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Low genetic relatedness among linked individuals in the social network of an Australian lizard.

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Abstract

Social networks are increasingly being used to describe animal social structure, however we still have a limited understanding of the factors that shape networks, and this is particularly so for more solitary species. We investigated the genetic relatedness of individuals in a social network of a solitary living Australian scincid lizard, *Tiliqua rugosa*. We derived genetic relatedness of 46 lizards from analysis of genotypes at 15 microsatellite DNA loci, and described social networks from GPS locations of all the lizards every 10 minutes for 81 days during their main activity period of the year. We found low relatedness among lizards in our study population and inferred a high level of female-biased dispersal. Observed social associations (inferred through synchronous spatial proximity) were lower than, but correlated with, expected associations (calculated from home range overlap), and many close neighbours did not contact socially, suggesting a deliberate avoidance of some neighbouring individuals. Overall, there were no relationships between social associations and relatedness, however among neighbouring males, and male-female dyads, the strongest relationships were between lizards that were the least related. Explanations of this pattern may include the avoidance of inbreeding in male-female dyads, or the direction of aggressive behaviour towards less related individuals in male-male dyads. The results suggest that lizards can discriminate among different levels of relatedness in their neighbours and tend to direct their social interactions towards those that are less related. This may suggest there is a major difference in the way that social links are formed between species that are solitary (where links are to less related conspecifics) and species that form stable social aggregations (where links are to more related individuals).

Keywords: social network, relatedness, Scincid, lizard, space use, male-male interactions, pair bond

Introduction

Animal species range from solitary to eusocial in their social organisation (Michener 1969; Linksayer 2010), but all interact socially with conspecifics at some times, in some of their activities. An ongoing question is how genetic relatedness influences these social associations (Wilson 1975). There are two main mechanisms by which genetic relatedness may influence social interactions. Firstly, where individuals have limited opportunity for dispersal, they may avoid inbreeding through avoiding social contact with related individuals of the opposite sex, either through sex-biased dispersal or behavioural avoidance (Pusey and Wolf 1996). Secondly, interactions with kin may be favoured when the benefits from cooperative interactions exceed the costs associated with close living (Alexander 1974). Even in reptiles, benefits may be gained from social interactions among kin. For example, the gidgee skink (*Egernia stokesii*) lives in highly related groups with one or more cohorts of their offspring (Gardner et al. 2001), and have enhanced vigilance to predators from this group living (Lanham & Bull 2004). Thus there are several ways in which genetic relatedness may influence social interactions among individuals and shape social network structure.

Increasingly, social networks are being used to explore the structure of social associations within populations and within aggregations (Krause et al. 2007; Sih et al. 2009). They provide a framework for quantifying associations among individuals on a dyadic level, by representing a population as a series of nodes (representing individuals) connected by edges (representing associations) and are particularly useful for testing hypotheses about the factors influencing social structure (Wey et al. 2008). For instance, network analysis has shown consistent social network associations among members of fission-fusion aggregations (Croft et al. 2012), which are sometimes stronger in one sex than the other (Stanley and Dunbar 2013; Carter et al 2013). However, there is conflicting evidence about whether these social associations are influenced by genetic relatedness (Lukas et al. 2005). There is growing evidence to suggest that relatedness can influence social structure, and social networks provide an ideal framework in which to test these hypotheses. For example, Wisniewski et al. (2010) showed that related female dolphins form stable coalitions in the fission-fusion dynamics of pod formation, and Best et al. (2013) found that groupings of female kangaroos had higher relatedness than average for the population. Similarly, Chiyo et al. (2011) reported stronger associations among related than unrelated male elephants, and Kurvers et al. (2013) found that foraging barnacle geese preferentially associated with related individuals and familiar individuals. In contrast, Croft et al. (2012) found no evidence that related individuals associated more strongly in shoals of wild guppies, although this result does not suggest avoidance of related individuals.

For more solitary living and subsocial species, social networks can be derived from the occasional contacts during courtship and mating, or while foraging at a common source (Hamede et al. 2009). Our hypothesis is that even in some solitary species, genetic relatedness should still influence aspects of social interactions, although Hirsch et al. (2013) reported no influence of relatedness in social networks of solitary living racoons.

In solitary species, kin selection should favour associations of more related individuals during any collaborative activities, but may lead to associations of less related individuals during antagonistic encounters. Similarly, selection to reduce the degree of inbreeding should favour associations of less related individuals for mating activity. Thus, we suggest, species that are largely solitary should still have a signal of genetic relatedness built into social network structures. Separate components of the social network associated with different behaviours can be teased apart by examining different subsets of the social interactions (Godfrey et al. 2012). We tested these hypotheses, that genetic relatedness influences social network links, by comparing social network associations among individuals of known genotype in a population of a largely solitary living Australian scincid lizard.

