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Integrating social networks, animal personalities, movement ecology and parasites: a framework with examples from a lizard

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We describe a conceptual framework integrating animal personalities, movement ecology, social networks and parasite transmission. For directly transmitted parasites, parasite transmission depends on social interaction patterns that can be quantified using social network metrics. For indirectly transmitted parasites, the key can be transmission networks that quantify time-lagged contacts (e.g. where potential hosts visit locations used earlier by infected hosts). Social network connections (time-lagged or not) often result from shared space use determined by individual movements in response to key environmental factors. Movement ecology provides a framework for understanding these responses. Finally, individuals with different personalities likely respond differently to environmental factors in ways that influence the movements and space use that underlie network connectivity, which, in turn, affects parasite loads and transmission. We illustrate these key points with recent work on sleepy lizards, *Tiliqua rugosa*, and their ticks. By GPS tracking of nearly all adult lizards at our site, we found that lizards that more frequently shared the same refuges (where ticks detach and reattach to a new host) used earlier by other lizards tended to indeed have higher tick loads. Higher shared refuge use was associated with greater shared space use, in general. Shared space use with conspecifics was reduced by the lizards' general propensity (quantified by analyses of 279 985 GPS locations for 72 lizards) to avoid conspecifics, but enhanced by their general tendency to prefer areas with more resources and better refuge (in particular, late in the season when food was scarce and conditions were hotter and drier). Both of these tendencies were personality dependent. Less aggressive lizards exhibited both a stronger attraction to areas with more food and better refuge, and a stronger tendency to avoid other lizards. We conclude by discussing implications of our results for the general conceptual framework and suggest future directions.

Numerous recent studies have noted the value of using a social network approach to quantify social structure, the pattern of interactions among individuals in a social group (Pinter-Wollman et al., 2014; Wilson, Krause, Dingemanse, & Krause, 2013). Key related issues include understanding (1) determinants of social networks – factors that explain differences among individuals or groups in social network metrics (Aplin et al., 2013; Boogert, Farine, & Spencer, 2014; Ilany, Booms, & Holekamp, 2015; Sih, Hanser, & McHugh, 2009) and (2) consequences of social networks – how social networks affect individual or group outcomes (e.g. parasite transmission (Keiser et al., 2016), information flow (Aplin et al., 2015; Pinter-Wollman, Guetz, Holmes, & Gordon, 2011), dispersal (Blumstein, Wey, & Tang, 2009), evolution of cooperation (Ohtsuki, Hauert, Lieberman, & Nowak, 2006) or patterns of sexual selection (McDonald, 2007; Oh & Badyaev, 2010). Here, we combine information on determinants and consequences of social networks in an integrated framework focusing, in particular, on parasite transmission. Specifically, we outline connections between animal personalities (Sih, Bell, & Johnson, 2004), movement ecology (Hansson & Akesson, 2014; Nathan et al., 2008), social networks and parasite loads and transmission. We suggest that in many systems, spatial and temporal variation in the ecological and social environment interact with individual differences in personality to influence individual movements that underlie social networks, which, in turn, drive parasite transmission (as well as numerous other important ecological and evolutionary outcomes). We next outline our conceptual framework and review key components in more detail. We then illustrate main

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portions of this framework by summarizing data from a study on Australian sleepy lizards, *Tiliqua rugosa*, and their ticks. Although much of the data we present was published in earlier papers (during 2010–2016), the integration of the separate parts is new, and in the discussion we highlight new insights from this integration.

CONCEPTUAL FRAMEWORK

Social networks can play an important role in determining parasite (or information) transmission whenever social interactions directly or indirectly facilitate transmission (Pastor-Satorras, Castellano, Van Mieghem, & Vespignani, 2015; Stegehuis, van der Hofstad, & van Leeuwaarden, 2016; Wang, Andrews, Wu, Wang, & Bauch, 2015). As a broad generality, higher social connectivity should tend to result in greater parasite transmission; hence a key issue is to explain individual differences in social network position. Individuals can have social interactions when they overlap spatially either when individuals live in cohesive, social groups, or simply because they are attracted to the same resources or refuges (Spiegel, Leu, Sih, Godfrey, & Bull, 2015). That is, understanding 'movement ecology' (Hansson & Akesson, 2014; Nathan et al., 2008), the individual movements and space use that underlie shared space use with neighbours, is important for understanding social networks.

A growing body of literature focuses on how individual differences in movements and space use depend on consistent individual differences in behavioural tendencies (i.e. animal personalities) such as aggressiveness, boldness or exploratory tendency (Cote, Clobert, Brodin, Fogarty, & Sih, 2010; Cote, Fogarty, Weinersmith, Brodin, & Sih, 2010; Spiegel, Leu, et al., 2015). At large scales, transmission is influenced by personality-dependent dispersal that shapes the introduction of parasites into new patches (VanderWaal & Ezenwa, 2016) and by migration tendencies and associated behaviours that can move parasites over large distances (Altizer, Bartel, & Han, 2011). At the local scale, individual differences in personality can affect the tendency for individuals to be attracted to (or avoid) conspecifics, or to be attracted to the same resources or refuges (Spiegel, Leu, et al., 2015). For example, more social individuals are, by definition, more attracted to conspecifics (than less social ones), and bolder individuals likely differ from shyer ones in their response to resources, and refuges from danger. Of course, actual transmission depends not only on social contact or shared space use, but also on the nature of interactions and on host resistance, which can both also be personality dependent (Barber & Dingemanse, 2010; Koprivnikar, Gibson, & Redfern, 2012).

