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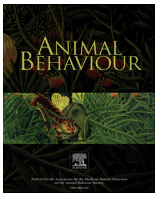

Structure of male cooperation networks at long-tailed manakin leks

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Social networks arise from complex interactions among multiple individuals and affect the emergent properties of groups (e.g. cooperation, disease spread, information transfer, etc.). Cooperation among nonkin is generally predicted to be favoured in structured social networks where individuals primarily interact only with certain individuals. Long-tailed manakins, *Chiroxiphia linearis*, form lek groups of as many as 15 unrelated males, whose members can attend multiple leks. At each lek, several top-ranked males perform the majority of obligate cooperative courtship displays. We used exponential random graph (ERG) modelling to analyse manakin cooperation networks constructed from 2-year time intervals over a 14-year study period. ERG modelling evaluates how local processes contribute to formation of global social network structure. We found that four local processes of link formation largely explained the overall structure of male manakin cooperation networks: (1) the spatial proximity of birds: males were more likely to cooperate if they primarily displayed at the same or neighbouring leks; (2) social status of birds: males were more likely to cooperate as they moved up the social queue at leks; (3) triad closure: males were more likely to cooperate with a ‘friend of a friend’ than with males with which they did not share a mutual partner; and (4) link persistence: males were more likely to cooperate with males whom they had cooperated with in the past. Other plausible mechanisms, such as selective mixing (the tendency to interact with individuals of similar or dissimilar social status) and preferential attachment by degree (whereby individuals with many social links gain additional links) did not consistently explain the structure of male cooperation networks at leks. These local processes may facilitate cooperation among long-tailed manakins by creating structured social networks in which males interact with only a subset of the population.

Social structure (i.e. the pattern of relationships among individuals) emerges from the decisions and attributes of a society's constituents. Individuals may have multiple social relationships, which influence subsequent relationships and the generation of interdependent and intricate social structure (Byrne, 1997; Connor, Heithaus, & Barre, 2001). The organization of these social relationships can affect a variety of important population phenomena including disease spread, fitness, genetic structure, information transfer, goods exchange and resource use (Baird & Dill, 1996; Cauchemez et al., 2011; Fritsch & Kauffeld-Monz, 2010; Lusseau et al., 2006; McDonald, 2007; McGregor, 2005; Naug, 2008; Ryder, Parker, Blake, & Loiselle, 2009). In particular, social structure may have a strong influence on the evolution and maintenance of cooperation in populations (Nowak, 2006; Ohtsuki, Hauert, Lieberman, & Nowak, 2006; Santos, Rodrigues, & Pacheco, 2006).

By definition, cooperators incur a direct fitness cost (e.g. lower survivorship or reproductive success) by providing a benefit to other individuals in a population. In contrast, defectors are individuals that benefit from cooperative acts but pay no costs, because they do not provide benefits to others. Defectors have higher average fitness than cooperators in traditional theoretical models of well-mixed populations where all individuals are equally likely to interact (Nowak, 2006). As a result, natural selection favours defectors in these models, and cooperators are predicted to disappear from the population (Nowak, 2006; Nowak & Sigmund, 2007). Natural populations are usually structured, such that individuals interact more often with certain individuals because of factors such as social structure and spatial effects. Graph theory provides a powerful framework for studying cooperation in structured populations because it uses mathematical structures to model pairwise relations between objects, (Abramson & Kuperman, 2001; Lieberman, Hauert, & Nowak, 2005). Using

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graph theory, cooperation among individuals can be mapped on a social network, where nodes (also called vertices) represent individuals and links (also called edges) characterize social interactions between them. By modelling links between individuals, social networks can be used to tease apart the various factors that influence social structure (Croft, James, & Krause, 2008) and behaviours such as cooperation (McDonald, 2007). Several theoretical models have demonstrated how cooperation can be maintained on structured social networks (Nowak, 2006; Ohtsuki et al., 2006; Santos et al., 2006).

