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.

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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

networks and shed light on how emergent social structure favours cooperation among unrelated males.

METHODS

Social Network Construction

Data on social interactions among male long-tailed manakins were collected as part of a long-term study in Monteverde, Costa Rica, described in previous publications (McDonald, 1989a, 1989b, 2010). Males were considered to be linked if they were seen to engage in at least one dual-male or multimale display together at leks. Many such displays and interactions occur even in the absence of any females. Because these links represented observable affiliative behaviours, they did not rely on the 'gambit of the group', and it was not necessary to filter them in the way recommended for analysis of links based on co-occurrence in fission–fusion groups (James, Croft, & Krause, 2009). We constructed eight undirected, unweighted (i.e. binary) 2-year networks from 9288 h of behavioural observations of 139 colour-banded males during 1983–1998. Networks were constructed for 2-year periods because this was the shortest time frame that resulted in highly connected networks (Fig. 1). Unweighted links were used in constructed networks as ERG modelling does not yet incorporate weighted links (Robins et al., 2007). The long-tailed manakin networks ranged in size from 29 to 46 nodes (mean $\pm$ SE = 37.7 $\pm$ 2.3 nodes, $N = 8$) with relatively sparse links (mean $\pm$ SE = 73.7 $\pm$ 8.3 links, range 43–99, $N = 8$). The network density (i.e. actual number of links/potential number of links) was low (mean $\pm$ SE = 0.106 $\pm$ 0.007, $N = 8$). Males were assigned to a primary lek, based on where they were observed most frequently during the 2-year period (approximate average distance between leks was about 200 m). A lek was defined as having one to four alternative dance perches that were spatially proximate to each other and used by the same alpha–beta pair and their lower-ranking associates, comprising a total team of 8–15 males (McDonald, 1989a, 2010). Males were classified into five social status categories (McDonald, 2007): predefinitive (age 3 years or younger, based on a strictly age-based sequence of plumage maturation; Doucet, McDonald, Foster, Clay, & Lank, 2007), definitive (age 4 years or older, but never documented to have danced for a female), dancer (one or more documented dances for a female, but not yet at alpha or beta rank), beta (the subordinate partner for the dual-male cooperative courtship displays) and alpha (the senior partner, to whom any copulations at that lek accrued). A male's status was assigned on the last date for which he was included in each 2-year network. All banding complied with the appropriate regulations of the Servicio de Vida Silvestre of Costa Rica and, during the later years of the study were approved by the Institutional Animal Care and Use Committee of the University of Wyoming (permit number UWMcDonald2005).

Exponential Random Graph Modelling

The effects included in our full ERG models were spatial proximity, social status, triad closure, link persistence, selective mixing by social status and preferential attachment. An intercept term for the number of links in the network was also included in the models to account for the sparseness of networks. In ERG models, the logodds coefficients, analogous to those in logistic regression, indicate the probability of forming a social link for every unit change in the predictor variable (Lusher, Koskinen, & Robins, 2013). Spatial proximity was assessed as the metric link distance. Link distance estimated the effect of spatial distance on the probability of link formation between birds, based on a distance matrix (i.e. pairwise distances in metres between the primary leks of all the birds in the network divided by 100 for easier interpretation). Note that link distance is not social distance, which would be assessed as the number of links separating individuals in the social network. Social status assessed the probability of forming a link depending on social status, where social status was coded according to the following scheme: alpha = 4; beta = 3; dancer = 2; definitive = 1; predefinitive = 0. To quantify the effect of triad closure (i.e. the tendency of triads containing two links to form a third link), we used the geometrically weighted edgewise shared partner distribution (GWESP). A shared partnership occurs when two birds are linked and both are also linked to a shared partner, forming a triangle (closed triad). The shared partner count is taken on each link, producing a distribution of counts. GWESP defines a parametric form of the edgewise shared partner distribution that includes a declining positive impact on the probability that two birds will form a link with each additional shared partner (Lusher et al., 2013). Link persistence estimated the effect that an existing social link between two birds in the immediately previous 2-year network would have on the probability of their forming a link in the current network. Link persistence was based on a pairwise matrix, where 1 denotes a previous link in the prior 2-year network between two birds and 0 denotes the lack of any such link. Because this covariate was not available for the first time period (1983–1984), we performed ERG modelling only on the remaining seven time periods. The influence of selective mixing on the probability of forming a link was examined for each social status separately in the ERG model (alpha, beta, dancer, definitive, predefinitive). A positive selective-mixing coefficient indicated that individuals were more likely to cooperate (form links) with individuals of the same social status (homophily), whereas a negative coefficient indicated the opposite (heterophily). We quantified preferential attachment by degree, the tendency for high-degree nodes to form new links, by using the geometrically weighted degree distribution (GWD). GWD estimates the degree distribution with a diminishing increase in the probability that an individual will increase its degree. A positive GWD coefficient indicates a degree distribution with centralization due to high-degree nodes (preferential attachment), whereas a negative coefficient indicates degree distribution is more equal among nodes (Lusher et al., 2013). We used the GWESP and GWD as metrics of triad closure and preferential attachment, rather than other possible metrics, because they produce better model fits and prevent model degeneracy, which can result in incorrect convergence on models where either all or no links exist in the networks (Goodreau et al., 2009; Hunter, 2007). Both GWESP and GWD have a decay parameter that we set to 0.7 in all ERG models. The 0.7 value was selected by examining the model fits of all observed networks for decay values ranging from 0 to 1 in 0.1 increments (Goodreau et al., 2009). All models showed little improvement in model fit beyond 0.7, but the specific decay value had relatively little effect on goodness-of-fit measures or statistical significance.

