Predicting fate from early connectivity in a social network

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In the long-tailed manakin (*Chiroxiphia linearis*), a long-lived tropical bird, early connectivity within a social network predicts male success an average of 4.8 years later. Long-tailed manakins have an unusual lek mating system in which pairs of unrelated males, at the top of complex overlapping teams of as many as 15 males, cooperate for obligate dual-male song and dance courtship displays. For as long as 8 years before forming stable ''alpha–beta'' partnerships, males interact with many other males in complex, temporally dynamic social networks. ''Information centrality'' is a network connectivity metric that accounts for indirect as well as shortest (geodesic) paths among interactors. The odds that males would rise socially rose by a factor of five for each one-unit increase in their early information centrality. Connectivity of males destined to rise did not change over time but increased in males that failed to rise socially. The results suggest that network connectivity is important for young males (ages 1–6) but less so for older males of high status (ages 10–15) and that it is difficult to explain present success without reference to social history.

delayed benefits | lek behavior | mating success | network models | social status

Scientists often seek to predict fate from earlier states that will change dynamically. Examples include the quest to explain early variation in helping behavior according to conflicting components of future fitness (1), the influence of juvenile experience on fitness-related adult behaviors (2), and the attempt to pinpoint the most likely perpetrator from earlier communications among a network of potential terrorists (3). In the context of social behavior, fitness may depend on complex networks of social interactions that precede reproduction by several or many years. In the lek-mating long-tailed manakin (*Chiroxiphia linearis*, Aves), long-standing male–male relationships culminate in a unique form of obligate dual-male cooperative courtship display. Beginning in their first year, males establish overlapping relationships at multiple display arenas, culminating in ''alpha'' and ''beta'' roles in which the top two males focus most or all of their time at a single display arena (4, 5). Males must often wait as long as 10 years (4) to move up to alpha rank and have any chance of reproducing, because only the top-ranking alphas in a team have any real prospects for copulatory success. Beta males gain direct but delayed benefits by cooperating with alpha males to whom they are unrelated (4). How, though, do males move through the ranks to ascend to alpha or beta positions? Do behavioral characteristics early in life predict the likelihood of later attaining alpha or beta rank? Because younger males interact with many others, often in multimale displays in the absence of females, it is plausible that early male–male social interactions might influence or determine a male's eventual acquisition of partner rank.

Network theory provides useful quantitative metrics for analyzing complex, reticulate social interactions (6, 7). These metrics account not just for dyadic interactions, but also for multiactor interactions whose complexity requires special analytical tools. Network models consist of ''nodes'' or ''vertices'' (in this case, individual birds) connected by ''links'' or ''edges'' (interactions among birds). The simplest formulation is to have binary links (1/0, presence/absence of interaction), the approach taken here. Numerous network metrics exist to assess the connectivity of nodes within networks. Many of these metrics assess some aspect of the ''centrality'' of an individual (node), asking how central the individual's place is in the network of interactions among individuals.

Here, I use network models to ask whether early social interactions predict the social trajectories of male long-tailed manakins. Because the interactions among males are dynamic and long lasting, I created five sequential subnetworks, in 2-year timeblocks, over a 10-year span from 1989 to 1998. I classified males into five categories, based on a progression in plumage and social status, culminating in the alpha and beta roles assumed by the males that perform nearly all of the dual-male song and dance displays for females. A basic measure of connectivity is a node's ''degree'' (6, 7), the number of other nodes to which it is connected. Other metrics of connectivity included ''information centrality'' (8), which assesses how often a bird lies along a ''path'' (a series of links) between other birds in the network. Information centrality is similar to the more familiar network metric ''betweenness'' (6, 7), except that betweenness credits only shortest paths (''geodesics''), whereas information centrality also credits more circuitous paths weighted by the inverse of the path length (the number of links along the path). I used binary logistic regression to assess seven such connectivity metrics as potential predictors of a male's likelihood of rising success. The seven metrics were information centrality, degree centrality, eigenvector centrality, power, closeness, distance-weighted reach, and betweenness (6, 7). Rising success was defined as moving upward to a role as a male that danced for a female, or a rise in the number of dances for females, or a rise to alpha or beta status, or an increase in copulatory success. Here I show that a male's early connectivity predicts his social trajectory an average of 4.8 years later.