The Australian sleepy lizard, *Tiliqua rugosa*, is a large, long-lived, Australian scincid lizard that occupies stable, overlapping home ranges (Bull 1994; Kerr & Bull 2006a). Although it has a largely solitary life, each spring, adult lizards form monogamous pair-bonds for up to 10 weeks before they mate, and individual pairs of lizards often re-establish those partnerships in subsequent years (Bull 1988; 1994; Bull et al. 1998; Bull 2000; Bull & Burzacott 2006; Leu et al. 2010a). The use of on-board activity and GPS loggers (Kerr et al. 2004a; Leu et al. 2010a), has allowed us to describe more cryptic and infrequent aspects of their social system beyond pair associations, that cannot be captured from snapshot observations.

Social networks based on frequency of contacts among active lizards have shown that individuals associate with some neighbours and avoid others, and that this social structure remains stable both within a year and over multiple years (Leu et al. 2010a; Godfrey et al. 2013). Our current study builds upon this previous research by exploring the genetic relationships between adult lizards in a social network. The aim of the study was to determine whether lizards that were connected in the social network were more (or less) related to each other than if there had been random associations. In any population, individuals that live closer together will have more opportunities to interact than those living further apart. In our analyses we specifically asked whether we could detect an influence of genetic relatedness on network structure after controlling for spatial proximity.

Methods

The study was conducted from October to December 2010, in a 1.0 x 1.5 km area of chenopod shrubland (33° 54' S, 139° 20' E), near Bundey Bore Station in the mid-north region of South Australia. The study period was during the austral spring and early summer, the time when these lizards are most active each year (Kerr & Bull 2006; Kerr et al. 2008).

All 60 adult lizards resident in the area (30 males, 30 females) were captured by hand in September 2010 and fitted with data loggers that were attached to the dorsal surface of the tail with surgical tape. Handling time was normally no longer than 30 mins, and usually only 10-15 mins. The 60 lizards were part of a larger continuous population inhabiting similar habitat surrounding the study area. The data loggers recorded synchronous GPS locations for each lizard every 10 min when it was active (determined by a step-counter attached to the lizard), for the duration of the study (Kerr et al. 2004a, Leu et al. 2010). GPS loggers were manufactured at Flinders University (Adelaide, Australia) (Kerr et al. 2004a). For our analyses, we considered all locations collected over the period 1 Oct - 20 Dec 2010 (81 days), when the majority (~ 90%) of lizards in the study area had data loggers attached. A radio transmitter (Sirtrack, Havelock North, NZ) with unique frequency allowed us to identify, locate and hand-capture each lizard every 12 days to download data and to change batteries. Each data logger plus radio unit weighed 37 g, or 4.5% of the average body weight of an adult lizard, and 5.6% of the body weight of the lightest lizard in our study. Data downloads were conducted at times before or after the diurnal period of activity, to avoid interfering with normal behaviours and to reduce the impact of handling on lizard behaviour (Kerr et al. 2004). The lizards do not grow substantially during the season, and for any lizards where they had noticeably gained (or lost) weight between captures (12 days), we completely refitted the logger. Lizard behave normally with the loggers on (they forage and mate with the loggers attached (Godfrey, pers. obs.), and are observed to gain weight throughout the season (at a rate comparable to other lizards in the study area). At the end of the study, all lizards were recaptured and we removed the units and released the lizards. We found no skin damage or irritation where the units had been attached and lizards naturally shed their skin in the following months. The lizards were treated using procedures formally approved by the Flinders University Animal Welfare Committee in compliance with the Australian Code of

Practice for the Use of Animals for Scientific Purposes and conducted with a Permit to Undertake Scientific Research from the South Australian Department of the Environment, Water and Natural Resources.

Network structure

We developed a social network from incidents of spatial proximity of dyads of active lizards. These were derived from synchronous GPS locations every 10 min for each of the 60 lizards. Following Leu et al. (2010), we considered that two lizards within 2 m of each other at any of the GPS location times had probably made, or would soon make a social contact. Allowing for a median GPS precision of 6 m, we included each pair of GPS derived locations within 14 m of each other at the same time as a record of social contact. To construct the social network we calculated the Simple Ratio Index (SRI) for each dyad, as the number of recorded contacts divided by the number of observations when both lizards were active. This was a measure of association strength, which on a biological level, represents the amount of time two lizards spent together. This is an appropriate association measure because sleepy lizards have infrequent contact with other lizards, which in some cases (especially male-male contacts) can be brief. Thus, our measure captures the length and frequency of interactions, given the cryptic nature of most sleepy lizard interactions. Higher SRI values represented more frequent and stronger associations. The network consisted of 60 nodes, representing the 60 lizards. An edge was included for each pair of lizards that was recorded in contact at least once (SRI > 0) over the study period. Edge weight was determined by the SRI, with a higher weighting for pairs of lizards that were in close proximity more often. The network was non-directional in that contacting lizards were assumed to have equal roles in a contact interaction. Although that may not have been the case, for example if a more aggressive lizard was more likely to initiate contacts, the data did not allow any inference of directionality.