Performance of different model selection methods has not been extensively studied for ERG models. As a result, it is recommended that several complementary methods be used to compare different models. Effects included in the final ERG models were selected through a combination of backward selection and examination of goodness-of-fit graphs (Simpson, Hayasaka, & Laurienti, 2011). Beginning with the full model, the least significant effect was deleted and the nested model was compared using a likelihood ratio test. We considered P values of <0.05 statistically significant. For each model, we visually examined three network-level metrics (distributions of edgewise shared partners, minimum geodesic distance and degree) between the observed network and 100 simulated networks generated from the fitted model, to determine whether the removal of model predictors reduced goodness of fit. Nested models that produced simulated networks that were a
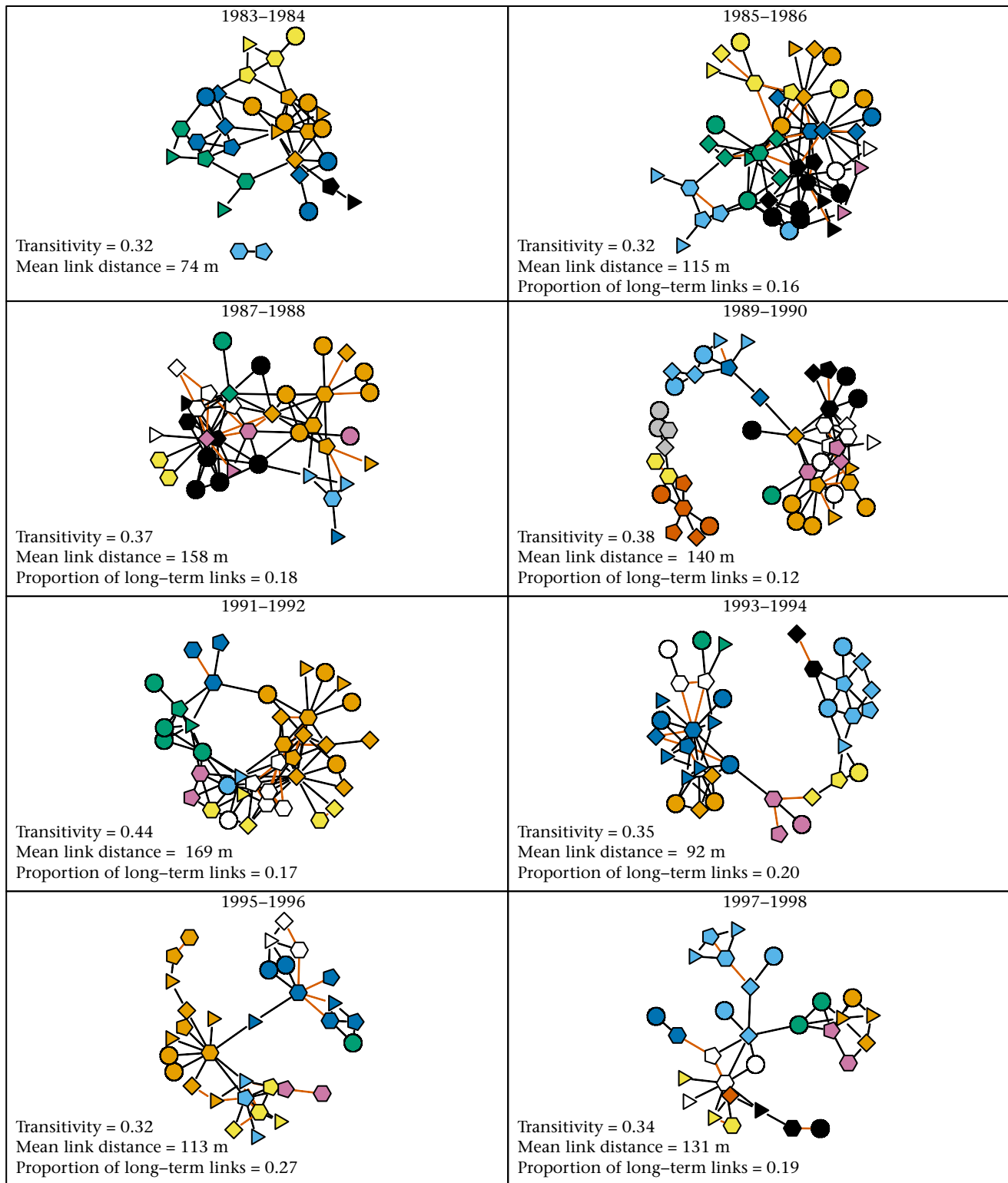
Figure 1. Male long-tailed manakin cooperation networks at leks for each 2-year period during 1983–1998. Node colours denote main lek affiliations; red links represent interactions present in the previous 2-year network (i.e. long-term links). Social status: alpha (hexagon); beta (pentagon); dancer (square); definitive (triangle); predefinitive (circle). Global transitivity, proportion of long-term links and mean link distance are listed below each network.

