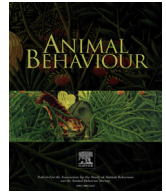




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Where should we meet? Mapping social network interactions of sleepy lizards shows sex-dependent social network structure

Orr Spiegel ^{a,*}, Andrew Sih ^a, Stephan T. Leu ^{b,1}, C. Michael Bull ^b^a Department of Environmental Science and Policy, University of California, Davis, CA, USA^b School of Biological Sciences, Flinders University, Adelaide, Australia

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Social network analyses allow researchers to describe patterns of social interactions and their consequences in animal societies. Since direct observations in natural settings are often difficult, researchers often use tracking technologies to build proximity-based social networks. However, because both social behaviour (e.g. conspecific attraction) and environmental heterogeneity (e.g. resources attracting individuals independently) affect rates of interaction, identifying the processes that shape social networks is challenging. We tracked sleepy lizards, *Tiliqua rugosa*, using global positioning system (GPS) telemetry to investigate whether they show conspecific attraction or avoidance beyond any shared space use driven by environmental heterogeneity. Since these lizards have strong pair bonds and nonoverlapping core home ranges, we predicted different interaction rates between inter- and intrasex dyads and compared social network indices among dyad types (male–male, female–female and intersex) using node-identity permutation tests. We also mapped interactions onto the home ranges (using distance from the centre as an index) and contrasted observed social networks with those expected from a spatially explicit null model. We found that dyad types differed in their interaction patterns. Intersex dyads had stronger connections (higher edge weight) than a null expectation, and stronger than for same-sex dyads. Same-sex dyads did not differ in edge weight from the null expectation, but were significantly more common (higher degree). Males had larger home ranges than females and consequently male–male dyads interacted further away from their home range centres. Moreover, the locations of these interactions also differed from the null expectations more strongly than other dyad types. Hence, we conclude that males predominantly interacted with each other at the peripheries of their home range, presumably reflecting territorial behaviour. By applying a novel analysis technique, we accounted for the nonsocial component of space use and revealed sex-specific interaction patterns and the contribution of conspecific attraction to the social structure in this species. More generally we report how mapping the locations of nonrandom interaction rates provides broad information on the behaviours they represent.

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Social networks offer a powerful tool for exploring processes such as information transfer, disease spread and collective movements in animal societies (Bode, Wood, & Franks, 2011; Krause, James, & Croft, 2010; Pinter-Wollman et al., 2014). Individuals in the population can differ in their number of partners (termed degrees in network theory), or interaction rates with a given partner (i.e. edge weight), and these differences may have implications for

the ecological process in question. Thus, quantifying the variation in social network metrics and the mechanisms underlying it are key issues for social network studies (Sih, Hanser, & McHugh, 2009; Spiegel, Leu, Bull, & Sih, 2017). Yet, application of social networks to free-ranging species is limited by our ability to collect data and by the availability of appropriate analytical methods for extracting biologically meaningful insights from these data sets. Many social network studies from natural settings focus on species with relatively strong group cohesion and sociality, where social interactions within groups can be easily observed. Examples include studies of baboons (Wittig et al., 2008), guppies (Croft et al., 2009) and zebras (Sundaresan, Fischhoff, Dushoff, & Rubenstein, 2007). Direct observations of social interactions are harder for species in which individuals are solitary or spend little time within groups, but those

* Correspondence and present address: O. Spiegel is now at the Mitrani Department of Desert Ecology, Jacob Blaustein Institutes for Desert Research, Ben Gurion University of the Negev, Midreshet Ben-Gurion, Israel.

E-mail address: orr.spiegel@mail.huji.ac.il (O. Spiegel).

¹ S. T. Leu is now at the Department of Biological Sciences, Macquarie University, Sydney, Australia.

methodological obstacles can be overcome with various biologging techniques. Proximity sensors, passive transponders and global positioning system (GPS) tags allow simultaneous tracking of multiple individuals in their natural habitat, broadening the spectrum of species whose social networks can be studied to include songbirds (Firth, Sheldon, & Farine, 2016), lizards (Leu, Bashford, Kappeler, & Bull, 2010) and badgers (Böhm, Palphramand, Newton-Cross, Hutchings, & White, 2008), among others.

