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## Environment modulates population social structure: experimental evidence from replicated social networks of wild lizards



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Social structure is a fundamental component of a population that drives ecological and evolutionary processes ranging from parasite transmission to sexual selection. Nevertheless, we have much to learn about factors that explain variation in social structure. We used advances in biologging and social network analysis to experimentally test how the local habitat, and specifically habitat complexity, modulates social structure at different levels in wild populations. Sleepy lizards, *Tiliqua rugosa*, establish nonrandom social networks that are characterized by avoidance of some neighbours and frequent interactions with one opposite-sex individual. Using synchronous GPS locations of all adult lizards, we constructed social networks based on spatial proximity of individuals. We increased habitat structural complexity in two study populations by adding 100 short fences across the landscape. We then compared the resulting movement behaviour and social structure between these populations and two unmanipulated populations. Social connectivity (network density) and social stability, measured at weekly intervals, were greater in populations with increased habitat structural complexity. The level of agonistic interaction (quantified as scale damage) was also higher, indicating a fitness cost of greater social connectivity. However, some network parameters were unaffected by increased complexity, including disassortative mixing by sex, and at the individual level, social differentiation among associates (coefficient of variation of edge weights) and maximal interaction frequencies (maximal edge weight). This suggests divergent effects of changed ecological conditions on individual association behaviour compared to the resulting social structure of the population. Our results contrast with those from studies of more gregarious species, in which higher structural complexity in the environment relaxed the social connectivity. This shows that the response to altered ecological conditions can differ fundamentally between species or between populations, and we suggest that it depends on their tendency for gregarious behaviour.

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Local populations or subpopulations within species can vary in how individuals interact or associate with each other (Aplin et al., 2013; Dammhahn & Kappeler, 2009; Schradin & Pillay, 2005). Variation in this social structure can have profound implications for key ecological and evolutionary processes, including information transfer (Aplin et al., 2015; Webster, Atton, Hoppitt, & Laland, 2013), parasite transmission (Fenner, Godfrey & Bull, 2011; Leu,

Kappeler, & Bull, 2010) and selection pressures on individuals (Farine & Sheldon, 2015; McDonald, James, Krause, & Pizzari, 2013). Theory suggests that social structure reflects individual behaviour that maximizes fitness in the current environmental conditions (Emlen & Oring, 1977). That is, individuals should balance the benefits derived from social grouping or individual associations, which include social foraging, access to mating partners and group vigilance, against the costs of group living such as within-group competition for resources and parasite transmission through social contact (Cote & Poulin, 1995; Hamilton, 1971; Kappeler, Cremer, & Nunn, 2015; Kappeler & van Schaik, 2002; Komdeur, 1992; Vahl,

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Lok, van der Meer, Piersma, & Weissing, 2005). An important factor that can determine this balance is the habitat in which individuals live. Studying how social structure varies under different habitat structures will provide insight into the ecological drivers of sociality.

Habitat complexity is a ubiquitous aspect of the ecological environment. In this study, we examined its effects on social network structure and explored how different levels of complexity affect population processes relevant to social structure and individual fitness. Habitat complexity has been defined in many ways, but generally refers to the complexity of physical or topographic structure in the environment (Kovalenko, Thomaz, & Warfe, 2012). Increased habitat complexity may benefit individuals if it, for instance, reduces predator effectiveness (Warfe & Barmuta, 2004), improves escape behaviour from predators (Jensen, Gray, & Hurst, 2003) or reduces male – male competition for females (Myhre, Forsgren, & Amundsen, 2013). Conversely it may be disadvantageous if it reduces the ability to detect predators or increases intraspecific competition and agonistic behaviour for food (Petren & Case, 1998).

The level of habitat complexity might reflect resource and risk distribution patterns and it influences individual habitat use and where and when animals move to certain resources. This affects social interaction patterns among conspecifics. Habitat structural complexity might also affect social structure, if it has reached a level that reduces efficient movement or the detection of attractive conspecific cues, so that individuals may contact each other less frequently, reducing social network connectivity (Edenbrow et al., 2011; Orpwood, Magurran, Armstrong, & Griffiths, 2008; Webster et al., 2013). However, increased habitat complexity might also increase social connectivity by reducing the number of paths available and funnelling movements along particular pathways, or by inhibiting the spread and detection of conspecific cues that animals might use to avoid conspecifics.

We propose that the effects of habitat complexity on social behaviour will depend on the underlying social system. In some species, individuals form cohesive aggregations such as schools, flocks or herds. In other species, individuals are largely solitary and tend to avoid each other, or may only interact because of external (but not social) factors such as clumped resources that bring them together. Hence, the level of sociality may determine how habitat can shape movement and interaction rates. Some naturally aggregating species form larger groups in open spaces that lack refuges (presumably for individual safety in numbers), but separate into smaller groups or become solitary in more structurally complex habitats in which predators are less efficient (Caro, 2005; Orpwood et al., 2008). In these aggregating species, greater habitat complexity might reduce the ability of individuals to detect and join up with conspecifics, thus reducing group size independent of predation pressure (Gerard & Loisel, 1995). In social network terms, previous studies have reported that increased habitat structural complexity reduces network connectivity in gregarious, clustering species. For instance, sticklebacks, *Gasterosteus aculeatus*, form smaller subgroups and establish fewer social associations (lower network density) in more structured habitats (Webster et al., 2013). In contrast, in more solitary species in which social structure is predominantly driven by avoidance of conspecifics with overlapping home ranges, the effect of increased structural complexity can depend on whether it increases or decreases the ease of avoidance. For instance, Michael, Cunningham, and Lindenmayer (2010) reported that largely solitary tree skinks, *Egernia striolata*, aggregate with conspecifics more often in heterogeneous, complex habitats than in more homogeneous environments. Note that real social systems can feature both attraction (e.g. between mating partners or

family members) and avoidance (e.g. between same-sex competitors), influenced by a mix of the functional aspects of habitat complexity discussed above.