significantly poorer match to observed networks than more complex models based on goodness-of-fit measures were not classified as best-fitting models even if likelihood ratio tests suggested otherwise. To prevent isolates (i.e. nodes of zero degree), all models included a constraint that birds must have at least one link. This

constraint was reasonable given that individuals needed to engage in a cooperative display (have degree ≥1) to be included in the network in the first place. All ERG model estimation, simulation and goodness-of-fit diagnostics were performed using the Statnet package in R (version 3.0.3, R Foundation for Statistical Computing,

Vienna, Austria). Because our ERG model lacked statistical independence among observations, the maximum likelihood could not be calculated using traditional methods. Instead, we used a Markov-chain Monte Carlo (MCMC) estimation technique to approximate the maximum likelihood (Lusher et al., 2013). This method generated a sample from the space of possible networks to estimate the maximum likelihood (Robins et al., 2007). The MCMC technique was also used to generate the simulated networks for construction of goodness-of-fit graphs (Hunter, Goodreau, & Handcock, 2008). Visual representation of networks relied on the Fruchterman–Reingold layout algorithm.

RESULTS

Likelihood ratio tests (Supplementary Table S1) and examination of goodness-of-fit plots (Fig. 2) resulted in the best-fitting ERG model for each 2-year cooperation network (seven total), including effects for three of our six hypothesized predictors of link formation: spatial proximity (link distance), social status and triad closure (GWESP; Table 1). Link persistence was also an important effect, appearing in the best-fitting model for five of the seven networks (Table 1). Selective mixing for alpha (heterophily) and predefinitive males (homophily) were included in the best-fitting models for only three networks each (Table 1). Neither selective mixing for the other social status levels (beta, dancer, definitive), nor preferential attachment by degree (GWD) were included in any of the best-fitting models. Based on the log-odds coefficients of all best-fitting models, the direction and magnitude of the main model effects were similar across all 2-year periods (Table 1), signifying that the processes shaping manakin networks did not vary greatly over time. The negative coefficient for spatial proximity indicated that birds tended to interact more with individuals of the same or nearby leks. Two individuals with the same lek affiliation were 1.7 times more likely, on average (range 1.6–2.7 times, $N = 7$), to form a link than two birds with lek affiliations 100 m away from each other. The positive coefficient for social status specified that individuals of higher status tended to cooperate with more partners than individuals of lower status. A higher-ranking male was 1.3 times more likely, on average (range 1.3–1.4 times, $N = 7$), to form a link than a male immediately below him in social status (e.g. alpha compared to beta). The positive coefficient for triad closure (GWESP) signified that links that closed a triangle were more likely to occur in the network than links that did not close a triangle. Links that closed one triangle were 2.5 times more likely to occur, on average (range = 1.7–3.4 times, $N = 7$), than links that did not close a triangle. Note that the odds ratio of the triad closure effect decreased geometrically as the number of triangles closed by an additional link increased. Link persistence also had a positive coefficient, indicating that previous links between birds were more likely to occur than new links. Birds that had interacted in the