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It takes two to tango: reproductive skew and social correlates of male mating success in a lek-breeding bird

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Variance in reproductive success among individuals is a defining characteristic of many social vertebrates. Yet, our understanding of which male attributes contribute to reproductive success is still fragmentary in most cases. Male–male reproductive coalitions, where males jointly display to attract females, are of particular interest to evolutionary biologists because one male appears to forego reproduction to assist the social partner. By examining the relationship between social behaviour and reproductive success, we can elucidate the proximate function of coalitions in the context of mate choice. Here, we use data from a 4-year study of wire-tailed manakins (*Pipra filicauda*) to provide molecular estimates of reproductive skew and to test the hypothesis that male–male social interactions, in the context of coordinated displays, positively influence a male's reproductive success. More specifically, we quantify male–male social interactions using network metrics and predict that greater connectivity will result in higher relative reproductive success. Our data show that four out of six leks studied had significant reproductive skew, with success apportioned to very few individuals in each lek. Metrics of male social affiliations derived from our network analysis, especially male connectivity, measured as the number of males with whom the focal male has extended interactions, were strong predictors of the number of offspring sired. Thus, network connectivity is associated with male fitness in wire-tailed manakins. This pattern may be the result of shared cues used by both sexes to assess male quality, or the result of strict female choice for coordinated display behaviour.

Keywords: coordinated display; manakins; *Pipra filicauda*; reproductive skew; social networks

1. INTRODUCTION

The non-random apportionment of reproductive success among individuals (i.e. reproductive skew) is a defining characteristic of many animal societies (Mackenzie *et al.* 1995). Understanding the reasons for and the adaptive significance of these inequalities has become a major focus of both empirical and theoretical research (Haydock & Koenig 2003). Measures of skew are often used to model reproductive strategies of dominants and subordinates under different social and ecological conditions (Reeve *et al.* 1998; Cant & Johnstone 1999; Kokko & Johnstone 1999; Magrath & Heinsohn 2000). Moreover, such indices provide an important framework for understanding the evolution and maintenance of social behaviour because they assess the fitness benefits that are associated with group living and cooperation (Keller & Reeve 1994; Clutton-Brock 1998; Griffin *et al.* 2003).

At the centre of skew research are lekking taxa in which males are spatially aggregated, presumably because individuals cannot profitably control or monopolize resources that are essential for the acquisition of females

(Emlen & Oring 1977). Male reproductive coalitions, in which two or more males join together to display for females (e.g. coordinated displays), are of particular interest among avian lekking taxa. Such coalitions represent an evolutionary paradox because one individual often accrues all the reproductive benefits, while the other individuals appear to sacrifice their own reproductive potential to assist the social partner. Males in several species of manakins, family Pipridae, engage in ritualized social partnerships for coordinated displays (e.g. *Chiroxiphia* and *Pipra aureola* clades). Previous behavioural and molecular work have revealed strong reproductive skew between male *Chiroxiphia* partners (McDonald 1989; DuVal 2007), yet, to date, no work has quantified skew for coalitions in the *P. aureola* clade.

One potential adaptive benefit of coordinated displays is that such behaviour might attract more females and lead to greater reproductive success (Foster 1981; McDonald 1989). Despite the potential fitness benefits of social relationships, the direct fitness correlates of such behaviours are rarely shown (Wey *et al.* 2008). Understanding the relationship between male social behaviour and variance in reproductive success will help to elucidate the proximate function of these reproductive strategies in the context of mate choice. Of late, the application of

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network analysis has begun to advance our understanding of the fitness implications of social structure at the individual level (Krause *et al.* 2007; McDonald 2007; Ryder *et al.* 2008). Social network analysis provides a statistical framework for quantifying individual associations within and among groups (Croft *et al.* 2004) by using metrics that help interpret reticulate multi-actor interactions (Wasserman & Faust 1994; Newman 2003). Moreover, correlative analyses between quantitative network metrics and fitness attributes have the potential to identify the selective pressures for different aspects of sociality (Wey *et al.* 2008). Despite the enormous potential of network analyses for understanding aspects of animal behaviour, there have been few applications (reviewed in Krause *et al.* 2007; Wey *et al.* 2008), especially in birds (but see McDonald 2007; Ryder *et al.* 2008).