We experimentally tested the effect of increased habitat complexity on social network structure, and the consequences for social processes, in populations of sleepy lizards, *Tiliqua rugosa*. The sleepy lizard is a large, long-lived Australian skink (adult snout – vent length  $\geq 28$  cm), with a mainly herbivorous diet (Bull, 1995; Dubas & Bull, 1991). Individual lizards occupy overlapping home ranges within which they move around to forage. Across years with different food availability, sleepy lizard social networks have been shown to be relatively stable, despite interannual differences in the intensity of their pairing behaviour (Godfrey, Sih, & Bull, 2013). Here, we took an experimental approach and manipulated habitat structural complexity within lizard home ranges by introducing a maze-like structure of short lengths of fencing. Barriers that affect movement are common components of the environment for most populations and include rivers, habitat edges (Hansbauer et al., 2008; Rittenhouse & Semlitsch, 2006) and artificial structures such as roads, paths and fence lines (Taylor & Goldingay, 2010; Vanak, Thaker, & Slotow, 2010). Other structures, such as road underpasses and rope bridges, are used as conservation tools to redirect movement paths and to increase habitat connectivity (Taylor & Goldingay, 2010). Importantly, even permeable structures, such as human walking trails, can also alter movement paths of wildlife species, such as wolves, *Canis lupus* (Whittington, St Clair, & Mercer, 2004).

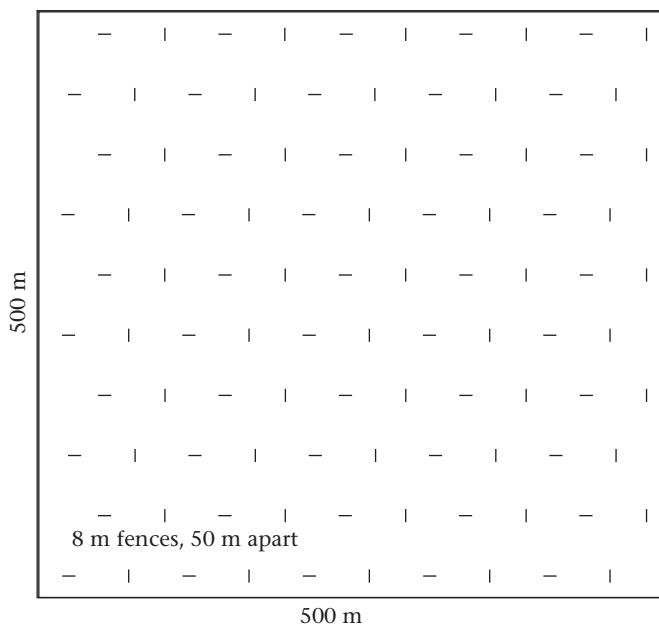
We tracked all adult individuals in four independent study groups with GPS data loggers to address three questions. First, we asked whether a change in the level of habitat complexity affected activity and movement patterns within individual home ranges. We predicted that during natural movement, for example when foraging, lizards in the more structurally complex habitats would need to move around the added fences to reach destinations, and would spend more time active and move further each day. Second, we asked how habitat complexity affected social network connectivity and stability. Sleepy lizards do not aggregate and their social networks are characterized by avoidance of some neighbouring conspecifics (Godfrey, Ansari, Gardner, Farine, & Bull, 2014; Leu, Bashford, Kappeler, & Bull, 2010). We predicted that network connectivity and temporal stability would be higher in the structurally more complex sites, either because the increased path lengths provide more opportunity for random encounters among individuals, or because the maze-like structure would channel movements of individuals along the same common paths. Finally, we asked how changes in the social network resulting from increased habitat complexity impacted local social processes. If individuals, which normally avoid each other, interacted more frequently, then we had two predictions. First, we predicted that many of these interactions would be agonistic and that we should expect to find evidence of higher levels of aggression. The second prediction was derived from the important exception to conspecific avoidance, which is that sleepy lizards form stable pair bonds and often stay in close proximity to one other individual for much of each day during early spring (Bull, 1988; Leu, Bashford, et al., 2010; Leu, Kappeler, & Bull, 2011). This typically results in a high coefficient of variation in interaction rates among associates. We predicted that, with greater habitat complexity, increased interaction rates with other neighbours would result in a smaller coefficient of variation in contact rates among associates, that is less differentiation between preferred and nonpreferred contacts (Whitehead, 2008). Our multifaceted approach explored experimental evidence to understand how environmental conditions modulate social structure at different levels, the consequences of changes in social structure, and how movement patterns can provide a

mechanistic link between the environment and the social structure.

