A contact-based social network of lizards is defined by low genetic relatedness among strongly connected individuals

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Social organization is widespread; even largely solitary species must organize themselves to enable contacts with mates and reduce competition with conspecifics. Although the forms of social structure can be subtle in solitary species, understanding the factors that influence them may be important for understanding how different forms of social organization evolved. We investigated the influence of genetic relatedness and spatial structure on social associations in a solitary living Australian scincid lizard, *Tiliqua rugosa*. We derived the 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 min for 81 days during their main activity period of the year. We found that connected male dyads were significantly more related than expected by chance, whereas connected male–female and female–female dyads had lower relatedness than expected. Among neighbouring male–male and male–female dyads, the strongest social 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. Observed social associations (inferred through synchronous spatial proximity) were generally lower than expected from null models derived from home range overlap, and many close neighbours did not make social contact. This supports our hypothesis for the presence of deliberate avoidance between some neighbouring individuals. We suggest that lizards can discriminate between different levels of relatedness in their neighbours, directing their social interactions towards those that are less related. This highlights differences in how social associations are formed between species that are solitary (where associations form between un-related conspecifics) and species that maintain stable social groups structured by kinship.

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Animal species range from solitary to eusocial in their social organization (Linksvayer, 2010; Michener, 1969), 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. First, if individuals have limited opportunity for dispersal, they may avoid inbreeding by reducing social contact with related in-dividuals of the opposite sex (Pusey & Wolf, 1996). Second, indirect fitness accrued through interactions with kin may be favoured when the benefits from cooperating exceed the costs associated with close living (Alexander, 1974). Even in reptiles, benefits can be gained from kin-structured social interactions. For example, the gidgee skink, *Egernia stokesii*, lives in highly related groups that include a breeding pair and one or more cohorts of their offspring (Gardner, Bull, Cooper, & Duffield, 2001), with related individuals benefiting from the resulting enhanced vigilance against predators (Lanham & Bull, 2004). The alternative ways in which genetic relatedness may influence social interactions among individuals may shape social network structure.

Increasingly, social networks are being used to explore the structure of social associations within populations and within ag-gregations (Krause, Croft, & James, 2007; Sih, Hanser, & McHugh,

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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, Blumstein, Shen, & Jordán, 2008). For instance, network analysis has shown consistent social associations among members of fission–fusion aggregations (Croft et al. 2012), with these associations sometimes stronger in one sex than the other (Carter, Brand, Carter, Shorrocks, & Goldizen, 2013; Farine, 2014; Stanley & Dunbar, 2013). However, there is conflicting evidence about whether these social associations are influenced by genetic relatedness (Lukas, Reynolds, Boesch, & Vigilant, 2005). On the one hand, several studies suggest that relatedness can influence social structure. For example, Wisniewski, Lusseau, and Moller (2010) showed that related female dolphins, *Tursiops aduncus*, form stable coalitions in the fission–fusion dynamics of pod formation, and Best, Seddon, Dwyer, and Goldizen (2013) found that social groupings of female kangaroos, *Macropus giganteus*, had higher relatedness than average for the population. Similarly, Chiyo et al. (2011) reported stronger associations among related than unrelated male elephants, *Loxodonta africana*, and Kurvers et al. (2013) found that foraging barnacle geese, *Branta leucopsis*, preferentially associated with related and familiar individuals. On the other hand, Croft et al. (2012) found no evidence that related individuals associated more strongly in shoals of wild guppies, *Poecilia reticulata*, although their results did not suggest avoidance of related individuals.

In subsocial or solitary species, patterns of association might be affected by relatedness in different ways, with fewer benefits from cooperative behaviours. Among these species, social network structure is primarily shaped by contacts during courtship and mating, by aggressive encounters to maintain territory boundaries (Lattanzio & Miles, 2014) or by contacts while foraging at a common source (Hamede, Bashford, McCallum, & Jones, 2009). For example, in solitary living woodchucks, *Marmota monax*, nonaggressive interactions were more frequent among pairs of individuals with higher genetic relatedness (Maher, 2009). Similarly, normally solitary mountain brush-tailed possums, *Trichosurus cunninghami*, preferred to share tree hollow dens with kin when tree hollows were limited (Banks et al. 2011). In contrast, Hirsch, Prange, Hauver, and Gehrt (2013) reported no influence of relatedness in social networks of solitary living racoons, *Procyon lotor*. Although solitary species are less likely to show cooperative behaviours, kin selection should normally favour higher tolerance and thus stronger associations between related individuals. But avoidance of kin competition should reduce associations among related individuals (or increase aggression) when resources are indivisible (e.g. Foster & Briffa, 2014). Selection to reduce the degree of inbreeding should also favour associations of less related individuals for mating activity. Thus, social structure should still be influenced by relatedness in predominantly solitary species. We tested this hypothesis by comparing social network associations among individuals of known genotype in a population of a largely solitary living Australian scincid lizard. We predicted that tolerance of kin would lead to stronger social associations among more related individuals of the same sex, whereas avoidance of inbreeding would lead to stronger associations among less related individuals of the opposite sex.

The Australian sleepy lizard, *Tiliqua rugosa*, is a large, long-lived, Australian scincid lizard that occupies stable, overlapping home ranges (Bull, 1994; Kerr & Bull, 2006). 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 these partnerships in subsequent years (Bull, 1988, 1994, 2000; Bull & Burzacott, 2006; Bull, Cooper, &

Baghurst, 1998; Leu, Bashford, Kappeler, & Bull, 2010). The use of onboard activity and GPS loggers (Kerr, Bull, & Cottrell, 2004; Kerr, Bull, & Mackay, 2004; Leu et al. 2010) has allowed us to describe more cryptic and infrequent aspects of their social system beyond pair associations, which cannot be captured from snapshot observations.

Social networks based on synchronous spatial proximity 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 (Godfrey, Sih, & Bull, 2013; Leu et al. 2010). Our current study builds upon this previous research by exploring the genetic relationships between adult lizards in a social network. We tested the hypothesis that social associations among lizards were influenced by relatedness by determining whether the strength of social connections among lizards in the social network were positively (or negatively) correlated with relatedness to each other, compared with whether there had been random associations. Given that individuals that live closer together will have more opportunities to interact than those living further apart, we used a null model to generate expected rates of interaction based on shared space use. By controlling for spatial proximity (using the null model), we could specifically ask whether there was a social influence of genetic relatedness on network structure.

METHODS

The study was conducted from October to December 2010, in a 1.0×1.5 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, Bottema, & Bull, 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 min, and usually only 10–15 min. 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, Bull, & Cottrell, 2004; Kerr, Bull, & Mackay, 2004; Leu et al. 2010). GPS loggers were manufactured at Flinders University, Adelaide, Australia (Kerr, Bull, & Cottrell, 2004; Kerr, Bull, & Mackay, 2004). For our analyses, we considered all locations collected over the period 1 October–20 December 2010 (81 days), when the majority (ca. 90%) of lizards in the study area had data loggers attached. A radiotransmitter (Sirtrack, Havelock North, New Zealand) 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, Bull, & Cottrell, 2004; Kerr, Bull, & Mackay, 2004). The lizards did not grow substantially during the season, and for any lizards that had noticeably gained (or lost) weight between captures (12 days), we completely refitted the logger. Lizards foraged and mated normally with the loggers on (S. Godfrey, personal observation), and maintained weight levels throughout the study comparable to other lizards without loggers attached in adjacent areas. At the end of the study, all lizards were recaptured and we removed the units and released