Given the potential importance of coordinated displays for mate choice, an examination of how quantitative measures of male network connectivity relate to variation in reproductive success is of particular value. Here, we quantify reproductive skew and assess the potential fitness benefits of coordinated display in the lekking wire-tailed manakin (*Pipra filicauda*). Our previous work on wire-tailed manakins showed that measures of network connectivity predicted a male's ability to rise in the social hierarchy and that territory tenure predicted a male's probability of either siring or not siring offspring (Ryder *et al.* 2008). To extend those findings, we examined the hypothesis that male–male interactions, which occur in the context of coordinated display, are the target of female mate choice and thus positively affect male reproductive success. This hypothesis predicts that males with a greater number of display partners will achieve higher reproductive success. To test this prediction, we quantified male–male interactions using direct and indirect network metrics of connectivity, and examined their ability to explain differences in the relative reproductive success of males.

2. MATERIAL AND METHODS

(a) *Field methods*

We studied a population of wire-tailed manakins from 2003 to 2007 at the 650 ha Tiputini Biodiversity Station (TBS) within the Yasuní Biosphere Reserve located in Orellana province of eastern Ecuador (0° 38' S, 76° 08' W). During this time, we located 13 leks by systematically searching along trails as well as within two 100 ha study plots established by J.G.B. and B.A.L. Over the 4 years of the study, we captured 419 individuals, consisting of 133 females, 250 males and 36 of unknown sex, using mist nets. Captured manakins were weighed, sexed, aged and banded with aluminium and unique colour–band combinations. A blood sample of approximately 20–25 µl was taken from the brachial vein of all individuals and stored in lysis buffer (Longmire *et al.* 1988) for later genetic analyses.

We searched for manakin nests between November and March from 2002 to 2006. These months correspond to the drier part of the year and encompass the main avian reproductive period in the region. Nests were located via systematic searches within two 100 ha study plots as well as around known lek localities off the study plots. In 2005, 2006 and 2007, we concentrated our systematic efforts within known female territories as well as near sites where nests were

found in previous years. Systematic nest searching was supplemented by following radio-tagged females to their nests. Radio transmitters (Holohil Systems, Ltd, Carp, Ontario) weighed 0.70 g (i.e. less than 5% of the bird's body weight) and were attached using a Rappole harness (Rappole & Tipton 1991). Females were tracked using Advanced Telemetry Systems Field Master receivers and three element Yagi antennas. Once the nest was located, females were recaptured and radios were removed.

(b) *Social system and male classification*

Male wire-tailed manakins form exploded leks in both upland *terra firme* and seasonally flooded forest. Leks average one hectare in size (Heindl 2002) and are separated by a distance of 300 m or more (Loiselle *et al.* 2007a). The number of territorial males per lek at TBS ranges from 4 to 12, with each male defending a territory roughly 40 m in diameter; territory edges are typically 10–15 m apart. The frequency of solitary versus coordinated display varies among males, and stable display partnerships are formed between males that differ in social status (Ryder 2008). Male wire-tailed manakins undergo a series of plumage (Ryder & Durães 2005) and social transitions (age-graded social queue) from when they leave the nest until they become territory holders (Heindl 2002). Changes in male plumage and social status have four transition phases: formative plumage floaters are young males in female-like plumage who move freely between leks and male territories but lack territories themselves; predefinitive plumage floaters have mixed formative and definitive plumage and have established social relationships with territory holders but lack territories; definitive plumage floaters are the same as predefinitive plumage floaters except they have attained definitive adult plumage; and definitive plumage territory holders have attained the apex of social and plumage status.

(c) *Molecular analyses and paternity assignments*

DNA was isolated using standard phenol–chloroform extraction followed by dialysis in TNE₂ buffer (10 mM Tris, 10 mM NaCl, 2 mM EDTA). Once DNA was extracted and concentrations were checked, we screened 25 microsatellite primers (McDonald & Potts 1994; Piertney *et al.* 2002; DuVal & Nutt 2005; R. Brumfield & M. Braun 2003, personal communication) and isolated seven polymorphic markers for the genotyping of individual wire-tailed manakins. PCR reagents and reaction conditions are detailed elsewhere (Loiselle *et al.* 2007b). We tagged our PCR products using fluorescently labelled forward primers (Applied Biosystems, Inc., Foster City, CA). PCR amplicons from different markers were mixed in the appropriate dilution ratios for multiplexes to run on an ABI 3100 automated capillary sequencer. Fragments were sized using GENESCAN LIZ (500), and genotypes were assigned using GENEMAPPER v. 4.01 (Applied Biosystems, Inc.). All homozygotes were run at least twice; any questionable allelic calls were repeated to avoid spurious results and discarded when necessary.