## METHODS

### Study Site and Experimental Design

We conducted our study near Bunday Bore Station in the mid-north of South Australia (33°54'16"S, 139°20'43"E). The area is semiarid with an annual average rainfall of 238 mm (1925–2006). It is characterized by chenopod shrubland, dominated by blue-bushes, *Maireana sedifolia*, which cover approximately 20% of the area, with a ground cover of annual plants in between bushes (Kerr, Bull, & Burzacott, 2003). The study area experiences rapid changes in vegetation structure as the abundance and distribution of annual plants respond to periods of rainfall or drought. The sleepy lizard is most active during the austral spring and early summer of each year (mid-September to mid-December; Bull, 1987; Firth & Belan, 1998), the time when we conducted our study. In early spring 2012, we established four 500 × 500 m sites within the study area, separated by 0.5–1.0 km. We considered these sites to be independent because individual lizards have stable home ranges that are normally less than 200 m across (Bull & Freake, 1999). We used a one-factorial design with two replicates. We increased habitat structural complexity at two sites (maze sites) by building a maze of 100 fences within each of them. Each fence was an 8 m length of 15 cm high, brown plastic mesh, pegged to the ground with 30 cm high plastic stakes at 2 m intervals. Fences were arranged in 10 rows, 50 m apart. Each row contained 10 fences, also 50 m apart along the row, with fence orientation alternating by 90° for adjacent fences (Fig. 1). Half of the fences were oriented in a north–south direction, the other half in an east–west direction. The 100 fences, with a total length of 800 m, provided obstacles that lizards had to move around and increased the structural complexity in this open habitat. The other two unmanipulated sites acted as controls.



**Figure 1.** Fence design (fence length is not to scale). In each of the two manipulated maze sites 10 × 10 fences were built in an area of approximately 500 × 500 m. Fences were 8 m long, 50 m apart, along 10 rows that were also 50 m apart. The first fence in each fence row was offset 25 m relative to adjacent rows.

### Biologging Lizard Movement

We located and captured by hand all adult lizards resident in each site during August and September. There were 13 and 11 lizards in the two control sites, and 17 and 15 lizards in the two maze sites (we accounted for the difference in the number of lizards by using permutation tests, see below). The methods used to derive social networks and movement patterns have been described previously (Godfrey, Bradley, Sih, & Bull, 2012; Leu, Bashford, et al., 2010). Briefly, we attached GPS units to the dorsal surface of the tail of each lizard using surgical tape. GPS units weighed 37 g, or 4.9% of an average 750 g adult lizard and 7.4% of the lightest lizard in our study population. Synchronized locations of each lizard were recorded every 10 min every day, over the entire 3 month study period. The units also included a step counter, and new GPS locations were only recorded if a lizard had been active, defined as having taken at least one step in the previous 10 min. Each unit also contained a radiotransmitter with a unique radiofrequency allowing us to identify, locate and hand-capture each lizard, every 12 days, to download the GPS data and to renew batteries. Handling time was usually 15 min, and normally no longer than 30 min. Lizards with GPS units attached foraged normally (S. T. Leu, personal observation) and throughout the season maintained body mass levels similar to lizards without units attached living in adjacent areas. At the end of the study, we removed the units and released all lizards. We did not detect any adverse effect of the units on the lizards, which naturally shed their skin in the following months. We followed 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 our work under a Department of Environment, Water and Natural Resources Permit to Undertake Scientific Research.

### Effects on Activity, Movement and Home Range Size

We calculated for each lizard (1) its mean activity per day (total number of 10 min intervals during which the lizard was recorded as active divided by the number of days observed), (2) its mean movement per day (total distance moved in metres divided by number of days observed), and (3) its 95% minimum convex polygon home range size (in ha). This home range includes the exploratory zone outside the core home range area, important for encounters with neighbouring animals (Kerr & Bull, 2006a), but excludes outlier locations. Home ranges were calculated with the program Ranges 6 (Kenward, Walls, South, & Casey, 2008). We also calculated for each lizard the relative frequency of movements along the orientation of the fences. If, after encountering a fence, lizards changed their movement direction and followed the fence line we predicted a higher proportion of movement directions coinciding with the orientation of the fences in the maze than in the control treatment. We calculated movement directions by assuming straight line movement between consecutive location records. We considered that directions coincided with the orientation of the fence lines if they deviated by 10 degrees or less from either fence line orientation, and calculated for each lizard the proportion of all 10 min movements in these directions. For the lizards of the control sites, we used the same orientation as the fences and calculated the proportion of movements along the north–south and east–west directions, allowing for 10 degrees or less of deviation.

We separately analysed whether activity, movement, home range size (natural log-transformed) and the proportion of movement directions along fence lines (arcsine transformed) differed between maze and control sites. We used univariate two-factor

nested ANOVAs with treatment as a fixed factor and replicate as a random factor nested within treatment. We performed these analyses in IBM SPSS Statistics Version 20, with model syntax DESIGN = Treatment Replicate(Treatment).