Results

Connectivity varied both for individual males over time and among males of the same category within each timeblock (Fig. 1). A male's information centrality in his starting subnetwork, relative to that of males of the same category, was the best predictor of his odds of social rise ($P = 0.014$ following Bonferroni correction; see Fig. 2). Each unit increase in a male's information centrality (scale 0–2) increased his odds of rising socially by a factor of 5 (95% CI; 1.8–13.95). The mean time interval between assessing early connectivity and later rise, or lack thereof, was 4.8 years (range: 2–9). The metric dwReach (the weighted sum of path lengths from actor to all other nodes, weighted by the reciprocal of path length) was the only other connectivity metric that was a significant predictor of social rise ($P = 0.028$ following Bonferroni correction, odds ratio
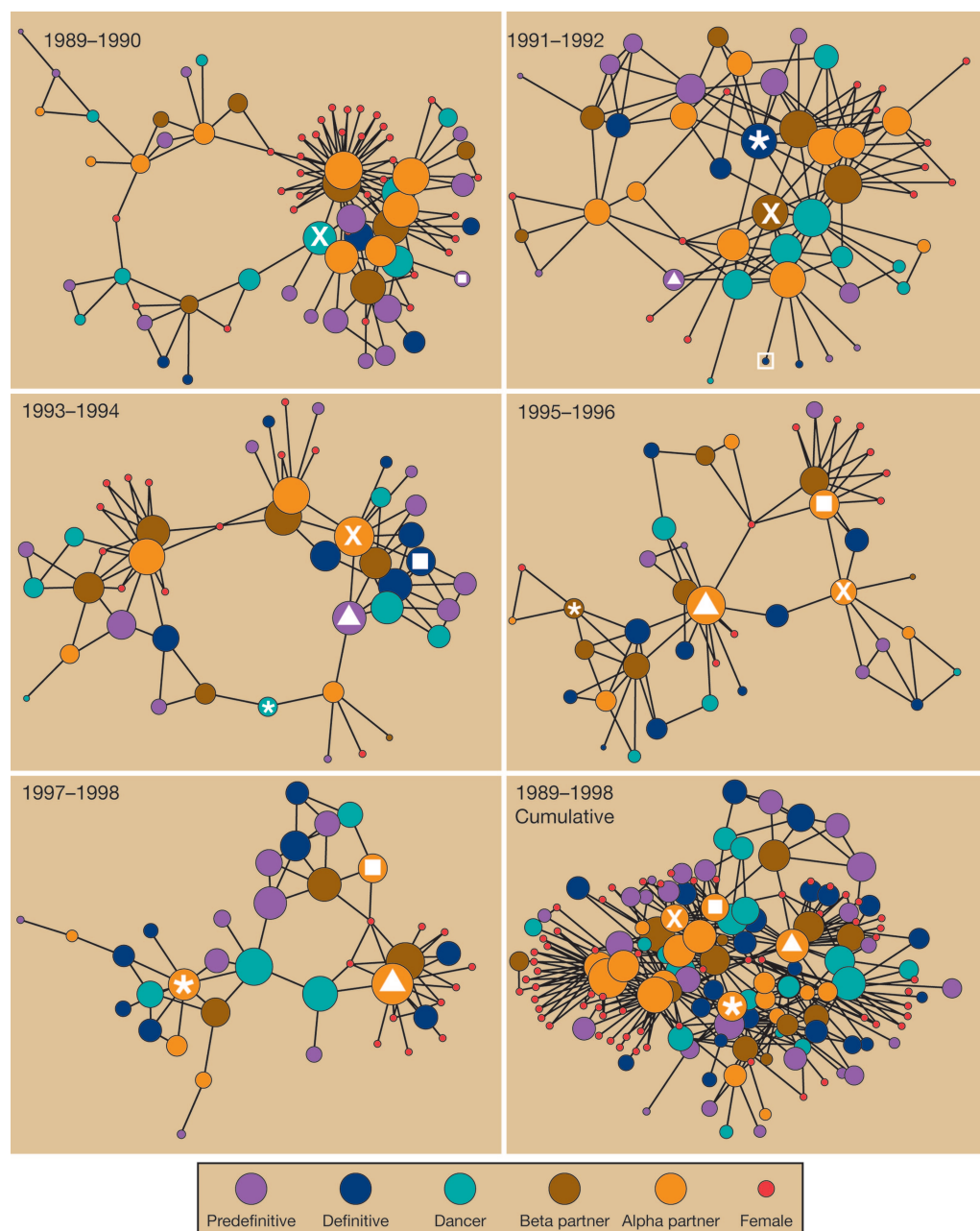
Fig. 1. Social networks in long-tailed manakins. (*Left Top–Bottom* and *Right Top* and *Middle*) Subnetworks in successive 2-year timeblocks. (*Right Bottom*) The cumulative network (1989–1998) for 95 males and 61 females. Early connectivity, assessed by the network metric information centrality, predicts later fate. Circles (nodes), colored by category, represent individuals, and lines (undirected, unweighted links) represent social interactions at lek display perches. Node size (males only) represents information centrality, which is defined in the text. In *Left Top–Bottom* and *Right Top* and *Middle*, node size represents information centrality relative to males of the same category in that subnetwork. In *Right Bottom*, node size represents information centrality in each male's last timeblock adjusted by the mean in that subnetwork. White symbols (X, triangle, asterisk, and enclosed or enclosing square) track four individual males through time. Note that, as successful alphas (*Right Bottom*), all four tracked males had moderate information centrality. The number of banded females linked to alpha males is a reasonable proxy for male mating success.

