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Social networks in the lek-mating wire-tailed manakin (*Pipra filicauda*)

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How social structure interacts with individual behaviour and fitness remains understudied despite its potential importance to the evolution of cooperation. Recent applications of network theory to social behaviour advance our understanding of the role of social interactions in various contexts. Here we applied network theory to the social system of lek-mating wire-tailed manakins (*Pipra filicauda*, Pipridae, Aves). We analysed the network of interactions among males in order to begin building a comparative framework to understand where coordinated display behaviour lies along the continuum from solitary to obligately cooperative dual-male displays in the family Pipridae. Network degree (the number of links from a male to others) ranged from 1 to 10, with low mean and high variance, consistent with the theory for the evolution of cooperation within social networks. We also assessed factors that could predict social and reproductive success of males. Four network metrics, *degree*, *eigenvector centrality*, *information centrality* and *reach*, some of which assess circuitous as well as the shortest (geodesic) paths of male connectivity, predicted male social rise. The duration of a male's territorial tenure during the 4 years of the study predicted his probability of siring offspring.

Keywords: cooperation; coordinated display; Pipridae; social networks; wire-tailed manakin

1. INTRODUCTION

Social interactions are a ubiquitous characteristic of many animal taxa; yet our understanding of how social structure affects selective pressures, and resulting behaviour, is incomplete. Recently, social network theory, developed for the study and analysis of human social behaviour (Wasserman & Faust 1994), has been applied to vertebrate animal systems (Lusseau 2003; Croft *et al.* 2004; Lusseau & Newman 2004; McDonald 2007; Sundaresan *et al.* 2007). These novel applications of network theory represent a 'natural history' phase where empirical data can inform theory, while theoretical work develops a predictive framework for network function (Proulx *et al.* 2005). Thus far, the analysis of animal social networks has provided insight into the complex dynamics of animal social behaviour, while concurrently establishing similarities with human social systems (Connor *et al.* 1999; Lusseau & Newman 2004).

Social network analysis provides a statistical framework for quantifying individual associations, within and among groups, that are characterized by structured interactions (Croft *et al.* 2004). More specifically, network analysis produces quantitative metrics that help interpret reticulate multi-actor interactions (Wasserman & Faust 1994; Newman 2003). In its simplest form, a social network is a graph consisting of *nodes* (individual actors) connected by *links* (social interactions; Wasserman & Faust 1994; Newman 2003). A *path* is the number of unitary links required to connect individuals within the network. Individuals that interact directly do so along a path of length 1 those separated by one intermediate individual are connected by a path of length 2 and so on. The shortest path between a pair of nodes is called a *geodesic*. *Degree* measures the number of links to other actors, and is the basic measure of social connectivity.

Thus, the networks can be characterized by their degree distribution (Albert & Barabasi 2004), defined as the fraction of actors (nodes) in the network, p_k, that have degree k (Newman 2003), where k ranges from zero (i.e. no interactions) to the degree maximum (i.e. an actor that is fully connected to all other actors in the network). Many real-world networks (e.g. power grids, World Wide Web) are 'scale free', with a degree distribution that obeys a power law, where a few nodes of high degree link many nodes of lower degree (Santos & Pacheco 2006; Santos *et al.* 2006*a*,*b*). The networks constructed from vertebrate social interactions, however, are smaller with fewer links and therefore limit our ability to fully assess all scale-free network properties. In addition to degree distributions, the topology of a network (i.e. the arrangement and lengths of paths among nodes) has obvious implications for the dynamics of network processes (Newman 2003). For example, the extent to which nodes are clustered, and the length of paths among them, influence the speed with which information travels through the network.

Recently, evolutionary game and network theories have been applied jointly to investigate the evolution of

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cooperation, altruism and indirect reciprocity (Nowak & Sigmund 2005; Santos & Pacheco 2005, 2006; Ohtsuki *et al.* 2006; Santos *et al.* 2006*a*). These models have shown that certain network structural components can drive selection gradients that affect behavioural outcomes. The networks exhibiting low average degree (k) and preferential attachment, where new actors tend to attach to the nodes of high degree, provide sufficient conditions for the evolution of cooperation (Santos *et al.* 2006*b*; Ohtsuki *et al.* 2006).

