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REPRODUCTIVE AND SOCIAL DYNAMICS OF A LEK BREEDING BIRD

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ABSTRACT

Sociality and the unequal apportionment of reproductive success among social individuals is a common characteristic of many vertebrate taxa. To date, our understanding of what factors drive high variance in reproductive success (i.e., intra vs. inter-sexual selection) and which male attributes contribute to that variance, are still fragmentary for most species. Moreover, how social structure interacts with individual behavior and fitness remains understudied despite its potential importance to the evolution of cooperation. This dissertation research focused on understanding this complex synergistic interplay between social and reproductive dynamics in a lek-breeding bird, the wire-tailed manakin. The first chapter examines the complex display ritual of this species of manakin (*Pipra filicauda*). More specifically, it quantifies and compares the frequency of individual behavior among males of different age and social status. In addition, the first chapter examines in detail the genetic relatedness of male partnerships to test the kin selection hypothesis. The second chapter uses these complex reticulate interactions to build social networks. This chapter details the emergent properties of these networks and examines their role in determining male social ascendancy and access to reproduction. The third chapter uses a combination of molecular tools and network analysis to create a synthetic understanding of variance in male reproductive success. This chapter presents molecular estimates of reproductive skew and examines the social correlates of male reproductive success. Our primary results show 1) that males within leks are not more related than expected by chance, enabling us to reject the role of kin selection in the lek evolution of wire-tailed manakins; 2) that the complex networks of social interactions among males contain the ingredients needed for the evolution of cooperation; 3) that social connectivity of young males was predictive of their later social ascendancy; 4) that the number of male affiliations was strongly predictive of the number of offspring he sired. Overall our findings greatly advance our understanding of social relationships and the role they play in the evolution of cooperation and reproductive variance.

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CHAPTER 1- DISPLAY DYNAMICS AND RELATEDNESS OF MALE WIRE-TAILED MANAKINS

ABSTRACT

Understanding the social organization involved in group behaviors remains integral to the field of behavioral ecology. In particular, systems where animals engage in apparent cooperative acts despite unequal apportionment of reproductive success continue to be of interest in evolutionary biology. Wire-tailed manakins (*Pipra filicauda*) engage in communal displays in which some males appear to forego individual reproductive success. Here, we investigate the social organization of males engaged in coordinated display behavior, the relatedness of male display partners, and the proximate role of this complex display using data from a three-year study of the wire-tailed manakin. Males in our system followed an age-graded queue which was specifically facilitated by the coordinated-display behavior. We found variation in the frequency of display behaviors among males within leks but not among the leks themselves. Our analysis of male relatedness showed that male coordinated display partners are not more related than expected by chance and ruled out the possibility of indirect fitness benefits to display partners. Coordinated displays functioned in maintaining social dominance via non-aggressive competition and influenced the probability of territorial inheritance for subordinate partners. Our examination of this social behavior helps to understand how it has been maintained over evolutionary time.

Keywords: *Coordinated display, leks, manakins, Pipridae*

INTRODUCTION

Animal sociality is a widespread phenomenon yet its function varies among taxa. Of special interest is the maintenance of coordinated behaviors in social systems where there are clear costs and no obvious benefits. In particular, coordinated display as seen in some members of the manakin family Pipridae (e.g. *Pipra aureola* clade) are complex social behaviors that remain poorly understood with respect to their social function and the associated fitness consequences for participants.

Manakins in the family Pipridae are small, sexually dimorphic sub-oscine passerines found in warm, humid regions of Central and South America (Hilty and Brown 1986; Ridgely and Tudor 1994). Manakins are well known for their marked secondary sexual characteristics, and their displays performed at communal lek sites. Males aggregate at leks where they attract and court females (Beehler and Foster 1988) and leks are traditionally thought not to be resource-based (but see Ryder et al., 2006). Manakin leks are located at established sites and adult males tend to show strong philopatry, whereas younger satellite males progress in social status and fidelity with age (Snow 1962b; Snow 1962a; Lill 1976; Foster 1981; Foster 1987; McDonald 1989). Moreover, where it has been studied, behavioral estimates of male mating success on manakin leks are highly skewed (Snow 1962b; Lill 1974; McDonald and Potts 1994).

