwise relatedness values for our Tree Skink population, which was used in three independent downstream analyses. First, we combined this genetic relatedness data with our sociality data to test whether kinship plays a role in Tree Skink sociality (see section "Relationships Between Social Associations, Spatial Overlap, and Genetic Relatedness"). Second, we carried out a

spatial autocorrelation analyses to explore broad-scale genetic structure at the population-level (see section "Dispersal: Spatial Autocorrelation"). Third, we combined this genetic relatedness data with parentage analyses to describe the mating system of our population (see section "Mating System").

Relationships Between Social Associations, Spatial Overlap, and Genetic Relatedness

To investigate relationships between social associations, spatial overlap, and relatedness, we used the Multiple Regression Quadratic Assignment Procedure (MRQAP) following Dekker et al. (2007) with 10,000 permutations (using the function "mrqap.dsp" from the "asnipe" R package; Farine, 2013; Farine and Whitehead, 2015) and the double permutation approach for our hypothesis-testing as described in Farine and Carter (2020). This double permutation approach has been shown to reduce both type I- (false positives) and type-II error rates (false negatives) that are often a concern in social network analyses (Farine and Carter, 2021).

Our first analyses assessed whether Tree Skink social associations were correlated with relatedness (i.e., directed toward kin; see Piza-Roca et al., 2019 for a similar analysis framework). To achieve this, we ran two separate MRQAPs correlating either the overall or preferred association strength matrices against the relatedness matrix. Second, we assessed if spatial overlap occurred between relatives by running two separate MRQAPs correlating either the home- or core-range overlap matrices against the relatedness matrix. We analyzed the relationship between Tree Skink relatedness vs. association strength and spatial overlap separately because the latter two matrices were significantly related to one another (see **Supplementary Materials**). This avoided any confounding effects of including both these matrices in the same MRQAP. The relationship between association strength and spatial overlap is, indeed, logical, especially based on our definition of Tree Skink social groups. Third, with a separate MRQAP, we examined if skink demographics and size affected Tree Skink social associations. In this analysis, the overall association strength matrix was the dependent matrix, and three predictor matrices were included in our model: the relatedness matrix, demographic similarity (i.e., whether dyads were between two adult females, adult males, or juveniles), and size (SVL) similarly (details in **Supplementary Materials**). These predictor matrices were not strongly correlated ($r < |0.05|$ in all cases), as assessed via pairwise comparisons with a Mantel test (function "mantel" in the R package "vegan" using 1,000 permutations; Oksanen et al., 2019).

Dispersal: Spatial Autocorrelation

We used a multi-locus spatial autocorrelation analysis in GENALEX 6.5 (Peakall and Smouse, 2006), as described in Peakall et al. (1995, 2003) and Smouse and Peakall (1999) to investigate Tree Skink dispersal and philopatry. The output of this analysis is a measure of genotypic similarity between dyads (r ; also termed the autocorrelation coefficient) at predefined distance classes. For this analysis, we calculated matrices of genotypic

distance based on our SNP dataset and Euclidean spatial distance based on the location each skink was most often observed during our 2-year study. These matrices were calculated separately for adult females, adult males, and juveniles to allow testing for differences in spatial genetic structure among demographic groups (Chapple and Keogh, 2005; Banks and Peakall, 2012; Piza-Roca et al., 2019). Juvenile SVL was also included in the analyses to reflect differences in age—if a juvenile was captured multiple times we used average SVL across repeated measures. Only skinks with all data (spatial, genetic, and morphometric) were included in the analyses ($n_F = 112$, $n_M = 52$, $n_J = 34$). Tests for significance of r were performed through 9,999 spatial permutations and we calculated 95% confidence intervals for estimates of r using 10,000 bootstraps (Peakall et al., 2003). We examined the spatial autocorrelation across the whole study population by analyzing pairwise genotypic data grouped into four distance categories (i.e., pairwise comparisons at 0.0–3.0 m, 3.1–10.0 m, 10.1–50.0 m, and 50.1–127.0 m). Selection of the distance classes strongly influences the ability to detect differences in genetic structure (Peakall et al., 2003; Banks and Peakall, 2012). By comparing a range of distance categories, we determined that these categories provided an adequate sample size while providing fine-scale information about spatial genetic structure (see **Supplementary Materials**).

Mating System

To determine the mating system of our Tree Skink population, we assessed the relatedness of offspring within litters of known mothers. In both field seasons, we collected gravid females (during January 2015 in the 2014/15 field season, and December 2015 in 2015/16 field season) and then transported them to, and maintained them at, Macquarie University, New South Wales, Australia until parturition (housing and husbandry details in **Supplementary Materials**). We visually checked enclosures twice daily to see if females had given birth. Within 12 h after birth, we recorded offspring morphometrics, marked each individual uniquely with a toe-clip (Borges-Landaez and Shine, 2003), and took a tissue sample for genetic analyses. We released offspring and their mothers at their site of capture a month before the final survey period of each season in March. Temporary removal of gravid females was required because the genetics of entire litters need to be sampled to quantify rates of multiple paternity and, in the wild, capturing full litters of offspring is unachievable due to high mortality and low capture rates of neonates. Other studies of Egernia-group skink sociality have previously used this approach (O'Connor and Shine, 2004; While et al., 2009b) with no effect on natural social behavior, and, similarly, in our study we did not observe any impact on female social behavior post-release.

We aimed to quantify the mating system for females in our main study population in Albury (**Supplementary Figure 1**) by identifying paternity of each litter. Unfortunately, we ended up with a low sample size of litters from this population ($n = 17$); even though a total of 53 females were caught and brought back to the laboratory to give birth across both study years, which represented 45% of known females within the population. In 2014/15, we collected 42 females, and only 1 of these females gave birth to 2 offspring across 2 days (5 and 6 February 2015). It is

unknown if females gave birth before being caught in 2014/15, or if skinks were not gravid at our study due to other factors (e.g., biennial reproduction, consequences of drought). In 2015/16, we captured 28 females (17 that were also sampled the year before) and 16 gave birth to 35 offspring. Parturition occurred between 10 January and 11 March 2016. In total, only 2 and 57% of females sampled each year gave birth, which suggests Tree Skinks might not reproduce annually (see similar findings in *L. whitii*: While et al., 2009b; and in other Egernia-group skinks: Chapple, 2003). During the same time, we also captured 39 gravid female Tree Skinks from sites nearby our main study population for an experimental study investigating the effect of social environment on behavioral development (Riley et al., 2016, 2017, 2018a,b). No genetic samples were taken from males in these areas, so paternity could not be identified; sibship, however, can be genetically quantified and the likely mating system thereby established. A total of 39 litters of 88 offspring from wild-caught females were born from 10 February to 12 March 2014, and 17 January to 22 February 2015.

To maximize our sample size, we used genetic data from all litters ($n = 55$) for parentage analysis. The parentage analysis included genotypes from known mothers, as well as all males within our main study population. We used COLONY (Jones and Wang, 2010) and CERVUS (Marshall et al., 1998) to estimate paternity, and then verified paternity using our relatedness estimates (see more details in **Supplementary Materials** and a similar approach in Riley et al., 2021). In all cases, the results from all three methods agreed. These data give an indication of the mating system of Tree Skinks, which is important information about the sociality of this species (Whiting and While, 2017).

RESULTS

Habitat Use

Lizards made use of both rock and tree habitats at our study site (see **Supplementary Materials**), and all sexes and life stages showed strong site fidelity. Specifically, while both females and males were observed at a variety of rock and tree locations (an average of 6 ± 3 standard deviation, and 6 ± 4 , respectively), they were observed at just one of those locations in most of their observations (55 and 61%, respectively). Juveniles showed even higher site fidelity, as they were observed at their primary location in 75% of their observations.

Social System

Social Organization

In 28% (1,007/3,593) of behavioral observations, individual skinks were observed within an aggregation. Of the 438 aggregations we observed during our study, 190 were unique (i.e., consisted of a distinct set of individuals). The size of these unique Tree Skink aggregations varied between 2 and 5 individuals (**Supplementary Table 3**). The most observed composition was one male and one female (33% or $n = 62/190$) followed by multiple females (with no males; 22% or $n = 42/190$ female pairs, 6% or $n = 11/190$ groups of three females, and $n = 1/190$ group of four females) (**Supplementary Table 4**). Juveniles were

more likely to aggregate with only females than with males or adults of mixed sexes (**Supplementary Table 4**). Of these unique aggregations, we observed 73 more than once during our study and 30% of these ($n = 22/73$) remained consistent across active seasons. In addition, Tree Skink social associations and spatial overlap were highly correlated across years (see **Supplementary Materials**), which suggests these aggregations reflect consistent social groupings.

Kinship, Social Associations, and Spatial Overlap

We found evidence that social associations were stronger between Tree Skinks that are more genetically related to one another (i.e., kin). Genetic relatedness was a significant predictor of overall [MQRAP estimate corrected with double-permutations ($r = 0.061$, $p < 0.001$; **Figure 3**] and preferred association strength [MQRAP estimate corrected with double-permutations ($r = 0.061$, $p < 0.001$]. These results were driven largely by associations between full siblings and between parents and offspring (**Figure 3**). Further supporting this pattern, we also observed that aggregations with adults and juveniles generally had higher within-group relatedness than adult-only groups (**Supplementary Table 4**). The average association strength (HWI) in our overall social network was 0.002 ± 0.0001 (SE), but,

when only HWI > 0 are considered, the average is 0.094 ± 0.005 , and the range of HWI > 0 is 0.013–0.762. Overall association strength was not significantly influenced by skink age or sex, or size similarity (**Supplementary Table 5**). This is evidence that the degree to which Tree Skinks associate with one another is not simply restricted between particular age classes, sexes (as is also shown in **Supplementary Table 4**), or individuals of a similar size.