4.6). Model selection procedures, using Akaike's information criterion (AIC), favored the model with information centrality as the lone predictor over other models, including more complex models.

Whereas time-lagged prior connectivity predicted fate, concurrent connectivity did not. In contrast to the predictive ability of early connectivity, a male's information centrality in his last subnetwork, which is usually the time when males achieve their peak success in terms of female visits or matings, did not predict his odds of social rise ($P = 0.37$). Further, the information centrality of socially rising males did not differ between their starting timeblock ($\bar{x} = 1.22$) and their ending timeblock ($\bar{x} = 1.18$; $n = 28$, paired t test, $P > 0.5$). In contrast, the information centrality of males that did not rise socially did increase from the starting timeblock ($\bar{x} = 0.88$) to the ending timeblock ($\bar{x} = 1.10$; $n = 22$, paired t test, $P = 0.004$).

Discussion

The most surprising result of the network analysis was that greater temporal remove between predictor (connectivity) and response (social rise) improved predictive power. Concurrent
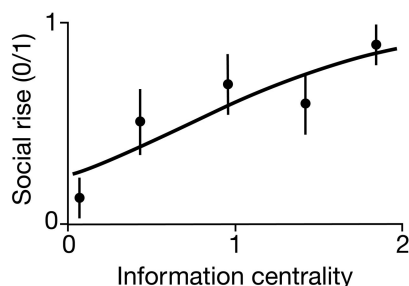
Fig. 2. Logistic regression for binary rise in success (response) as a function of information centrality (predictor) in long-tailed manakin social networks. Early connectivity predicted fate (social rise) 4.8 years later on average. A male's information centrality score was relative to that of others in the same category for the 2-year timeblock (Fig. 1) in which he was first seen interacting. Curve plots probability of success as a function of information centrality (logit[p] = $-1.21 + 1.6 \times$ information centrality). Points are response averages binned in groups of 10 ($\pm$SE). A male's odds of later social rise were 4.96 times higher for each unit increase in his relative information centrality (scale 0–2). In contrast, information centrality in the final timeblock subnetwork was not correlated with contemporaneous success.

connectivity was not correlated with social rise, whereas connectivity 5 years prior was a strong predictor of rise. The strong predictive ability of early information centrality, coupled with its lack of change in males that rose socially, suggests that social connectivity is crucial for a male early in his career, but less so once he attains high status. In contrast, the connectivity of males that did not rise socially increased over time, suggesting that high connectivity was still important to them, if they were to have any hope of later rise.