The ritualized courtship behaviors of manakins are among the most complex interactions known among passerine birds (Snow 2004). In most manakin species, males display solitarily on a territory within a lek. Less common are species with true coordinated or cooperative displays, in which pairs or groups of males engage in complex ritualized behaviors (Schwartz and Snow 1978; Foster 1981; Robbins 1985;

Foster 1987; Heindl 2002). Of particular interest are species that engage in coordinated display routines where multiple members of a social group exhibit ritualized behaviors in which some individuals play a subordinate role and, potentially, forego individual reproductive success. Coordinated displays among males can take two forms; males may express intra-sexual aggression as ritualized behaviors in a competitive fashion (Snow 1962b; Tello 2001); or male ritualized behavior could have reproductive benefit by enhancing the attraction of females, favoring cooperative displays (Snow 1971a; Snow 1971b; Foster 1981; McDonald 1989). Such displays among manakins appear to have evolved independently at least twice: in *Chiroxiphia* and in the *Pipra aureola* clade (Prum 1994). Previous studies of *P. aureola* complex (i.e., *aureola* and *filicauda*) have provided different evidence on the function of coordinated display (Robbins 1985; Heindl 2002).

Pipra filicauda, the wire-tailed manakin, has a true communal display but shows variation in the frequency of coordinated male partnerships (Heindl 2002). Males maintain dispersed display sites (i.e., exploded lek *sensu* Bradbury, 1981) in which territory-holding males interact with other territory holders and non-territorial males (Schwartz and Snow 1978; Heindl 2002). Thus, within a single lek we may find some court holders who display alone and others who engage in coordinated displays with neighboring court holders and non-territorial individuals. Further, there is variation in the frequency with which individuals coordinate, potentially resulting in differential costs and benefits.

Of late, the evolution of lekking and sociality among male manakins has received significant attention. Recent work has focused on the kin-selection model which has been used to explain why individuals might join in social behaviors (Dugatkin 1997). Under the kin-selection model, individuals join leks with close relatives to obtain indirect benefits through the passage of shared genes. To date, kin selection does not appear to have played a role in the evolution of lekking or sociality among manakins (Loiselle et al., 2007b; McDonald and Potts, 1994, but see Shorey et al. 2000). Despite the lack of support for kin selection as an ultimate mechanism in the evolution of lekking, it still could be a proximate explanation for social partnering in the *P. aureola* clade. To date no studies have examined finer scale relatedness patterns of social display partners.

Over three years, we have examined the nature of coordinated display in the wire-tailed manakin to specifically examine the complex nature of social dynamics among males, the proximate function of coordinated display, and the potential role of kin selection. Here we detail the frequency, stability and social nature of male relationships as well as test the kin selection hypothesis for coordinating male partners. Further we examine two potential benefits involved in social coordination, 1) territorial inheritance and 2) indirect benefits via kin selection. Lastly, we describe how males progress in the social queue and how that progression is related to their plumage sequence as well as their social role in the lek. Overall, our findings advance understanding of the complex male affiliations found in the family Pipridae.

METHODS

Field sampling

We conducted our field study during 2003, 2004 and 2005 at Tiputini Biodiversity Station (TBS), Orellana Province, Ecuador (0º 38′ S 76º 08′ W), a 650-ha biological station located at ~200 m above sea level adjacent to Yasuní National Park yet embedded within the 1.5-million ha Yasuní Biosphere Reserve. The site is dominated by upland *terre firme* forest but also includes some *varzea* habitat (Ryder et al., 2006). During 2001, two 100-ha plots (~1 km x 1 km each) were established at TBS by J. G. Blake and B. A. Loiselle (for description of Harpia and Puma plots see Loiselle et al., 2007a; Loiselle et al., 2007b; Ryder et al., 2006).

