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ORIGINAL PAPER

Young-boy networks without kin clusters in a lek-mating manakin

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Abstract I use 10 years of data from a long-term study of lek-mating long-tailed manakins to relate the social network among males to their spatial and genetic structure. Previously, I showed that the network connectivity of young males predicts their future success. Here, I ask whether kinship might shape the organization of this "young-boy network". Not surprisingly, males that were more socially distant (linked by longer network paths) were affiliated with perch zones (lek arenas) that were further apart. Relatedness (r) among males within the network decreased as social distance increased, as might be expected under kin selection. Nevertheless, any role for indirect inclusive fitness benefits is refuted by the slightly negative mean relatedness among males at all social distances within the network (overall mean $r=-0.06$). That is, relatedness ranged from slightly negative (−0.04) to more negative (−0.2). In contrast, relatedness in dyads for which at least one of the males was outside the social network (involving at least one blood-sampled male not documented to have interacted with other banded males) was slightly above the random expectation (mean $r=0.05$). The slight variations around $r=0$ among males of different categories likely reflect dispersal dynamics, rather than any influence of kinship on social organization. Relatedness did not covary with the age difference between males. These results, together with previous results for lack of relatedness between alpha and beta male partners, refute any role for kin selection in the evolution of cooperative display in this lek-mating system.

Keywords Leks · Kin selection · Social network · Relatedness · Kinship · Cooperation · Manakin

Introduction

Social network techniques (Wasserman and Faust 1994) provide a useful tool for assessing complex social interactions because they explicitly accommodate the obvious fact that many social processes involve more than dyadic (two-way) interactions. Network analyses have proven useful for several different kinds of problems in behavioral ecology, as suggested in the introduction to this special issue of the journal (Krause et al. 2009). Examples include demonstrations that: (1) a young individual's position in a social network can predict that individual's later social trajectory (McDonald 2007); (2) key individuals can play important roles in stabilizing social relationships that favor social orderliness (Flack et al. 2006; Williams and Lusseau 2006); (3) group decisions may depend on the network position of signalers (Lusseau 2007); and (4) social network interactions can help explain cooperative predator inspection (Croft et al. 2006). All these examples feature emergent properties that arise from the complex interactions that are described by network metrics. They also tend to reflect an intersection between the resource distribution focus of ecological studies and the social interaction focus of animal behavior studies. They can, therefore, provide the sort of synthetic approaches that served as cornerstones for behavioral ecology as a discipline, such as the review by Emlen and Oring (1977) of the ecological underpinnings of mating systems. An important contributor to the progress of behavioral ecology has been

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the application of molecular markers as a tool for understanding the interaction between patterns of genetic structure and relatedness and the dynamics of social systems (Hughes 1998). It seems likely that bringing molecular data to bear on social network analyses could be similarly fruitful.

The complex social interactions of lek-mating long-tailed manakins (*Chiroxiphia linearis*) are particularly well suited to examination in the light of network techniques. Males form complex partnerships that culminate in cooperative dual-male courtship displays that are virtually unique in the animal kingdom. Each partnership consists of an alpha and a beta partner that top a team comprising as many as 15 males that collectively constitute a lek (defined as a cluster of males). The members of a lek are affiliated with a perch zone, which includes several spatially clustered dance perches used for the dual-male backwards leapfrog dance display (McDonald 1989a). The unison *toledo* calls (Trainer and McDonald 1995) and coordinated dance performed by alpha and beta are the basis for female choice and are an absolute prerequisite for mating success (McDonald 1989b). Younger males may be simultaneously members of more than one lek. The variance in male mating success is among the highest known for vertebrates (McDonald 1993a). Long-tailed manakins have long life spans, such that the estimated mean age for copulating males is 10.1 years (McDonald 1993a). Because the social interactions of males take place over the span of many years, and because males move among perch-zones over the years, the resulting social fabric has a richness of both temporal and spatial complexity. “Information centrality,” a network metric describing how often a young male lies along paths connecting other pairs of males in the network (Stephenson and Zelen 1989), is a good predictor of his later social rise (McDonald 2007). These “young-boy” network interactions have effects that bear fruit almost 5 years later. The same metric (information centrality) that predicts the probability of social rise for young males does not help explain differences in success among older males. That is, network connectivity is critically important for young males, but less so once they become established, higher-ranking members of a lek.