Why might information centrality be a particularly good predictor of the likelihood of social rise? Information centrality credits circuitous paths across the network, emphasizing a role for even indirect and weak ties (9). In contrast, the metric betweenness assesses only geodesic (shortest) paths among individuals. In systems as disparate as ecological food webs (10, 11) and population genetics (12), the cumulative importance of weak (indirect) links may be similarly crucial to capturing fully the dynamics of reticulate interactions. The dynamism of the social network in male long-tailed manakins may help explain the importance of circuitous as well as direct pathways. Because of the orderly, age-graded queues for social rank (4, 5, 13), a crucial step for young males (ages 1–6) is to establish relationships in those leks where they stand the best chance of becoming one of those very few alpha males with high copulatory success. Most young males establish and maintain at least loose relationships with males in as many as five different leks, each consisting of partially overlapping sets of 5–15 males. Persistence, interactivity, and the proper combination of dominance over males of equivalent category and submission toward males of higher rank likely determine a male's social capital. The predictive force of information centrality suggests that success may stem from early, indirect connections to many other males. Whereas Akaike's information criterion selected information centrality as the lone predictor, other predictors (e.g., distance-weighted reach) had only slightly lower likelihoods. The more important point may be that any of several possible time-lagged connectivity metrics predict fate well in advance, whereas concurrent connectivity is uncorrelated with fate.

The direct delayed benefits hypothesis (4) for cooperation among unrelated males posits that cooperation leads to payoffs delayed by several years. The essential point is that lack of present options forces young males to adopt a strategy, i.e., male–male cooperation, that enhances future prospects of success. The present study demonstrates that a male's trajectory

depends crucially on youthful interactions. The natural history of long-tailed manakins clearly supports the importance of such early interactions. Males move through an unusually distinct series of age-specific predefinitive plumages (photos in ref. 14). In each of their first 5 years of life, they have a different and easily distinguished plumage: green, red-cap, black-face, blue-back, and finally the definitive red, black, and blue plumage. Younger males interact at more perches than do older males (ref. 5, p. 719). Thus, young males with high information centrality spend time at several different leks accruing links to males at several distinct leks, any one of which may later be a key player as they jockey for social success. Thus, male–male interactions are fluid in both time and space, but we cannot understand present success solely by present phenotype and performance. A male's history is a critically important predictor.

Age, rank, and gender interact in several intriguing ways in the network. First, connectivity of males (assessed by information centrality or degree) did not change as they attained high rank and rose socially, whereas it increased in males that did not rise socially. Decreasing connectivity coupled to increasing success applies especially to links with other males, because many of the links involving the most successful alphas and betas are with females (Fig. 1). Second, males of high status were often linked to fewer males, but those few links involved very high numbers of interactions, a factor not considered in the present analysis. Third, although the queues are largely age-graded, age alone does not guarantee success. One of the lower-ranked dancers (the blue-green nodes in Fig. 1) was at least 18 years old when last seen in 1997. No other male during the 1989–1998 period was known with certainty to be older. Finally, the complex cooperation and social networking among males stands in stark contrast to the essentially solitary behavior of females, which visit dance perches only briefly and otherwise interact socially only with their nestlings. Note that females were linked mostly to just a few alphas and betas (Fig. 1), reflecting the high variance in male mating success.

