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An analytical framework for quantifying and testing patterns of temporal dynamics in social networks

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Change is fundamental to all social systems. Temporal dynamics are critical in understanding how relationships form and change over time but rarely are studied explicitly in animal groups. Social network approaches are useful in describing association patterns and provide promising tools for investigating the dynamics of change in social structure but have rarely been used to quantify how animal associations change over time. In this study, we describe and test a framework for temporal analysis of social structure. We propose an analytical framework of methods that integrates across social scales and comparatively analyses change in social structure across multiple types of social association. These methods enable comparisons in groups that differ in size and are flexible to allow application to weighted and unweighted networks, where ties can be directed or undirected, and relationships can be symmetric or asymmetric. We apply this analytical framework to temporal social network data from experimentally formed captive groups of monk parakeets, *Myiopsitta monachus*, to both evaluate our analysis methods and characterize the social structure of this species. We compared dynamics of dyadic network formation, ego network formation and global network stabilization patterns across neutral, affiliative and agonistic associations. We found that social structure of captive monk parakeets formed and stabilized over a short period, but patterns differed by social association type. We also found evidence for consistency in the temporal dynamics of formation and stabilization of social structure between replicate social groups. Our analysis methods successfully identified change in social structure that corresponded well with qualitative observations. This framework is likely to be useful in characterizing patterns of temporal dynamics in social structure in longitudinal data in wide variety of social systems and species.

Change is fundamental to all social systems. Social associations vary over time as individuals are incorporated into social groups through birth and immigration and leave through emigration and death. This process can be somewhat predictable in cases of long-lived species with stable social groups. In contrast, this process is less predictable when mortality rates are higher or when individuals alter their group membership more frequently, as in the case of species with high fission–fusion dynamics. The importance of an individual's social associates can also be context dependent and can shift with changes in developmental, environmental or social conditions (Hinde 1976a; Sapolsky 2005). Once formed, relationships among individuals are unlikely to remain static, and the consistency or stability of relationships is important to consider when characterizing social patterns (Hinde 1976a).

Temporal Dynamics of Social Networks

Temporal dynamics are key to understanding how relationships form and change over time but are rarely studied explicitly in animal groups (Whitehead 2008; Krause & Ruxton 2010). One method for analysing social relationships is social network analysis (Wasserman & Faust 1994; Wey et al. 2007; Croft et al. 2008). Social network analysis is a flexible, model-free technique applicable to a wide range of social situations. It provides methods for quantifying relationships and how individuals fit into the social landscape on a global scale. Although social network analysis provides promising tools for investigating the dynamics of change in social structure, it has rarely been used to quantify how animal associations change over time. Where temporal dynamics of social

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structure have been studied, the focus has generally been on gross structural patterns obtained when data are aggregated over long timescales. For example, social network structure in some groups changes with season (Hamede et al. 2009; de Silva et al. 2011), reproductive state (Fischhoff et al. 2007; Sundaresan et al. 2007; Patriquin et al. 2010), individual attractiveness (Oh & Badyaev 2010) and resource availability (Henzi et al. 2009; Foster et al. 2012). Other studies have found evidence for stable social associations across years (e.g. Silk et al. 2006a; Mitani 2009) and correlations with individual fitness across years (McDonald 2007; Ryder et al. 2008). Data in these analyses were generally aggregated over relatively long periods such as months or years. This type of data aggregation is a snapshot method of comparing static networks to one another and does not allow for detailed exploration of dynamic change. Studies of the fine details of network change are much less common (but see Blonder & Dornhaus 2011).

Methods have been developed to study temporal dynamics in human social networks to predict patterns of formation of social ties. Exponential random graph modelling or p^* models (reviewed in: Wasserman & Pattison 1996; Anderson et al. 1999; Robins et al. 2007) can be used to determine the probability of the occurrence of network ties based on predictor values (Robins et al. 2007). However, parameters for these methods are complex, results can be difficult to interpret and the models are best used to differentiate between tie occurrence based on peer influence or self-driven selection (Borgatti 2010). To quantify and test how patterns of social associations and structure change over time, methods that are more easily interpreted and that can be generalized to a broader range of study questions are needed (Borgatti 2010). In addition, most of the development of tools in the social sciences has focused on dichotomous ties between individuals, where a tie is either present or absent; much less work has focused on development of statistical analysis of continuous weighted tie strengths or valued relations (Robins et al. 1999). There has been a recent push to move towards use of continuous measures of dyadic association strength in network studies, especially in nonhuman animals (see Lusseau et al. 2008; Croft et al. 2011).