previous 2-year period were 3.6 times more likely, on average (range 2.9–5.9 times, $N = 5$), to form links again with each other in the following 2-year period than were birds without previous social links. Coefficients for selective mixing by social status indicated that alphas were more likely to form links with individuals of lower social status (heterophily), whereas predefinitives were more likely to form links among themselves (homophily). An alpha was 3.9 times more likely, on average (range 1.0–4.7 times, $N = 3$), to form a link with a bird of lower social status than with another alpha. A predefinitive was 4.7 times more likely, on average (range 3.9–7.5 times, $N = 3$), to form a link with another predefinitive than with individuals of other social statuses.

We evaluated three common metrics of global network structure to determine goodness of fit for best-fitting ERG models (i.e. how well the fitted models captured the structure of observed networks): edgewise shared partner distribution, geodesic distance distribution and degree distribution. Although there were slight variations between time periods, the observed networks typically were well within the range of values for network structural characteristics generated from the 100 simulated networks of the best-fitting models, indicating a strong goodness of fit (Fig. 2; Supplementary Table S1).

DISCUSSION

Four of the six factors that we hypothesized might explain link formation among male manakins proved to be important (Fig. 3). Males were more likely to cooperate with partners that were spatially close (link distance), to interact with more partners as they moved up in social queue (social status), to cooperate with partners of partners (triad closure) and to continue to cooperate with previous partners (link persistence). ERG modelling allowed us to assess robustly the combined influence of these key local processes on social network structure. These four effects, in concert, explained the quantitative global social network properties (Fig. 2) during all 14 years of observations, the approximate life span of these manakins. The importance of these processes in shaping manakin social network structure and promoting cooperation can be attributed to the unique lek-mating system that requires long-term queuing and cooperative display.

Spatial proximity is an important, if underappreciated, factor that strongly influences social relationships in a variety of animals (Lusseau et al., 2006; Preciado, Snijders, Burk, Stattin, & Kerr, 2012; Wiszniewski, Allen, & Möller, 2009). Obviously, individuals that share the same geographical area are more likely to interact than individuals that are geographically separated. Many studies, however, ignore spatial effects or minimize them by focusing on a small group of spatially proximate individuals (Kasper & Voelkl, 2009). Given that male manakins, especially young individuals, can and do move between different leks, we chose to examine the cooperative interactions at the scale of the local population. Our results indicate that spatial proximity between manakins increases the likelihood of forming cooperative interactions and support general findings from theoretical models suggesting that cooperation is more likely to evolve and be maintained when individuals interact with a limited subset of the population (Ohtsuki et al., 2006). It is important to note that, based on the ERG models, spatial proximity alone cannot explain manakin social network structure. While spatial proximity probably influences the initial pool of individuals from which manakins can select partners, other factors are also important in determining whether two individuals will cooperate.