Distance-weighted reach, the other connectivity metric that was a predictor of social rise, is a weighted sum of the reciprocal of path lengths from actor to all other nodes. The use of the reciprocal of path length makes it similar to information centrality in assessing indirect connections. In contrast, degree, which was not a significant predictor, assesses the number of individuals directly connected to actor. The latter would credit males with links to females. Links to females rarely formed parts of longer paths; that is, female were often linked only to alphas and betas and not onward to other birds in the network. Thus, successful alpha males tended to have highest degree, but had relatively lower information centrality and distance-weighted reach, because the one-link paths to females did not substantially increase those metrics.

Much recent research on networks has addressed their overall ontogeny and structural dynamics. For example, disparate types of networks share structural characteristics such as "small-world" features (15). Ecological analyses have tended to focus on the robustness (10) of the network as a whole. Outside of the sociological literature, however, few have asked whether the connectivities (position and context, as assessed by metrics such as information centrality) of individual nodes can predict their fate. In contexts as diverse as economics, engineering, and criminology, early connectivity among nodes (network members) may serve as a state that predicts later fate (e.g., likelihood of criminal acts). In the study of social behavior, full understanding of group behavior often requires understanding of the history of the social network context (16–18). When the connectivity of individual nodes is dynamic, as will often be the case in real-world networks (19), early connectivity may predict fate, even when later connectivity cannot. In such cases, connectivity may act not only as a predictive tool but also help to raise

questions that suggest previously unsuspected mechanisms for changes in state, such as tradeoffs or dynamic interactions between the number of links and their strength. My results also suggest that detailed scrutiny of spatially and temporally fluid interactions among individuals in social networks may elucidate behavioral strategies by which individuals establish relative status, even when the payoffs do not become evident for many years.

Methods

Behavioral Observations and Network Model Building. Observers sat in blinds 8–10 m from dance perches for 2-h periods between March and June, for a total of 9,288 h of observation. In any given year, as many as seven major perches and three to five minor perches were observed at least once a day for most days of the breeding season, within the 80-hectare (ha) study area in Costa Rica (5). All alpha and beta males were color-banded, as were a large majority of the definitively plumaged males. Male–male interactions constituting a link usually consisted of unison "toledo" calls (20), or of elements of the dance display ("butterflying," "side-by-side jumps," or "leapfrogging"), which often occur in the absence of any females. Male–female links consisted of dance displays by males. Interactions involving unbanded birds were not included. Alpha–beta partners perform most dances for females, but one of the partners sometimes dances for females with a lower-ranking male (the blue-green nodes in Fig. 1).

Network Metrics. I constructed social network models from detailed behavioral observations of color-banded birds seen to interact with other banded birds between 1989 and 1998 (Fig. 1). To relate a male's early network connectivity to his later social trajectory, I computed a subnetwork for each of the five 2-year timeblocks over the 10-year interval. I classified males into five generally age-graded categories (5, 14): predefinitive-plumaged (ages 1–3), definitive-plumaged (age 4 or older) that had never danced for a female, males who had danced at least once for a female (generally age 6 or older) but that were not yet in alpha–beta partnerships, beta partners (often age 8 or older), and alphas (often age 10 or older).

Connectivity metrics were assessed relative to the connectivity of males in the same status category. Because of the largely age-graded queuing for social status (5, 13, 14), males in different age and plumage categories tend not to be competitors. For a predefinitive male, for example, what matters is not his connectivity relative to that of alpha males, but relative to that of other predefinitive males. Within each timeblock, I therefore computed network metrics for each male, relative to the metrics for males in the same status category.

Subnetwork 1 (1989–1990 timeblock) included 78 birds, with 30 multiblock males first joining the network (seen interacting) then. Subnetwork 2 (1991–1992) had 53 birds, with 11 multiblock males starting then. Subnetwork 3 (1993–1994) had 48 birds, with 6 males starting then. Subnetwork 4 (1995–1996) had 43 birds, with 4 males starting then. Subnetwork 5 (1997–1998) had 41 birds and was used only to assess the fates of birds whose trajectories began in earlier subnetworks. I constructed the full network model (Fig. 1 *Right Bottom*) using all of the cumulative interactions over the 10-year period.