We also found evidence that Tree Skinks that overlapped in their space-use were also more likely to be relatives because genetic relatedness was significantly, positively related to home- [MQRAP estimate ($r = 497.956$, $p < 0.001$)] and core-range overlap [MQRAP estimate ($r = 60.177$, $p < 0.001$)]. Thirty-one percent of skink dyads (3,255/10,585) overlapped in their home ranges, of which the home-range overlap averaged $378 \pm 10 \text{ m}^2$ and ranged between 1 and $6,078 \text{ m}^2$. Core-range overlap occurred in 8% of skink dyads (848/10,585), which averaged $41 \pm 4 \text{ m}^2$ and ranged between 1 and $1,309 \text{ m}^2$.

Social Structure

From our analysis of social network metrics (see section “Social Network Analysis”), we found that the nature of Tree Skink social associations differed depending on their sex and age (**Table 1**). Juveniles associated with more individuals (aka. binary degree)

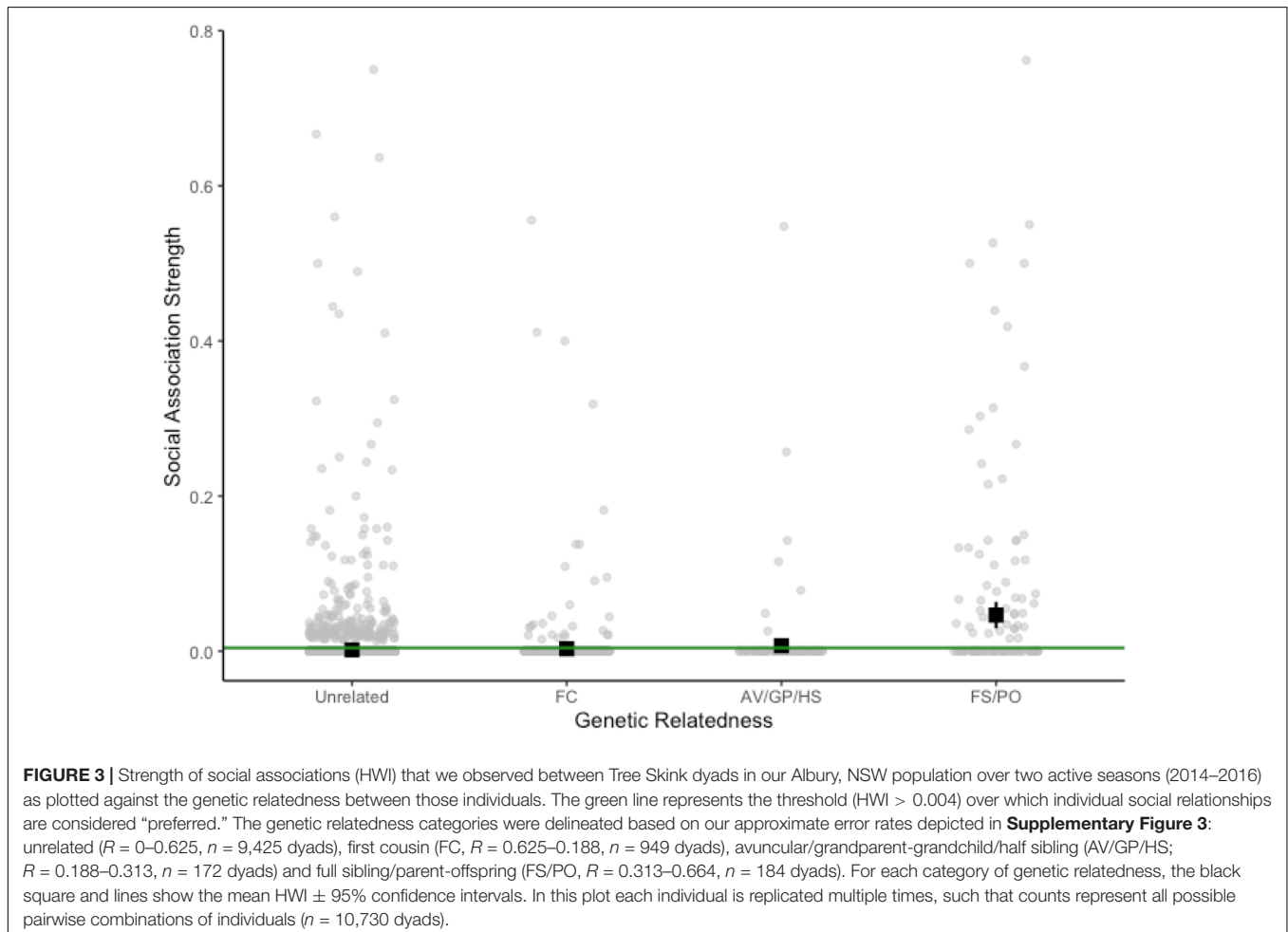


TABLE 1 | Summary of our linear models testing for the effects of demographic classes (adult female, adult male, or juvenile) on social network metrics (see **Supplementary Materials** section 1.3.2 for details).

	Binary degree			Weighted degree			Coefficient of variation		
	β_{corr}	β_{rand}	P_{rand}	β_{corr}	β_{rand}	P_{rand}	β_{corr}	β_{rand}	P_{rand}
Intercept (Female)	-6.368	5.095, 10.316	<0.001	0.174	0.321, 0.362	<0.001	212.924	435.627, 635.202	<0.001
Sex (Juvenile)	4.522	-4.421, 0.129	<0.001	0.128	-0.135, 0.137	0.042	-84.332	-104.357, 192.093	0.052
Sex (Male)	1.129	0.031, 1.874	0.447	-0.016	0.001, 0.081	<0.001	58.672	-86.073, 66.709	0.040

The corrected model coefficient (β_{corr}) and the range of model coefficients generated from randomized data (β_{rand}) are presented. P_{rand} is also presented, which is the comparison between the coefficients from corrected data to the distribution of model coefficients from the randomized data. Effects are considered significant if corrected coefficient values are outside the 95% range of random coefficient distributions; we have bolded these significant effects. Please note, to generate contrasts between adult males and juveniles we re-leveled the demographic classes and re-ran the models to extract coefficient estimates; these contrasts are reported in the Results (see section "Social Structure").

than females and males ($\beta_{corr} = 3.393$, β_{rand} 95% range: 0.031–1.874, $P_{rand} < 0.001$). Male and female skinks did not differ in the number of conspecifics they associated with. Juveniles also had stronger social associations (aka. weighted degree) than females and males ($\beta_{corr} = 0.044$, β_{rand} 95% range: 0.001–0.081, $P_{rand} < 0.001$). Males had weaker social associations than females. Juvenile social associations were also more homogeneous (i.e., less variable) than females and males ($\beta_{corr} = -143.003$, β_{rand} 95% range: -86.073 to 66.709, $P_{rand} < 0.001$). Males had more variable social associations (aka. a greater CV of edge weights) than females.

Dispersal

We found that adult Tree Skinks of each sex are largely philopatric with no genetic evidence for sex-biased dispersal. The juveniles appeared to be pre-dispersal (i.e., a higher r than adults from 0.0–3.0 m). For adults of each sex and juveniles, there was a significant decline in genetic relatedness with spatial distance. These patterns were relatively consistent among adult females, adult males, and juveniles, as well as distance classes (see **Supplementary Materials**). In general, there was a gradual decline in r -values after about 50 m and, after this, values become negative with increasing geographical distance (**Figure 4**).

Litter Size, Birthing Asynchrony, and Mating System

The average litter size was 2.27 individuals (standard deviation = 0.80, median = 2), and ranged from 1 to 4 offspring ($n = 56$). Females that gave birth to more than one offspring ($n = 46$) gave birth across 1.67 days (standard deviation = 0.60, median = 2, min = 1, max = 3). Thus, Tree Skinks in this population do experience birthing asynchrony (i.e., a spread in birth separated by a minimum of 12 h; While et al., 2007) like other Egernia-group skinks (Chapple, 2003; While et al., 2007). In fact, 28/46 (61%) of litters with more than one offspring were born asynchronously.

Parentage analyses showed that the mating system of Tree Skinks is predominantly monogamous. Of the 46 litters with more than one offspring, only 13% ($n = 6$) had mixed parentage. In total, 45 males sired the 55 litters born in this study. Parentage within a litter was only ever mixed between 2 males. There was little evidence for strong male reproductive skew: most males

(68% or 31/45) only mated with one female, and the remaining males contributed to the litter of either 2 or 3 females.

For known mating pairs from our main study site (where mother identity was known and paternity was identified during parentage analyses, $n = 15$), the majority were unrelated (87% or $n = 13/15$). Of the related mating pairs, one represented a first-cousin relationship, and the other represented a half-sibling/avuncular/grandparent-grandchild relationship. On average, the genetic relatedness between mating pairs was 0.034 (standard deviation = 0.067, range = 0.000–0.234). The average association strength between these known mating pairs from our overall social network was 0.175 (standard deviation = 0.168, median = 0.111, ranged = 0.000–0.489). Thus, 73% ($n = 11/15$) of mating pair associations are preferred (i.e., association strength, HWI, values > 0.004), and this is suggestive of social, in addition to genetic, monogamy.