We typed all individuals using seven microsatellite markers that varied in the number of independently assorting alleles and polymorphic information content (table 1). Allelic frequencies were determined from the proportion of individuals that were completely typed (0.96), and all markers had a low proportion of typing error (table 1). We assessed departures from Hardy–Weinberg equilibrium and linkage using FSTAT v. 2.9.3.2 (Goudet 2002). None of the loci

Table 1. Details of the seven polymorphic microsatellite markers used in the paternity analysis of wire-tailed manakins at TBS, Ecuador. (The significant deviation from Hardy–Weinberg equilibrium for MAN7 is denoted with asterisks. *K*, number of independently assorting alleles; *N*, number of individuals typed; PIC, polymorphic information content; Exc, average exclusion probability of first parent; Fnull, frequency of null alleles.)

locus	<i>K</i>	<i>N</i>	Ho	He	PIC	Exc	H–W	Fnull	error
LAN10	15	508	0.797	0.801	0.779	0.454	n.s.	0.002	0.000
LAN20	24	505	0.828	0.849	0.837	0.562	n.s.	0.012	0.000
MAN13	8	495	0.521	0.550	0.471	0.156	n.s.	0.029	0.000
MAN3	18	494	0.858	0.890	0.879	0.634	n.s.	0.017	0.049
MAN6	5	479	0.526	0.506	0.460	0.132	n.s.	–0.019	0.000
MAN7	30	495	0.743	0.902	0.894	0.670	***	0.095	0.074
MAN(AC)-13	11	471	0.703	0.747	0.716	0.362	n.s.	0.031	0.018

examined showed linkage and only one out of the seven failed to meet Hardy–Weinberg expectations (MAN7), probably due to a higher frequency of null alleles (table 1). The loci yielded high exclusion power for paternity (1st parent = 0.98, 2nd parent = 0.99 and combined = 0.99). Paternity assignments based on exclusion probabilities alone can be misleading, particularly when potential sires are relatives (Double *et al.* 1997; Marshall *et al.* 1998). Thus, we used the maximum-likelihood approach for paternity assignments to minimize assigning males that matched offspring by chance (CERVUS v. 3.03, Marshall *et al.* 1998; Kalinowski *et al.* 2007). The likelihood assignment approach of CERVUS uses Monte Carlo simulations to calculate confidence levels for putative parents via simulations that incorporate population allelic frequencies, the number of candidate sires and the proportion of those potential sires sampled. The confidence measure of CERVUS is based on delta, which is the difference between the likelihood score (hereafter referred to as LOD) for the most likely candidate and the second most likely candidate (Marshall *et al.* 1998). Our preliminary simulations used 10 000 cycles and (0.02%) as per locus genotyping error. True typing error was measured by CERVUS as the percentage of mismatches between identified mothers and offspring.

Owing to small sample sizes in some years, we performed paternity analyses on the cumulative data across the 4 years of the study to increase power. We assumed all males had the potential to be candidate fathers and, thus, included all individuals captured in male plumage or sexed as males using the P2 and P8 primers (Griffiths *et al.* 1998). The number of candidate males was 250; given our complete sampling of territorial individuals at leks of interest, we assumed that we had sampled approximately 95 per cent of candidates across our 4 year study. High male survival (see Blake & Loiselle 2008) and strong male site fidelity also contribute to confidence in our sampling assumptions. Post-fledging individuals can be aged as less than a year old using moult limits within their greater-coverts (Ryder & Durães 2005). We also attempted to assign paternity to any post-fledging individual that was born during the 4 years of our study.

We assigned offspring using both strict 95% and relaxed 80% confidence as well as using a ‘total evidence’ approach (Prodohl *et al.* 1998; Webster *et al.* 2004). Under all three scenarios, assignments were only made when assigned fathers had one or fewer mismatches with the offspring. Using the total evidence approach, we rejected CERVUS assignments and assigned paternity to a lower ranking male under three circumstances: (i) if the other chick in the brood was assigned with confidence to the same male and the candidate had a

similar LOD score to the CERVUS-assigned male, (ii) if two males with the same number of mismatches had similar LOD scores but the assigned male was compared with the offspring at fewer loci, and (iii) if both males had similar LOD scores and the same number of mismatches, but only the mismatches of the male with the lower LOD score were consistent with null alleles.