Expected associations among lizards

In order to account for the influence of spatial proximity on social associations, we developed an expected association network using the ideal gas model (Hutchinson & Waser 2007), which estimated expected association rates if individual lizards moved randomly within their home ranges. For each dyad, we calculated f, the expected encounter rate per day, using the formula [1] derived from Leu et al. (2010):

[1] $f = \frac{8v(14)o}{\pi hr_i hr_j}$

where v is the mean velocity of the two lizards (average distance (m) travelled/day), o is the area of home range overlap between the two lizards, and hr_i and hr_j are the home range areas of individual i and individual j, respectively. We included all GPS locations to derive, using Ranges 6 (Kenward et al. 2003), both the 95% minimum convex polygon home range, and the area of home range overlap between each dyad. We used the estimated f as encounter rates to determine edge weights in expected association networks. We used the expected association network in the MR-QAP analyses to test the influence of space use and relatedness on social associations.

Microsatellite DNA genotypes

We collected blood onto a 3 mm^2 area of an FTA card by clipping the tip of one toe of each lizard in the social network using a pair of sterilized, sharp, dog nail clippers. An analgesic (Meloxicam) was administered orally prior to toe clipping to reduce pain and discomfort. Lizards were gently restrained by hand during the procedure. About 30% of lizards flinched briefly during the procedure with limb movement, but became calm again within 1 minute.

We ensured bleeding had ceased before the lizard was released, and all lizards behaved normally upon release. The persons conducting the surgery had at least a full-years' experience in conducting the procedure. We recaptured all lizards 12 days later, and in all cases the clipped area had healed and we could observe no signs of infection. We recaptured all toe-clipped lizards throughout the duration of this study, and the method had no observable impact on survival, movement or body condition, compared with other studies, or with other conspecifics we encountered in adjacent sites. Sleepy lizards do not use their claws for digging or climbing so toe-clipping should not affect their ability to seek refuge. They are slow-moving reptiles so toe clipping should not affect their locomotor performance to the detriment of the individual movement speed. Many lizards are found with natural toe loss, and with no obvious loss of body condition. In other studies of the same species, several hundred toe-clipped individuals, with several toe-tips removed for individual recognition, have been recaptured over periods of up to 20 years (Bull and Burzacott 2006) with no apparent loss of body condition compared with unmarked animals. Thus we consider there were no short- or long-term adverse effects of removing the tip of a single toe on the lizards in this study. Alternative methods of DNA collection are unreliable (caudal vein blood sampling), impractical (tail tipping), or untested (buccal swabs) in this species. In particular, caudal vein sampling can extend handling time because the vein is difficult to find in this species.

We extracted DNA from blood samples on 3 mm^2 squares of the FTA cards following the Whatman® FTA Elute card procedure (GE Healthcare, Buckinghamshire, UK). We then used the procedures described by Gardner et al. (2008) to determine lizard genotypes at 15 microsatellite DNA loci (Trl1, Trl3, Trl9, Trl10, Trl12, Trl14, Trl16, Trl19, Trl21, Trl22, Trl27, Trl30, Trl32, Trl36 and Trl37). Genotypes were successfully scored for 46 lizards (26 males and 20 females) using GENEMAPPER v4.0 and were checked manually.

General patterns of relatedness within the population

We used the program Coancestry (Wang 2010) to calculate coefficients of relatedness (r) between pairs of individuals with a moments estimator that assumes there is no inbreeding (Wang 2002). Allele frequencies used in the calculations were simulated from all genotyped individuals in the sample. Additionally, we estimated mean relatedness values separately for all male-male dyads, for all female-female dyads, and for all male-female dyads in the sample. To test whether mean relatedness values differed among dyadic combinations, we randomised the derived relatedness values with 10 000 permutations and determined if the observed (absolute) differences in mean relatedness between two groups (e.g male-male dyads and female-female dyads), or between one group (e.g. male-male dyads) and the population mean, were significantly greater than expected by chance. Node permutation tests were performed using PopTools 3.2 (Hood 2010) in Excel 2007.

Social networks, spatial relationships and genetic relatedness

We explored how the spatial relationships and genetic relatedness of the 46 genotyped lizards influenced their social associations. We used Multiple Regression Quadratic Assignment Procedure (MRQAP) analysis (Krackhardt 1988), which regresses multiple predictor matrices onto a dependent matrix, using semi-partialling, and then assesses, using permutation procedures (permuting the dependent matrix), the significance of each regression while accounting for the influence of other measured variables. Our dependent matrix was derived from association strengths of the edges in the social network (pair-wise values of SRI), so that the analysis asked what factors influenced the strength of social associations within our lizard population. The predictor matrices came from the dyadic genetic relatedness estimates, and from the dyadic expected association networks.

We structured our analyses into three components. First we asked, across the entire study social network, what most influenced social association strength among lizards; genetic relationships or spatial relationships. Second, because lizards further apart were less likely to encounter each other and form social contacts, we restricted our analysis to lizards that had home range centres within 200 m of each other (that is, analysing a subset of the dataset used in the first analysis). We called these lizards neighbours, because 200 m is within the distance across a normal home range for this species (Bull and Freake 1999; Kerr and Bull 2006), and asked whether genetic relationships or spatial relationships influenced association strength among all neighbouring lizards. Third, we conducted similar analyses separately for three subgroups of neighbouring lizards, male-male, female-female and male-female dyads. Within neighbouring male-female dyads, we also performed separate analyses for dyads we had previously defined as paired (those with an SRI > 0.1) and for dyads we had previously defined as having formed an extra-pair association ($0 < \text{SRI} < 0.1$), allowing us to distinguish between strong pair bonds, and weaker links among males and females (Leu et al. 2010; Godfrey et al. 2012). These analyses were performed to address specific hypotheses about differences in what influences association strength within different sub-groups, and different behavioural interactions in the population. We performed the analyses using UCINET 6.461 (Borgatti et al., 2002) and, in each case, ran 10,000 permutations to assess the significance of the relationships.