Following Hamilton (1964), Ohtsuki *et al.* (2006) derived an elegant rule for the evolution of cooperation within the social networks: the ratio of benefit to cost must exceed average degree (k). The networks with low average k and high variance in k have the highest probability of promoting cooperation over the entire cost–benefit range (Santos & Pacheco 2005). Despite theoretical advances towards explaining the evolution and maintenance of cooperation, few real-world networks have been shown to have the characteristics predicted to foster the evolution of cooperative behaviours. The lack of evidence for this relationship, however, probably reflects the recent origin of the models rather than a lack of the necessary conditions, given the prevalence of cooperation in vertebrate social systems. We are aware of no studies linking theory to empirical data for taxa that exhibit a range of behaviours from non-cooperative to strongly cooperative. Manakins (Pipridae) provide a useful opportunity to examine how network structure and social behaviour interact, given the continuum from solitary to obligate cooperative male display behaviours across roughly 40 species in the family.

Lek-mating manakins (Pipridae) are neotropical birds well known for their exaggerated courtship displays that involve complex movements by, and sometimes interactions between, males. These displays have been described as the most complex behaviours known among passerine birds (Snow 2004). All manakin species engage in displays; yet the degree of coordination between the displays of males varies greatly, ranging from solitary to obligately cooperative. In most species, males aggregate at leks and defend individual display territories where male–male interactions often consist mainly of brief antagonistic encounters. Less common are species with true coordinated or cooperative displays, in which pairs or groups of males engage in complex ritualized courtship displays.

True coordinated or cooperative displays occur only in the genus *Chiroxiphia* and three species in the *Pipra aureola* clade (Schwartz & Snow 1978; Robbins 1983, 1985; Foster 1987; McDonald 1989*b*; Heindl 2002; DuVal 2007*b*) and are thought to have evolved independently on two occasions (Prum 1994). *Chiroxiphia* species can range from frequent but not obligate cooperation (*Chiroxiphia lanceolata*, DuVal 2007*a*,*b*) to strict obligate cooperation (*Chiroxiphia linearis*, McDonald 1989*a*,*b*). In addition, all three species of the *P. aureola* clade engage in dual-male coordinated display behaviours (Snow 2004). The wire-tailed manakin (*Pipra filicauda*), the focus of this study, is a member of the *P. aureola* clade, and is intermediate on this continuum, exhibiting intermittent or special-context coordinated display behaviours (Schwartz & Snow 1978) that appear to represent incipient cooperation. Associations among males in all these species appear to be based on linear dominance hierarchies (Foster 1981, 1987) and may serve two functions: either competition to establish reproductively beneficial dominance or cooperation to attract females (Prum 1994). In manakins, these functions appear not to be mutually exclusive. In both *Chiroxiphia* and the *P. aureola* clade, joint male displays function in establishing and maintaining dominance (i.e. age-graded queuing for social status), while concurrently providing benefits to subordinate display partners (McDonald 1989*a*; McDonald & Potts 1994; DuVal 2007*a*).

Reproductive success in male manakins is wholly dependent upon a male's ability to rise in social status and attract mates. Nevertheless, virtually nothing is known about the ontogeny of male status (but see McDonald 2007). In *C. linearis*, social rise depends upon a multi-year history of social interactions (McDonald 2007), but no studies have yet examined the link between interaction history and genetically based paternity assignments. Here we examine three social networks over 4 years to quantify the structure of multi-male social interactions in the wire-tailed manakin. Specifically, we examine how network structure and topology (i.e. average degree, variance in degree distribution and extent of clustering) relate to the incipient cooperation involved in the intermittent phenomenon of coordinated courtship displays. Furthermore, we examine the power of network metrics to predict male social rise and reproductive success. Each of the three social networks contained two spatially clustered leks that were linked socially by young males that moved between the paired leks. We expand upon the previous work of McDonald (2007) by examining the relationship between network structure and male social status and reproductive success in the wire-tailed manakin. This work begins building a comparative framework for understanding variation in the levels of cooperative display within manakins and, more broadly, the evolution of cooperation.

2. MATERIAL AND METHODS

(a) *Field work*

We studied social dynamics of male wire-tailed manakins from November to March 2003–2007, the height of the reproductive period, at Tiputini Biodiversity Station (TBS), Orellana Province, Ecuador (0°38′ S, 76°08′ W). TBS is a 650 ha biological station operated by the Universidad San Francisco de Quito; the site has approximately 30 km of trails and two gridded 100 ha study plots (Loiselle *et al.* 2007). The station is in primary lowland rainforest dominated by upland *terra firme* and *varzea* habitats (Ryder *et al.* 2006).