(d) Network analyses

Network analyses are useful for characterizing social structure at the level of the individual and can be used in conjunction with traditional statistical measurements (Krause *et al.* 2007). Specifically, networks are graphs of nodes (individuals) connected by vertices (social interactions) (see Wasserman & Faust 1994; Newman 2003). We constructed social networks based on two techniques: (i) data from behavioural observations collected over a 4 year period (414 hours; $\bar{x} = 16.2 \pm 0.89$ h male⁻¹, range: 8–20 h male⁻¹) and (ii) daily scan sampling alternating between leks that yielded 818 resights of colour-banded males. Network links among males represent male–male social affiliations (excluding aggressive interactions), the minimum definition of which was perching within 20 cm of each other for at least two minutes. Although some links represent only the minimum requirement, most (90%) were assigned based on coordinated display events observed during both observations and scan sampling (Ryder *et al.* 2008). All links were undirected and unweighted so that the frequency of male interactions was not incorporated. We took this approach because some males were observed for multiple, 2 hour periods, while others were recorded only during scan sampling, resulting in an uneven sampling effort. Despite uneven sampling efforts, previous analyses showed no relationship between observer effort and social connectivity of males (Ryder *et al.* 2008). Links between males and females for figures represent affiliations as determined by paternity and were only used for graphical purposes.

Cumulative male interactions at six leks yielded three social networks in which neighbouring leks were joined by floater males that visited territorial males at both localities (see Ryder *et al.* 2008). We used the cumulative social network to calculate all network metrics because within-year subnetworks were not fully connected. Node level network metrics were calculated with only male–male contributions (excluding links between males and females). All network metrics were calculated using the program UCINET v. 6.0 (Borgatti *et al.* 2002). Specifically, we calculated seven network metrics for each node (*degree*, *nEigenvector centrality*,

power ($\beta=0.05$), *nCloseness*, *dwReach*, *information centrality* and *nBetweenness*); metrics were used as explanatory variables for variance in reproductive success. *Degree* measures the number of direct links (edges) between a node (male) and the males to whom he was affiliated (i.e. the number of display partners); *nEigenvector centrality* assesses how central a node is in the network; *power* is a measure of the degree of nodes to which the focal node is connected (a positive β parameter confers greater power to nodes of higher degree); *nCloseness* is the mean geodesic (shortest) path between the focal node and all other nodes in the network; *dwReach* is a path length-weighted measure of the percentage of nodes within two links of the focal node; *information centrality* is a path length-weighted measure of how often a node lies along paths connecting other pairs of nodes, including paths longer than the geodesic path (Stephenson & Zelen 1989); and *nBetweenness* measures the number of geodesic paths between pairs of nodes that run through the focal node (for more detailed descriptions see Wasserman & Faust 1994; Newman 2003; Albert & Barabasi 2004). Network diagrams were created using NETDRAW v. 2.504 (Borgatti 2002) with nodes arranged using a spring-embedding algorithm.

(e) *Skew estimation and statistical analyses*

Measures of skew vary widely and may depend upon differences in group size, differences in survival, length of group membership and the *per capita* productivity of groups (reviewed in Nonacs 2003). Although many skew measures have been developed, there is no consensus on which measure is best (Nonacs 2003). Our data suffered from two known problems with traditional measures of skew: differences in the length of group membership and differences in the *per capita* productivity of groups. Consequently, we used the binomial skew index, in which observed group variance is corrected by variance expected if each member has an equal probability of gaining reproductive opportunity (Nonacs 2000). We used the SKEW CALCULATOR v. 1.2 to calculate indices and present the binomial index because it has the fewest statistical limitations, corrects differing lengths of group membership and provides a method for the calculation of confidence intervals (Nonacs 2003).