Two major aspects of the dynamics of social networks that have received little attention are (1) analyses of temporal dynamics across different social scales and (2) comparative analyses of dynamics across different association types. First, social structure has generally been examined at a single scale. Representations of social structure are usually constructed based on characteristics of dyadic relationships (Wasserman & Faust 1994; Whitehead 2008), and then analysis focuses on dyadic relationships (Silk et al. 2006a, b, 2009), individual connections within the network structure (Stanton et al. 2011), or the group's global network structure (Lusseau et al. 2006; Henzi et al. 2009). However, changes in social structure may be better understood by using a scaled approach that considers aspects of temporal dynamics across different social levels. Social networks can be examined at multiple levels to determine how change occurs over time in dyadic relationships, how individuals interact within local social structure, and characteristics of the entire network on a global scale. A multiscale approach could thus provide a more comprehensive perspective on the drivers and characteristics of temporal dynamics in networks (Mucha et al. 2010; de Silva et al. 2011).

Second, analyses of temporal dynamics generally focus on a single type of social association. Associations among individuals may be affiliative, agonistic or behaviourally neutral. There are few comparative studies of social structure dynamics across multiple association types to examine differences in the speed of formation of different types of social structure. For example, previous studies on the temporal dynamics of dominance hierarchy formation solely incorporate information on agonistic associations (Chase 1980; Chase et al. 2002). Comparisons of temporal dynamics across multiple association types, or a 'multiplex' approach to social structure analysis (Hinde 1976b; Wasserman & Faust 1994; Hamill 2006; Croft et al. 2008; Mucha et al. 2010), could provide a more comprehensive and comparative perspective on social change. Even in groups structured by aggression, mutual dependencies exist between group members (de Waal 1986). Comparisons across multiple association types are especially important because an individual's connections within a group have been shown to have important fitness consequences. For example, neutral associations, through shared group membership, can increase foraging efficiency in vultures (*Coragyps atratus* and *Cathartes aura*; Buckley 1996; Rabenold 1987) and access to other essential resources in Grevy's zebra, *Equus grevyi* (Sundaresan et al. 2007). Affiliative associations increase reproductive success in wire-tailed manakins, *Pipra filicauda* (Ryder et al. 2008, 2009), and a mother's affiliative grooming network is positively correlated with infant survival in baboons (*Papio cynocephalus*; Silk et al. 2009). Agonistic associations, especially in species with linear dominance hierarchies, are often correlated with increased access to reproductive opportunities and the potential to pass rank on to offspring in spotted hyaenas, *Crocuta crocuta* (Holekamp & Smale 1991; East et al. 2009). In yellow-bellied marmots, *Marmota flaviventris*, aggressiveness or bullying is positively associated with male reproductive success (Wey & Blumstein 2012). Studies have also documented that changes in one association type can affect associations in another context. For example, patterns of social associations at one life stage can affect future associations, status and reproductive success in male manakins (*Chiroxiphia linearis*: McDonald 2007; *Pipra filicauda*: Ryder et al. 2008, 2009).

Despite previous research, large gaps remain in our understanding of complex sociality in many taxa (Silk 2007), which hampers efforts to understand broader patterns in the evolution of social structure. More detailed understanding of the temporal dynamics of social structure within and across association types could help provide insight into the processes driving complex sociality (Krebs & Davies 1996; Croft et al. 2008).

Analytical Framework

In this study, we describe and evaluate a framework to address questions about the temporal dynamics of social structure. We provide methods for quantifying and testing temporal dynamics that integrate across social scales and compare change in social structure across multiple association types for a more holistic view of formation and stabilization patterns over time. This framework is particularly applicable to studies with short-term temporal data sets that are difficult to analyse with more traditional time series analysis methods. We outline analyses in increasing order of social scale, from the micro social scale of dyadic relationships through the macro social scale of global network structure. This framework is built in part on a conceptual model developed by Hinde (1976a) for studying primate social structure using concepts derived from human social sciences. Importantly, this model did not specify analyses that could be used, nor did it explicitly include temporal dynamics, although Hinde stressed that patterns and stability of relationships are important characteristics to include (Hinde 1976a, b). A similar conceptual framework was more recently used to quantify dynamics of elephant social structure through time at three social scales (de Silva et al. 2011), but the study focused on a single association type within a single population and thus lacks the multiplex approach described here.

We build on previous work to propose a framework that incorporates analyses that are broadly applicable to comparisons across multiple association types in a wide range of social systems.