DISCUSSION

Our study of a single population of Tree Skinks revealed a social system based on small, relatively stable, kin-based groups. Associations most commonly consisted of one adult male and one adult female, but adult females also aggregated with one another (up to a maximum of 4 skinks, and sometimes with one male present). These female-only groups were often made up of relatives ($R = 0.125$, or a "first cousin" relationship, and above) with 68% of these relatives either full-sibling or parent-offspring relationships. Juveniles were usually found associating with adult females. We only observed one juvenile-only group, which was made up of two full siblings, during the 2 study years (**Supplementary Table 4**). Although we observed a diversity of social associations and intra-population variability in social behavior throughout our study, the spatial overlap and social associations of Tree Skinks were strongly biased toward kin. The strongest social associations occurred within full-sibling and parent-offspring relationships, which suggests that many consistent social associations may be of nuclear families that share crevice sites and spend their time together. To further support this idea, their mating system reflected both social and genetic monogamy, as most females and males mated with the one partner with whom they had a preferred association. That said, the term "nuclear family" is typically used describe a social

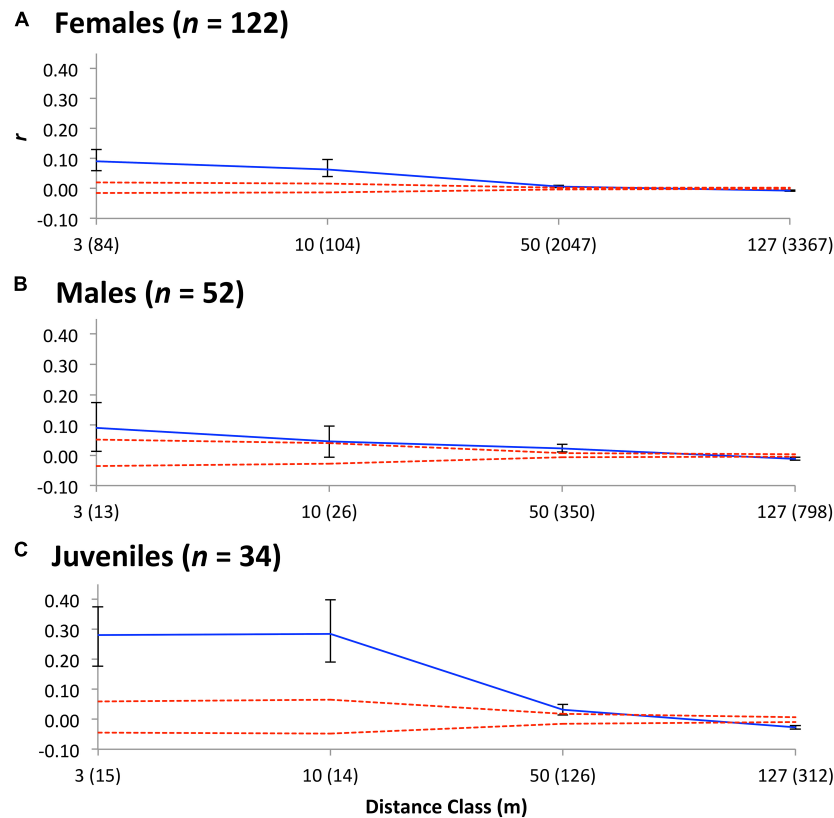


FIGURE 4 | Correlograms displaying the genetic correlation (r) for Tree Skink **(A)** adult females, **(B)** adult males, and **(C)** juveniles over a function of distance (m). Sample sizes at each distance are shown in brackets following each class label. Dotted lines represent 95% confidence intervals reflecting the null hypothesis of a random distribution of genotypes, which were determined with 10,000 bootstraps.

group consisting of parent(s) caring for the offspring of a single reproductive event (Kramer and Meunier, 2019). Thus, more research is needed to establish the care system of this species and determine whether offspring from one (or more than one) reproductive event are present in Tree Skink social groups. We discuss this and other future research topics our study has highlighted below.

Comparison of Sociality Across Studies and Species

Comparing our findings to previous work on Tree Skink sociality may approximate the degree of inter-population variability in Tree Skink social organization. In our population, Tree Skinks were gregarious—28% of behavioral observations of skinks were of individuals aggregating. This is likely a conservative estimate of their aggregative tendency, because this percentage includes only direct observations of associations between individuals and does not consider individuals who co-occurred together but who were not directly observed with one another (such as inside crevices). Such cryptic social associations are relatively common particularly for social species that do not display particularly overt social behavior. Previous studies have reported the percentage of observations of Tree Skinks in groups as 13% (Bustard, 1970), 47% (Michael et al., 2010), 63% (Duckett et al., 2012), and 78%

(Bonnett, 1999). Maximum group size was 5 at our study site, which is similar to the range of maximal group sizes observed in other studies: 3 (Bustard, 1970), 4 (Michael et al., 2010; Duckett et al., 2012), and 6 (Bonnett, 1999). The most common group composition observed in our study was one female and one male, presumably breeding pairs. Breeding pairs, or groups of two when Tree Skinks were not sexed, were the most-observed group composition in other studies too (Bonnett, 1999; Michael et al., 2010). Variation in social structure amongst studies is not just related to adult group composition but also the frequency of adult-offspring associations. Indeed, in all studies, including ours, adults and juveniles were observed sharing crevices and basking together; however, the frequency of those associations varies among studies (Bustard, 1970; Bonnett, 1999; Derez, 2004; Michael et al., 2010; Duckett et al., 2012). Our study found evidence that suggests aggregations are stable in this species. Notably, spatial overlap and social associations were highly correlated between study seasons. Also, 30% of aggregations consisting of the exact same composition of individuals were observed over both study seasons. In addition to similarities in Tree Skink social organization, our study and the two others that included molecular analyses have all found that Tree Skink groups consist of kin (Bonnett, 1999; Duckett et al., 2012). Our study also found that both spatial overlap and social associations

were positively correlated with relatedness—indicating that both space use and social interactions were biased toward kin in our population. Overall, our study was largely congruent with previous work on this species. This demonstrates there is considerable consistency in the basic components of sociality across Tree Skink populations, despite substantial variation in social behavior at the individual level (e.g., social plasticity).

Tree Skinks, across all sex and age classes, exhibited high site-fidelity and dispersal appeared limited. Philopatry is a trait common in gregarious and family-living animals (Waser and Jones, 1983; Ekman, 2006), so it is not surprising that family-living Tree Skinks also exhibit it. For example, in the Yakka Skink (*E. rugosa*), on average, 50% of individuals remained at their original site of capture for at least 5 years (Peck et al., 2017). The lack of evidence we found for sex-biased dispersal in Tree Skinks was unexpected, as either female- or male-biased dispersal is often viewed as a mechanism to avoid inbreeding in social species (Pusey, 1992; Gardner et al., 2013; Whiting and While, 2017). In our study, the majority of known mating pairs were unrelated, and, thus, it appears that Tree Skinks can avoid inbreeding, and perhaps do so through kin recognition (Bull et al., 2001).

Most females and males in our Tree Skink population produced offspring with one partner. Rock-dwelling Tree Skinks in South Australia also exhibited low levels of genetic polygamy (1 of 6 litters had multiple paternity: Bonnett, 1999). Despite the low sample size, this is comparable to our observed rate of 13% multiple paternity. This level of polygamy is on the low-end of the variation documented in Egernia-group species (Chapple, 2003; Whiting and While, 2017). For example, the socially monogamous Sleepy Lizard (*Tiliqua rugosa*) exhibits a rate of multiple paternity of 19% (Bull, 2000). Several other *Egernia* spp. or close relatives also show modest rates of multiple paternity within litters: Cunningham's Skinks (*E. cunninghami* 3%: Stow and Sunnucks, 2004) White's Skinks (*Liopholis whitii* 11.6–17%: Chapple and Keogh, 2005; While et al., 2009b), Black Rock Skinks (*E. saxatilis* 20%: Chapple, 2003), and Gidgee Skinks (*E. stokesii* 25%: Gardner et al., 2002). The evidence of multiple mating within a socially monogamous mating system observed in most group- and family-living Egernia-group species including Tree Skinks, is consistent with studies of socially monogamous bird species (Birkhead and Møller, 1995; Brouwer and Griffith, 2019). Outside of the Egernia-group of skinks, multiple paternity within clutches or litters is the norm in lizards (an average of 53% and ranges between 11 and 87%: summarized from Table 15.1 in Wapstra and Olsson, 2014). Based on our data, we suggest that Tree Skinks are both socially and genetically monogamous. For females whose mates were identified, the majority exhibited preferred social associations. However, most of our paternity data were collected within 1 year, and only multiple years of sampling could tell us if there is consistency in mating partners and patterns in this species, similar to what has been seen in Sleepy Lizards (Bull et al., 1998; Bull, 2000) and White's Skinks (While et al., 2009b). Future research is needed to tease out consistency in mating systems and mate choice in Tree Skinks.

Our evidence that social associations between parents and offspring are largely preferred, and our observation that adult and juveniles are often aggregating in our populations (25% or 47/190

of unique aggregations observed), raises interesting questions regarding the nature of these groupings. We know from other Egernia-group species that such parent-offspring associations have the potential to provide significant benefits to offspring in terms of reduced risk of infanticide (O'Connor and Shine, 2004), reduced predation risk (Watson et al., 2020), increased access to resources (Munch et al., 2018) and, in the long-term, potential inheritance of territories (Gardner et al., 2001). Targeted study of the nature of Tree Skink parent offspring aggregations, perhaps through the use of focal individual observations or trail cameras which have been enlightening in regard to the extent of parental care present in Cunningham's skinks (Watson et al., 2020), may afford novel insights into direct parental care and communication (see **Supplementary Materials** for anecdotal observations) within Egernia-group skinks. The potential for communication, and potentially, cultural transmission, is significant in this species, because both juveniles (Riley et al., 2018a) and adults (Whiting et al., 2018) learn socially from one another.

Variation in Social Behavior at the Individual and Population Level

Our study highlights intra-population variability in social organization and structure occurring within our Tree Skink population. We observed a substantial variety of group compositions across 2 years. We also found individual social behavior differed among Tree Skink age classes and sexes. Our detailed observations revealed that juvenile skinks associated with more individuals and these associations were stronger and less variable than the associations of adult males and females. Female skinks, although they had a similar number of social connections to males, their connections were stronger and less variable (i.e., were observed more often within their groups than males). These sex- and age-class-specific differences in Tree Skink social behavior may have the capacity to underpin inter-population variability in sociality depending on demographic differences between populations. Future work is needed to understand the role this variation plays both in individual fitness and the evolution of sociality. First, how does variation in individual social behavior link to fitness? Previous work has shown, within an experimental context, that Tree Skinks can be plastic in their social associations, potentially maximizing individual benefits within a dynamically changing environment (Riley et al., 2018b). In the field, Bonnett (1999) found that individual vigilance rates (head movements per minute) were lower for grouped sub-adults than lone sub-adults, but this trend was not observed in adults. These studies both suggest potential benefits of aggregation for Tree Skinks, but clear links to individual fitness are yet to be determined. Second, future research should aim to identify a link between inter-individual variation in social traits and the degree of inter-population variability in sociality that has often been discussed in Tree Skinks, and ultimately, between Egernia-group species too.