We used step-wise multiple regression to examine the social correlates of male reproductive success. We used the number of offspring sired, based on molecular paternity assignments, as our response variable and the seven network metrics produced from our network analyses as potential predictors to explain variance among successful and unsuccessful males. We also included territory tenure as an eighth predictor to control for the effect of male longevity on the number of offspring sired. Given that territoriality is a strong prerequisite for reproductive success (see §3) and tenure, we examined only correlates of success among male territory holders. Given that multiple regression is often hindered by multicollinearity (Graham 2003), we used ridge regression to examine multicollinearity among our predictors. Variance inflation factors (VIFs) less than 10 were used as a sign of severe collinearity (Chatterjee *et al.* 2000). As a solution to multicollinearity, we removed independent variables that had high VIFs and were significant in bivariate correlations (Legendre & Legendre 1998). We included only those independent variables with low VIF (range: 1.3–3.5) and high tolerance (range: 0.28–0.77). Variables were entered into the model in a step-wise fashion to find the best-fit overall

model. All analyses were run in JMP v. 7.0.2; means and standard errors are reported unless otherwise noted.

3. RESULTS

(a) *Molecular paternity and reproductive skew*

Over 4 years, we sampled 125 offspring from 63 broods (clutch size, $\bar{x}=1.79\pm 0.05$) and 76 post-fledging individuals and typed them at seven polymorphic microsatellite loci for paternity analyses (table 1). Mother-offspring relationships were known for 101 out of 125 (81%) nestlings and 0 out of 76 (0%) individuals less than 1 year of age. Of the total offspring ($n=201$), we successfully assigned paternity to 114 (57%) (99 out of 125 nestlings (79%) and 15 out of 76 juveniles (20%)). Of offspring sampled as nestlings, 16 out of 99 (16%) were assigned using the total evidence approach, 31 out of 99 (31%) were assigned at relaxed 80% confidence and 52 out of 99 (53%) were assigned at 95% confidence for the nestlings. Of the young individuals sampled, for which neither mother nor father were known, all 15 individuals were assigned at the relaxed 80% confidence.

Given that some broods contained only a single egg, we assessed detailed paternity patterns for 52 broods and found that within broods, 7 out of 38 (18%) females had mixed paternity in their nests while a single male sired each of the remaining clutches. Within a single year, we observed six females that made repeated nesting attempts, each represented by two broods. Three of these females switched mates between broods and three did not. Between years, females were more likely to switch mates (6 out of 8 females; 75%) than to remain with the same partner from the previous year (2 out of 8 females). In all cases of mate switching between broods within a year, the previous partners were present; however, in four out of six mate switches between years, the previous mate had disappeared. Mate switching between leks was relatively rare and only occurred twice.

Our results show that territoriality is a strong prerequisite for reproductive success. Out of the 114 offspring to which we assigned paternity, 112 (98%) were sired by territorial males, whereas only 2 (2%) were sired by definitive plumage floaters (i.e. non-territorial individuals). In both instances, the non-territorial floaters sired a single chick and were the partners of more successful male territory holders. The measured skew (binomial index) at six leks varied widely, with the largest lek having the lowest skew (table 2). Skew, however, only differed significantly from random expectations at four out of the six leks (figure 1). All six estimates of the binomial index differed from values expected under equal distribution or total monopolization of reproductive benefits (for binomial index comparison see table 2).

(b) *Social correlates of male mating success*

The number of territorial males that sired offspring within each lek ranged from 3 to 11 with an average of 5.3 ± 1.1 successful individuals per 10 territories. Although multiple males sired offspring in some leks, on average only three top-ranked males per lek sired more than 80 per cent of the total offspring (males were sequentially ranked based on the number of offspring sired). We further examined the relationship between male rank and proportion of offspring sired at a larger spatial scale by

Table 2. Distribution of reproductive benefits among group members at wire-tailed manakin leks of different size at TBS, Ecuador. (Binomial index for actual reproductive skew (B), equal distribution among group members (equal) and monopolized distribution by a single group member (monopoly) are shown. Note that index values for equitable distribution of reproductive benefits are all negative. N , number of males, both court holders and their floater affiliates; N_b , number of males that sired offspring.)

lek	N	N_b	B	equal	monopoly
Tower	20	3	0.563	-0.038	0.847
Chichico	26	6	0.137	-0.052	0.906
Puma 2.5-800	16	6	0.080	-0.085	0.844
Puma 2-200	16	5	0.238	-0.050	0.832
Huaira/Lago	28	10	0.010	-0.050	0.923
Danta	6	3	0.090	-0.104	0.715