We located 13 wire-tailed manakin leks by systematically searching the habitat along all trails and within the two 100 ha gridded study plots. All captured males were fitted with aluminium leg bands and unique colour combinations to aid in individual recognition. Blood was taken from the brachial vein of all individuals for genetic analyses (see below). Leks range from 7 to 10 territorial males, and to quantify male–male interactions we employed two sampling techniques: (i) observations of 27 territory-holding male manakins at six leks during the 2 hour focal observation periods totalling 414 hours of observation and (ii) systematic scan samples at all other male territories within those leks. The two techniques over 4 years yielded 818 individual male colour-band resights from which we quantified male social interactions. Analyses of male social interactions were restricted to the cases where the colour combinations of

both males were positively identified. Male social interactions often occurred between males of differing status. Male plumage categories included *formative plumage* males characterized by green plumage with moult limits showing them to be less than 1 year of age, *predefinitive plumage* males characterized by green plumage intermittently flecked with yellow in the breast, black in the back and red in the head, which are approximately 2 years of age, and *definitive plumage* males characterized by adult plumage and which were at least 3 years of age (see Ryder & Durães 2005). Female–male interactions (almost exclusively for mating) were excluded from the analyses owing to brevity and rarity and because our goal was to assess the dynamics of male–male social structure.

(b) *Male social and reproductive success*

Males were categorized by plumage and territoriality as follows: *formative floaters* were all-green males, less than 1 year old, which did not hold territories, but which were seen visiting other males on leks; *predefinitive plumage floaters* were males with some red head feathers and black back feathers, which did not hold territories, but which were seen visiting lek territory holders; *definitive floaters* were definitively plumaged males without territories that regularly were seen visiting territorial males; and *definitive territory holders* were males in definitive plumage with their own display territory. Males in the formative or predefinitive plumage stages never held territories. Changes in male plumage were determined across the 4 years of the study by subsequent resightings and interactions with other males. Changes in male social status or social ascendancy occurred only when a male changed from definitive floater status to a definitive territory holder status. As such, only males that had the opportunity to rise socially were considered for this analysis (i.e. all pre-existing territory holders were excluded). Male status was coded as 0 if a male failed to change status and 1 if he inherited a territory during the 4 years of the study. Rises in male social status were always maintained within and across years (i.e. there were no reversals in status).

Male reproductive success was determined using molecular markers to assign paternity. Paternity was assigned using the likelihood approach (Marshall *et al.* 1998) and reproductive success was quantified in a binary fashion 0/1, where any male that sired an offspring with at least 80% confidence was coded 1, and any male that could not be assigned at least one offspring with 80% was coded 0 (see the electronic supplementary material for detailed information on genetic analyses). We used binary coding instead of a weighted measure of success in this study because our intent was to examine differences between successful and unsuccessful territory holders as they relate to network metrics. We view this as the first step towards later investigating more fine-grained variation in success.

(c) *Network metrics*

We constructed social network models based on 4 years of behavioural observations of colour-banded individuals. Network links (1 versus 0 in the corresponding *adjacency matrix*; Wasserman & Faust 1994) represented social interactions among males and were unweighted and undirected (0/1), so that frequency of interactions was not incorporated. Several applications of the social network theory have applied filtering to data for the co-occurrence in groups in fission–fusion type societies (see Rubenstein *et al.* 2007; Sundaresan *et al.* 2007). The usual procedure for such filtering is to require a threshold number of joint occurrences as the criterion for constituting a link. Such filtering reduces the effect of random or chance co-occurrence that does not represent any real interaction or partner choice. The links in the manakin network do not occur in the fission–fusion context of a flock or herd, but rather result from explicitly defined affiliative behaviours in the context of coordinated displays. The minimum requirement for a link (1 versus 0 in the corresponding adjacency matrix) was joint perching within 20 cm for several minutes. A subset of coordinated display data ($n=45$) from our 2 hour focal observations showed that joint perching and short perch-to-perch flights with non-vocal mechanical sounds (termed *klokking*) always preceded coordinated male displays. Moreover, the vast majority of links (more than 90%) among males were assigned based on joint coordinated display events in which males engaged in ritualized coordinated displays (for a detailed description, see Schwartz & Snow 1978). We also explicitly examined the relationship between observer effort and social connectivity to make sure that our results were not biased towards certain males. Our investigation of these patterns yielded no relationship between the number of hours observed and the number of male interactions ($r^2=0.0081$) or the time in the network and the number of male interactions ($r^2=0.069$).

We created three social networks, hereafter referred to as the Tower, Huaira and Puma networks, from male interactions at six leks. Each of the three networks included two leks that were spatially adjacent. The different networks, however, were not spatially contiguous; all were separated by at least 2 km, i.e. each network comprised a distinct pair of leks and had a non-overlapping set of individuals, making each a statistically independent replicate. The links between spatially adjacent leks were created by a few floater males that interacted with territory holders in each of the paired leks within a network. We used the cumulative interactions over the entire 4-year study period to compute all network metrics and statistical measures, because individual year sub-networks were not fully connected. The change and the reproductive status analyses were conducted on data combined from the three networks, to increase statistical power.