We located leks of wire-tailed manakins by systematically searching and mapping singing male manakins along 36 km of transects that form the grids of two 100-ha study plots as well as along 30 km of trails outside of the plots. Wire-tailed manakin leks tend to vary in size from 4 to 10 territorial individuals with as many as 10-15 other associating individuals, based on 12 leks in Ecuador. Leks were found in both seasonally flooded forests as well as in adjacent *terra firme*. Leks were typically in low elevation flat areas near streams (Loiselle et al. 2007a). The under-story vegetation at leks varied from extremely open to marginally closed with old tree falls and vine tangles.

We used ground-level mist-nets (12.5 m X 2.8 m, 36-mm mesh) to capture manakins over the course of the three year study. Captured manakins were weighed, sexed, aged, and banded with aluminum and individual color-band combinations. Overall, 414 individuals consisting of 133 females, 245 males and 36 of unknown sex were individually color marked. Blood samples were taken (~ 50 µL per individual) via puncture of the brachial vein and stored in lysis buffer (Longmire et al. 1988). To determine optimal times for observation we assessed male activity at five leks using song frequency across the day as an indicator of number of males present and active. We then sampled 25 different territorial male manakins from seven different leks with 2-hour continuous focal sampling (Martin and Bateson 1986) during periods of peak activity (e.g., morning 6:30-8:30 and afternoon 13:30-15:30) (see results).

During observations, we recorded the frequency of all display behaviors, songs and interactions with other individuals. Wire-tailed manakin displays took two forms, either solitary or coordinated, each including a variety of complex ritualized behaviors. Coordinated displays engaged two or more males in alternating and, at times, highly synchronized display routines. Display elements included the *side to side*, short back and forth jumps or hops on a display perch, the *stationary display*, back feathers raised and quivering wings drooped, the *twist*, rapid twisting while sidling backwards with tail raised, the *flutter*, an awkward stumbling maneuver, the *hover flight*, a rapid hovering flight typically to grab a piece of a nearby leaf, the *swoop-in-flight*, a rapid upward flight trajectory which culminates in an s-shaped return over the display perch and partner, and the *butterfly flight*, a slow fluttering flight from perch to perch where the white wing patches are displayed (for detailed description of display behaviors see Heindl, 2002; Schwartz and Snow, 1978).

Male status was classified by plumage and territoriality over the three years of observation, as follows: *Definitive territory holders* were males of at least three-years of age in definitive plumage with their own display territory that did not visit other territories; *Definitive territorial visitors* were definitive-plumage males of at least three-years of age with their own territory who were frequently seen visiting neighboring male territories; *Definitive floaters* were definitive plumage males of at least three-years of age without territories but regularly seen visiting territorial males; *Pre-definitive-plumage floaters* were males approximately two-years of age with some red head feathers and black back feathers, without territories, but seen visiting lek territory holders; and *Formative-plumage floaters* were young males less than one-year of age in green plumage without territories seen visiting other males on leks.

Molecular techniques

We isolated DNA from blood samples via standard phenol-chloroform extraction (Sambrook et al. 1989), with a cleaning step of dialysis in 1X TNE_2. Concentration of samples was determined using spectrophotometry and verified through electrophoretic gels stained with ethidium bromide. We screened 25 microsatellite loci developed for other species of manakins and chose a subset of 7 markers with sufficient polymorphism (DuVal and Nutt, 2005; McDonald and Potts 1994; Piertney et al., 2002; Brumfield R and Braun M, personal communication). All polymerase chain reactions (PCR) were run in 5 µl volumes consisting of genomic DNA, 1mM DNTP's, 10X reaction buffer, 25 mM $MgCl_2$, forward and reverse primer pairs, DMSO additive, and Taq DNA polymerase (Bioline). For fragment analysis we tagged PCR products using fluorescently-labeled forward primers (Applied Biosystems, Inc.). PCR conditions are described in more detail in Loiselle et al. (2007b). PCR amplicons were multiplexed and run on an ABI 3100 automated capillary sequencer. Each sequencing plate contained up to five positive controls. Fragment sizes were determined using a size standard GENESCAN$^{©}$ LIZ (500) and genotypes were assigned using Genemapper 4.01 (Applied Biosystems, Inc.). Most individuals, and all homozygotes, were run at least twice; any questionable allelic calls were repeated to avoid spurious results and discarded when necessary.