Results

All dyads in the social network

Mean values of network edge weight (SRI), distance between home range centres, percentage home range overlap, and relatedness (R) among dyads of the 46 genotyped lizards in the social network are shown in Table 1. The mean relatedness differed significantly among different dyadic groups, with male-male dyads more related than male- female dyads, and with female-female dyads the least related (Fig. 1).

Association strength was strongly positively correlated with expected associations (derived from the spatial overlap among dyads), although observed association strength was substantially lower than expected association rates (Fig. 2). Association strength was not significantly influenced by genetic relatedness at this spatial scale (Table 2).

Among neighbouring dyads (< 200 m apart)

Most (75%) social network edges (dyads with SRI > 0) occurred between neighbouring lizards that had home range centres less than 200 m apart (Fig. 2). For this subset of dyads, association strength was also positively correlated with expected association rates (Fig. 2, Table 2), although again, observed associations were substantially lower than expected association rates. Note also, that among dyads of neighbouring lizards, 84.6% had very low association strength (SRI < 0.01) and 40.9% never contacted each other (SRI = 0). Close proximity did not necessarily mean strong social association. In these analyses, there was no effect of genetic relatedness on social association strength (Table 2).

Neighbouring lizards of the same sex

Among genotyped neighbouring lizards, there were 64 male-male dyads and 48 female-female dyads (Table 1). The mean values of association strength of neighbouring male-male dyads and female-female dyads did not differ significantly (Table 1, mean difference = 0.0002, 95% CI = 0 – 0.002, P = 0.928). Nor were there spatial differences between these two dyadic groups. For instance mean home range overlap was similar between neighbouring male-male dyads and female-female dyads (Table 1, mean difference = 0.031, 95% CI = 0 – 0.055, P = 0.219). However, there was a significantly higher mean genetic relatedness between neighbouring males than between neighbouring females (Table 1, mean (absolute) difference = 0.055; 95% CI = 0 – 0.034; *P* < 0.001).

Again, social associations were positively correlated (but lower) than expected association rates for both male-male and female-female dyads (Table 3, Fig. 3a). Genetic relatedness had a significant negative effect on male-male social associations, but no significant effect on female-female associations (Table 3). Males had a higher association rate with other neighbouring males when they had lower genetic relatedness (Fig. 3c).

Neighbouring lizards of the opposite sex

Among genotyped neighbouring lizards, there were 128 male-female dyads (Table 1). Neighbouring male-female social associations were significantly stronger (mean SRI difference = 0.028, 95% CI = 0.009 – 0.024, *P* < 0.001), and had a significantly higher percentage of home range overlap (mean overlap difference = 18.4%, 95% CI = 14.2 – 18.1%, *P* = 0.012) than for other neighbour dyad types (male-male and female-female dyads). However, relatedness among neighbouring male-female dyads was not significantly different from the mean for other neighbour dyad types (mean difference = 0.044, 95% CI = 0.039 – 0.055, *P* = 0.741).

Social association strength was positively correlated with expected association rates, both overall, and for pairing and extra-pair associations (Table 4, Fig. 4a). Genetic relatedness also had a significant effect on the strength of social association among pairs (with the analysis using home range overlap), and among extra-pair associations (for analyses using either spatial parameter). In each case social association was stronger among less related individuals (Fig. 4b).

Discussion

We noted three major results from our study population. The first concerned genetic structure within the population. Among the adult lizards in our social network, there were generally low levels of relatedness, and only a small number of dyads had relatedness values that exceeded 0.25, a level that would indicate close familial relatives. This implies that the social structure among adult lizards was not based on associations of close kin. Rather, the results suggest that dispersal that separates related individuals is the normal strategy in this species. Furthermore, both at the level of the whole study population, and at the level of neighbouring lizards, female-female dyads were significantly less related to each other than were male-male dyads (Table 1). An implication is that related females disperse further from their natal sites and from each other than males. Sex biased dispersal has been widely reported among many animal groups, with a common explanation that inbreeding is avoided if one sex disperses more than the other (Greenwood 1980; Pusey 1987). Our data confirm that most neighbouring males and females that are potential mating partners are only distantly related.

Our second result was the strongly significant influence of expected association rates on observed social associations. Our expected association rates were derived from the extent of home range overlap between each dyad, and assumed that lizards moved randomly within their home ranges. Thus, this suggests that a component of lizard interactions can be explained by their spatial ecology. However, even among neighbouring lizards with home range centres less than 200 m apart, or with overlapping home ranges, a proportion of dyads showed very low levels of social association, and observed social association strength was much lower than the expected association rates (Fig. 2). This observation confirms previous analyses from this species showing social structure is characterised by individuals apparently deliberately avoiding contact with some close neighbours (Leu et al. 2010; Godfrey et al. 2013).