Social status has clear and important consequences for the functioning of links in the social network. We found that the probability of link formation increased as social status increased. Higher-ranking males (alpha, beta and dancers) engage most frequently in cooperative calls and displays at a lek (McDonald, 1989a), contributing to their increased probability of forming network links. Lower-ranking males (definitives and predefinitives) perform cooperative displays much less frequently (McDonald, 2007), resulting in fewer partners. These findings are also in accordance with the results of a previous study (McDonald, 2007). For young males in the predefinitive and definitive status categories, high network connectivity (in the form of the network metric information centrality) is a predictor of later social rise. Young males tend to have links across leks (increasing information centrality without necessarily increasing degree), but they interact relatively infrequently with any particular partner. In contrast, no correspondence occurs between information centrality and success for males of high status. At the top of each lek queue is an alpha male, and even though he may interact with many other males (has
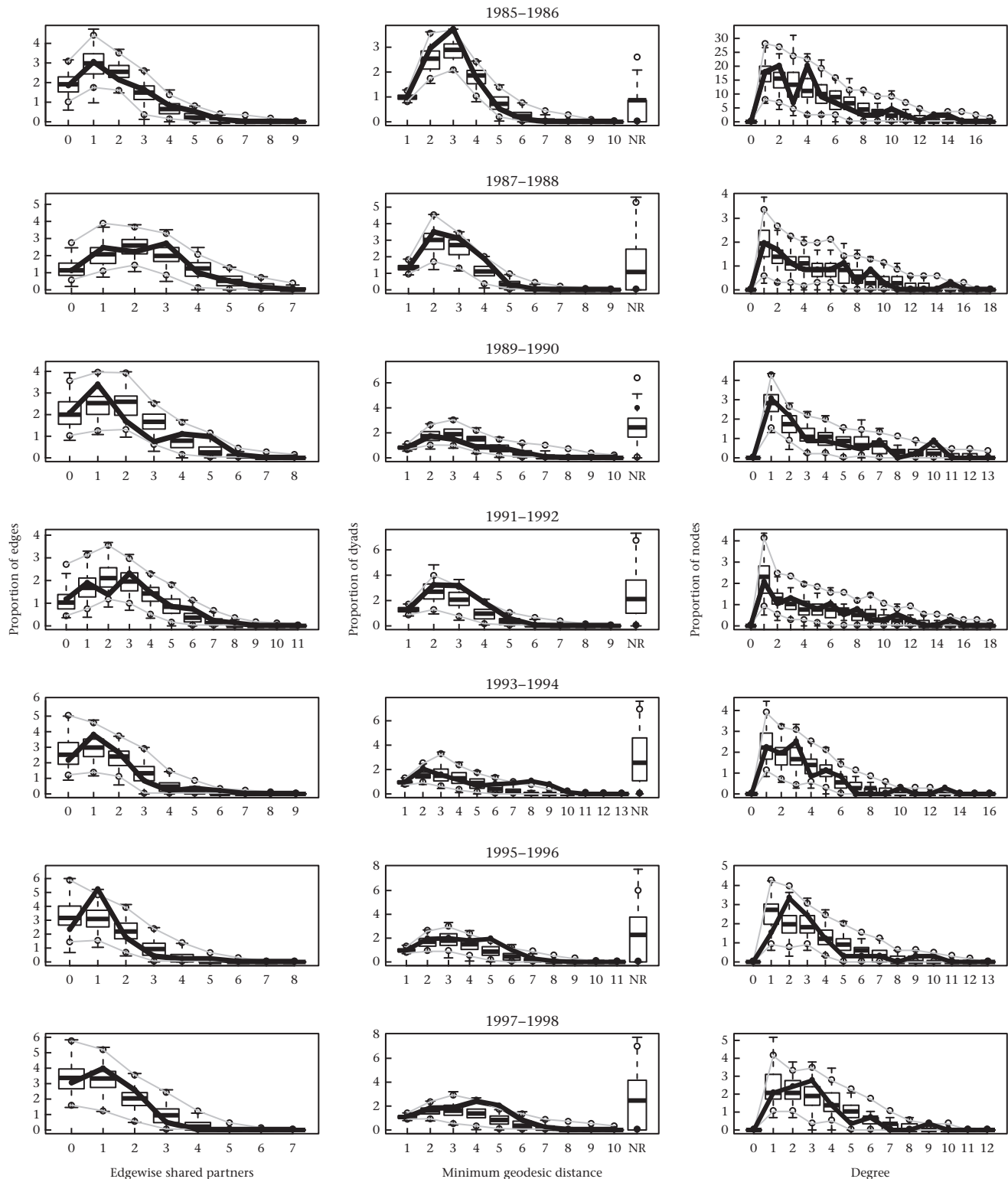
Figure 2. Networks simulated from best-fitting exponential random graph models containing effects for link distance, social status, triad closure and link persistence closely matched the quantitative network structure of observed male manakin cooperation networks during 1985–1998. Distributions of edgewise shared partners, geodesic distance (NR denotes nonreachable dyads) and degree from the observed networks (black lines) typically were well within the range of values generated from 100 simulated networks (box-and-whisker plots include median and interquartile range and grey lines denote 95% bounds) of the corresponding exponential random graph models.