Statistical analyses

We examined display variation in eight response variables (song, side to side, stationary display, twist, flutter, hover, butterfly flight and swoop-in-flight) as predicted by lek and males nested within those leks. In a second analysis, we examined variation in only four of the most common display elements as predicted by age/social class and display type. All variables were tested for normality and homoscedasticity prior to data analysis. We used DSTLM (Anderson 2004) to analyze our behavioral data, because many variables were non-normally distributed. DSTLM, calculates either multivariate ANOVA or multivariate regression of any symmetric distance matrix using permutations of the observed data (for theoretical background see Anderson, 2001a; Anderson, 2001b; McArdle and Anderson, 2001). This non-parametric statistical tool accommodates more complex statistical designs, including covariates, unbalanced ANOVA designs and tests of individual terms in a multi-factorial ANOVA. DSTLM enabled us to examine variation in behavior as predicted by males nested within leks. We used XMATRIX (Anderson 2003) to produce design matrices (i.e., dummy variable coding) for the predictor variables, lek and male, in our unbalanced nested design and display type and age/social status for the second analysis. In an unbalanced design, the terms are no longer orthogonal and the two X matrices were therefore fit sequentially (i.e., Type I SS) as is appropriate for a nested design (Anderson, M. J., pers. comm.). DSTLM generates a pseudo F-statistic based on our distance measure, Bray-Curtis dissimilarity, and the P-value is obtained by recalculating this statistic for a large number of random re-orderings of the observations (Anderson 2004), in our case 999 permutations. To examine which display maneuvers differed among males and between display types, we conducted post-hoc univariate ANOVA's with DTSLM, using Euclidean distance as our distance metric. Means ± standard error are reported unless otherwise noted.

Descriptive information for each locus (i.e., allele frequencies, richness, linkage and H-W equilibrium) was determined using FSTAT v. 2.9.3.2 (Goudet 2002). We assessed equilibrium departures using randomization procedures and applied Bonferroni corrections when appropriate. We included only the loci that were in Hardy-Weinberg equilibrium and showed no significant linkage (Loiselle et al. 2007b).

We estimated pair-wise, within-lek and population-baseline relatedness using RELATEDNESS Version 5.0 (Queller and Goodnight 1989; Goodnight and Queller 1999). Relatedness patterns of males within leks were compared to background levels of relatedness among the rest of the population sampled both within the 100-ha study plot or around outside leks. All relatedness values were bias-corrected for population allele frequencies by excluding the focal individual and all other lek members from the calculation of population allele frequencies. Bias correction prevents an underestimate of true relatedness for small sample sizes or samples with large numbers of relatives (Queller and Goodnight 1989; Goodnight and Queller 1999). Standard error estimates and 95% confidence intervals were obtained by jackknifing over loci.

RESULTS

Male Activity and Display Patterns

Male wire-tailed manakins sang throughout the day; however, their song frequency varied greatly and peak activity was bi-modally distributed (Figure 1). Males typically arrived at the lek at sunrise and stayed until mid to late afternoon with peak periods of activity occurring from 0630 to 0800 and from 1300 to 1500 (Figure 1). Male activity was greatly reduced after 1530 and was nearly complete by 1630. During periods of peak activity, we observed 25 males during 181.5 observation periods that totaled 363 hours of observation. Observation time per male ranged from 7.5 to 20 hours ($\bar{\chi}$ = 14.5 ± 0.91 hrs). During the observations, we observed 145 displays, of which 31% (45/145) were coordinated and 69% (100/145) were solitary. The frequency with which individual males engaged in coordinated display ranged from 0 to 100% ($\bar{\chi}$ = 31.3 ± 5.50 %). The number of visitors per displaying male ranged from 1 to 5 ($\bar{\chi}$ = 2.6 ± 0.25) over all observations.