It seems possible that patterns of kinship might influence patterns of interactions in the social network. Clustering of male kin on leks has been hypothesized to suggest a role for kin selection in the evolution of leks (Höglund et al. 1999; Shorey et al. 2000). Krakauer (2005) convincingly demonstrated indirect inclusive fitness benefits for cooperatively displaying subordinate male turkeys (*Meleagris gallopavo*). Other studies of lek-mating species, however, have failed to corroborate the generality of kin groups on leks (Gibson et al. 2005; Loiselle et al. 2007). Furthermore, the simple presence of kin does not guarantee indirect benefits or the evolution of cooperative behavior (West et al. 2002). Any search for the a priori most plausible circumstances for indirect benefits in lek mating systems would surely focus on the tightly coordinated cooperative displays of long-tailed manakins. The partners who display together are, however, unrelated, and the kin selection hypothesis for alpha-beta cooperation can, therefore, be rejected (McDonald and Potts 1994). Nonetheless, it is still possible that early kin associations, such as those seen in the sibships of peacocks (*Pavo cristatus*; Petrie et al. 1999) could underlie social ties among young males as they begin to associate with different perch zones, even if those ties dissipate by the time males achieve alpha and beta status. That is, kin selection could shape early “young-boy network” interactions, even though it does not contribute to the eventual alpha–beta interaction.

Here, I ask how social network relationships relate to the spatial and genetic organization of male long-tailed manakins. First, I ask whether the spatial distance between the perch zones with which males were affiliated was related to the degree of social separation between males. Second, I ask whether relatedness is a predictor of the degree of social separation among males, as measured by path lengths between males in the social network. Third, I ask whether relatedness among males that interacted in the social network was higher than that among males outside the social network. Finally, I ask whether the age differential between males was correlated with their coefficient of relatedness. That is, were males that were more similar in age more closely related than males that differed more in age? Taken together, these questions address the fundamental issue of whether kin selection plays a general role in the evolution of leks (Kokko and Lindstrom 1996; Shorey et al. 2000) or whether kin selection is at most a rare feature of lek systems (Gibson et al. 2005; Loiselle et al. 2007) and whether the occasional clusters of kin observed in some systems can be best explained as a simple consequence of patterns of dispersal with no further fitness consequences.

Methods

Social network construction The data on social interactions among male long-tailed manakins came from a long-term study in Monteverde, Costa Rica that is described in McDonald and Potts (1994) and references therein. The social network models were built according to procedures outlined in McDonald (2007). Here, I summarize the essentials pertinent to this paper. I constructed a cumulative 10-year network from 9,288 h of behavioral observations of 95 color-banded males and 61 color-banded females between 1989 and 1998. Males were classified into five status categories: predefinitive (age three or younger, based on a strictly age-based sequence of plumage maturation; Doucet et al. 2007), definitive (four 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 perch zone accrue). A male's status was assigned at the last date for which he was included in the network. The reason for this was that as males age, they spend more and more time at fewer and fewer different perch zones, such that top-ranking males are rarely sighted at more than one perch zone (McDonald 1989a). Thus, although males often move widely among different perch zones (McDonald 1989a) through their lifespans, a male's last sighting is most likely to represent his "core" perch zone. Males were credited as interacting if they were seen to engage in dual- or multi-male displays at lek arenas. Many such displays and interactions occur in the absence of any females. Because these interactions represent observable affiliative behaviors, the interactions do not rely on the "gambit of the group" and need to be filtered in the way recommended for analysis of co-occurrence in fission-fusion groups (e.g., James et al. 2009). Further, because the sampling was conducted at stable lek sites (dance perches), the problem of edge effects is reduced. Males sighted at the physical boundary of the study area were not notably less likely to be resighted than were males at the core. This is particularly true for high-ranking males, especially alphas, who are sighted almost exclusively at their "home" lek site. Nevertheless, some young males were spottily sighted at various lek sites and might be subject to a form of temporal censoring.