Here we examine the local processes that contribute to formation of cooperation networks of male long-tailed manakin, *Chiroxiphia linearis*, leks. Manakins (Aves, Pipridae) include about 51 species (McDonald, 2010) of small Neotropical birds with a lek-mating system. No other family of vertebrates has a larger proportion of lek-mating species (McDonald, 2010). Within the family, all of the species in the genus *Chiroxiphia* show obligate male–male cooperation in courtship display (DuVal, 2007; Foster, 1981; McDonald & Potts, 1994). In a few other species of manakins (e.g. crimson-hooded manakin, *Pipra aureola*; band-tailed manakin, *Pipra fasciicauda*; wire-tailed manakin, *Pipra filicauda*), coordinated courtship displays appear to occur sporadically or in facultative fashion (Robbins, 1985; Ryder, McDonald, Blake, Parker, & Loiselle, 2008; Snow, 2004). Most other manakin species perform only solo courtship displays, and cooperative courtship display is otherwise rare in the animal kingdom (but see Krakauer, 2005). The spectrum of cooperative courtship display in manakins raises interesting questions about the fitness benefits of cooperation (McDonald & Potts, 1994; Ryder et al., 2008). Long-tailed manakins, the species considered here, have an unusual lek-mating system in which males cooperate to perform courtship displays (McDonald & Potts, 1994). Each lek (centred at a perch) consists of a team of 8–15 unrelated males of various ages and social statuses. Younger, lower-ranking males can be members of more than one lek simultaneously or sequentially. To attract females to their lek, the two top-ranking males (alpha and beta) perform sustained unison songs (Trainer & McDonald, 1995). If a female chooses to visit a lek, the duo performs a synchronized dance display that determines whether a female will copulate (McDonald, 1989a, 1989b). Most dual-male displays for females at a lek are performed by the alpha male and beta male, or occasionally by other high-ranking males, but lower-ranking lek members also engage in cooperative displays when females are absent (McDonald, 1989a, 2009). Fitness benefits for beta males are delayed, because alpha males obtain almost all copulations (McDonald, 1989a; McDonald & Potts, 1994). After the death of the alpha male, the beta male almost always ascends to alpha rank at that lek (McDonald & Potts, 1994). Males move up through an age-graded queue at leks over many years, ultimately reaching alpha status and perhaps achieving copulations (average age of males engaged in copulations is 10.1 years; McDonald, 1993b). Queues are orderly, with little aggression between males, and a male's rank depends heavily on age. Female choice maintains orderly queues, because females avoid leks if males are disorderly (McDonald, 1989a, 1993a, 2010; McDonald & Potts, 1994). By understanding processes that govern link formation (i.e. cooperative displays), we seek to illuminate both how these complex networks form and the potential consequences of that structure for the origin and maintenance of cooperative courtship display in these lek-mating birds.

To explore the ontogeny and consequences of male–male cooperation, we considered the following six candidate processes that could drive formation of cooperative links: spatial proximity, social status, triad closure, link persistence, selective mixing and preferential attachment. Each of the six might, in principle, influence the structure of male long-tailed manakin cooperation networks. Spatial proximity should increase the likelihood of forming cooperative links. In manakin networks, spatial proximity is an obvious candidate, perhaps even a prerequisite, for cooperation. Previously, McDonald (2009) showed that links cannot be explained by relatedness, but do tend to occur between males affiliated with the same lek or spatially proximate leks. Thus, we predicted that manakin cooperation networks would exhibit a strong influence of spatial proximity, tending to produce structured populations. Individual attributes like social status can affect the tendency for individuals to form links. We predicted that male manakins of higher social status (e.g. alpha and beta) would cooperate most. This prediction was based on the observation that alpha and beta males perform most of the courtship calls and displays at a lek (McDonald, 1989a). Males of lower status tend to spend time at several leks but interact relatively infrequently with any particular male (McDonald, 2007). Triad closure promotes local clustering (also known as transitivity) and is a common feature of many social networks (Wasserman & Faust, 1994). Triad closure occurs when individual A is socially linked both to individuals B and C, and B and C form a link more readily than do individuals lacking a mutual partner. Triad closure can occur because of shared time among three individuals or because of cognitive processes such as trust (Goodreau, Kitts, & Morris, 2009). In manakins, males spend many years at leks, both displaying and watching other males display; therefore, we predicted that triad closure may contribute to emergence of structured networks in this species. In many networks, established links are more likely to persist across time and can be particularly important in maintaining cooperation. Because high-ranking older males (e.g. alpha and beta) tend to display with each other over long periods (McDonald, 1989a, 2007, 2010), we predicted that pre-existing links would also be important in maintaining cooperation in long-tailed manakins networks. These persistent interactions have important long-term consequences for male mating success (McDonald, 2007). The tendency of individuals to form links with others based on certain attributes, known as selective mixing, can also lead to local clustering in networks, creating structured populations (Goodreau et al., 2009). Positive selective mixing, called homophily, occurs when individuals link to others with similar attributes, whereas negative selective mixing, known as heterophily, occurs when individuals link to those with dissimilar attributes. We predicted that negative selective mixing by social status would likely occur among male manakins of higher social status because most cooperative displays are between males of differing social status such as the alpha and beta (McDonald, 1989a). Finally, theoretical modelling suggests that cooperation can evolve and be maintained on networks where new individuals preferentially attach to cooperators of high degree (where degree is the network term for the number of links per node), creating a network of interconnected high-degree hubs (Santos et al., 2006). In manakins, we predicted that if preferential attachment by degree is an important process in creating structured cooperation networks, then highly interactive males should be more likely to form links compared to less interactive males.

We used exponential random graph (ERG) modelling to examine which combination of our six hypothesized processes contribute to the structure of male manakin cooperation networks. ERGs model how multiple local processes combine to form global social network structure (Pinter-Wollman et al., 2014; Robins, Pattison, Kalish, & Lusher, 2007). ERG modelling, similar to multiple logistic regression, estimates the probability in logit form that a social link exists between individuals as a linear function of the predictor variables. ERG modelling differs from logistic regression because it can explicitly account for the inherent nonindependence of network nodes. Our goal was to see whether a few candidate factors could both explain the observed structure of male manakin