We used the program UCINET v. 6.0 (Borgatti *et al.* 2002) to calculate seven network metrics for each node (*degree*, *nEigenvector centrality*, *power* ($\beta=0.05$), *nCloseness*, *dwReach*, *information centrality* and *nBetweenness*). *Degree* is the number of links (edges) from a node (male) to the males with whom he was directly affiliated; *eigenvector centrality* assesses how central a node is in the network from eigen analysis of the *adjacency matrix* (the matrix equivalent of the network graph/diagram, which is the computational basis for most network metrics); *power* is a measure of the degree of nodes to which the focal node is connected; *nCloseness* is the mean geodesic (shortest) path between the focal node and all other nodes in the network, where path length is the number of unitary links separating the pairs of nodes (each link contributes one unit to total path length); *dwReach* is a measure of the percentage of nodes within two links of the focal node, weighted by path length; *information centrality* is a path length-weighted measure of how often a node lies along the paths connecting other pairs of nodes, including paths longer than the geodesic (Stephenson & Zelen 1989) and *nBetweenness* is a measure of the number of geodesic paths between the pairs of nodes that run through the focal node (see Wasserman & Faust 1994; Newman 2003; Albert & Barabasi 2004). Average network

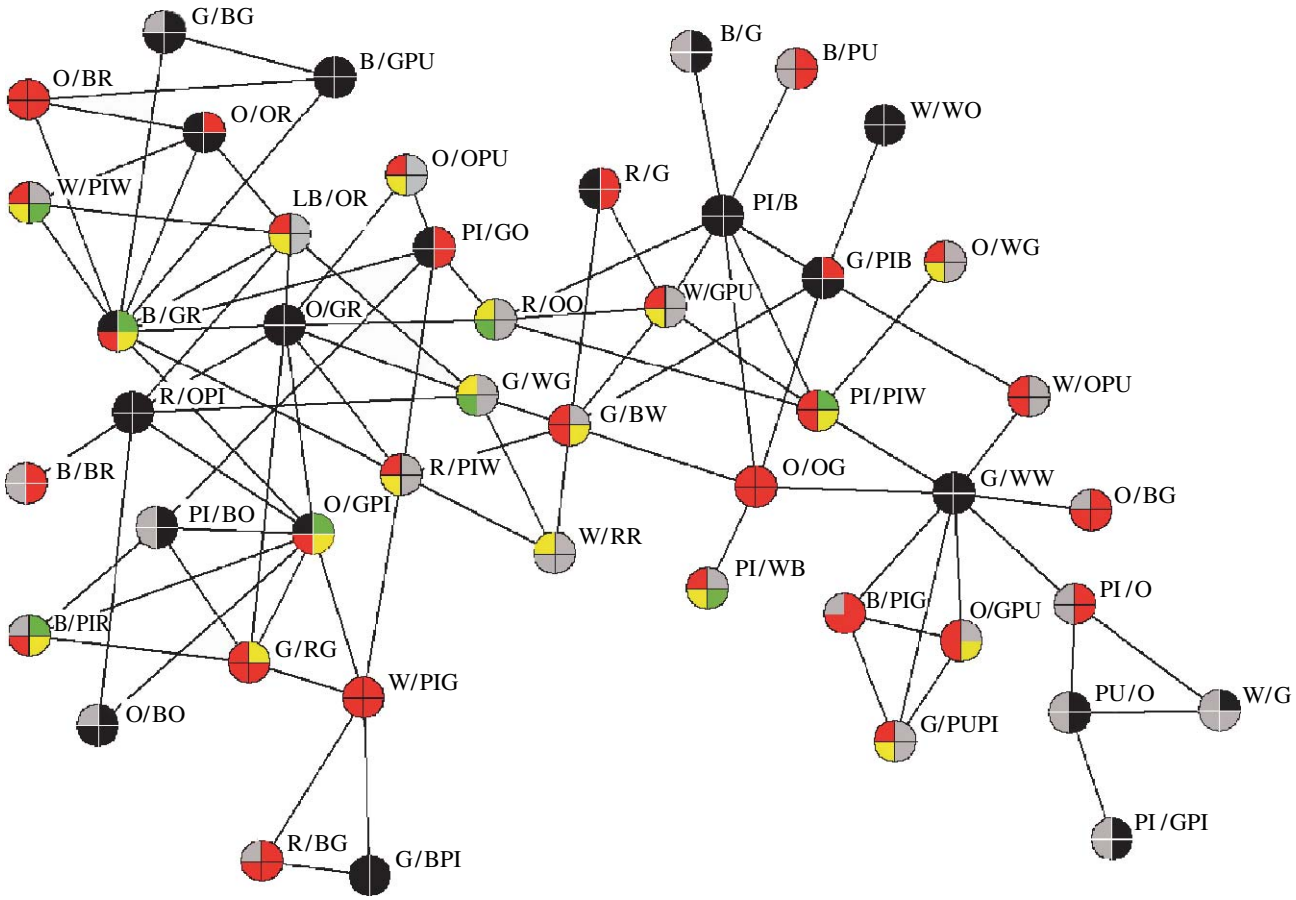

Figure 1. A representative social network for male wire-tailed manakins during a 4-year period at TBS, Ecuador. Each node represents a male, and the links represent social interactions among males. Path lengths are integer-valued counts of the number of links separating males. Note that the placement of nodes represents social, rather than spatial, proximity, although the two may often be correlated. The nodes are divided into four sections, representing a male's status during each year of the study, moving clockwise from the upper right quadrant. Grey, not present in the network; green, formative plumage floater; yellow, predefinitive plumage floater; red, definitive plumage floater; black, definitive plumage territorial holder. The network shown is the Tower network, comprising 46 males and 89 social links, from two spatially contiguous leks. The cluster of nodes on the left represents one lek and the cluster on the right represents a nearby lek linked socially by floater males. Bridging links between the leks pass through two non-territorial floater males (G/BW and R/OO). Removing those two males would disconnect the two leks. Note that several males of high connectivity (social hubs, usually court holders) link males of lower connectivity (often floaters), resulting in distinct clusters of affiliated males.