Our third result, and the result that directly addresses the questions we asked in this study, was that genetic relatedness influenced the strength of social associations among neighbouring male-male dyads, and male-female dyads. But, contrary to a kin association hypothesis, the significant results showed a negative effect, with the strongest associations among the least related individuals. Even with the low level of genetic relatedness that we recorded in our study population, close neighbours were more likely to associate if they were less related to each other, and the neighbours that were avoided were the ones that were genetically more related.

We considered four possible explanations for this pattern. One is that the lack of association among more related individuals reflects the lack of any general cooperative behaviour in this species. We have never observed cooperative foraging, or collaboration in defending resources in this species, so there would be little opportunity for kin-selection to favour associations of closer relatives, as reported in species which form social aggregations (e.g. Kurvers et al. 2013). And while kin selection may favour higher tolerance of related lizard individuals, for instance by a greater level of overlap of home ranges, this would not necessarily result in more social contacts. A second explanation concerns parasite transmission. We have already shown for this species that gut bacteria are transmitted along social network connections rather than among spatially adjacent individuals (Bull et al. 2012). Similarly ectoparasitic ticks are transmitted along network pathways (Leu et al. 2010; Wohlfiel et al. 2013). Thus more socially connected lizards are more likely to transmit parasitic infections among themselves. Other studies have demonstrated that higher genetic variability, particularly at MHC (major histocompatibility complex) loci, confers higher resistance to pathogens (Coltman et al. 1999; Penn 2002; Bonneaud et al. 2006). If infection is influenced by host resistance genotype, then transmission from one host to another is likely to be more successful if host genotypes are similar (Shykoff & Schmid-Hempel 1991). Thus to reduce the risk of infection from parasites that are transmitted along network pathways, it would be advantageous to prefer social contacts with more distantly related individuals.

The third explanation comes from our analyses of male-male dyads. Males often interact aggressively with each other (Kerr and Bull 2002; Murray and Bull 2004; Godfrey et al. 2012), so that the social contacts we detected between dyads of males may have been primarily agonistic. Bull (1990) previously suggested that younger males may fight for home range positions and access to females. The inclusive fitness of an individual male may be increased by directing aggressive encounters, and thus stronger social associations, towards less related males. The result for males may be further enhanced by the generally higher levels of relatedness among males, meaning that differentiating between related and unrelated individuals may have more impact on inclusive fitness for males than for females, where relatedness is generally very low.

In a fourth explanation, social contact among male – female dyads may be predominantly related to courtship, with a sustained association between monogamous partners that extends over some weeks before mating (Bull 2000). Even within the low levels of relatedness among lizards in the study population, they appeared to associate most often with less related potential partners, a result that confirms previous analysis of inbreeding avoidance in these lizards (Bull and Cooper 1999).

Independent of the mechanisms that might explain why there are stronger social interactions among less genetically related lizards, the results suggest a remarkable ability in this species for individual lizards to detect small differences in the degree of relatedness. We have previously suggested that olfactory signals are used by scincid lizards to differentiate among familiar and unfamiliar adult (Bull et al. 1999; 2000) or neonate conspecifics (Main and Bull 1996), and among siblings and non-siblings (Bull et al. 2001). The current result extends those conclusions to suggest that differentiation of the degree of relatedness even among distantly related conspecific lizards can form the basis of a social structure. Wolf and Trillmich (2008) reached a similar conclusion in their study of Galapagos sea lions, where individuals associated more strongly with genetically more similar conspecifics, even with low levels of relatedness among neighbours in a colony.

In sleepy lizards, other analyses have shown that this social network structure remains stable across time and across a range of ecological conditions (Godfrey et al., 2013). Here we show that social structures in this lizard population are not random with respect to genetic relatedness, but are based largely on avoidance of genetic relatives, particularly among males and between males and females. We suggest that this might be a more common form of social structure in species where cooperative behaviours are infrequent and where selection favours directing attention away from more related individuals, for instance in acts of aggression or in mating. This represents an alternative social structure to the more commonly reported kin associations in species where individuals are more likely to aggregate.

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Figure list

Figure 1. Mean genetic relatedness among male-male dyads, male- female dyads, and female-female dyads, for adult lizards in our study area. *P* values correspond to those comparing the differences in means between each pair of groups using a randomisation test with 10,000 permutations.

Figure 2. Relationships between social association strength in the network (SRI) and expected association rates (calculated using the ideal gas model) for neighbouring lizards (dyads < 200 m apart, black symbols) and for dyads > 200 m apart (grey symbols).

Figure 3. Relationships between social association strength in the network (SRI) and (a) expected association rates for neighbouring male-male (black symbols) and female-female (grey symbols) dyads, and (b) relatedness among neighbouring male-male dyads.

Figure 4. Relationships between social association strength in the network (SRI) and (a) expected association rates, and (b) relatedness, for neighbouring male-female dyads. Pairing associations (SRI > 0.1) are represented with grey symbols, and extra-pair associations (SRI < 0.1) are represented with black symbols.

