Animal Behaviour 111 (2016) 23–31

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

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

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ARTICLE INFO

Article history:
Received 1 June 2015
Initial acceptance 7 July 2015
Final acceptance 16 September 2015
Available online
MS. number: 15-00467R

Keywords:
environmental variation
habitat complexity
lizard
movement
Scincidae
social network
social structure

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.

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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http://dx.doi.org/10.1016/j.anbehav.2015.10.001
0003-3472/

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 ≥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