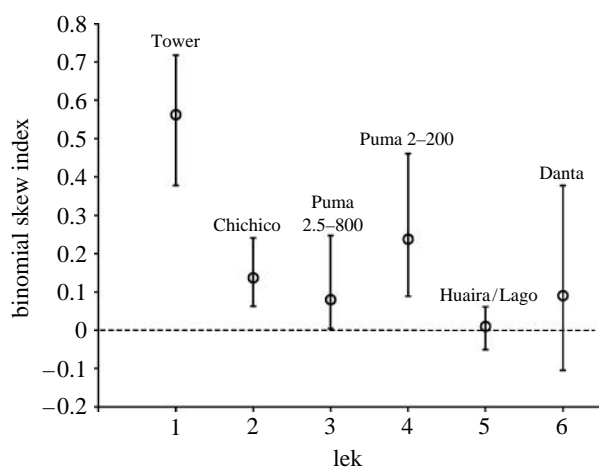


Figure 1. Binomial skew index with 95% confidence intervals for six wire-tailed manakin leks of different sizes at Tiputini Biodiversity Station, Ecuador. The binomial skew index ranges from -1 to 1 and is a measure of variance in male reproductive success. Indices and their confidence intervals that do not overlap zero are considered statistically different from random.

combining males from spatially contiguous leks linked by floater individuals. In all three instances, we found that only the three top-ranked males sired 70–90% of the offspring in these pairs of contiguous leks defined by social networks (figure 2).

In a step-wise multiple regression analysis, both network metrics and territory tenure were predictive of the number of offspring sired. In our best-fit model to explain variance in reproductive success among males, we found that *degree* ($\beta = 0.91 \pm 0.21$, $t = 4.33$, $p < 0.0001$), *eigenvector centrality* ($\beta = -0.11 \pm 0.03$, $t = -3.69$, $p = 0.0006$) and territorial tenure ($\beta = 1.297 \pm 0.36$, $t = 3.58$, $p = 0.0008$) all contributed to overall model significance ($F_{3,51} = 9.82$, $p < 0.0001$, $r^2 = 0.37$). However, *degree*, which is a direct measure of a male's social connectivity, was the best predictor of the number of offspring sired (figure 2). A reduced model examining variance among only reproductively successful males was largely explained by *degree* ($t = 4.12$, $p = 0.0004$), *eigenvector centrality* ($t = -3.86$, $p = 0.0008$) and, to a lesser extent, tenure ($t = 1.95$, $p = 0.062$) ($F_{3,24} = 8.0$, $p = 0.0007$, $r^2 = 0.50$). The lower predictive power of tenure in the second model suggests that territorial longevity differentiates successful from unsuccessful males, but explains less variance in the relative number of offspring sired.

4. DISCUSSION

These data on wire-tailed manakins demonstrate the importance of reproductive and social dynamics in a lek-mating system with male–male coordinated displays. Four out of the six leks we studied showed significant reproductive skew with only a few territorial males receiving most of the reproductive benefits. Overall, our data show that territoriality is a strong prerequisite for access to reproduction in this system (i.e. 98% of offspring). Metrics of male social affiliations derived from our network analysis, especially male connectivity, measured as the number of males with whom the focal male has extended interactions, were strong predictors of the number of offspring a male sired.

(a) *Molecular paternity and reproductive skew*

Previously documented strong skew in lekking systems (Wiley 1991; Höglund & Alatalo 1995; Mackenzie *et al.* 1995) suggests that females often make unanimous mate choices (Bradbury *et al.* 1985). Unanimity, however, by definition implies a singularity not observed in our data; hereafter, we use 'concordance' to refer to this general agreement among females. Concordance in female mate choice can be achieved either if females use the same cues to assess and select males, or if females copy other females' choices (reviewed in Balmford 1991). Strong skew within four out of our six leks indicated that a few individuals received most of the reproductive benefits and suggests strong concordance among females (e.g. in one lek a single male sired 20 of 24 offspring). Given that the beta estimator of skew corrects for tenure and overall lek productivity, our data provide strong support for non-random mating at four out of six leks.