Note that for many parasites that have a free-living (or spore) stage between consecutive hosts (e.g. ticks, cold or flu viruses), transmission likely depends not only on direct social contact, but on time-lagged, shared use of space. I can catch a cold from you by handling the doorknob that you handled earlier, even without direct social interaction. Understanding time-lagged interactions among hosts can be important for disease dynamics (Leu, Kappeler, & Bull, 2010; Schauber, Storm, & Nielsen, 2007; Wohlfiel, Leu, Godfrey, & Bull, 2013).

Finally, animal personalities are not necessarily stable over the long term. They can change in response to ecological stressors. In particular, an individual's parasite load can feedback to affect its behaviour, or even its personality. This could happen because parasites influence an individual's state (e.g. energy reserves, condition), and behaviour and personality are often state dependent (Houston & McNamara, 1999; Luttbeg & Sih 2010; Sih et al., 2015; Wolf & Weissing 2010), or because parasites manipulate host behaviour (Poulin, 2010, 2013; Vyas, Kim, Giacomini, Boothroyd, & Sapolsky, 2007). Parasite loads can thus feedback to affect host movements and social networks that govern further parasite transmission.

This overall framework is summarized in Fig. 1. Below, we discuss important nuances on each of these points in more detail.

Social Networks and Heterogeneity in Parasite Transmission

Parasites, both rare catastrophic epidemics and the far more common, low-level infections, often have important effects on host behaviour, fitness, populations, communities and ecosystems (Fitze, Tschirren, & Richner, 2004; Hatcher & Dunn, 2011; Smith, Acevedo-Whitehouse, & Pedersen, 2009). Simple models of directly transmitted parasite spread (where transmission is from one host to another without intermediate phases) assume random mixing among individual hosts that differ only in whether they are infected or not. Recent models, however, emphasize heterogeneity among hosts in transmission potential due to variation in contact rates, infectiousness or susceptibility to infection following contact (Lloyd-Smith, Schreiber, Kopp, & Getz, 2005). This heterogeneity can have major effects on transmission dynamics and can determine whether a parasite dies out or becomes epidemic (Pastor-Satorras et al., 2015). The social network approach provides a useful framework for quantifying heterogeneities in host contacts and for predicting how they affect transmission dynamics (Bull, Godfrey, & Gordon, 2012; Paull et al., 2012). At the individual level, a variety of social network metrics can be used to quantify the number of other hosts directly contacted by a focal host ('degree') and an individual's potential importance in linking others that are not directly connected ('betweenness'). At a group level, modelling suggests that the overall network structure influences how parasites and pathogens spread through a population, but specific predictions are complex (Eames, Tilston, Brooks-Pollock, & Edmunds, 2012; Hamede, Bashford, Jones, & McCallum, 2012). While social network models have generated excitement about the importance of networks in understanding parasite transmission, empirical evidence, and especially experimental testing of these models in natural populations lags behind theoretical work.

Time-lagged Transmission Networks

For many parasites, transmission involves a time lag determined by the parasite's life cycle; for example, due to a parasite incubation period or, in ticks, a moulting period between life history stages

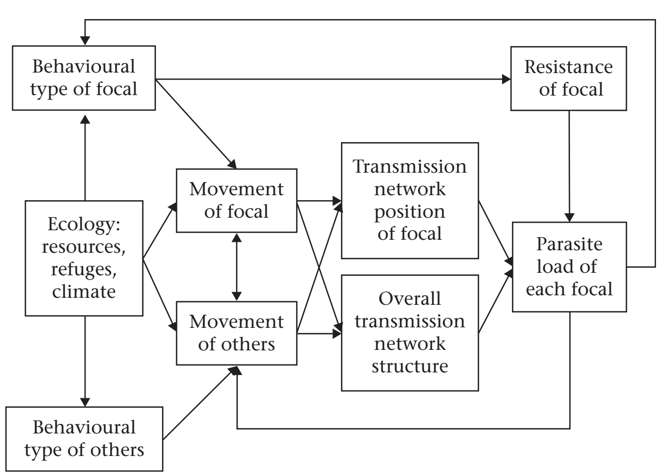

Figure 1. Conceptual flowchart. The ecological environment and individual behavioural types interact to influence movement patterns both of each focal host and of other hosts that result in shared space use that underlies social networks. Along with individual differences among hosts in resistance to parasites, these social networks explain parasite loads that may feedback to influence behavioural types and movements.