high degree), he spends most of his time with his beta partner. He therefore has one all-important link of high weight (i.e. interactions occur very frequently). The concentration of weight on one or a few links is concordant with the theoretical expectation of high

viscosity in network-based models for the evolution of cooperation (Ohtsuki et al., 2006). In the model of Ohtsuki et al., Hamilton's rule $b/c > r$ is replaced by $b/c > k$, where k is the number of interactors (here, social partners). That is, having few partners increases social

Table 1
Log-odds coefficients ±SE of effects from best-fitting ERG models for 2-year male manakin cooperation networks during 1985–1998 ($N = 7$), with P values for each model effect given in parentheses

Model effect	1985–1986	1987–1988	1989–1990	1991–1992	1993–1994	1995–1996	1997–1998
Intercept	−3.04±0.39 (<0.0001)	−4.58±0.55 (<0.0001)	−4.35±0.51 (<0.0001)	−4.87±0.53 (<0.0001)	−3.06±0.57 (<0.0001)	−3.41±0.60 (<0.0001)	−2.10±0.64 (0.0011)
Link distance	−0.65±0.08 (<0.0001)	−0.34±0.06 (<0.0001)	−0.57±0.07 (<0.0001)	−0.30±0.04 (<0.0001)	−0.60±0.10 (<0.0001)	−0.47±0.08 (<0.0001)	−0.61±0.11 (<0.0001)
Social status	0.23±0.06 (<0.0001)	0.26±0.07 (0.00044)	0.35±0.08 (<0.0001)	0.25±0.04 (0.00012)	0.29±0.09 (0.00079)	0.23±0.10 (0.018)	0.24±0.09 (0.013)
Triad closure	0.76±0.16 (<0.0001)	1.22±0.22 (<0.0001)	1.09±0.19 (<0.0001)	1.40±0.22 (<0.0001)	0.65±0.21 (0.0023)	0.68±0.21 (0.0014)	0.52±0.23 (0.024)
Link persistence	1.13±0.39 (0.0039)	1.05±0.38 (0.0060)	1.17±0.50 (0.021)		1.23±0.51 (0.015)	1.78±0.48 (0.00023)	
Alpha selective mixing		−1.54±0.78 (0.048)	−1.50±0.63 (0.018)	−1.02±0.55 (0.042)			
Predefinitive selective mixing		1.36±0.47 (0.0041)		1.26±0.62 (0.065)		2.01±0.98 (0.041)	

viscosity and promotes cooperation among unrelated individuals. The subtle additional factor in the manakin network is that the total number of partners (degree) for alphas is relatively large, but the effective interaction is heavily weighted on just the single link to the beta (low effective k). Additional weighted analysis of manakin networks (not currently possible with ERG modelling) should reveal how interaction strength influences social network structure.

Manakin social networks exhibited a strong tendency towards triad closure, whereby two individuals with a shared partner were more likely, in turn, to become partners, which often is called the 'friend of a friend' effect. Triad closure in long-tailed manakins could occur as the result of a variety of potential mechanisms such as shared time together at leks, as well as from trust developed through cooperative displays (e.g. if A trusts B and B trusts C, then A should also trust C). In addition, while cooperation in long-tailed manakins appears superficially to be just a dyadic relationship between the alpha and beta male, interactions among all the members of the team play a crucial role in orderly queuing. For example, reaction to experimentally placed taxidermic mounts (i.e. intruding males) was often strongest by nonalpha/nonbeta males (McDonald, 1993a). Furthermore, successful partnerships are the culmination of years of multimale interactions that extend beyond the simple alpha–beta dyad. For example, the importance of connectivity for young males (McDonald, 2007) is an emergent property of all the males in the network, not of any particular dyad. Interestingly, blue manakins, *Chiroxiphia caudata*, often dance in threesomes, but show little in the way of unison singing (Foster, 1981).