Although mate choice concordance represents the general trend in our data, we did find that some females mated with more than one male, producing broods with mixed paternity. Moreover, between-brood and among-year differences in female choice indicate that females may mate with more than one male in their lifetime. Our data contrast with data from two other species of manakins, which showed high between-brood female fidelity (e.g. *Manacus manacus* (68.8%) and *Pipra erythrocephala* (66.6%), Lill 1974, 1976); however, use of molecular tools, as in this study, probably increases the likelihood of detecting polyandry. Female polyandrous behaviour has been documented in other lekking taxa (e.g. peacocks *Pavo cristatus*; Petrie *et al.* 1992; buff-breasted sandpipers *Tryngites subruficollis*; Lanctot *et al.* 1997), yet, current

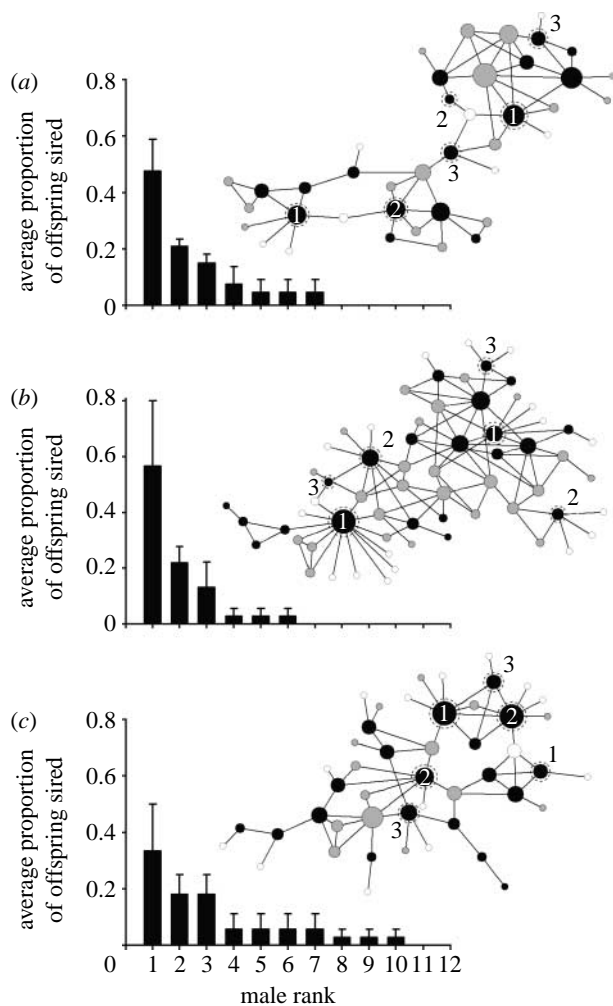


Figure 2. Males ranked by the number of offspring sired within three social networks, each consisting of two linked leks of male wire-tailed manakins. Each bar with its associated standard error represents the average proportion of offspring sired by territorial males of that rank. Inset within each graph is the corresponding social network. The three top-ranked males in each lek are designated with numbers and dashed circles. Each node is sized by degree, which is a strong predictor of male reproductive success. Territorial males are shown as black nodes, floater males are shown as grey nodes and females are shown as white nodes. Note that the larger black nodes (territorial males) with high degree are often found at the periphery of the social network while it is primarily grey nodes that create the connections among territory holders and between leks. Male–female links are included for graphical purposes only and were not used in the calculation of male degree for analyses. (a) Puma network, (b) Tower–Chichico network and (c) Huaira–Lago network.

evidence suggests it has a less significant role in the reproductive strategies of female wire-tailed manakins.

The evolution of lekking behaviour implies that male territoriality is a prerequisite for reproductive opportunity, and that male aggregation was favoured because of the fitness benefits associated with this strategy. Our documentation of reproductive skew at the lek level and among individual wire-tailed manakin partners show that, while engaging in coordinated displays does provide access to reproduction, few offspring are sired by subordinate partners (less than 2%) and no significant immediate benefits are gained. These results mirror previous findings for two other manakin species that engage in coordinated

male–male display, *Chiroxiphia linearis* and *Chiroxiphia lanceolata* (McDonald 1989; DuVal 2007). Ultimately, the benefits to males of participating in coordinated displays are likely to vary by age class and social status.