#### *Inferring Lizard Social Networks from Spatial Locations*

From the location data we inferred social interaction between two lizards if they were close to each other. We used methods previously described (Leu, Bashford, et al., 2010) that allow for variation in the precision of the GPS readings and considered two lizards to have been in contact if their synchronized location records were within 14 m of each other. This distance is well within the visual perceptual range of a sleepy lizard (Auburn, Bull, & Kerr, 2009) and could quickly be covered as lizards may move more than 2000 m a day (Kerr & Bull, 2006b). We, nevertheless, acknowledge that our estimate of proximity could overestimate the real frequency of lizard social contacts. However, this would affect contact frequencies estimated for both maze and control groups equally, allowing comparisons between treatments. A special case of contact was when two individuals were on opposite sides of a fence. The 8 m length of each fence constituted a small fraction of the 2000 m a lizard can move during a day, which would minimize the likelihood of two lizards encountering each other directly at a fence. Furthermore, the fences were made of plastic mesh that should allow visual or olfactory awareness of other lizards on the other side of the fence, and justifying our classifying these as social contacts.

#### *Statistical Significance Testing Using Permutation Tests*

Social networks can appear to be structured and nonrandom even when derived from random data (Farine & Whitehead, 2015). We wanted to know whether our networks were differently structured than expected from random. Hence, all of our hypothesis testing was based on null models constructed by multiple permutations of the observed data within each study site (Farine & Whitehead, 2015). Following Godfrey et al. (2014), we used a hybrid between node-based and data-stream permutations to account for the temporal autocorrelation structure in the GPS tracks. This involved randomizing the lizard identities of entire daily tracks through randomly assigning different identities from among the lizards at the same site across different days. We then reconstructed the network, derived the same network parameters and conducted the same analysis as we did for the observed data. Randomizations were repeated 1000 times and *P* values for each effect were calculated by comparing the coefficient from the model based on the observed data to the distribution of coefficients from the same model based on the randomized data (herein  $P_{\text{rand}}$ ) (Boogert, Farine, & Spencer, 2014). Hence, because each instance of the randomized data contained the same number of individuals and associations as the observed data, our analysis accounted for the potential for significant effects resulting from our sampling regime (see Box 5 in Farine and Whitehead (2015) for an example). We considered effects to be significant if the coefficient values fell outside the 95% range of the random coefficient distribution.

#### *Effect on Weekly Binary Network Structure*

We analysed whether social network density, stability and assortativity in relation to sex were different in structurally more complex habitats compared to control sites. For each of the four sites, we derived a social network from each of the 12 weeks of the study period, forming 12 replicated observations of social structure per site. Binary networks were created using the package *asnipe*

(Farine, 2013) in R (R Core Team, 2013), with association matrices defining an edge between nodes if two individuals were observed in direct contact at least once during the week. For each weekly replicate we calculated network density, a measure of connectedness, as the number of connecting edges in the network relative to the number of possible edges ( $\frac{N \times (N-1)}{2}$  possible edges,  $N$  = number of individuals). We also measured network stability each week as the proportion of network edges that remained present in each consecutive week. To derive this parameter we divided the number of edges that were consistent between two consecutive time steps ( $t_i$  and  $t_{i+1}$ ) by the sum of the total number of unique edges present across both time steps. We calculated assortativity by sex for each weekly network, a measure of whether associations were typically between individuals of the same or different sex, using the R package *assortnet* (Farine, 2014). Finally, we constructed generalized linear mixed models (GLMMs) with treatment as a fixed effect and site and time period (week) as random effects to test how spatial complexity affected the observed network density, network stability and network assortativity. We ran these same models with randomized permutations of the network data to evaluate statistical significance.

#### *Effect on Long-term Social Differentiation*

To investigate how habitat structural complexity affected social differentiation among associated individuals over an extended period, we aggregated all association data and constructed one weighted network for each site for the whole study period (12 weeks). Network edge weights were calculated using the simple ratio association index (SRI), which represents the proportion of times while active that a pair of individuals was recorded in contact (i.e. the number of times a pair of individuals was detected active and in contact divided by the total number of times when both individuals were recorded as active). This is a relative measure of contact frequency and allows direct comparisons of association strength among lizard dyads with different numbers of observations. To determine whether habitat structural complexity affected the heterogeneity in association patterns, we calculated the coefficient of variation (CV) of edge weights for each individual and used that as a measure of social differentiation among its contacts (Whitehead, 2008). High values of CV represent repeated interactions (high edge weights) with a few individuals and few interactions (low edge weights) with other individuals. This pattern is generally associated with social differentiation or preferred and avoided relationships. Low values of CV represent a more even level of interaction with other individuals in the population, often associated with a low level or no social differentiation. We also measured the maximum edge weight for each individual. As above, we used GLMMs to estimate the effects of treatment (habitat structural complexity) on social differentiation and maximum association strength. In these analyses, with only one network per site, we used site as a random effect.