Maintenance of long-term partnerships (here between unrelated males) is a key feature of manakin social networks. Stable bonds can enhance endeavours that promote the common goals of both parties (Dunbar & Shultz, 2007; Emery, Seed, von Bayern, & Clayton, 2007). Alpha and beta male manakin partnerships are the epitome of stable, long-term bonds, entailing thousands of cooperative displays, songs and dances, often over many years (McDonald, 1989b, 2010). The stability of this bond is critical to male reproductive success. Alpha–beta pairs that are highly successful in attracting females to leks perform unison calls and dance displays with greater quality of coordination as well as higher total output (McDonald, 1989b; Trainer & McDonald, 1995). Alpha males reap the immediate benefits of these cooperative relationships, because they obtain almost all of the copulations occurring at their leks. Although beta males rarely mate with females, they typically benefit in the long term, through inheritance of the alpha male's position. In addition, females show lek fidelity, resulting in a correlation between the reproductive success of alpha males and that of their successor beta males (McDonald, 2010; McDonald & Potts, 1994). Persistence of stable partnerships also contributes to higher fitness in other species of manakins with cooperative courtship (DuVal, 2007; Ryder et al., 2008), suggesting a broad generality to the importance of stable configurations of males. Link persistence may, therefore, be a prerequisite for high longevity in male long-tailed manakins (McDonald, 2010) and, more generally, for the evolution of cooperation among unrelated individuals in lek-mating animals. Ryder, Blake, Parker, and Loiselle (2011), and Ryder et al. (2009) found that number as well as stability of partnerships was correlated with male success in wire-tailed manakins. The importance of number of partnerships (links) is lower in long-tailed manakin networks, where alpha and beta males tend to have lower connectivity (assessed by information centrality) than lower-ranking males (McDonald, 2007). This difference probably reflects the more hierarchical and skewed reproductive success in long-tailed manakins, where only alpha males have any real prospects of mating success, and where alpha males virtually never move between leks; younger males that move between leks tend to
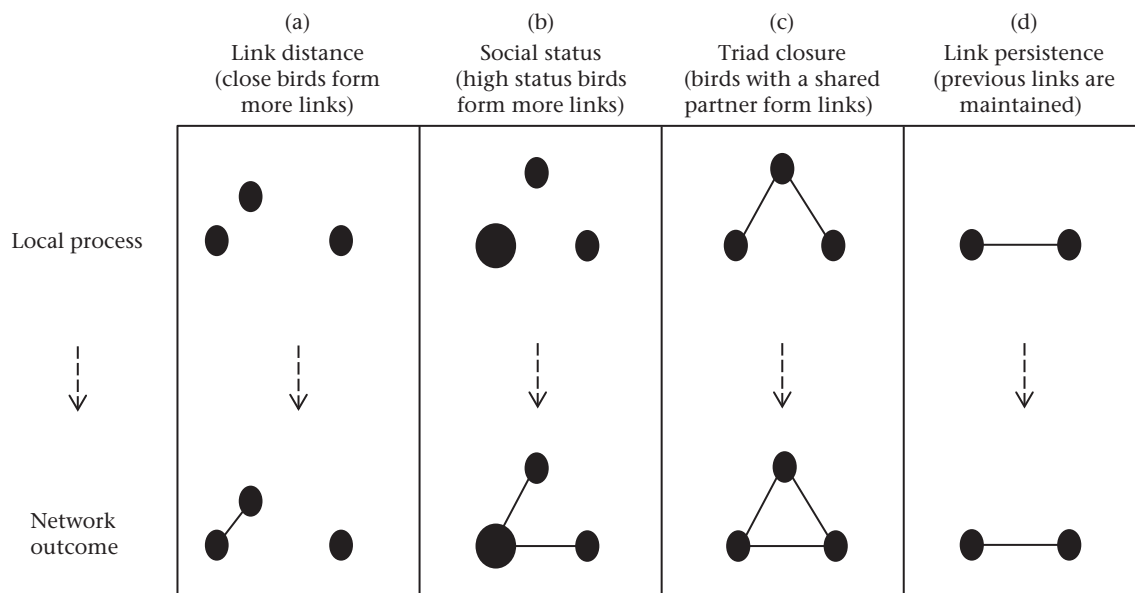
Figure 3. Diagrammatic representation of processes that contribute to formation of male long-tailed manakin cooperation networks. Males that were socially proximate tended to form links (a), males of higher social status (larger node size represents higher social status) tended to develop more links (b), triad closure tended to occur between males that had a shared partner in common (c), and previous links were likely to persist (d).