Table 1. Summary of mean values of network edge weight, distance between home range centres, home range overlap and relatedness among dyads of lizards in the social network.

		Network edge weight (SRI)		Distance between home range centres (m)		Home range overlap (%)		Relatedness (R)	
	N	Mean (SE)	Range	Mean (SE)	Range	Mean (SE)	Range	Mean (SE)	Range
All dyads	1035	0.004 (0.001)	0 - 0.495	377.4 (6.7)	0 - 1024.1	4.2 (0.3)	0 - 83.2	0.052 (0.002)	0 - 0.661
Neighbouring dyads									
All dyads	240	0.017 (0.004)	0 - 0.495	131.7 (3.1)	0 - 198.8	16.2 (1.1)	0 - 83.2	0.047 (0.004)	0 - 0.618
Male-male dyads	64	0.004 (0.001)	0 - 0.024	138.7 (5.7)	7.1 - 198.1	14.9 (1.6)	0 - 56.5	0.074 (0.013)	0 - 0.618
Female-female dyads	48	0.004 (0.001)	0 - 0.063	131.9 (6.6)	5.8 - 197.4	11.9 (1.9)	0 - 61.9	0.019 (0.006)	0 - 0.199
Male-female dyads	128	0.028 (0.008)	0 - 0.495	128.2 (4.5)	0 - 198.8	18.4 (1.7)	0 - 83.2	0.044 (0.004)	0 - 0.247

Table 2. Results of MRQAP analyses of the effects of spatial relationships (expected associations) and genetic relatedness on social network structure among all lizards, and those within 200 m of each other.

	All lizards		**Within 200 m**	
	Regression Coefficient	***P***	**Regression Coefficient**	***P***
Expected associations	0.659	**<0.001**	0.686	**<0.001**
Relatedness	-0.002	0.485	-0.012	0.361

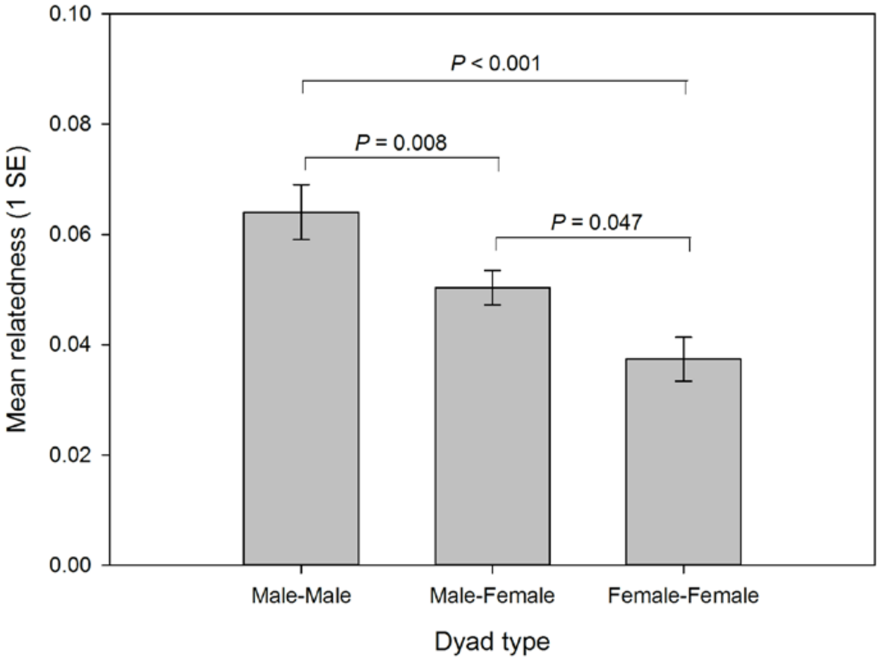
Table 3. Results of MRQAP analyses of the effects of spatial relationships (expected associations) and relatedness on social network structure among males and among females within 200 m of each other.

	Among males		**Among females**	
	Regression Coefficient.	***P***	**Regression Coefficient**	***P***
Expected associations	0.570	**<0.001**	0.387	**<0.001**
Relatedness	-0.146	**0.002**	0.005	0.367

Table 4. Results of MRQAP analyses of the effects of spatial relationships (expected associations) and relatedness on social network structure among males and females, and separately for pair associations and extra-pair associations, for dyads within 200 m of each other.

	Males and females		**Among pairs**		**Extra-pair associations**	
	Regression Coefficient	***P***	**Regression Coefficient**	***P***	**Regression Coefficient**	***P***
Expected associations	0.743	**<0.001**	0.278	**0.002**	0.305	**0.001**
Relatedness	0.034	0.105	-0.177	**0.005**	-0.078	**0.002**

Figure 1



$P < 0.001$
$P = 0.008$
$P = 0.047$
Mean relatedness (1 SE)
0.10
0.08
0.06
0.04
0.02
0.00
Male-Male
Male-Female
Female-Female
Dyad type