We also investigated the effect of structural complexity on rates of agonistic interaction. At the end of the study we recorded the cumulative scale damage on each lizard. Visual observations of fights between two lizards are rare (Kerr & Bull, 2002), but damaged scales that result from these fights can be used as an indirect measure of agonistic and aggressive interactions (Murray & Bull, 2004). Under natural conditions, sleepy lizards shed their skin once a year, in between activity seasons. New scale damage acquired after shedding is clearly identifiable as being from the current activity season. We were interested in whether accumulated scale damage counts, recorded at the end of the season, differed between lizards from the maze and control sites. We further investigated what patterns of interactions were most



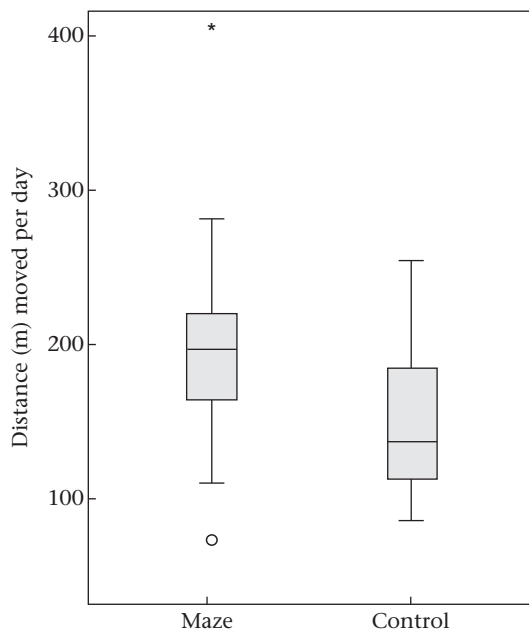
strongly associated with scale damage. For each individual, we identified whether their strongest associate was or was not of the same sex and derived a categorical variable which we called ‘sex of strongest associate: same or different’. We constructed a GLMM with treatment, sex and sex of strongest associate: same or different as fixed effects and with site as a random effect to test whether scale damage differed in relation to habitat complexity or between males and females. This also enabled us to test whether individuals most strongly connected to associates of the same sex experienced higher rates of agonistic interactions. We did not include an interaction term in the model due to our limited sample size. Because these data are also based on the associations inferred from the social network, we calculated significance for each effect using the randomization procedure described above.

## RESULTS

The average number of observation days per lizard did not differ between treatments (median for maze sites = 70 days, control sites = 72 days; Mann – Whitney test:  $U = 347.000$ ,  $N_1 = 32$ ,  $N_2 = 24$ ,  $P = 0.539$ ), and thus we did not account for individual observation length in further analyses.

### Effects on Activity, Movement and Home Range Size

Lizards at the maze sites did not differ in the mean duration of their daily activity over the study period (estimated marginal mean number of 10 min intervals per day = 17.616) from lizards at the control sites (mean = 14.976;  $F_{1,52} = 6.434$ ,  $P = 0.120$ ), but moved longer mean distances per day ( $F_{1,52} = 19.977$ ,  $P = 0.039$ ; Fig. 2). Home range size (in ha) did not differ between maze sites (estimated marginal mean of natural log transformed data = 0.971) and control sites (mean = 1.330;  $F_{1,52} = 5.098$ ,  $P = 0.146$ ). The proportion of movements along the orientation of the fences did not differ between maze sites (estimated marginal mean of arcsine transformed data = 0.262) and control sites (mean = 0.251;  $F_{1,52} = 1.126$ ,



**Figure 2.** Lizard movement per day at the maze and the control sites (data were pooled across the two replicates). Box plots show the median, first and third quartile; whiskers extend to 1.5 times the interquartile range. Circles and stars indicate values greater than 1.5 times and 3 times the interquartile range, respectively.

$P = 0.398$ ). Lizard behaviour was not significantly different between replicates nested within treatments, either for mean duration of daily activity ( $F_{2,52} = 0.829$ ,  $P = 0.442$ ), mean daily distance moved ( $F_{2,52} = 0.458$ ,  $P = 0.635$ ), home range size ( $F_{2,52} = 0.842$ ,  $P = 0.437$ ) or proportion of fence line oriented movements ( $F_{2,52} = 2.792$ ,  $P = 0.071$ ).

### Effect on Weekly Binary Network Structure

At the level of the population, the density of the weekly social networks was significantly higher in the maze sites (mean density = 0.073,  $N = 24$ ) than in the control sites (mean density = 0.050,  $N = 24$ ; Table 1, Fig. 3a). Although our study populations were slightly larger in the maze sites than in the control sites, our analysis method accounted for this, and the difference in network density between experimental treatments exceeded any effect of the different population sizes. Network stability over time was also higher for maze sites (mean = 0.3) than for control sites (mean = 0.17; Table 1, Fig. 3b). Network assortativity by sex of the weekly binary networks was not significantly different between maze and control sites (Table 1, Fig. 3c).

### Effect on Long-term Social Differentiation

Fig. 4 shows the social networks of the four study groups, based on aggregated data over the 12 weeks. All four networks showed disassortative mixing by sex ( $r = -0.652$ ,  $P_{\text{rand}} = 0.003$ ,  $r = -0.491$ ,  $P_{\text{rand}} = 0.118$  for both maze sites and  $r = -0.812$ ,  $P_{\text{rand}} = 0.061$ ,  $r = -0.813$ ,  $P_{\text{rand}} = 0.005$  for the control sites, respectively), illustrating the predominantly pair-living social organization of the sleepy lizard. At the local level of the individual in the network, we found no effect of habitat complexity on the coefficient of variation of dyadic association frequencies (Table 1, Fig. 5a) nor on the value of the maximum association frequency (Table 1, Fig. 5b). There appeared to be a trend for higher scale damage in maze sites than control sites, although this was not significant (Table 2). Individuals whose strongest edge was with individuals of the same sex had significantly more scale damage than those more strongly associated with the opposite sex. Sexes did not differ significantly in the amount of scale damage (Table 2).