increase their social network connectivity metrics such as betweenness and information centrality. High network connectivity matters for young males that are attempting to establish relationships, but not as much for high-ranking males, which focus their interactions intensely on their display partner and females (McDonald, 2007).

Selective mixing according to social status, in the form of homophily and heterophily, was not a consistent feature of manakin social network formation. Social status terms for either alpha heterophily or predefinitive homophily were included in only three of the seven 2-year network models each. Long-tailed manakin leks (subclusters within the network) tend to consist of males interacting across all five social status categories, although the strength of these interactions differ among specific partnerships, such as the intense cooperation between alpha and beta males and the less frequent cooperation of lower-ranking males (McDonald, 1989b, 2007). Analysis of weighted network links that account for strength of cooperative interactions could reveal a stronger effect of selective mixing by social status on network structure. Homophily by behavioural phenotypes such as boldness (often linked to social status) has been found to exist within other social networks (Pike, Samanta, Lindström, & Royle, 2008; Schürch, Rothenberger, & Heg, 2010). Nevertheless, that we were consistently able to capture most of the important features of the manakin networks with four other main processes (link distance, status sociality, triad closure and link persistence) suggests that behavioural phenotypes may not be essential to the overall structure of the lek networks of male long-tailed manakins.

In contrast to the theoretical model of Santos et al. (2006), long-tailed manakin cooperation networks did not exhibit any direct evidence of preferential attachment by degree, in which high-degree nodes would attract more links, resulting in a degree distribution with centralization. Preferential attachment by degree should not be confused with the influence of individual attributes, such as social status, in manakins. The ERG model suggested that individuals form more links as social status increases, but there was no support for the idea that high degree in itself increases the likelihood of forming links. Instead, all males, when holding other effects constant, had an equal probability of forming new links regardless of their degree. These findings are supported by the relatively dispersed degree distributions in manakin networks (Fig. 2). Further analysis of weighted manakin networks, in which frequency of interactions are included, should be explored for evidence of preferential attachment.

Our results show that just a few local processes can explain the major features of the cooperation networks of long-tailed manakins. ERG modelling allowed us to robustly examine which combination of effects contributed to network structure while accounting for the inherent nonindependence of the network data (Pinter-Wollman et al., 2014). The four main processes we uncovered (Fig. 3), spatial proximity, social status, triad closure and link persistence, are also important to formation of complex social networks in humans (Capocci et al., 2006; Faust, 2007; Goodreau et al., 2009; Preciado et al., 2012; Simmel & Wolff, 1950). However, unlike human societies, in which preferential attachment by degree and homophily can be important and related to the other four processes (Goodreau et al., 2009; Newman, 2002), manakin networks showed little to no influence of preferential attachment or selective mixing processes (Table 1). From our results, we can conclude that local processes drive the formation of cooperative links among male long-tailed manakins. Those local processes, in turn, produced networks in which cooperators tended to interact only with certain individuals in the population, as generally predicted in some theoretical models for the evolution and maintenance of cooperation among unrelated individuals (Nowak, 2006; Ohtsuki et al., 2006). Our results indicate that long-tailed manakins form highly structured networks in which cooperators interact with a spatially proximate subset of the population, variation in interactivity of males is based on social status, individuals with a shared partner form links, and pre-existing partnerships are maintained (Fig. 1).

Acknowledgments

Supplementary Material

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