Figure 2

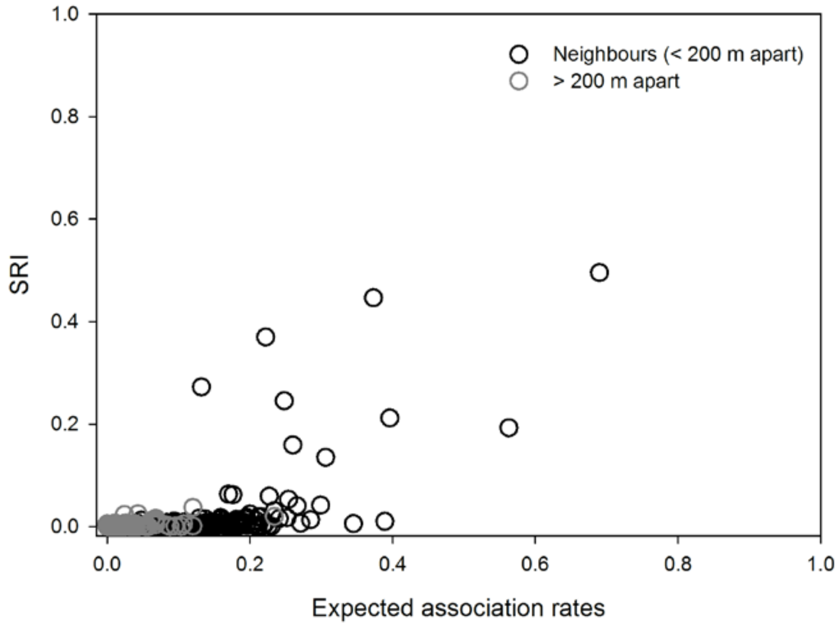

Neighbours (< 200 m apart)
> 200 m apart
SRI
1.0
0.8
0.6
0.4
0.2
0.0
0.0
0.2
0.4
0.6
0.8
1.0
Expected association rates