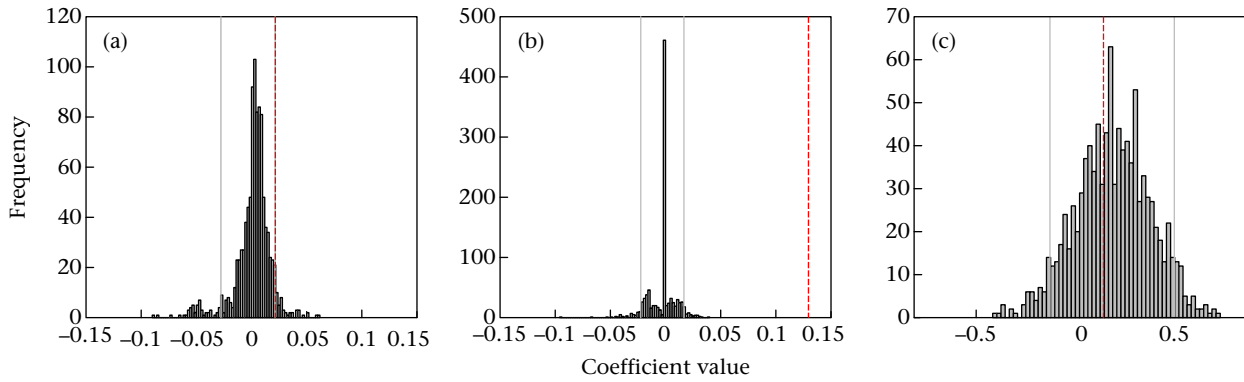
## DISCUSSION

Our results suggest that the habitat occupied by a population, in particular the level of habitat structural complexity, can modulate the social structure of a nongregarious species. While the social structure of the populations we examined differed between habitats of different structural complexity, social differentiation within the populations was similar. This illustrates the divergent effects of an environmental factor at different levels of the social structure.

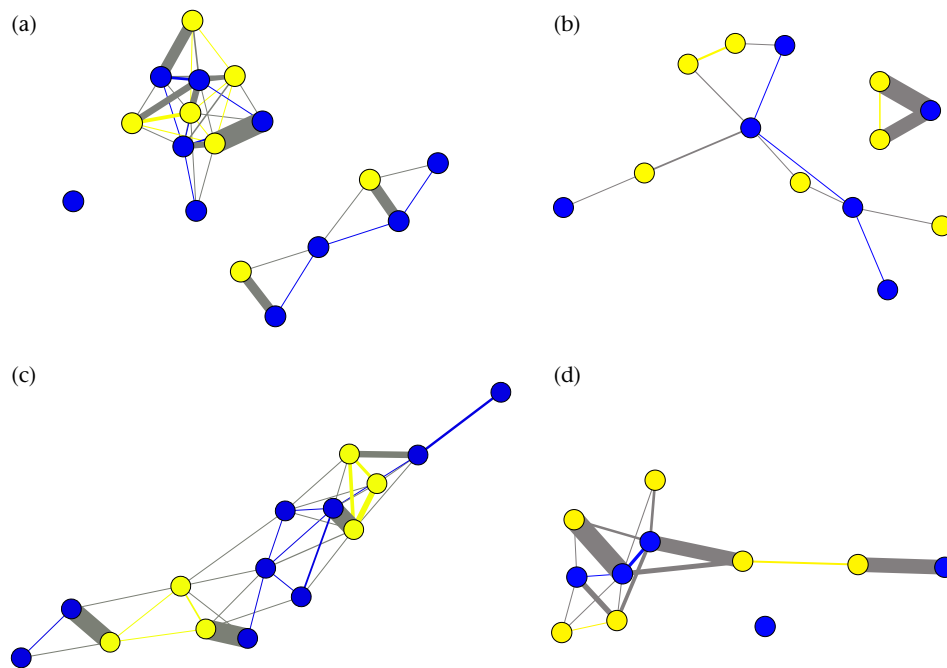
**Table 1**  
Effects of habitat structural complexity on social network structure

	Coefficient	SE	<i>t</i>	$P_{\text{rand}}$
<b>Global population level</b>				
Density of weekly social network	0.022	0.015	1.453	0.035
Network stability over time	0.128	0.052	2.433	<0.001
Assortativity of weekly social network	-0.302	0.096	-3.147	0.219
<b>Local individual level</b>				
Coefficient of variation	8.873	28.767	0.308	0.622
Maximum association frequency	0.046	0.036	1.262	0.111