There are challenges associated with comparing social systems across studies with differing methodologies (Whitehead, 2008; Castles et al., 2014). For example, concerns regarding experimental designs needed to detect kin-based sociality (i.e.,

minimum sample sizes; Foroughirad et al., 2019, the type of molecular analyses; Santure et al., 2010; Hauser et al., 2011) are critical to guide future research in this field. However, the similarity between studies on Tree Skinks sociality spanning ~20 years suggests that some categorizations of sociality may be robust to variation in methodology. The value of insights generated by long-term field studies on vertebrate sociality (e.g., acorn woodpeckers, Koenig et al., 2019; meerkats, Russell et al., 2007; sperm whales, Gero et al., 2015 and as reviewed in Clutton-Brock and Sheldon, 2010; Hughes et al., 2017) is clear. Yet, for the purposes of an initial description of a species' social system, simpler sampling methods, such as that used in Duckett et al. (2012), may suffice. With limited resources for research, and the huge knowledge gaps we face in the field of reptile sociality, it is important to have accessible methodologies to start studying the sociality present in promising, understudied reptile groups (e.g., Cordylidae; Mouton, 2011, and Iguanidae; Burghardt et al., 1977). Further, simpler sampling methods may be more easily replicated across populations of one species or multiple species, which could offer a logistically feasible comparative approach to study the drivers of variation in sociality.

CONCLUSION

The combination of our findings indicates that Tree Skinks live in small, kin-based social groups centered around their use of rock and tree crevices and are monogamous. Tree Skinks are unique in that multiple investigations of their social, and to a lesser extent, their mating system, have been undertaken, with varying methodologies and time scales. This is rare in a field where less than 1% of squamates' aggregation tendency has been studied (Gardner et al., 2016). Interestingly, the social and mating systems of Tree Skinks appear to be largely consistent across their range despite a high degree of intra-population variability in social behavior, social organization, and structure occurring within populations. This raises the question of whether this species' social system is facultative (as suggested in Chapple, 2003; Riley, 2017; Whiting and While, 2017), and if it is, what circumstances are necessary for Tree Skinks to transition to solitary life rather than family-living. Future research examining variation in sociality using a comparative approach across populations or species, or an experimental process that teases apart potential sources of variation (as per Visagie et al., 2005; Schutz et al., 2007) may allow us to gain a greater understanding of the evolution of reptile family life. The detailed understanding of the complexity of Tree Skink sociality our study provides a foundation from which more targeted research can be undertaken.

DATA AVAILABILITY STATEMENT

The data for this study are available from Open Source Framework (OSF) and can be found at the following link: <https://osf.io/bn9te/> (doi: 10.17605/OSF.IO/BN9TE).

ETHICS STATEMENT

The animal study was reviewed and approved by the Macquarie University Animal Ethics Committee (ARA # 2013/039).

AUTHOR CONTRIBUTIONS

Initials of authors are presented in alphabetical order by first initial and do not represent relative contributions. DWAN, GMW, JLR, MJW, and RWB all conceptualized this study. JLR, MJW, and RWB obtained research funding for this study. DWAN and MJW obtained ethics approval and permits. JLR led fieldwork, and DWAN, GMW, and MJW all contributed to field data collection. AJS, PB, and SD provided guidance and training on molecular analyses that JLR completed. JLR conducted data summaries, as well as social network and statistical analyses and led the writing of this manuscript. All authors contributed to editing and finalizing the final manuscript for publication.

FUNDING

Financial support for this research was provided by The Australian Research Council (ARC DP130102998 grant to MJW and RWB), the Australian Government (Endeavour Fellowship to JLR), the Australian Museum, the Australasian Society for the Study of Animal Behaviour, the Natural Science and Engineering Council of Canada (scholarship to JLR), and Macquarie University (research funding and scholarship to JLR).

ACKNOWLEDGMENTS

We thank S. Attersley, J. Baxter-Gilbert, M. Berry, R. Brent, I. Damas-Moreira, S. Deventer, R. Everett, M. Favre, M. Francis, G. Heard, O. Monck-Whipp, J. Ocock, J. O'Hanlon, D. Paris, F. Passas, S. Perkins, R. Robinson, R. Shepard, B. Smagala, and A. Tak for their assistance in the field. Also, thanks to F. Kar, P. Vine, C. Wilson, and the exceptional volunteer team at Macquarie University's Lizard Lab for their care of lizards. K. Bilgmann, P. Momigliano, J. Thompson, L. Waldon, and S. Yadev deserve thanks for their help with genetic analyses. We thank to J. Paterson for his help with spatial analyses, C. Rouleau for his inspiration on plotting social association and kinship data, and H. Whitehead and D. Farine for their advice on social network analyses. We also thank M. Gardner and J. Clayton for supplying hard-to-obtain literature, as well as two reviewers and M. Elgar for their feedback that greatly improved this manuscript.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2021.722455/full#supplementary-material>

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SUPPLEMENTARY MATERIALS

for

Socioecology of the Australian Tree Skink (*Egernia striolata*)

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Please note: there is repetition in the Supplementary Materials with the manuscript to ensure clarity.

1 Supplementary Methods and Results

All analyses, unless stated otherwise, were completed in R version 3.4.4 (R Core Team, 2018).

1.1 The Natural History of Tree Skinks

The Tree Skink, *Egernia striolata*, is a medium-sized skink (180 to 220 mm in total adult body length; Cogger, 2014). Their dorsal coloration (grey to brown with white mottling; Figure 1) affords them superb camouflage on rocks or trees. Their ventral coloration varies among individuals from light grey, cream, or a pale pinky-orange within our study population (J. Riley, unpublished data). Tree Skinks do not exhibit sexual dimorphism in their coloration or morphology, with the exception of slight sex-specific differences in head shape and size. In our study population at Albury, New South Wales (Figure S1), females ($n = 116$) had an average SVL of 100 mm (standard deviation = 8 mm, range = 82 to 117 mm) and an average total length of 183 mm (standard deviation = 20 mm, range = 125 to 232 mm). Males had an average SVL of 102 mm (standard deviation = 5 mm, range = 88 to 111 mm) and an average total length of 195 mm (standard deviation = 14 mm, range = 161 to 234 mm).

Female Tree Skinks are viviparous and have Type 1 placentas (Weekes, 1935; Chapple, 2003). Females give birth to offspring from January to March each year, and litter size ranges from 1 to 6 offspring (Chapple, 2003). Tree Skinks may take several days to complete parturition of a litter, also termed prolonged parturition (Chapple, 2003) or asynchronous birth (While et al., 2007). Female Tree Skinks have been reported to take between 1 to 7 days to complete parturition of one litter (Chapple, 2003). The Tree Skink lifespan is unknown, but it is estimated to be between 10 to 20 years based on data from similar species (i.e., White's Skink, *Liopholis whitii*: G. While, pers. comm.). Juveniles reach sexual maturity in the wild at 2 to 3 years of age (Chapple, 2003), and, within captivity, at 1.5 years of age (Riley et al., 2017).

Tree Skinks are one of the most widely distributed *Egernia*-group species, and can be found in dry sclerophyll forest, woodlands, and rock outcrops throughout south-eastern Australia. Tree Skinks live in cracks, hollow limbs, and beneath the bark of standing trees or fallen timber, and they also inhabit crevices in rock outcrops (Cogger, 2014). Tree Skinks aggregate in these crevices and hollows, and the size and structure of these social groups is thought to vary among and within populations. Tree Skinks are hypothesized to be a species' complex or group (M. Gardner, pers. comm.), so phylogenetic differences may account for the inter-population variability observed but sociality may also affect their fine-scale genetic structuring (Pearson et al., 2020).

Within arboreal populations, like the forested habitats of the Pilliga region in northern New South Wales, the social structure has been described as non-gregarious with only 13% (33/250) of skinks observed in groups, which had a maximum size of three individuals (Bustard, 1970). Yet, a later study in the same region found Tree Skinks aggregating in 63% of observations (12 groups of up to 4 individuals in 29 trees; Duckett et al., 2012). Similarly, in the mallee woodlands of South

Australia, Derez (2004) observed adults and neonates sharing crevices and group basking. In mainly saxicolous populations, like rock outcrops at Para Wirra Recreation Park in South Australia, Tree Skinks were observed in groups, of up to six, 78% of the time (57/78 observations; Bonnett, 1999). Similarly, in rock outcrops throughout the southern South-Western Slopes bioregion of New South Wales, Tree Skinks were found in groups, of up to 4, during 47% (191/403) of observations, (Michael et al., 2010). From this mix of published and unpublished reports, it is clear there is variability the size, structure, and occurrence of Tree Skink groups among populations. Yet, the majority of studies (4/5), as well as anecdotes (Swanson, 1976; Ehmann, 1992), have described Tree Skinks as social and gregarious, and it is unknown whether the variability reported in these studies may also be due to substantial differences in methodology.

Tree Skink behavior is very cryptic. They are sit-and-wait foragers that, in the wild, spend on average 98% of their time stationary (Riley, 2017). Generally, Tree Skinks spent their days waiting beside or within crevices to capture passing invertebrates. That being said, occurrences of active foraging have been observed; in the spring Tree Skinks would eat flowers and insects while moving on the ground (J Riley, pers. obs.) and similar behavior has been observed in other populations (Bonnett, 1999). They are omnivorous, and no ontogenetic changes in diet have been found in this species (Bustard, 1970). Prey groups for this skink include Coleoptera, Dictyoptera, Orthoptera, Hymenoptera, and Hemiptera (Bustard, 1970), and over a third of their diet consists of plant material (39.7%; Chapple, 2003).