Each of the 2-year subnetworks, as well as the cumulative 10-year network, was fully connected. That is, at least one path connected every bird to every other bird; each link adds one unit to the path length between nodes. I required that links be documented at each time step to be included in a subnetwork; that is, I credited links only when observed in the current timeblock, regardless of past links. Links were undirected and unweighted (i.e., number or intensity of interactions was ignored), and nodes were arranged on the network diagram (Fig. 1) by a spring-embedding algorithm. Node sizes in the cumula-

tive network (Fig. 1 *Right Bottom*) were adjusted by the mean information centrality in the last timeblock in which a male was sighted; note that the basis for node size therefore differs between the cumulative diagram and the five subnetworks. Within each subnetwork, I calculated seven connectivity metrics (6, 7) for each bird, using UCINET software (Analytic Technologies, Needham, MA): degree centrality, nEigenvector centrality, power ($\beta = 0.05$), nCloseness, dwReach, information centrality, and nBetweenness. Each of these seven node-based connectivity metrics is defined in ref. 6 or 7 or in the documentation for UCInet. Each of the seven metrics quantifies, by disparate algorithms, some aspect of the node's centrality in the network.

Statistical Analyses. Using binary logistic regression, I asked whether early connectivity predicted later social rise. For the logistic regression, each male's connectivity was assessed twice: once in the timeblock subnetwork in which he was first sighted (predictor = relative connectivity) and once in the subnetwork in which he was last sighted. Over that interval, each was assessed as rising socially (response = 1) or not (response = 0). Males received a percentile score within their category (e.g., the male with the highest percentile connectivity received a 1, the middle male received a 0.5 and the lowest 0). I then adjusted the percentile-based scores so that they ranged from 0 to 2. I adjusted the range because logistic regression assesses the odds of an increase in the response variable for each unit increase in the predictor. Adjusting the predictor range changes (reduces) the odds ratio but not the P value for significance testing. The odds ratios resulting from the change of scale are more interpretable. Consider, for example, comparing a 1-unit increase in connectivity score from 0.7 to 1.7, versus the limited spectrum of 0 (unconnected) to 1 (connected). The (arbitrary) change in scale is analogous to a change of scale from centimeters (too fine) to meters (suitable and more interpretable) in a spatial analysis. In summary, for the 50 males sighted in at least two different timeblocks (multiblock males), I ran logistic regression with the seven relative connectivity metrics in their first timeblock as predictors, and rise in social success as the binary response. Because I had seven predictors, I used Akaike's information criterion to decide among candidate models involving combinations of predictors.

I defined a rise in social success as a transition from nondancer (predefinitive or definitive) to dancer, from dancer to beta, or from beta to alpha. Alphas or betas rose socially if they danced for increasing numbers of females or if their copulatory rate (corrected for observer effort) increased. Copulatory success was not a feasible metric for success; over the entire 10-year interval only 14 males copulated, 8 of them only once or a few times. Because plumage maturation is strictly age-graded (14), I did not consider the (inevitable) transition from predefinitive to definitive plumage as constituting a social rise. I did, however, separate these two plumage categories (purple vs. dark blue nodes in Fig. 1) when calculating initial state (relative connectivity). Separating these two categories prevented any bias arising from greater connectivity due solely to changes in acquisition of links with age.

I assessed temporal change in connectivity (information centrality) using two-tailed paired t tests. For each male, I paired his information centrality in his first timeblock with that in his last timeblock. The first test asked whether connectivity changed from first to last timeblock for the males that rose socially ($n = 28$). The second asked the same question for those males that did not rise socially ($n = 22$). Because mean connectivity varied by timeblock, largely as a function of total number of birds detected, I adjusted the connectivity metrics by the mean in the starting and ending timeblocks for each male. I accounted for multiple comparisons in both the logistic regression and changing con-

nectivity *t* test cases by using a Bonferroni correction (adjusting α by the number of tests).

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