(b) Social correlates of male reproductive success

Sociality is a nearly ubiquitous characteristic of most vertebrate taxa, yet our understanding of how social structure impacts individual fitness and affects selection for behavioural phenotypes is incomplete. Recent applications of network theory have showed that detailed investigations of dynamic social interactions can elucidate the fitness benefits of specific behavioural strategies (McDonald 2007). More specifically, recent work on two species of manakins have documented that measurable, delayed and direct-fitness benefits are associated with coordinated displays, where the frequency of social partnerships predicts social ascendancy and territory acquisition (McDonald 2007; Ryder *et al.* 2008). In addition, Ryder *et al.* (2008) found direct support for the role of territory tenure and indirect support for the role of network metrics in predicting binary reproductive success (successful versus unsuccessful). Here, our results show that tenure, as well as both direct and indirect metrics calculated from a male's social network, were predictive of a male's relative reproductive success. More specifically, we found that longer tenure increased a male's probability of siring young, but that direct and indirect social connectivity were better predictors of the number of offspring he sired. Viewed cumulatively, these results suggest that fitness for male wire-tailed manakins is associated with network connectivity.

Assuming our findings are robust, we ask what functional hypotheses might explain the link between network connectivity and male fitness? The strongest predictor of the number of offspring sired was a direct measure of male connectivity (i.e. degree). Degree quantifies the number of male social affiliations in the context of coordinated displays and, as such, approximates the frequency of joint male displays. Greater connectivity could either be the cause of greater male reproductive success via female choice for joint male display, or the consequence of a relationship between connectivity and some other target of selection.

Reproductively successful males, for example, could attract more display partners if females and males use similar cues (e.g. phenotypic, behavioural, genetic, etc). Given the complex nature and energetic cost of even solo male displays, it is highly plausible that females might select mates based on display quality or frequency (also see Durães *et al.* in press), independent of display type (solitary versus coordinated). Moreover, given that males probably learn the complex display repertoire and perfect it over time (T. B. Ryder 2003–2007, personal observation), display quality could also be the target of male partner selection. Alternatively, if coordinated display enhances signal intensity, females might select males that engage in coordinated display more often. Currently, we do not have direct evidence that the number of offspring sired is correlated with the frequency of coordinated displays, because we did not make detailed observations of all males. Previous work, however, did show a significant per male increase in the frequency of display manoeuvres when social partners were present (Ryder 2008). Moreover, if

females select males based on coordinated display frequency, it would indicate a potential fitness advantage of male partnerships. Regardless of the mechanism, the two processes are not mutually exclusive and cannot be differentiated with our current data.

In addition to degree, we also found that a male's indirect connectivity, as measured by eigenvector centrality, predicted his relative reproductive success. Importantly, this metric is not a measure of a male's spatial position within a lek but rather his social centrality. The significance of indirect connectivity suggests that it is not only how connected a male is, but also to whom he is connected that is important. Our data show that males with lower centrality sired more offspring. Unlike degree, eigenvector centrality credits indirect network paths and, therefore, incorporates the importance of weak social ties. More specifically, the centrality measure of each male is determined by the centrality of those males to whom he is connected. Thus, males with high reproductive success are highly connected, but associations with males of lower degree dominate those connections. Our previous work has shown that social interactions are a form of social capital for young wire-tailed manakins. These interactions undoubtedly function in learning coordinated displays, and they may also establish dominance hierarchies through time as males queue for status. Given the importance of linear dominance hierarchies in *Chiroxiphia* social systems (Foster 1981; McDonald 1989), social links among territorial male wire-tailed manakins may reflect lek-level hierarchies established throughout a male's life. Overall, our data strongly suggest that coordinated display has an adaptive function and has been the target of selection, given its role in male social ascension and reproductive success.

Social systems of lekking species have long been at the centre of empirical and theoretical research on reproductive skew. Here, we have coupled molecular and novel analytical tools to better understand the fitness implications associated with these complex social systems. DuVal (2007) recently has noted that selection for complex male behaviours requires long-term male social affiliations, which in turn reinforce the evolution of complex social structure. Here, we emphasize that understanding the evolution of behavioural strategies necessitates investigating the existence of social connectivity as well as measures of individual variation associated with those metrics. Undoubtedly, future research using social network theory will continue to underscore the broader importance of social relationships in a fitness context and begin building comparative frameworks to better understand the evolutionary pathways that lead to complex social behaviour.

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