1.2 Population Size and Structure

Using the mark-recapture data, we estimated the size of our Tree Skink population using the R packages ‘*EasyMARK*’ to manipulate and organize our data and ‘*Rcapture*’ to run our population size estimation (Baillargeon and Rivest, 2007; Waller and Svesson, 2016).

From December 2014 to April 2016, we surveyed areas immediately surrounding our main site. The total surveyed area, outside of our main site, was 32.2 ha in size. In total we captured $n = 114$ individuals (70 females, 38 males, and 5 juveniles), and only 1.8% ($n = 2$) of which were previously marked during surveys on our main site and then migrated offsite. Overall, this reflects a closed population structure, because there is negligible emigration, immigration, and high site fidelity. Thus, we used the function ‘*closedp*’ from the R package ‘*Rcapture*’ to fit a variety of log-linear models for closed population size estimation. We assessed model fit using Akaike information criterion (AIC) values to select the most appropriate size estimate (Baillargeon and Rivest, 2007), which in our case was a capture-recapture model with heterogeneity and behavioral response (i.e., the Mbh capture-recapture model; Norris and Pollock, 1995).

Population size was estimated to be 240 ± 42.2 (standard error, *SE*) skinks. Across three years of field surveys on our main study site in Albury, we captured and observed 203 unique individuals. These observations were split across an initial trip in December 2013, and then capturing 169 individuals in the 2014/15 season, and 134 individuals in the 2015/16 season (56% of which were recaptures; Table S1). Over all surveys we found that the population consisted of 17% juveniles and 83% adults, and these proportions remained relatively consistent across seasons (Table S1). The sex ratio was female-skewed, and this skew was similar across field seasons (Table S1).

1.3 Additional Analyses Quantifying Skink Sociality

1.3.1 Social Associations Across Years

Using the same methods as described in the main manuscript, we calculated separate overall and preferred social networks for both study years (2014/15: $n_{ind} = 139$, $n_{obs} = 1308$, the number of observations varied between 1 to 28 per individual; 2015/16: $n_{ind} = 127$, $n_{obs} = 2285$, the number of

observations varied between 1 to 57 per individual). To test if social associations were related between field seasons, we used a multiple quadratic assignment procedures (MRQAP) following (Dekker et al., 2007) with 10,000 permutations (using the function ‘*mrqap.dsp*’ from the ‘*asnipe*’ R package; Farine, 2013) and using a double-permutation approach (Farine and Carter, 2020). We used separate MRQAPs to test correlations between overall and preferred association strength (HWI) matrices between field seasons. These matrices contained data from 98 skinks whose grouping behavior was observed in both study seasons. Our fieldwork protocol and effort was similar across field seasons, but our sample size of individuals and observations that were collected did slightly differ. Regardless, the comparison between seasons gives an indication of Tree Skink social association stability and indicate whether data can be pooled.

The results from our analyses indicate that the strength of Tree Skink social associations are correlated between seasons. Specifically, overall association strength matrices were significantly, positively related across years (MRQAP estimate controlled using double-permutations [r] = 0.657, $p < 0.001$, $R^2_{adj} = 0.367$), and the same trend was found between preferred association strength matrices (MRQAP estimate controlled using double-permutations [r] = 0.656, $p < 0.001$, $R^2_{adj} = 0.367$).

1.3.2 Analysis of Social Network Metrics

We used three separate linear models (using the function ‘*lm*’ from the R package ‘*stats*’; R Core Team, 2018) to test if the observed network metrics (binary degree, weighted degree, and CV of edge weights) differed between skink demographics (i.e., adult females, adult males, and juveniles). To generate contrasts between all demographic classes from our linear models, we re-levelled the demographic variable and re-ran the models to extract coefficient estimates of the comparison between males and juveniles. The data used within these linear models was explored prior to statistical analyses to investigate normality, the presence of outliers, and collinearity. Additionally, the assumptions of normality of residuals and homogeneity of variance were verified for all linear models (Zuur et al., 2010).

Skink snout-vent length (SVL; reported as an estimated marginal mean $\pm$ standard error calculated using the function ‘*emmeans*’ from the ‘*emmeans*’ R package) (Lenth, 2020) was confounded with their age and sex classes: females (99 ± 1 mm) and males (101 ± 1 mm) did not significantly differ in SVL (‘*eemmeans*’ contrasts [β] = -1.61, $SE = 1.36$, $t = -1.18$, $p = 0.24$). However, juveniles (67 ± 2 mm) were significantly smaller than females (‘*eemmeans*’ contrasts [β] = 32.55, $SE = 1.76$, $t = 18.48$, $p < 0.01$) and males (‘*eemmeans*’ contrasts [β] = -34.16, $SE = 1.94$, $t = -17.64$, $p < 0.01$). Differences in SVL were assessed using a linear model, and then post-hoc multiple comparisons between demographic classes were completed using the function ‘*emmeans*’ from the ‘*emmeans*’ R package with no p -value adjustment (Lenth, 2020). Due to the relationships between skink SVL and their age and sex, we opted to only include the latter in models.

We used the double permutation approach described in Farine and Carter (2020) for hypothesis testing regarding these network metrics. This is necessary because of non-independence of the data from social networks. This approach uses pre-network permutations to calculate the deviation of the network metrics from their expected random values given the structure of the observed data (i.e., the median value of the same network metric over 10,000 permuted networks); this is the equivalent to a residual value. These ‘residual’ network metrics were then analyzed using the linear models described above. We then calculated the significance of each effect (p_{rand}) by comparing model coefficients (β_{corr}) to the distribution of model coefficients (β_{rand}) based on randomized data (Farine and Whitehead, 2015). The randomized data we used for our calculation of significance was based on our original association matrix, which was randomized 10,000 times by randomly swapping individuals between groups (Farine and Whitehead, 2015). This permutation technique maintains the structure of our observed dataset: 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). From this randomized data, we then reconstructed a social network, calculated the same three network metrics, and conducted the same linear models as we did for the observed data. We considered effects to be significant if observed values fell outside the 95% range of the random coefficient distributions. Results from these analyses are reported in the main manuscript “Results” section and Table 1.

1.3.3 Spatial Overlap Across Years

Using the same methods as described in the manuscript, we calculated home- and core-range overlap separately for both field seasons (2014/15 $n_{ind} = 118$; 2015/16 $n_{ind} = 109$). Then, to assess if Tree Skink spatial overlap was stable across seasons, we used separate MQRAPs to test for correlations between home- and core-range overlap between field seasons. These matrices contained data from 82 skinks whose spatial data was sufficiently observed (i.e., more than 5 locations) in both active seasons. The results from our analyses indicate that spatial overlap between Tree Skinks is highly correlated between active seasons. Specifically, home-range overlap was significantly, positively related across seasons (MQRAP estimate $[r] = 0.122$, $p = 0.015$, $R^2_{adj} = 0.004$), and the same significant trend was found in core-range overlap from different seasons (MQRAP estimate $[r] = 0.199$, $p = 0.002$, $R^2_{adj} = 0.016$).

1.4 Genetic Analyses

1.4.1 DNA Extraction, Single Nucleotide Polymorphism (SNP) Sequencing, and Bioinformatics

DNA was extracted from skink tissue samples using GenCatch™ Blood and Tissue Genomic Mini Prep Kits (Epoch Life Science, Inc., Sugarland, Texas) in accordance with manufacturer instructions. Aliquots of all DNA samples were electrophoresed on 0.8% agarose gels pre-stained with GelRed™ (Biotium, Inc., Fremont, California; Huang et al. 2010) to confirm they contained high molecular weight DNA. After extraction, DNA samples were sent to a commercial genotyping service: Diversity Arrays Technology Pty Ltd (Canberra, Australia). This company has developed a widely used technique called DArTseq™ that identifies SNPs. Detailed descriptions of the DArTseq™ process of SNP identification are provided in Jaccoud et al. (2001) and Sansaloni et al. (2011). Using this process, we obtained a dataset of 15,187 SNPs with an average call and reproducibility rate of $95.16 \pm 0.09\%$ (mean $\pm$ standard error) and $99.45 \pm 0.01\%$, respectively.

We filtered this SNP dataset using the R packages ‘*Radiator*’ (Gosselin, 2017) and ‘*adegenet*’ (Jombart, 2008; Paradis, 2010), and ended with a final filtered dataset consisting of 2105 SNPs. During the filtering process, we removed any sequence clusters that were monomorphic. In cases where multiple polymorphisms were found within the same sequence length, only one SNP was retained and all other duplicates were removed in order to avoid bias due to physical linkage (Lemay and Russello, 2015). We only retained loci with a call rate $\geq 95\%$ and a reproducibility rate of $\geq 99\%$. We screened the data for allele coverage and removed any SNPs displaying a read depth of less than 8 and greater than 30 (Lemay and Russello, 2015). We also filtered SNPs for minor allele frequencies $< 2\%$, because low frequency SNPs can create biases in the data (Roesti et al., 2012). At this stage of filtering, we used the ‘*hw.test*’ function in the R package ‘*pegas*’ (Paradis, 2010) to assess if any SNPs significantly departed from Hardy-Weinberg equilibrium (HWE) and linkage disequilibrium using data from only adult skinks within our population. Loci that significantly departed from HWE were removed from the dataset. We are confident that the final filtered dataset consists of loci that are unlinked and conform to the expectations of HWE. After our SNP data was filtered, we ensured data integrity by identifying duplicate individuals using a combination of a likelihood method via the program COLONY (Jones and Wang, 2010) and

relatedness estimates (R) using the program COANCESTRY (Wang, 2011), as well as correcting any labeling errors as appropriate.