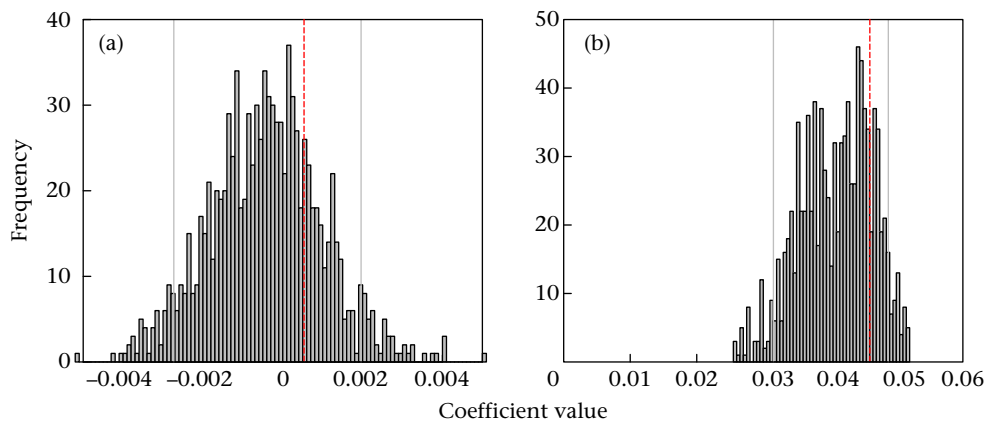
For the analyses on the global population level, the GLMM formula in R was  $\text{lmer}(\text{Density} \sim \text{Treatment} + (1|\text{Site}) + (1|\text{Period}))$ , and respectively for all other dependent variables. On the local individual level the GLMM was  $\text{lmer}(\text{CV} \sim \text{Treatment} + (1|\text{Site}))$ , and respectively for maximum association frequency.



**Figure 3.** Comparison of the coefficient from the GLMM based on the observed data (dashed vertical line) and the frequency distribution of coefficients from the same model based on the randomized data (95% CI shown by solid vertical lines): (a) network density, (b) network stability over time, (c) network assortativity by sex.



**Figure 4.** Weighted social networks of (a, c) sites with habitat manipulations and (b, d) control sites. We aggregated the association data over the study period of 12 weeks and constructed one weighted network for each site. Blue nodes are males; yellow nodes are females.



**Figure 5.** Comparison of the coefficient from the GLMM based on the observed data (dashed vertical line) and the frequency distribution of coefficients from the same model based on the randomized data (95% CI shown by solid vertical lines): (a) coefficient of variation of dyadic association frequencies, a measure of social differentiation and (b) maximum association frequency.

**Table 2**  
Factors that affected individual scale damage

	Coefficient	SE	<i>t</i>	<i>P</i> <sub>rand</sub>
Habitat structural complexity	0.249	0.196	1.269	0.062
Sex of strongest associate: same or different	0.507	0.254	1.997	0.010
Sex	0.341	0.190	1.759	0.361

The GLMM formula in R was `lmer(ScaleDamage ~ Treatment + SameSex + Sex + (1|Site))`.

### Effects on Activity, Movement and Home Range Size

Habitat structural complexity affected lizard movement. Individuals moved longer average distances per day in the more complex habitat, although their daily duration of activity and home range size did not differ between treatments. This suggests that lizards moved longer distances either at a faster pace or for more of the 10 min recording intervals. The 8 m long fences were short relative to the daily movement capabilities of sleepy lizards (Kerr & Bull, 2006b), and the observed difference in mean distance moved per day suggests that lizards moved around the fences to continue along their original path trajectories. Alternatively, we considered the possibility that lizards may have changed their movement more extensively, and after encountering a fence followed the direction of the fence line beyond its length before readjusting their path trajectories. However, we did not find empirical evidence from the maze treatment for a significantly higher proportion of path movements along the direction of the fences. Nevertheless, after encountering fences, lizards may have moved along their direction, but for less than 10 min. More frequent GPS locations would have been needed to detect this pattern.

### Effect on Weekly Binary Network Structure

In the maze treatment, with increased habitat structural complexity, sleepy lizard populations were significantly more connected (higher network density) and social structure was significantly more stable across weekly intervals than in the control treatment. Individuals interacted with more conspecifics and contacted them more often. While we recorded low network densities in both the maze and control sites, we argue that the observed 46% increase in network density represents a relatively large and biologically relevant increase, compared to the control sites. Low social network density is commonly reported in animal populations (Farine et al., 2015; Madden, Drewe, Pearce, & Clutton-Brock, 2009), particularly in those that are spatially structured and where spatial structure, such as partial home range overlap, constrains most individual interactions to those among neighbouring individuals. Our findings and study species fit this pattern.

One explanation for the increased network connectivity in the structurally more complex habitat can be derived both from empirical studies linking individual spatial behaviour and movement with interaction frequencies (Jeanson, 2012) and from the ideal gas model. The ideal gas model predicts encounter rates assuming random movement at a constant speed while taking the local population density, detection distance and group spread into account (Hutchinson & Waser, 2007). These empirical studies and the ideal gas model suggest that individuals that share space interact more frequently if they are moving more (Pinter-Wollman, Wollman, Guetz, Holmes, & Gordon, 2011). For the lizards in our study, the higher network density and network stability in the more complex habitats could simply result from a general increase in interaction frequencies, as well as repeated interactions among neighbouring individuals across time, owing to the greater

distances moved by individuals when mazes were present. However, we have previously shown that sleepy lizard interaction frequencies are not simply predicted by the random movements assumed in the ideal gas model (Leu, Bashford, et al., 2010).