degree ($\bar{k}$) was calculated following Albert & Barabasi (2004). D.B.M. programmed MATHEMATICA routines following algorithms in Wasserman & Faust (1994) and Newman (2003) to calculate network diameter, global clustering and mean geodesics (shortest path lengths). Network diagrams were created using NETDRAW v. 2.504 (Borgatti 2002), with nodes arranged using a spring embedding algorithm.

(d) *Statistical analyses*

We used binary logistic regression to determine whether network metrics predict (i) male social rise or (ii) reproductive success. Both logistic regressions used all seven network metrics as potential predictors. The reproductive success analysis added an eighth potential predictor, 'territorial tenure', a measure of how many years a male held his territory (range 0–4). Because each regression had multiple predictors, we used a best-model-subset analysis and Akaike's information criterion (AIC) to assess model fit among candidate models that involved combinations of predictors (Burnham & Anderson 2002). Best-subset analyses were done using MINITAB; all other statistical tests were carried out using SPSS v. 13.0. Means and standard errors are reported, unless otherwise noted.

3. RESULTS

(a) *Network properties*

The network diagram for the Tower network shows that the social relationships of male wire-tailed manakins have discernible structure, with a tendency for older, territorial males to be socially central (figure 1). Within-lek connectivity (figure 1) was primarily determined by a few territorial males and their associated partners (e.g. PI/B and G/WW), whereas among-lek links were created by younger floater males (e.g. R/OO and G/BW) that interacted with territorial males at the two different leks within each network.

The three manakin social networks varied in size (i.e. n = number of males) and average degree (Tower $n = 46$, $\bar{k} = 3.86 \pm 0.36$; Huaira $n = 32$, $\bar{k} = 2.63 \pm 0.28$; Puma $n = 31$, $\bar{k} = 2.83 \pm 0.29$). The manakin network had low mean degree and high variance in degree (combined three-lek analysis $\bar{k} = 3.34$, $\sigma_k^2 = 4.17$; figure 2). The high variance in degree was evident in the cumulative degree distribution of the three observed manakin networks, each of which also showed a strong positive skew (figure 2), with a few nodes of high degree linking many nodes of lower degree. The observed skew is in the 82nd percentile