1.4.2 Relatedness Estimator Determination

We used the program COANCESTRY (Wang, 2011) to determine the appropriate relatedness estimator to use, because relatedness estimator performance relies on understanding the underlying true population genetic structure (Van de Castele, 2001; Wang, 2011). In COANCESTRY we simulated multilocus genotype data, based on the allele frequencies of our observed dataset, for 100 individuals assuming predefined relationships as: unrelated ($R = 0$), first cousins ($R = 0.125$), half siblings/avuncular/grandparent-grandchild ($R = 0.25$), full siblings ($R = 0.5$), parent-offspring ($R = 0.5$), twins/clones ($R = 1$). We then calculated pairwise relatedness for this simulated data using seven relatedness estimators (two likelihood estimators: dyadic and triodic likelihood estimators from Milligan (2003) and Wang (2007), respectively, as well as five moment estimators: Ritland (1996), Lynch and Ritland (1999), Li et al. (1993), Wang (2002), and Queller and Goodnight (2002). We assessed correlation between relatedness estimates and expected relatedness using Pearson correlation coefficients (R^2 using the R function ‘*cor*’; R Core Team, 2018). Based on this analysis, we selected the dyadic likelihood relatedness estimator because it yielded the strongest correlation between estimated and expected values ($R^2 = 0.9986$, see Figure S2 and Table S2 for all comparisons).

1.5 Relationships between Social Associations and Spatial Overlap

Tree Skink social associations and spatial overlap were significantly related, which we tested using MRQAPs using the same methods as describe above. Specifically, overall association strength and home-range overlap matrices were significantly, positively related (MQRAP estimate [r] = 0.000005, $p < 0.001$, $R^2_{adj} = 0.004$), as well as overall association strength and core-range overlap matrices (MQRAP estimate [r] = 0.00008, $p < 0.001$, $R^2_{adj} = 0.011$). Preferred Tree Skink association strengths and home-range overlap (MQRAP estimate [r] = 0.000005, $p < 0.001$, $R^2_{adj} = 0.004$), as well as core-range overlap (MQRAP estimate [r] = 0.00008, $p < 0.001$, $R^2_{adj} = 0.011$), were also significantly, positively related. Thus, we separately analyzed the relationship between relatedness vs. social association strength and spatial overlap, as to avoid any confounding effects of including both these matrices (r ranged between 0.063 to 0.104, as assessed using the function ‘*mantel*’ in the R package ‘*vegan*’ using 1000 permutations; Oksanen et al., 2019) in the same MRQAP (Dekker et al., 2007).

1.6 Analysis of whether Demography and Size are Driving Skink Social Associations

Using the same methods as described above, we used a MRQAP, and data from 164 skinks, to test if skink demographics and size affected Tree Skink social association strength. In this analysis, the overall association strength matrix was the dependent matrix, and three predictor matrices were as follows:

1. The genetic relatedness matrix that contained relatedness estimates (R) between all skink dyads,
2. A demographic similarity matrix that was set to 0 if dyads differ in demographics (e.g., an adult female and adult male), and to 1 if dyad demographics agree (e.g., both juveniles), and
3. A SVL similarity matrix consisting of the difference in SVL (mm) between members of a dyad.

Predictor matrices were not strongly related to each other ($r < |0.05|$ in all cases), as assessed via pairwise comparisons with a Mantel test (function ‘*mantel*’ in the R package ‘*vegan*’ using 1000 permutations; Oksanen et al., 2019). Thus model outputs contain measures of how each factor

affects skink social associations while controlling for the others. From this analysis we determined that demographic (i.e., age class and sex) and size similarity did not affect Tree Skink social associations, and instead the only significant driver in this analysis was genetic relatedness (Table S5).

1.7 Comparison of Spatial Autocorrelation Distance Classes

We found evidence for strong positive genetic-spatial autocorrelation over short distances, and our results largely agreed across distance classes. We analyzed data at 3 m, 5 m, and 10 m intervals, as well as a combination of four distance classes (i.e., pairwise comparisons at 0.0-3.0 m, 3.1-10.0 m, 10.1-50.0 m, and 50.1-127.0 m; as presented within the manuscript), and similar findings were clear across all analyses.

For the 10 m distance class, r values were positive and significant at 10 m ($p_F = 0.000$, $p_J = 0.000$), 20 m ($p_F = 0.000$, $p_J = 0.002$), and 30 m ($p_F = 0.032$, $p_J = 0.012$) for females and juveniles. Male r values were positive and significant at 10 ($p_M = 0.000$) and 20 m ($p_M = 0.000$). The x -intercept was 40 m, 56 m, and 58 m for females, males, and juveniles, respectively.

For the 5 m distance class, r values were positive and significant at 5 m ($p_F = 0.000$, $p_M = 0.004$), 10 m ($p_F = 0.000$, $p_M = 0.010$), 15 m ($p_F = 0.000$, $p_M = 0.003$), 20 m ($p_F = 0.003$, $p_M = 0.000$), and 25 m ($p_F = 0.000$, $p_M = 0.027$) for both females and males. The x -intercept value for females and males were 29 and 30 m, respectively. The results were the same for juveniles, with the exception of 15 m ($p_{5m} = 0.000$, $p_{10m} = 0.000$, $p_{15m} = 0.199$, $p_{20m} = 0.001$, $p_{25m} = 0.003$), and an x -intercept value of 29 m.

For the 3 m distance class, r values were positive and significant at 3 m ($p = 0.000$), 6 m ($p = 0.000$), 9 m ($p = 0.000$), 12 m ($p = 0.026$), 15 m ($p = 0.001$), 18 m ($p = 0.034$), 21 m ($p = 0.002$), and 24 m ($p = 0.001$) for females (Figure 4). The female x -intercept was 27 m. Males had similar results, but with non-significance at 6 and 12 m ($p_{3m} = 0.002$, $p_{6m} = 0.310$, $p_{9m} = 0.006$, $p_{12m} = 0.433$, $p_{15m} = 0.000$, $p_{18m} = 0.000$, $p_{21m} = 0.004$, $p_{24m} = 0.051$) and an x -intercept of 12 m. The results were also similar between females and juveniles, with non-significance at 15 m and 24 m ($p_{3m} = 0.000$, $p_{6m} = 0.001$, $p_{9m} = 0.000$, $p_{12m} = 0.001$, $p_{15m} = 0.205$, $p_{18m} = 0.005$, $p_{21m} = 0.000$, $p_{24m} = 0.149$) and an x -intercept of 26 m.

1.8 Mating System

While we maintained females temporarily in captivity at Macquarie University to monitor birth, they were individually housed 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 provided light for each skink's tub, and each tub had an under-cage heating wire, restricted to one side. We cleaned tubs once weekly. We fed skinks 3 adult house crickets (*Acheta domesticus*) dusted with calcium and vitamins twice a week and puréed fruit (1.25 ml of Heinz® fruit baby food: mango, apple, and pear) once a week.

To assess parentage of Tree Skink litters, we used a combination of three programs and assessed agreement between the results. We used (1) COLONY (Jones and Wang, 2010) and (2) CERVUS (Marshall et al., 1998) to estimate paternity, as well as then (3) verified paternity using our relatedness estimates that were calculated in COANCESTRY (Wang, 2011). First, we used COLONY's maximum-likelihood method to assign parentage and sibship groups and to reconstruct genotypes of fathers (Jones and Wang, 2010). COLONY conducts simultaneous inference of multiple relationships among individuals and as such performs with greater statistical power compared to pairwise parentage analysis (Sieberts et al., 2002, Walling et al., 2010). Additionally,

COLONY assesses statistical confidence at an individual-level from the proportion of iterations that a specific relationship occurs and by the probability of configurations (Wang and Santure, 2009). Female and offspring genotypes were entered into COLONY, as well as known maternity and maternal sibships. A polygamous mating system was assumed for both sexes, thus permitting the assignment of half-siblings. An estimate of genotyping error (for all loci = 0.01) was included in the COLONY input, and the program was set to estimate and update allele frequencies throughout the analysis. The COLONY output clustered offspring into full- and half-sibling groups, as well as identifies fathers. The output from COLONY also contained reconstructed paternal genotypes, in the case that a father was not identified in the list of potential fathers, using the most-likely minimum-father combination (Wang, 2004; Phillips et al., 2013).

Second, we used CERVUS to find highly likely paternal assignments. CERVUS bases their confidence levels on simulated populations (specified to be 10,000 offspring genotypes in our case), which can increase the total number of parentage assignments at the possible cost of a larger number of inaccurate assignments (Walling et al., 2010). Assignments to potential fathers was carried out using a strict 95% confidence interval, and all adult males from our main site in Albury, New South Wales were included as candidate fathers. Mothers were known. The probability of a candidate father being present in the sample population was set at 0.9, because we sampled 203 out of a possible 240 individuals (estimated population size for Albury; see above). The genotyping error rate we assumed was 0.01 per locus for typing errors.

Finally, to determine paternity of Tree Skink litters, we assessed if the COLONY results identifying paternity of litters and sibship of juveniles within litters (i.e., half or full siblings) agreed with the father assigned with 95% confidence from CERVUS. We similarly verified these results using relatedness estimates (R). In the majority of cases, the results from all three methods agreed.

1.9 Summary of Tree Skink Habitat Use

We summarized the following variables using data from skinks with more than 10 spatial observations ($n = 132$). The ratio of observations on rocks:trees was, on average, 5:1 and this ratio reflects the presence of both habitat types on the landscape (i.e., there were more rocks than trees). The majority of Tree Skinks (63.6% or 84/132) were observed on both rock and tree habitats during our two-year study. Only 29.5% (39/132) and 6.8% (9/132) of individuals were observed solely on rock and tree habitats, respectively. The individuals that were restricted to only one habitat type (rocks or trees) spanned all life-stages and sexes.

1.10 Summary of Group Composition and Stability

Using our definition (≥ 2 individuals on the same rock or tree), we found that, in 1007/3593 of our observations, Tree Skinks were aggregating. In total, we observed 438 aggregations across our study's two active seasons. Of these 438 aggregations, we found that 190 were unique (i.e., consisting of a distinctive set of individuals). We used this observational data to summarize group size and composition and it was also what we used to construct our social networks and quantify Tree Skink social associations.