Network metrics For each dyad (pairwise set of males) in the network, I calculated "degree of social separation" as the geodesic (shortest path) distance between the two males. Degrees of separation alludes to the concept of "six degrees of separation" epitomized in popular culture by the game where one links any given actor to Kevin Bacon by a chain of intermediates who appeared together in the same film (Watts 2003). When degrees of separation are presented as the proportion of the maximum, they have sometimes been called "proximities" (Knoke and Kuklinski 1982, p. 48), and I modified that algorithm to calculate the degrees of social separation with a *Mathematica*™ program. A social separation of 0 is actor to self. A separation of 1 is the 1-unit path length connecting actor to any other individual with which it interacts directly. Path lengths are unitary—each link (line on the graph) has length 1, regardless of its apparent length in a network diagram such as Fig. 1. Each male was assigned a spatial location based on the perch zone with which he was affiliated at the end of his tenure in the social network. In the relatively few cases where a male (usually young) was observed at multiple perch zones in his final year in the network, I designated the perch zone at which he was sighted most often as his primary perch zone. End of network tenure

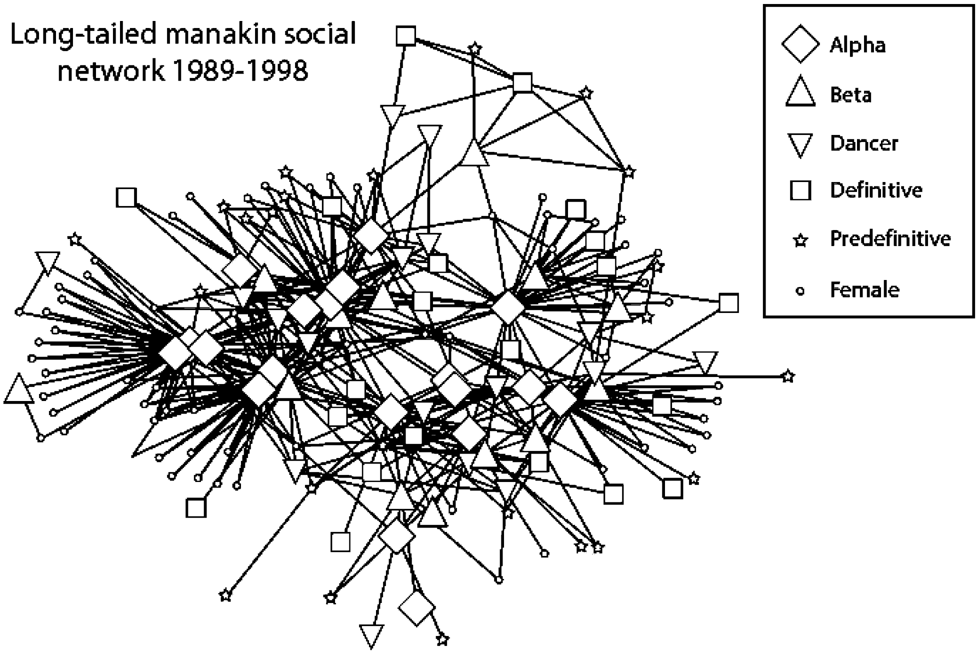

Fig. 1 Social network for 156 long-tailed manakins over the 10-year period from 1989 to 1998. Each *line* (regardless of apparent length in the diagram) is a one-unit path connecting an individual to another individual with which it has interacted directly (a path length of zero is interaction with self, which is usually ignored). The *shortest path* between pairs of individuals (geodesic) serves as the metric of "degrees of separation (social distance)" in the later figures, against which to compare geographic separation and relatedness. *Symbols* for the categories of male status become smaller as one moves down the social hierarchy. Banded females (*circles*) that visited male dance perches are shown in the network diagram but were not included in any of the analyses