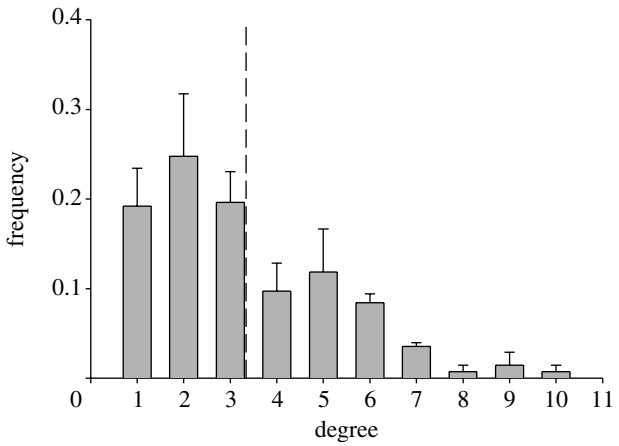

Figure 2. The cumulative degree distribution, averaged across the three manakin social networks, shows low average degree (dashed line), high variance, strong positive skew (calculated as the third central moment of the mean, divided by the cubed standard deviation) and a long tail. A few highly connected males (degree > 7) connected many males of lower degree ($\bar{k} = 3.34$, $\sigma_k^2 = 4.17$, skew = 0.95).

of the range of possible skews for a stretched beta distribution with the equivalent mean (Morris & Doak 2002, p. 281). Additional emergent properties of the three manakin networks were small mean diameter (8.33 ± 0.33 links) and low mean geodesic path length (3.92 ± 0.28 links), and fairly high node clustering (0.39 ± 0.03).

(b) *Social rise*

The best-fitting logistic regression model incorporated *degree*, *eigenvector centrality*, *information centrality* and *reach* as predictors of a male's probability of social rise (table 1). Predictors incorporated into the model varied in their explanatory power, with *degree* ($p = 0.001$, odds ratio = 7.31, 95% CI: 2.36–22.62) having the largest effect, i.e. each additional degree increased a male's odds of inheriting a territory by a factor of 7. Other predictors had lower predictive power, but did influence the overall fit of the model (*eigenvector centrality* $p = 0.034$, *information centrality* $p = 0.013$, *reach* $p = 0.007$). Other network metrics not selected by model fit criteria also varied between males that rose in status and those that did not (table 2).

(c) *Reproductive success*

Territory tenure best predicted the probability that a male would sire offspring ($p = 0.001$, odds ratio = 3.64, 95% CI: 1.66–8.02; table 1), i.e. a male's odds of siring offspring increased by a factor of about 4 for each additional year he was a territory holder (figure 3). The single-parameter tenure model was the best choice because it had the lowest AIC score, but a two-parameter model (*tenure* and *betweenness*) and a three-parameter model (*territory tenure*, *degree* and *reach*) were also good fits (i.e. ΔAIC < 2). None of the other network metrics contributed to the best-fit models for reproductive success. Moreover, models without *territory tenure* had much larger AIC values (i.e. ΔAIC > 2; table 1).

4. DISCUSSION

Results of the present study show that social network connectivity explained a male's ability to become a territory holder, and that the network topologies were consistent with the theory for conditions that facilitate the evolution of cooperation. *Territory tenure* was a strong predictor of a male's reproductive success. Obtaining a territory is a prerequisite for, but not the sole basis of, male reproductive success. The manakin networks also met other theoretical criteria favouring the evolution of cooperation. Although we did not measure the cost–benefit ratios, the manakin networks had low average degree (k) and high variance in k; such networks have the highest probability of promoting cooperative behaviour over the entire cost–benefit range (Santos & Pacheco 2005). The manakin networks have the low average degree and skewed degree distribution with a long tail that characterizes scale-free networks, although demonstrating a power-law distribution (versus alternative distributions) is virtually impossible in small networks (Keller 2005).

Table 1. AIC used to predict the best-fit models for male social rise and reproductive success in male wire-tailed manakins at TBS, Ecuador.

	P[a]	log (L)[b]	AIC[c]
social rise models			
degree + eigen + information centrality + dwReach	5	−27.200	64.400
degree + closeness	3	−33.027	72.054
degree + eigen	3	−33.299	72.598
degree	2	−34.785	73.570
power	2	−35.422	74.844
reproductive success models			
territory tenure	2	−29.141	62.282
territory tenure + betweenness	3	−28.495	62.990
territory tenure + degree + dwReach	4	−27.977	63.954
betweenness	2	−34.448	72.896
betweenness + dwReach	3	−33.876	73.752
betweenness + information centrality	3	−34.084	74.168
betweenness + closeness + information centrality	4	−33.379	74.758

[a] Number of model parameters including a constant.
[b] Maximized log-likelihood.
[c] AIC used in model selection.

(a) *Evolutionary implications of network topology*

The evolution of cooperation has long been an evolutionary puzzle. In spite of its relevance, understanding cooperation, particularly among unrelated individuals, remains a fundamental challenge for evolutionary biologists (Santos *et al.* 2006*b*). Graph-theoretical modelling of both static and dynamic networks has shown that selection can favour the evolution of non-selfish behaviour in the context of heterogeneous social ties (Santos & Pacheco 2005; Santos *et al.* 2006*a*).