Tree Skink aggregation size varied between 2 to 5 individuals; although the most commonly observed size was 2 skinks (Table S3). The demographic composition of aggregations was highly variable (Table S4). The most commonly observed group composition was one male and one female (33%; Table S4). Between adults, mixed-sex groups were the most common ($n = 84$ of 142 adult-only groups; Table S4). Most adult groups had either one ($n = 62$) or multiple females (2-4 individuals; $n = 19$) and only one male. In groups with multiple females, relatedness was higher among females ($R_{2F \& 1M} = 0.209 \pm 0.206$; $R_{3F \& 1M} = 0.305 \pm 0.198$; $R_{4F \& 1M} = 0.322 \pm 0.167$) than between males and females ($R_{2F \& 1M} = 0.102 \pm 0.182$; $R_{3F \& 1M} = 0.138 \pm 0.210$; $R_{4F \& 1M} = 0.035 \pm$

0.070). Same-sex aggregations were more often observed between females (varied in size from 2 to 4 individuals) than males (only observed in groups of 2), and an aggregation consisting of two adult females was the second-most commonly observed composition (22%; Table S4).

Aggregations with adults and juveniles ($n = 33/190$) generally had higher within-group relatedness than adult-only groups (Table S4). Juveniles were more likely to be in groups with only females ($n = 31$), than males ($n = 10$) and adults of mixed sexes ($n = 6$). Juveniles were rarely observed aggregating with one another ($n = 1$) without adults also present (Table S4).

1.11 Anecdotal Observation of Parent-Offspring Interactions

In addition to the observations we made during this study about Tree Skink aggregations, we also had the opportunity to observe other unique behaviors of Tree Skinks. These accounts are anecdotal, but we have included them and our speculations about them to inspire future research. On three occasions at our study site in Albury, New South Wales, we observed behavior that may reflect adult skinks acting as a ‘look-out’ or ‘sentinel’ as juveniles foraged nearby and using tactile signals to communicate the presence of predators. Of course, this behavior of lizards positioning themselves upon a high vantage is common, especially in territorial species (Fox et al., 2003), but it is rarer in Tree Skinks that typically cryptically bask within or at the edge of, their crevices, only quickly darting in-and-out for prey as they are sit-and-wait foragers (Riley, 2017). We observed this behavior when a predator approached, often a researcher (JLR) but sometimes a bird of prey, and adults, before retreating to the crevice themselves, would move towards a juvenile and repeatedly ‘nudge’ the juvenile’s back with their snout, as if to motivate them to move back the crevice (J Riley, pers. obs.). Thus, we think Tree Skinks may be an interesting model to investigate and quantify direct parental care and communication (i.e., visual and/or tactile) within a family group.

2 References

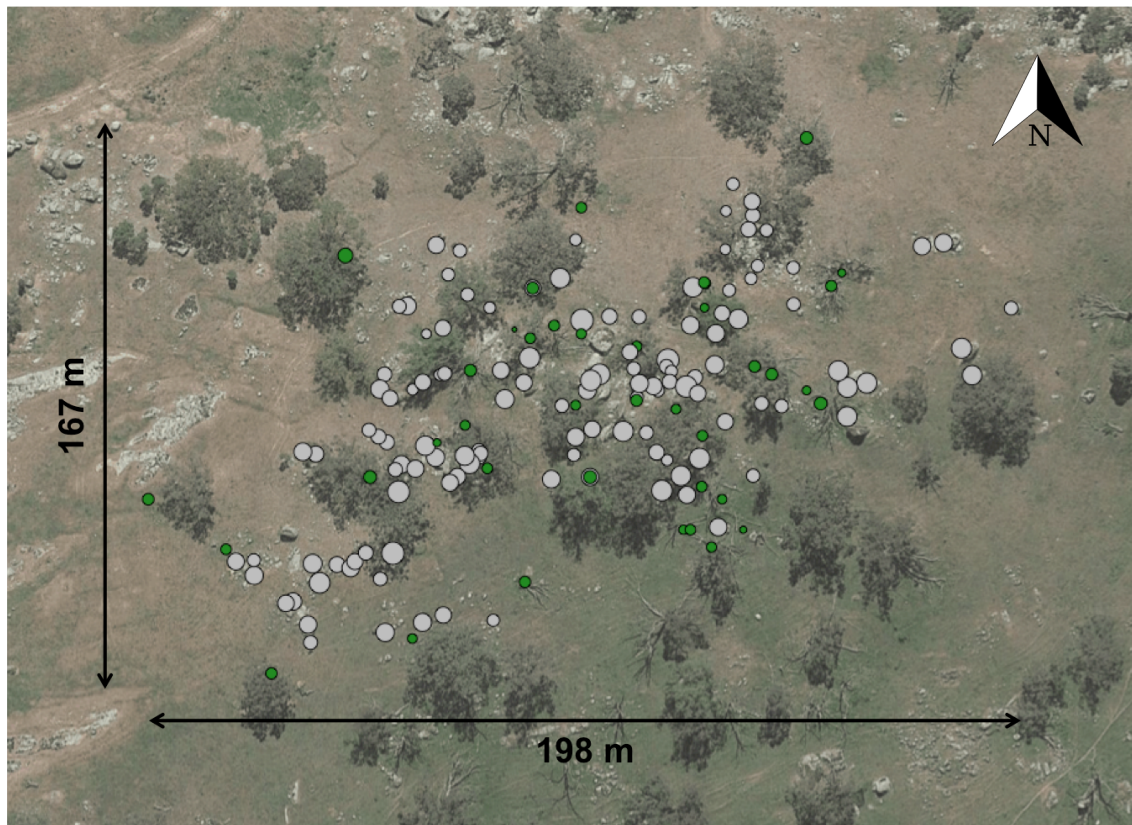
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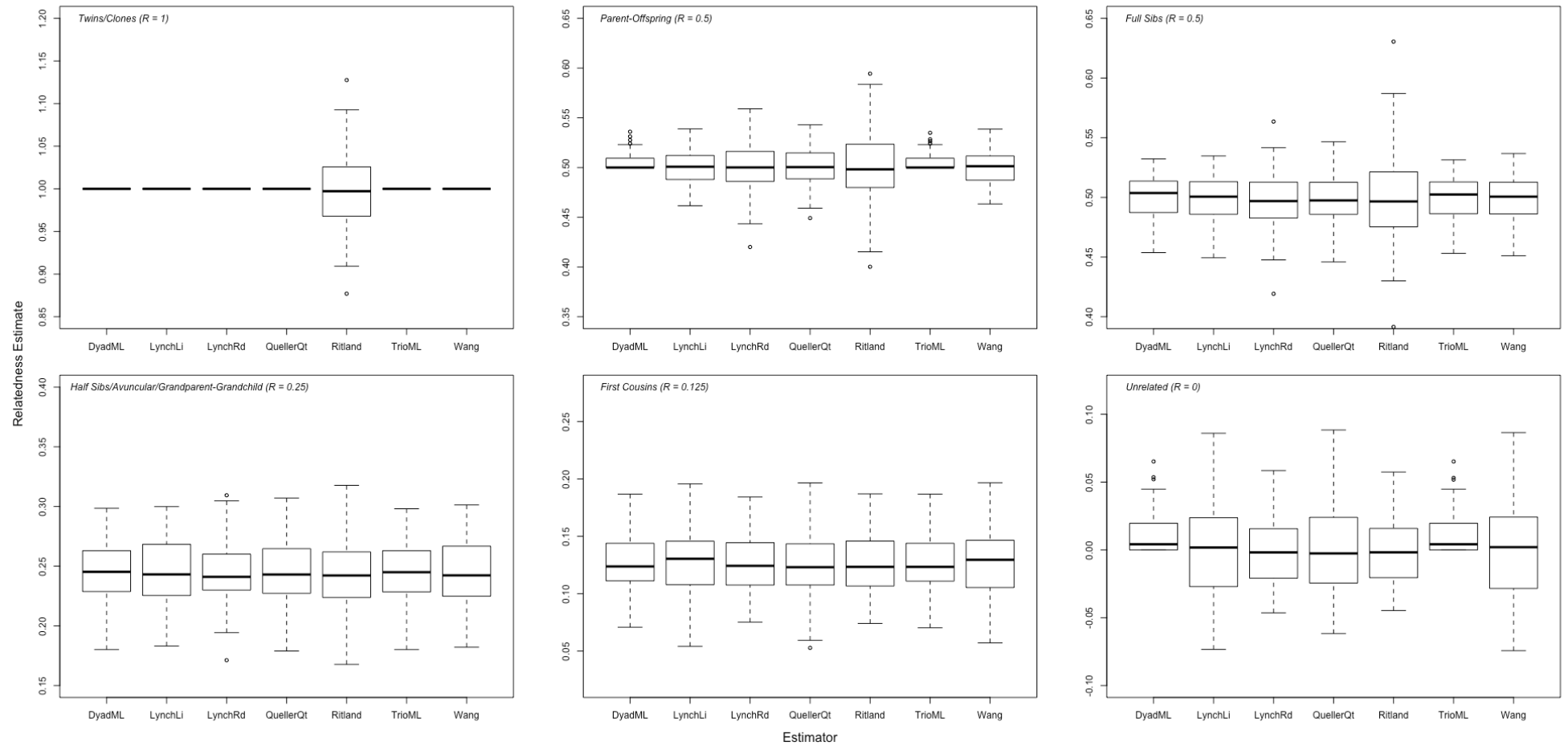
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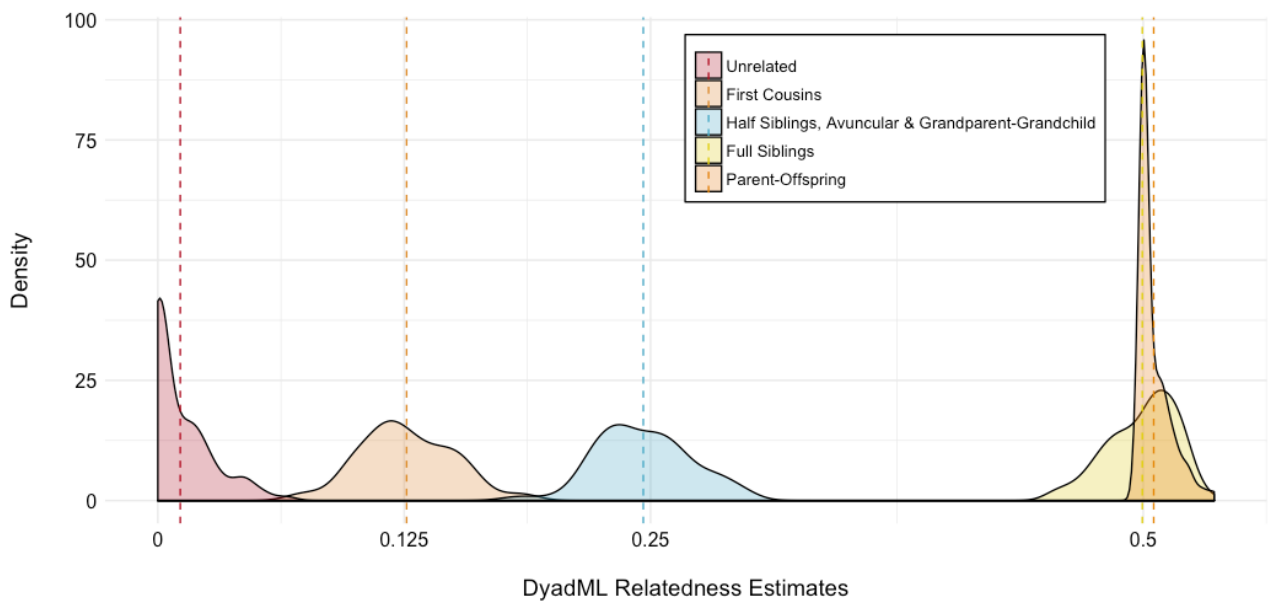
3 Supplemental Figures