could be due to disappearance (almost always meaning death in the case of senior males) or the right-censoring due to the end of the study period. Right-censoring is a demographic term meaning that the occurrence of an individual in a dataset ended because the study period ended rather than because the individual was observed to die or disappear.

Geographic distance tests For assessing the relationship of geographic distance between males to social network distance between males, the data points were pairs of males (dyads). For 95 males, 4,465 dyads are possible. Eliminating all dyads that consisted of males whose behavioral records did not overlap temporally reduced the sample to 2,122 dyads. I eliminated an additional 284 dyads by restricting the analysis to comparisons among males that had not interacted directly—avoiding the truism that males that interacted directly (network "degree of separation"=1) had to do so at the same perch zone (geographic separation=0). In contrast, indirect links between males quite often arose from interactions occurring at distinct perch zones. For example, males A and B might have interacted at perch zone X, whereas males B and C might have interacted at perch zone Y. That would mean two degrees of separation between males A and C, with a geographic separation corresponding to the distance between perch zones X and Y. Thus, "social separation" is a synonym for the path length between males in the social network. I was left with 1,838 dyads that co-occurred temporally and also had a degree of separation of at least two. Because each male was usually a member of multiple dyads, the 1,836 points are not independent. I, therefore, used a Mantel test, with a bootstrap sample size of 5,000, to test for a significant relationship between degrees of social separation and the geographic distance between primary perch zones.

Genetic relatedness tests The genetic data came from microsatellite DNA analyses of males collected as part of earlier studies of partner relatedness (McDonald and Potts 1994) and population genetic structure (McDonald 2003), which provide details of the sampling and laboratory methods. For the present study, I analyzed the genotypes of 69 males at four polymorphic microsatellite loci with the program *Relatedness* 5.0.8 to obtain the estimate of Queller and Goodnight (1989) for the relatedness coefficient, *r*. In principle, values of *r* can range from +1 (identical twins or clones) to 0 (the random expectation) to −1 (completely dissimilar genetically). The *Relatedness* 5.0.8 estimates, however, sometimes extend beyond those biologically meaningful boundaries (the most negative *r* value was −1.49). Of the 69 males in the genetic dataset, 44 were also members of the social network data set. These 44 males engendered 946 dyads that allowed pairwise comparisons of relatedness against degree of social separation, using a Mantel test with 5,000 replicates. I also used a two-tailed *t* test to compare the mean relatedness of the 44 males in the social network with that of the 25 males sampled in the study area but not observed to participate in the social network (i.e., that were not documented to interact with any other banded bird). Of the males with genotypic data, 46 were of known age, from cohorts spanning a 10-year period. I constructed a matrix of age differences between these males and compared that matrix to the matrix of their relatedness coefficients (*r*) using a Mantel test.

Results

The network was fully connected, meaning that at least one path connected every male in the network to every other male (Fig. 1). The mean geographic separation between the primary perch zones for the 2,122 temporally co-occurring dyads was 84±97 m. The mean degree of social separation (path length between males) was 2.5±0.9 and the maximum (also termed the "diameter" of the network; Wasserman and Faust 1994) was six degrees of separation. For the subset of 1,838 male dyads who were not directly connected (path length ≥2), the mean geographic distance between their perch zones was 97±98 m. The geographic distance between their perch zones was positively correlated with degree of social separation (Fig. 2; Mantel test, $P<0.001$).