Manakins show a spectrum of cooperation in courtship display from completely individual display to obligate cooperative display (*Chiroxiphia*). Coordinated male display, however, is rare among manakins and could represent intra-sexual aggression (Snow 1962; Tello 2001) or could produce reproductive benefits by enhancing attractiveness to females (Snow 1971*a*,*b*; Foster 1981; McDonald 1989*a*). Wire-tailed manakins show such intermediacy, with behavioural coordination (joint display) among males being common but not obligate (Schwartz & Snow 1978). The concordance between our social network topologies and theoretical predictions for conditions favouring the evolution of cooperation

Table 2. Measures of male network connectivity predict fitness components in male wire-tailed manakins at TBS, Ecuador. (Note that even network metrics not incorporated into the best-fit model varied across the response variables. All but two network metrics rose in concert with the response variables. Means ± s.e. are shown.)

	social rise[a]		reproductive success[b]	
network metrics	0	1	0	1
degree centrality	3.03 ± 0.2	4.47 ± 0.6	3.56 ± 0.41	3.89 ± 0.46
nBetweenness	7.44 ± 1.67	9.08 ± 1.76	6.39 ± 1.55	13.48 ± 3.04
nCloseness	27.66 ± 0.76	27.85 ± 1.50	26.14 ± 0.97	27.52 ± 1.20
power	4.04 ± 0.31	5.79 ± 0.91	4.65 ± 0.58	4.93 ± 0.62
nEigenvector centrality	16.58 ± 2.17	19.00 ± 4.62	15.53 ± 3.13	17.06 ± 3.18
information centrality	0.52 ± 0.03	0.56 ± 0.07	0.52 ± 0.04	0.49 ± 0.04
dwReach	14.16 ± 0.49	14.94 ± 1.20	14.38 ± 0.73	13.96 ± 0.80
territory tenure	n.a.	n.a.	2.56 ± 0.19	3.58 ± 0.15

[a] Male social status coded 0 (no social rise) and 1 (social rise).
[b] Male reproductive success coded as 0 (zero offspring sired) and 1 (at least 1 offspring sired).

suggests that cooperative benefits, at least as much as aggressive dominance-establishing benefits, may be important in the wire-tailed manakin social interactions.

The ingredients needed for the evolution of co-operation are present in the complex networks of social interactions among male wire-tailed manakins. Establishing that the social networks meet some of the necessary criteria specified by theoretical models is the first step towards the larger goal of specifying the set of necessary and sufficient conditions that could distinguish those species in which males cooperate in courtship display from those species that do not. We still do not know whether the observed network topology evolved as a precursor to, or concurrent with, the complex social interactions observed in the wire-tailed manakin. Comparative data from other manakin- and lek-mating taxa could help us distinguish features critical for evolving cooperation from features that are simply the inevitable consequences of interactions among spatially clustered males.

(b) *Social implications*

Recent evaluations of social networks (e.g. Croft *et al.* 2004; McDonald 2007) have shown that investigating social contacts can improve our understanding of complex behaviours. Moreover, because social interactions are dynamic in space and time, network metrics that integrate information on the history of interactions, phenotype and performance may best predict an individual's ultimate fate (McDonald 2007). Here, we present further evidence that the connectivity among males in a social network has a direct effect on individual fitness. Several related network metrics of connectivity predict male social rise in the critically important form of territorial inheritance. Those predictive metrics include measures that credit geodesic paths among nodes as well as longer, more circuitous paths across the network. *Degree* and path length-weighted *reach*, two of the best predictors of male social rise, take into account only geodesic paths between males. The other predictive metrics (*eigenvector centrality* and *information centrality*) also credit path lengths longer than the geodesic (shortest) path.

Our data support the recent findings for the long-tailed manakin, *C. linearis*, that social capital is a complex mix of male persistence and interactions, with multiple male partners of higher and lower social status (McDonald 2007). The existence of an age-graded queue in the wire-tailed manakins requires them to build social affiliations temporally that increase the probability of territorial inheritance. Over time, all males acquire social affiliations (network links) with both territorial males and non-territorial floaters, but males that acquire and maintain more links from the formative and predefinitive plumage stages are more likely to ascend socially (O/GPI and B/GR, figure 1). As noted above, male interaction history consists of social partnerships with both territorial and non-territorial individuals. As such, it is possible that successful dominance interactions with non-territorial individuals could contribute to social rise, especially if it contributes to the development of relationships with territory holders. Although de novo establishment of new territories does occur, the relationships with territorial individuals are an essential prerequisite for inheritance because most males acquire territories via a pre-existing social partnership (T. B. Ryder 2003–2007, unpublished data).