Supplemental Figure 1. Our Tree Skink (*Egernia striolata*) study site in Albury, NSW, Australia (-35.98°S, 146.97°E) with 166 marked trees and rocks (grey circles; size reflects tree or rock diameter) and trees (green circles) that were used by skinks as habitat (i.e., the majority of the rocks and trees that that were marked are ones we observed skinks using).



Supplemental Figure 2. Boxplots comparing relatedness estimates for seven relatedness estimators (two likelihood estimators: dyadic [dyadML] and triadic [TrioML] likelihood estimators from Milligan (2003) and Wang (2007) respectively, as well as five moment estimators: Ritland (1996) [Ritland], Lynch and Ritland (1999) [LynchRd], Li et al. (1993) [LynchLi], Wang (2002) [Wang], and Queller and Goodnight (2002) [QuellerQt]).



Supplemental Figure 3. Density of the relatedness estimates for our Albury, NSW population of Tree Skinks (*Egernia striolata*) using the dyadic likelihood estimator (Milligan 2003).

4 Supplemental Tables

Supplemental Table 1. Age class structure of our population of Tree Skinks (*Egernia striolata*) across both study years (2014/2015; 2015/2016).

Time period	Adult Females <i>n</i> (%)	Adult Males <i>n</i> (%)	Juveniles <i>n</i> (%)	Total <i>n</i>
All surveys	115 (57)	53 (26)	35 (17)	203
2014/2015	94 (56)	49 (29)	26 (15)	169
2015/2016	82 (61)	39 (29)	13 (10)	134

Supplemental Table 2. Pearson correlations (R^2) between relatedness estimates, for each relatedness estimator simulated ($n = 700$) and expected values. The estimator with the highest correlation (dyadic likelihood estimator; Milligan 2003) was selected for our study.

Pearson R^2	Relatedness Estimator
0.99856	triadic likelihood estimator (Wang 2007)
0.99724	Wang (2002)
0.99728	Li et al. (1993)
0.99771	Lynch and Ritland (1999)
0.9949	Ritland (1996)
0.99745	Queller and Goodnight (1989)
0.99857	dyadic likelihood estimator (Milligan 2003)

Supplemental Table 3. Composition of Tree Skink (*Egernia striolata*) aggregations in Albury, NSW. This includes a summary of how many times unique social groups ($n = 190$) of each size (varied from 2 to 5 individuals) were observed (n), the number of observed, a summary of the demography of each group (ordered based on the number of times observed) and habitat. The size (circumference) of and the number of crevices occurring on the habitat was summarized by group size, which indicates that habitat size/availability of crevices does not appear to limit group size of Tree Skinks.

Aggregation Size	n	Number of Unique Aggregations	Demography			Habitat		Circumference of Habitat (m)	Number of Crevices
			Female	Male	Juveniles	Rocks	Trees		
5	11	3	4 (6) or 2 (5)	1 (11)	0 (6) or 2 (5)	11	0	13.64 ± 6.52	5.30 ± 2.26
4	31	14	3 (19), 4 (5), 2 (2) or 1 (2)	1 (13), 0 (13) or 2 (2)	0 (19) or 1 (9)	23	8	11.26 ± 5.98	6.55 ± 3.02
3	60	38	2 (25), 3 (13), 1 (12) or 0 (6)	0 (30), 1 (18) or 2 (8)	0 (30), 1 (20) or 2 (6)	47	13	11.54 ± 4.72	9.39 ± 3.38
2	326	135	1 (205), 2 (98) or 0 (23)	1 (191), 0 (131) or 2 (4)	0 (278), 1 (44) or 2 (4)	252	74	11.62 ± 5.90	6.90 ± 3.77

Supplemental Table 4. Within 190 unique social aggregations of Tree Skinks (*Egernia striolata*) 21 different compositions of adult (F = female and M = male) and juvenile (J) skinks were observed. The number (*n*) of times each of these compositions was observed is provided, and the unique pairwise pedigree relationships within these aggregations are identified. For each of these compositions, we also provide the average ($\pm$ standard deviation with minimum and maximum values in brackets) of within-group relatedness. This table is presented over the following three pages.

Group Composition	Group Size	<i>n</i>	Pedigree Relationships	Within-Group Relatedness
1F 1M	2	62	7 parental/full sibling 0 half sibling/avuncular 4 first cousin 51 unrelated	0.072 ± 0.162 (0.000, 0.615)
2F	2	42	10 parental/full sibling 2 half sibling/avuncular 3 first cousin 27 unrelated	0.016 ± 0.199 (0.000, 0.528)
1F 1J	2	18	7 parental/full sibling 3 half sibling/avuncular 0 first cousin 8 unrelated	0.271 ± 0.204 (0.010, 0.523)
2F 1M	3	12	7 parental/full sibling 1 half sibling/avuncular 5 first cousin 23 unrelated	0.143 ± 0.196 (0.000, 0.500)
3F	3	11	13 parental/full sibling 2 half sibling/avuncular 2 first cousin 16 unrelated	0.252 ± 0.219 (0.000, 0.608)
1M 1J	2	8	4 parental/full sibling 0 half sibling/avuncular 1 first cousin 3 unrelated	0.248 ± 0.257 (0.002, 0.567)
3F 1M	4	6	10 parental/full sibling 1 half sibling/avuncular 3 first cousin 22 unrelated	0.192 ± 0.213 (0.000, 0.541)

2F 1J	3	6	8 parental/full sibling 1 half sibling/avuncular 0 first cousin 9 unrelated	0.300 ± 0.200 (0.010, 0.527)
3F 1J	4	4	12 parental/full sibling 3 half sibling/avuncular 1 first cousin 8 unrelated	0.321 ± 0.244 (0.000, 0.582)
2M	2	4	2 parental/full sibling 0 half sibling/avuncular 1 first cousin 1 unrelated 0 unrelated	0.181 ± 0.247 (0.000, 0.542)
1F 2J	3	3	4 parental/full sibling 1 half sibling/avuncular 1 first cousin 3 unrelated	0.442 ± 0.128 (0.252, 0.527)
2M 1J	3	2	2 parental/full sibling 0 half sibling/avuncular 2 first cousin 2 unrelated	0.154 ± 0.216 (0.012, 0.472)
1F 2M	3	2	0 parental/full sibling 0 half sibling/avuncular 1 first cousin 5 unrelated	0.039 ± 0.042 (0.000, 0.108)
1F 1M 1J	3	2	2 parental/full sibling 1 half sibling/avuncular 1 first cousin 2 unrelated	0.357 ± 0.191 (0.116, 0.514)
2F 1M 2J	5	2	6 parental/full sibling 0 half sibling/avuncular 0 first cousin 14 unrelated	0.203 ± 0.251 (0.000, 0.526)
4F	4	1	2 parental/full sibling 1 half sibling/avuncular 2 first cousin 1 unrelated	0.322 ± 0.167 (0.142, 0.506)

4F 1M	5	1	3 parental/full sibling 1 half sibling/avuncular 2 first cousin 4 unrelated	0.207 ± 0.198 (0.000, 0.506)
2F 1M 1J	4	1	2 parental/full sibling 0 half sibling/avuncular 0 first cousin 4 unrelated	0.013 ± 0.015 (0.000, 0.030)
2F 2M	4	1	3 parental/full sibling 0 half sibling/avuncular 1 first cousin 2 unrelated	0.260 ± 0.247 (0.000, 0.494)
1F 1M 2J	4	1	3 parental/full sibling 0 half sibling/avuncular 0 first cousin 3 unrelated	0.264 ± 0.283 (0.009, 0.526)
2J	2	1	1 parental/full sibling 0 half sibling/avuncular 0 first cousin 0 unrelated	0.418

Supplemental Table 5. Results of the MQRAP model examining if overall Tree Skink association strength was affected by demographic or size (based on snout-vent-length; SVL) similarity. Significant effects are bolded.

	<i>Regression Coefficient (β)</i>	<i>t-value</i>	<i>P</i>
Intercept	0.0004	1.4680	0.3699
Genetic Relatedness	0.0622	21.0543	<0.0001
Demographic Similarity	-0.0002	-0.3697	0.7564
SVL Similarity	-0.0000	-0.8747	0.5085
Multiple $R^2 = 0.032$			