Relatedness among males was negatively correlated with network degree of separation (Mantel test, $P<0.01$), largely driven by the negative *r* for males with four degrees of separation ($r=-0.2\pm0.5$; Fig. 3). For all five values of degree of separation, however, mean relatedness among network

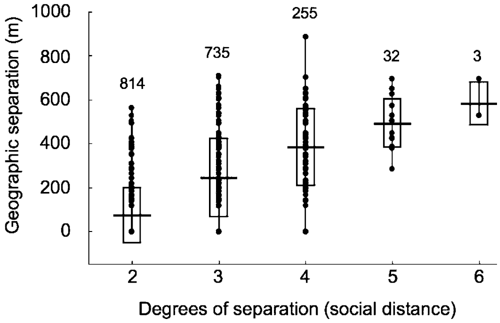

Fig. 2 Have friends, will travel, but not too far. The perch zones of males that were geographically proximate tended also to be socially closer (fewer degrees of network separation, measured as the length of the path between them across the network). Each point represents the metric for a male dyad. Note that male dyads that interacted directly (degree of separation=1) were excluded from the analysis, as were all dyads that involved combinations of males not overlapping temporally in the network. Thus, the degree of separation begins at two (at least one intervening male required) and extends to a maximum of six degrees of separation for a very few dyads. *Dark horizontal bars* mean for each degree of separation category; *boxes* mean±SD; *vertical line* range. *Number above each bar* is the sample size of dyads (pairwise comparisons)

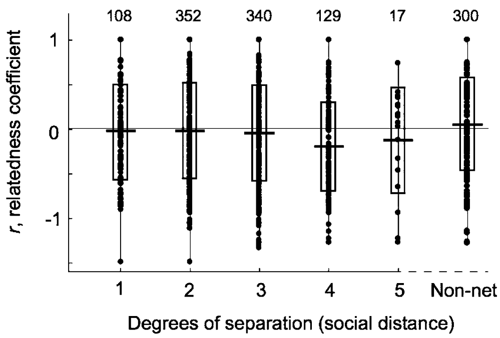

Fig. 3 Friendship is thicker than blood. Network social distance (degrees of separation, measured as the path length between males across the network) correlated negatively with the relatedness coefficient, *r*, reaching a minimum at four degrees of separation. Note, however, that within the network (*numbered bars 1 to 5*), mean relatedness was always less than zero (the random expectation). Interestingly, relatedness in male dyads for which one or both of the males was not in the network (*rightmost bar*) was positive and significantly higher than that among within-network dyads. Mean relatedness of dyads that interacted directly (degrees of separation=1) was −0.04, meaning that males did not interact preferentially with kin. Kinship, therefore, appears to play little role in social networking among males of any rank, consistent with previous results for lack of relatedness between alpha and beta male partners. *Dark horizontal bars* mean *r* for each degree of separation; *boxes* mean±SD; *vertical line* range. *Gray horizontal line* zero relatedness (random expectation). *Number above each bar* is the sample size of dyads. The algorithm used to estimate *r*, causes some dyads to have estimated *r* values below the minimum expectable value of −1

males was less than zero ($r=0$ is the random expectation). The mean relatedness of males with direct interactions in the network (one degree of separation) was −0.04±0.54. In contrast, the mean relatedness of 300 dyads of males sampled in the study area but with at least one member not observed to participate in the social network was slightly positive ($r=0.05$) and was higher ($t=3.09$, $df=1{,}244$, $P=0.002$) than the negative mean relatedness ($r=-0.06$) among the 946 dyads of genetically sampled males included in the social network. Relatedness did not vary with the age differential between males (Mantel test, $P=0.27$). For all measured age differentials (0 to 10 years) the confidence intervals for the coefficient of relatedness, *r*, overlapped zero. The only positive relatedness values were between males most different in age (6-year difference or greater).