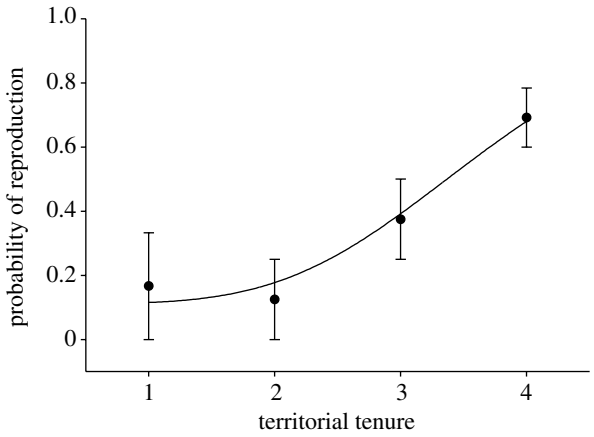

Figure 3. Territorial tenure in wire-tailed manakin social networks predicts the probability of reproductive success, using binary logistic regression. The probability of siring offspring is plotted as a function of territorial tenure (logit $(p) = -4.10 + 1.29 \times$ territory tenure). Points are response averages ± s.e. binned by tenure. The odds of territorial inheritance increased by a factor of 4 for each additional year a male held his territory.

(c) *Reproductive implications*

Variance in male mating success has been argued to be the single most important component of male fitness in lek-mating systems (McDonald 1989*b*). However,

understanding the sources of variation in male mating success continues to be a major challenge for behavioural ecology. Recent molecular estimates of reproductive skew in *Chiroxiphia* manakins are concordant with early observational estimates and suggest that a few males do most of the mating (DuVal 2007*a*). The wire-tailed manakin also exhibits reproductive skew, but with a more equitable distribution across males (T. B. Ryder 2003–2007, unpublished data). This lower variance in mating success in the wire-tailed manakins when compared with *Chiroxiphia* spp. means males have more options for mating success in the short term. The high variance in *Chiroxiphia*, skewed towards the oldest males, and hence fewer reproductive options for young males may have helped drive evolution towards the extreme of obligate cooperation.

Territoriality was a strong prerequisite to male reproductive success with nearly all chicks being sired by definitive territory holders (see the electronic supplementary material). Once a male had obtained a territory, his reproductive success was best predicted by the duration of his territorial tenure. Likewise, male tenure has previously been shown to predict male reproductive success in at least one other vertebrate (Engh *et al.* 2002). Unfortunately, male wire-tailed manakins cannot currently be accurately aged by phenotype after attainment of definitive male plumage late in their second year of life (Ryder & Durães 2005). It is likely, however, that territorial tenure is a good proxy for male age, given the nature of age-graded social queuing in other species of manakins (McDonald 1989*a*; Doucet *et al.* 2007; DuVal 2007*b*).

Two additional well-fitting models of male reproductive success incorporated additional network metrics. Those models included: *degree*, a measure of the number of other males with whom a male interacts directly; *betweenness*, a measure of the number of geodesic paths running through a given node (male); and *reach*, a measure of the proportion of nodes reachable by paths of length two or less. The inclusion of these metrics in two of the three models suggests the importance of indirect interactions involving intermediaries. The formal, quantitative framework provided by network models greatly enhances our understanding of these long-term reticulate multi-male interactions.

Previous network studies of animal social behaviour have focused largely on the emergent properties of networks, particularly classifications based on degree distributions. These studies have shown that interaction data, in a network theory context, provide useful quantitative measures of social interaction (Lusseau & Newman 2004). Fewer studies have addressed the evolutionary or fitness implications of dynamic network topologies at the level of individual nodes. Examining dynamic social interactions in spatial and temporal contexts may clarify behavioural strategies that previously lacked demonstrable fitness benefits (McDonald 2007). Here, we have demonstrated that connectivity plays a critical role in territory acquisition. Once established as a territory holder, a male's probability of siring offspring appears to be largely a function of *territory tenure*. Our results, therefore, provide a framework for beginning to partition the components of variance in male mating success. Further progress will require partitioning tenure into stochastic versus performance components and understanding in better detail how the complex social interactions described here result from the behavioural patterns of young males.

This research followed ethical guidelines set by the University of Missouri-St Louis Institutional Animal Care and Use Committee.

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