Figure 3

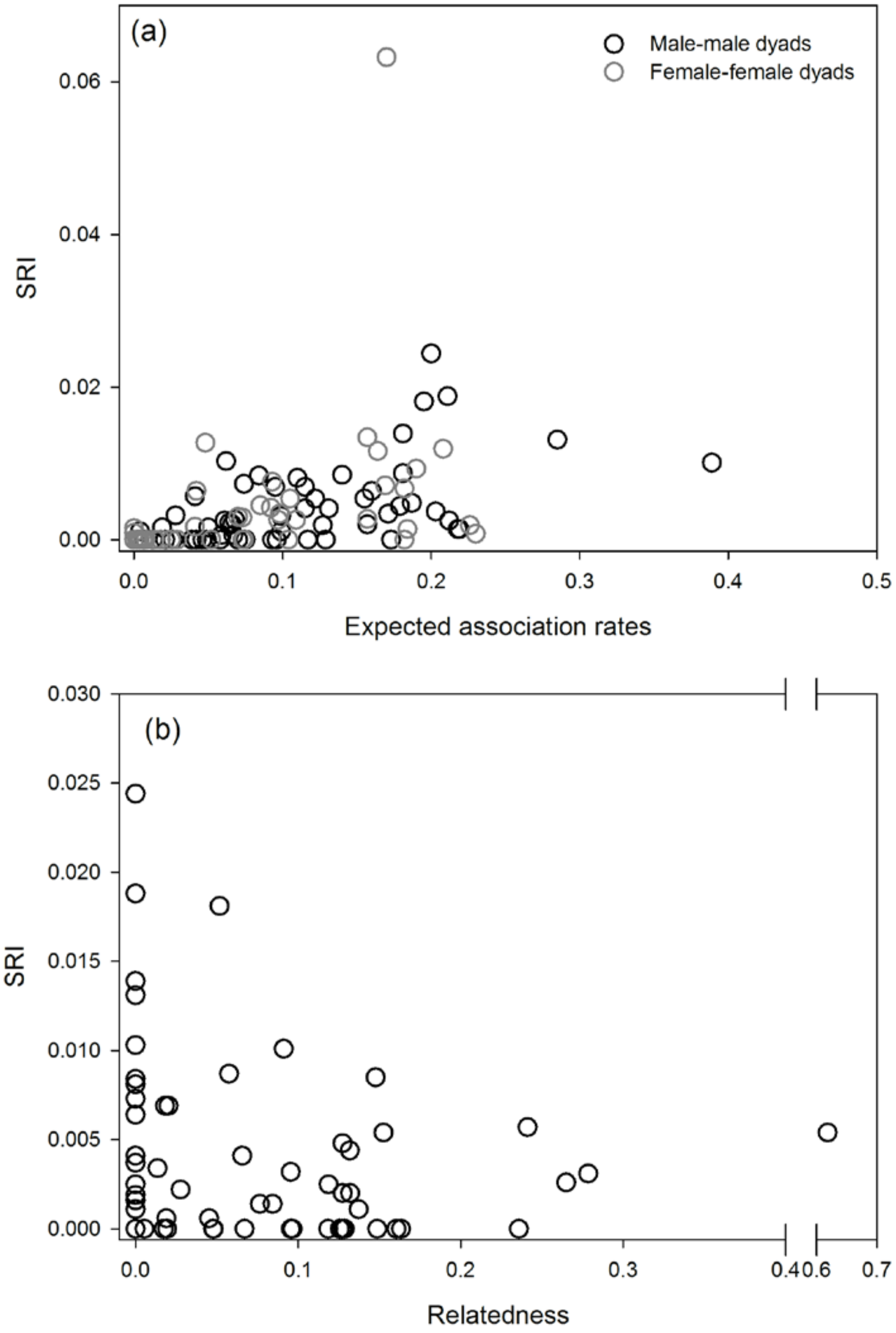
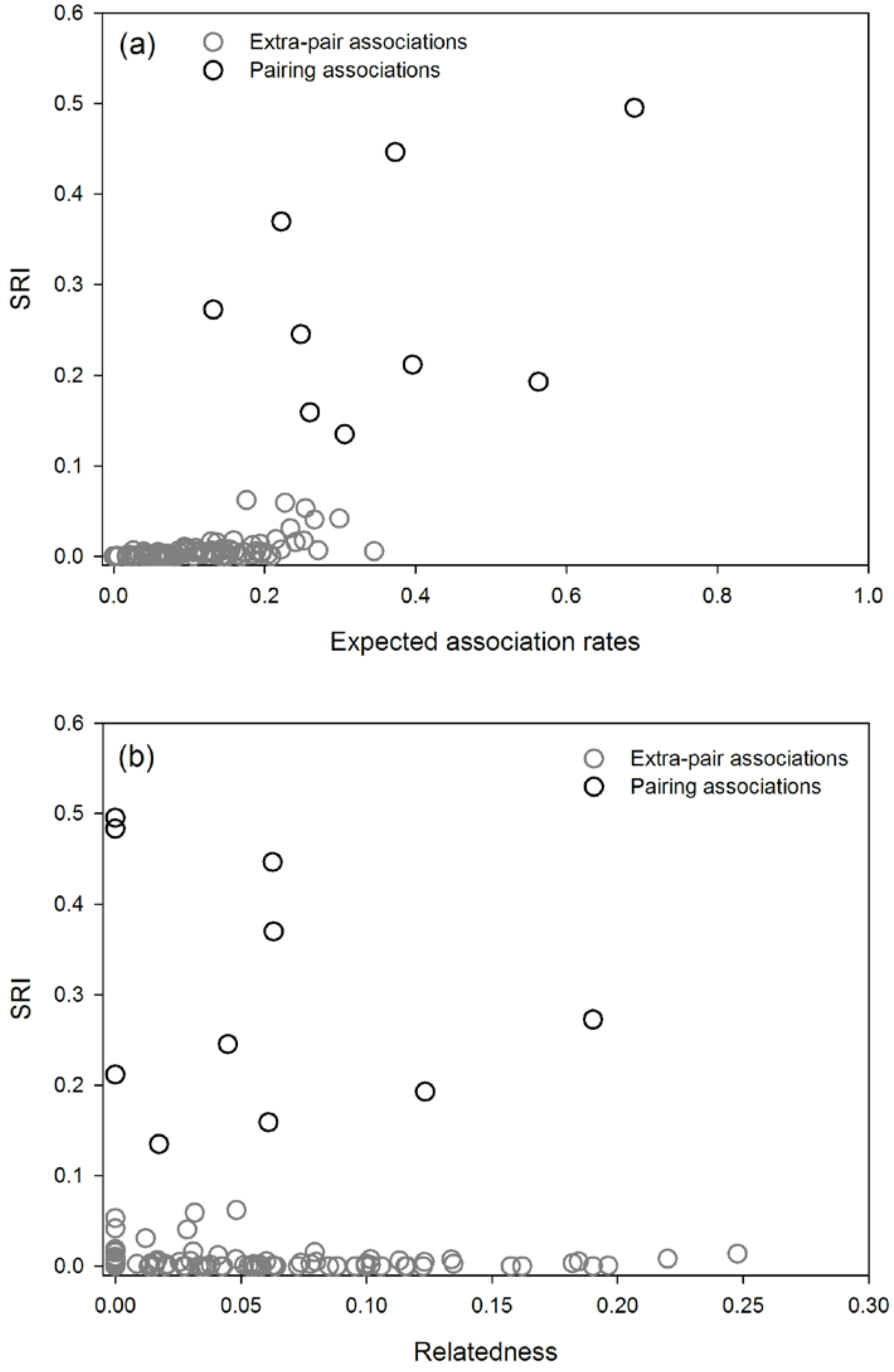

(a)
Male-male dyads
Female-female dyads
SRI
0.00
0.02
0.04
0.06
0.0
0.1
0.2
0.3
0.4
0.5
Expected association rates
(b)
SRI
0.000
0.005
0.010
0.015
0.020
0.025
0.030
0.0
0.1
0.2
0.3
0.4
0.6
0.7
Relatedness

Figure 4


(a)
Extra-pair associations
Pairing associations
SRI
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.0
0.2
0.4
0.6
0.8
1.0
Expected association rates
(b)
Extra-pair associations
Pairing associations
SRI
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.00
0.05
0.10
0.15
0.20
0.25
0.30
Relatedness