Social Partnerships

Visitors that engaged in coordinated display fell into several categories (formative-plumage floaters, pre-definitive-plumage floaters, definitive-plumage floaters and definitive-plumage territorial visitors). Formative-plumage birds known to be males were observed moving freely among leks and beginning to build associations with lek territory holders. Four males in this plumage class were observed visiting relatively distant (e.g., 500-700 meters) male territories at spatially contiguous leks within a breeding season. These males were never observed displaying during six social interactions but were often present during bouts either in a stationary role or observing other males during display activity. However, outside of formal observation periods, these males occasionally engaged in display with territory holders and also in apparent practice sessions with other floaters outside male territories. Pre-definitive-plumage males regularly engage in coordinated display bouts which contain most display elements (Table 1). Often more than one non-definitive male may be present during display bouts. Definitive-plumage males fall into one of three social classes. Definitive-plumage floaters had the highest frequencies of display maneuvers among birds of non-territorial status (Table 1), yet their subordinate status was especially apparent when territory holders flew off the perch before they completed their swoop-in-flights. Conversely, when visiting definitive-plumage floaters played the stationary role, they allowed the territory holder to do a complete swoop maneuver. Definitive territorial visitors were territory holders yet spent bouts of time in neighboring territories engaging in coordinated display (Table 1). Lastly, definitive territory holders are “dominant” territory holders who receive visits from both visiting neighbors and non-territorial floaters but were not seen leaving their territory to visit neighboring males.

Social relationships among males were typically stable over time yet complex and formed small networks of interacting members (Figure 2). More specifically, 76% (19/25) of males had stable display partners within breeding seasons (~ 5 months) and at least 44% (11/25) of males maintained partnerships between seasons. Particular males received a greater number of visitors (e.g., B/W and PU/PU) and this pattern repeated itself for all the leks observed (Figure 2). Of the 104 social interactions and corresponding displays by territory holders we observed, 31% (32/104) were with definitive-plumage territory neighbors, 47% (49/104) were with definitive-plumage floaters, 16% (17/104) were with pre-definitive plumage floaters and 6% (6/104) were with formative-plumage floaters.

Territorial turnovers

During the three year study we observed seven male territorial turnovers. In five of the seven cases, the floater male who inherited the territory had been previously identified as a non-territorial display partner of the former territory holder. In the other two cases, the floater males who inherited the territories had known display associations with other neighboring territory holders at the lek. In all seven instances of territorial turnover, the new territory holder was later observed displaying in contiguous male territories at the lek, apparently maintaining previously established affiliations.

Display Rate Variation

All age classes of visitors, except for formative-plumage floaters, engaged in active display routines and some singing while on the territory of another male (Table 1). Mean frequencies were, however, lower than those of territory-holding males and certain maneuvers (e.g., butterfly flight) were never done by visiting males (Table 1). Unfortunately, we can not determine male age past the attainment of definitive plumage and therefore can not relate display frequency to territory holder age. However, because of age-graded queuing, social status is a good proxy for male age in pre-definitive plumages. We found that social status was a predictor of display rate among male visitors during social interactions of coordinated display. Rates of performance of the four most common display maneuvers differed between pre-definitive, definitive floaters, and definitive territorial visitors (pseudo-$F_{2,49} = 2.76$, $P = 0.020$).