A second and not mutually exclusive explanation for the observed changes in network structure is that the fences forced lizards to move along similar paths. All fences were oriented along two axes. This could channel lizard movement along two main axes, and thus could increase the likelihood and rate of encountering neighbours that may otherwise be avoided. Although we found no evidence that the fences significantly channelled lizard movement along their orientation, we could not reject this hypothesis without more frequent location records. Independent of the relative importance of these two explanations, our results suggest altered movement behaviour is likely to be the mechanistic driver of the greater social connectivity in the more structurally complex habitats.

### Effect on Long-term Social Differentiation

We found sex disassortativity in both treatments, and lizards preferred to associate with opposite-sex individuals. This seems to be a common pattern among many animal networks (Farine, 2014). Neither the level of sex disassortativity nor, at the individual level, social differentiation and maximum interaction frequencies were significantly affected by different levels of habitat structural complexity in our experiment. Previous studies have shown that the social structure of the sleepy lizard differentiates into core units (opposite-sex pairs) with strong affiliative bonds and a series of weaker connections with other neighbours (Leu, Bashford, et al., 2010; Leu et al., 2011). Our analyses were consistent with that, and indicated that the core social organization (strong bonds among male – female pairs) was not affected by differential habitat complexity. The weaker interactions are often agonistic, and we have previously reported both that more aggressive males show more fresh scale damage and that males that interact more with other males than with females have relatively more scale damage (Godfrey et al., 2012). Thus, we consider scale damage to be a reliable measure of agonistic interaction. In the current study, a trend for lizards in more complex habitats to have more scale damage suggests a positive link between the greater social network connectivity and the frequency of agonistic interactions. Agonistic interactions in other species often result from an escalation of competition for resources. In our study, lizards with stronger network links to same-sex individuals sustained greater scale damage, consistent with reports that both male and female sleepy lizards normally exclude same-sex individuals from inner core areas of their long-term stable home range (Kerr & Bull, 2006a). In contrast with other studies (Murray & Bull, 2004), we found equal levels of scale damage in males and females. Although home ranges outside the core areas overlap among adjacent neighbours, they often avoid contact (Godfrey et al., 2012; Leu, Bashford, et al., 2010). Collectively, this suggests intrasexual competition in both males and females, which individuals can usually ameliorate through temporal avoidance in commonly used spaces.

At the population level, social structures are increasingly recognized as heterogeneous and dynamic, both in space and time and across contexts (Cantor et al., 2012). Our understanding of the ecological variables that drive those heterogeneities is still limited. Local food abundance (Foster et al., 2012) can affect social structure. For example killer whales, *Orcinus orca*, form a more interconnected social network when food is abundant (Foster et al., 2012). Other ecological factors that can influence social structure include predation pressure (Kelley, Morrell, Inskip, Krause, & Croft, 2011), habitat disturbance (Lattanzio & Miles, 2014) and habitat



shape, such as linear estuarine systems that affect ranging patterns (Murdoch Titcomb, O'Corry-Crowe, Hartel, & Mazzoil, 2015). Here, we have shown that higher levels of habitat structural complexity led to increased social connectedness at the population level in a nongregarious species. At the same time social differentiation at the individual level was unaffected by structural complexity, with similar levels of heterogeneous interaction frequencies and sex-disassortative mixing in both treatments. Our results contrast with those from more gregarious species, in which higher structural complexity relaxed the social connectedness (Edenbrow et al., 2011; Orpwood et al., 2008; Webster et al., 2013). We suggest that the response to altered ecological conditions can fundamentally vary among species and among populations within species, depending on their tendency for gregarious behaviour.

A change in environmental conditions that increases social connectivity could result in increased cooperation and improved information flow in gregarious and highly cognitive species (Aplin et al., 2015; Cantor & Whitehead, 2013). However, in less gregarious species, it could also result in increased parasite transmission (Cote & Poulin, 1995; Leu, Kappeler, et al., 2010; Naug, 2008) and greater conflict and competition for local resources with negative fitness consequences. Conflict, for instance, can reduce direct reproductive success due to fighting among group members and chronic stress (Young et al., 2006). An evolutionary feedback loop might develop in nongregarious species, driven by the opposing effects of the ecological environment (with greater connectedness as a response to habitat complexity) and the social environment (with lower connectedness as a response to agonistic interactions). This argument might extend to gregarious species so that social structures might generally respond dynamically to perturbations in the ecological environment to achieve a balance of benefits and costs. Future research is needed to validate this generalization. Nevertheless, social structures that both flexibly adjust to perturbed external constraints and also recover once the constraints are removed have been shown in a mixed-species bird community (Firth & Sheldon, 2015) and in dolphins, *Tursiops aduncus* (Ansmann, Parra, Chilvers, & Lanyon, 2012). In the sleepy lizard we have demonstrated both a flexible social structure that responded to structural habitat complexity (this study) and a stable structure across years that differed in rainfall and food availability (Godfrey et al., 2013). Hence, the social structure may respond differently to perturbation of different ecological factors. Alternatively, changes within one year may integrate into a stable social structure across years. This is consistent with suggestions by Cantor et al. (2012) that the spatiotemporal scale is important to identify social processes.

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