In biologged data sets, social interactions are often interpreted from spatial associations (two individuals co-occurring within a threshold distance) to build proximity-based social networks. This approach presents new challenges for data analysis and for identifying the processes that shape the observed social networks. First, determining the correct threshold distance that defines an interaction, or the nature of interaction (e.g. affiliative versus agonistic) are often problematic (Castles et al., 2014; Farine, 2015; Haddadi et al., 2011). Second, both environmental heterogeneity and 'true' social behaviour (i.e. when individuals actively attract or avoid others; Godde, Humbert, Côté, Réale, & Whitehead, 2013; Whitehead & James, 2015) might jointly affect observed network structure. Stochastic noise and the localized presence of an attractive resource (e.g. a waterhole) may lead to high association rates (independent of sociality) falsely suggesting conspecific social attraction. Third, the ambiguity between these alternative mechanisms (sociality versus environmental heterogeneity and pure chance) limits our ability to compare between social networks. Permutation tests, such as node-identity swapping, allow accounting for various dependencies in the data when comparing social networks (Croft, Madden, Franks, & James, 2011), but usually do not inform us about the reason(s) for observed differences. For instance, if individuals in network A are more connected than those in B, even after correcting for density-dependent effects, is this difference due to the fine-scale spatial arrangement of their home ranges, the way their resources are distributed, or their stronger conspecific attraction? Fourth, and superimposed on other issues, individuals with different phenotypes (e.g. different sex, morphology or behavioural type) can respond differently to their environment or to the composition of their social groups (Farine, Montiglio, & Spiegel, 2015). This challenges our ability to relate observed patterns to their biological causes. For instance, within a site, males may have higher network degree than females simply because their different food resources force them to move differently in space and encounter more individuals.

Many of these challenges can be addressed by contrasting observed networks with expectations from null models that test specific hypotheses, and that go beyond simple social network data permutations (Farine, 2017). Alternative null models that have been used in this context vary in complexity and realism of assumed processes (e.g. in the movements expected under the null hypothesis). Examples include the 'ideal gas model' (which assumes homogeneous space use within the home range; Godfrey, Sih, & Bull, 2013; Leu et al., 2010), the 'DigiRoo' model, which accounts for spatial, but not temporal, heterogeneity (Carter, Macdonald, Thomson, & Goldizen, 2009), and data stream randomization-based null models, which randomize track identity rather than the association matrix (Farine, 2015; Farine, Firth, et al., 2015; Spiegel, Leu, Sih, & Bull, 2016). A hypothesis-driven null model approach can also be used to explore phenotype-specific deviations from expectation, or to identify the specific network indices contributing to those differences. Identifying deviations in degree, edge weight or betweenness centrality can offer a better understanding of the biological processes and their implications. For instance, if a virulent disease is readily transmitted through superficial encounters, then deviations from null expectation in network degree will be important in modelling the spread of the

disease. In contrast, if an information transfer depends on extended interactions, deviations in edge weights from null expectations will be more informative.

Proximity-based social networks are typically data-rich compared to their alternatives (Farine & Whitehead, 2015). For many of the tracking sensors they also include data on where the interactions occur (i.e. in which habitat, or where in the home range), which can inform us on the factors that shape them, the behaviours they reflect (which is often missing in these networks) and their ecological outcomes. For instance, territorial birds may preferably interact at the territory periphery when defending it, and near the centre when engaging in reproduction (Giuggioli, Potts, & Harris, 2011). In nonterritorial species, interactions associated with foraging and competition are likely to happen near food patches. The importance of spatial context is well acknowledged in social network studies (Jacoby & Freeman, 2016; Wolf & Trillmich, 2008). Yet, surprisingly, potentially insightful spatial analysis is almost absent from social network studies. In a rare example, Pinter-Wollman (2015) mapped social interactions among foraging ants to demonstrate how nest architecture shaped both social network structure and the collective foraging performance of the colony. We propose that the locations of observed interactions could be compared with those expected from a null model (in addition to interaction rates). If observed interaction locations differ from expected (i.e. indicating preferential locations), then the traditional questions of 'who to interact with whom and how strongly' could be complemented with new questions about where individuals interact and whether they show spatial preference.

In this study we tracked sleepy lizards, *Tiliqua rugosa*, with GPS tags to ask whether they show conspecific attraction (or avoidance; note that here attraction refers to spatial associations and does not imply affiliative interactions) beyond expectations from constraints imposed by their environment, and whether social interaction patterns differ between inter- and intrasex interactions. Sleepy lizards form monogamous pair bonds, and both sexes occupy stable overlapping home ranges with more exclusive core areas, shared mostly with their sexual partners (Kerr & Bull, 2006a). Males are generally more active and aggressive (Leu, Kappeler, & Bull, 2011; Murray & Bull, 2004). Based on earlier work and the basic social system, counteracting predictions can be made. Males, for example, might have higher degree than females simply because they cover nearly twice the distance daily (Kerr & Bull, 2006b) but lower degree than females because of male–male aggression; applying the ideal gas null model to this system showed avoidance among males (Leu et al., 2010). Both of these effects may be mediated by differences in attraction to areas with more resources or refuges (Spiegel, Leu, Sih, Godfrey, & Bull, 2015). In this system, as in many others, new tracking and analytical methods allow us to finally test the above contradicting predictions about males' degree and understand the reasons for observed patterns. To do so, we construct social networks for the population, explore differences between dyad types (among males, among females and intersex), map interactions to their location in the home range and contrast observed patterns with those expected from a spatially explicit null model.

METHODS

The Study System and Tracking Methods

Sleepy lizards are large (ca. 30 cm snout–vent length), long-lived Australian scincid lizards. Their diet relies mostly on annual plants that grow after winter rains and become unavailable as they dry out during the hot, dry summer (Dubas & Bull, 1991). Their activity is constrained to periods of mild weather conditions during

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