We found display and song frequency did not differ among leks (pseudo-$F_{6,17} = 0.41$, $P = 0.969$) but that territorial males nested within those leks varied significantly (pseudo-$F_{17,159} = 2.12$, $P = 0.001$). Variation in the frequency of male behavior within leks stemmed from the twist (pseudo-$F_{17,165} = 2.68$, $P = 0.001$), swoop-in-flight display (pseudo-$F_{17,165}$ = 2.60, P = 0.001), hover flight (pseudo-$F_{17,165}$ = 2.45, P = 0.002), and the stationary display maneuvers (pseudo-$F_{17,165}$ = 1.65, P = 0.043), but not by the side to side display (pseudo-$F_{17,165}$ = 1.34, p = 0.161), flutter display (pseudo-$F_{17,165}$ = 1.25, P =0.237) or butterfly-flight (pseudo-$F_{17,165}$ = 1.19, P = 0.256).

We further tested for differences between solitary and coordinated display in the four most common display maneuvers. We found that coordinated displays had significantly higher maneuver frequencies than did solitary display (pseudo-$F_{1,144}$ = 9.36, P = 0.001). During coordinated displays males performed side to side (pseudo-$F_{1,144}$ = 40.11, P = 0.001), stationary display (pseudo-$F_{1,144}$ = 15.69, P = 0.001), twist (pseudo-$F_{1,144}$ = 12.92, P = 0.002) and swoop in flight (pseudo-$F_{1,144}$ = 29.28, P = 0.001) at higher rates than did those same individuals when engaged in solitary display bouts (Figure 3).

Male Relatedness

By measuring male relatedness, we assessed the potential for indirect male benefits. We investigated the possibility for kin selection by examining pair-wise relatedness for males who engaged in coordinated display. Our primary finding was that 15 of 21 of the pair-wise comparisons fell below the lek average, with relatedness values ranging from -0.3826 to 0.2344 (see stars in Figure 4). Those males whose pair-wise values fell within second order relatedness (see open circles leks 1,3 and 5) were never observed to engage in joint display. Average relatedness among male territory holders within leks ranged from -0.0567 to 0.0166 for five wire-tailed manakin leks (Figure 4). At every lek, mean relatedness was within the range expected by chance.

DISCUSSION

Coordinated Display and Male Partnerships

Our results show that males engaged in both solitary and coordinated displays but the frequency of these display types varied among males. On average, male territory holders had visitors 30% of the time as described by both Robbins (1983, 1985) and Heindl (2002). However, territorial males varied in the number and type of visitors they received, as reported by Heindl (2002). In contrast to Heindl (2002), however, our results show relatively common stable relationships among males through time as described for *P. fasiicauda* by Robbins (1983, 1985).

Age-graded Queuing, Social Partnerships and Dominance

Age-dependent sexual advertisement is a characteristic of lekking social systems and includes both aural and visual signaling (Kokko 1997). Moreover, some manakins have been shown to have age-graded social queuing where pre-definitive plumages are accurate indicators of status in an age-based dominance system (McDonald 1989; Doucet et al. 2007). Our observations of interactions among color-banded males of three plumages classes (i.e., formative-plumage, pre-definitive plumages and definitive plumage) combined with the knowledge that plumage is an accurate indicator of age up to definitive plumage support the supposition that males change status in accordance with their plumage ascension (i.e., age-graded queuing) (Schwartz and Snow 1978; Robbins 1985; McDonald 1989). Males less than a year old in formative-plumage had weakly established social bonds and spent very little time engaging in display. Two-year old males in pre-definitive-plumage contrastingly had developed lasting social bonds with one or more territory holders of a specific lek. Males of at least three years of age in definitive-plumage yet of floater status had the strongest social bonds with territory holders but have not yet attained a territory. Territorial subordinates who were also at least three-year of age had attained territories yet had lower with apparent lower ranking in social status based on behavioral dominance interactions. Lastly, changes in social status, as defined by age-class, were also a predictor of sexual advertisement in the form of the coordinated display.