Discussion

The social networks of long-tailed manakins are spatially structured so that males generally interact more closely with males at geographically proximate perch zones. In contrast, the social network shows no evidence for organization on the basis of kinship, because neither direct nor indirect associations within the network occurred preferentially with kin. If anything, males within the network (mean $r=-0.06$) tend to be related at slightly less than the random expectation, whereas males banded within the study area but not observed in the social network (mean $r=0.05$) had slightly positive relatedness. The results therefore extend earlier findings on the role of kinship in the cooperative behavior of long-tailed manakins. McDonald and Potts (1994) showed that alpha–beta partners are not related and, thus, that cooperative courtship display is not driven by inclusive fitness benefits to the cooperating beta male, who almost never obtains copulations during his several-year tenure as beta partner. Here, I have shown that social network interactions are not organized according to kinship. While kin selection may play a role in some lek mating systems (Kokko and Lindstrom 1996), the results presented here and those of others (Gibson et al. 2005; Loiselle et al. 2007) make it appear unlikely that kin selection plays any major role in the overall evolution of lek mating systems.

Given the complete lack of support for a kin selection hypothesis for male–male cooperation, why then were males that were more socially distant also less related? The key lies in where those decreasing relatedness values fall, along the possible spectrum from identical (twins or clones) to completely dissimilar. Male relatedness did decrease to a minimum at four degrees of separation (Fig. 3; mean $r=-0.2\pm0.5$). Nevertheless, for dyads with at least one member not connected to the social network, the relatedness was higher and, more importantly, positive. The most plausible explanation is that male dispersal sets a pattern whereby males that interact directly (degree of separation=1; mean $r=-0.04\pm0.54$) are related at essentially the random expectation and that relatedness gradually decreases for longer paths through the network (degrees of separation=2 to 5). The rise to positive for non-network dyads may reflect predispersal relatedness of some of the young males to a few highly successful male sires. Put differently, the significant negative relationship between social distance and relatedness may be statistically significant (because of the fairly large sample size) but is far from the prerequisite for creating meaningful indirect inclusive fitness benefits.

Further support for the hypothesis that kinship fails to explain social organization comes from the lack of relationship between the relatedness coefficient, *r*, and the age differential between males. Shorey et al. (2000) found some evidence for clusters of young, related males on white-bearded manakin (*Manacus manacus*) leks. Petrie et al. (1999) found evidence for kin association among young males in lek-mating peafowl. Nevertheless, male long-tailed manakins from the same cohort were related at essentially the random level. Somewhat positive relatedness between males very different in age is possibly consistent with the hypothesis that the sons of successful sires create ephemeral kinship patterns within the population at large, but nothing suggests that any such sire-son dyads interact in ways that would provide indirect inclusive fitness benefits to either young males or sires. Young males seeking establishment in leks interact primarily with males similar to them in age and signal their status with plumage badges directed mostly at males of their own, or similar, age (McDonald 1993b).

Knowledge of past social processes in a population, as encapsulated in social network metrics, can help us understand current patterns of social relationships, such as the importance of long term interactions between unrelated cooperators. The present analyses demonstrate that social interactions in the network are not a function of relatedness among males at any stage in their careers. Males did, however, exhibit a degree of social viscosity. They tended to be linked by shorter network paths to males at nearby perch zones than to males at more distant perch zones. Any of the 91 males in the 10-year cumulative network could be linked to any other male by a path of six links or fewer. In the present case, indirect inclusive fitness benefits can be almost entirely ruled out. In other systems, such as cooperative breeding, fairly close kinship among social interactants can be the norm. It seems likely that social network analyses, combined with molecular analyses of relatedness, will be very useful in at least two ways. First, they could provide a framework for quantifying kin vs. non-kin social interactions. Second, they could help quantify the way that complex social interactions affect higher-level population processes. An example is the dramatic difference between the population genetic structure of cooperatively breeding Florida scrub-jays (*Aphelocoma coerulescens*) and that of western scrub-jays (*A. californica*), which do not breed cooperatively (McDonald et al. 1999).

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