The social organization of *P. filicauda* in this study is similar to that of *P. fasiicauda* (Robbins 1983; Robbins 1985) and has many similarities to that described by Heindl (2002) for *P. filicauda* yet, here we present a previously unrecognized component of social complexity. Unlike *P. fasiicauda*, territorial males in our system may have as many as three to four beta partners whose associations appear to be maintained by dominance relationships. Moreover, these beta-male partners can include pre-definitive-plumage males, definitive floaters and even apparently subordinate territorial neighbors. Whereas Robbins (1985) found that *P. fasiicauda* males regularly excluded contiguous territory owners, we found that 31% of coordinated displays in *P. filicauda* were with territorial neighbors. The propensity for new or apparently lower-ranking territory holders to visit their neighbors for coordinated display may function to maintain dominance hierarchies within the lek after new members inherit territories. The hierarchy maintenance idea is evidenced by males which recently inherited territories yet maintained the same social bonds as during their floater status.

Our observations also suggest coordinated display visits to territorial males are skewed toward a few individuals within a lek. The variance in number of partners may be explained by age and social status. As a result of males building social networks over time and interacting with multiple lek territory holders as well as floaters, the assessments of dyadic dominance alone does not encompass all interactions. The more complex social network of male interactions described here suggests that dominance hierarchies may extend beyond close male associations as previously proposed by Heindl (2002). If males have social interactions with multiple partners over time, the potential exists for a global or whole-lek dominance hierarchy (Ryder, unpubl data). This suggests the need to examine social relationships of males as they progress through the social queue.

The duration of male partnerships in manakins has been shown to influence the synchronization of behaviors (Trainer and McDonald 1995; Trainer et al. 2002). In wire-tailed manakins, the key to highly coordinated interactions is male synchronization and consistent role alternation (for detailed display description see Schwartz and Snow, 1978). Although we lack specific data on the duration of male partnerships, our observations of coordinated interactions suggested an obvious pattern. Our data corroborate the finding that deterioration of coordinated displays appeared to occur when male partners were closer in status or lacked an established relationship (Schwartz and Snow 1978). We found that display bouts between males close in social status (e.g., territorial neighbors) lacked clear coordination. More specifically, partners close in status often interrupted the display maneuvers of their partner. In contrast, coordinated displays between males of different social status (e.g., definitive territory holder and pre-definitive male) were the most behaviorally coordinated, with high frequencies of display behavior exhibited by both males and consistent role alternation. Increased behavioral coordination between partners of different status suggests that partnership tenure influences behavioral coordination until a male becomes a direct competitor through territory inheritance. Thus, both social status and partnership tenure appear to affect behavioral coordination in the wire-tailed manakin.

Variation in Display Rate among Leks, Males and Age-classes

Variation in display rates among males has been shown for several lekking birds (Hoglund and Alatalo 1995) but few studies have examined inter-lek display-rate variation. We did not find differences in the mean frequency of male behavior among leks. The most parsimonious explanation for the lack of differences among leks is that all leks have some higher ranking and some lower ranking members that exhibit differences in display rate. Further, under the assumption that display behavior is a sexually-selected signal (for review see Searcy and Nowicki, 2005), leks with low display rates would eventually disappear because of lack of female visits and reproductive output of territorial males. Moreover, if age is a determinant of display frequency and frequency of coordinated male partnership, then older higher ranking males would be expected to display at higher rates than younger newer territory holders. We expect lek territory holders to be a mix of older more dominant males and newer younger territorial males because of turnover.

Joint Display Benefits and Functionality

Benefits for non-resident display partners can accrue if social partners are more likely to inherit territories from the former owner (Robbins 1985; Heindl 2002). Our data showed that multiple males inherited the territory of their previous partners. These observations support the supposition that subordinate males can gain the direct benefit of territory inheritance through the formation of social partnerships. Moreover, floater males may increase their chances of inheritance by maintaining social relationships with multiple territory holders in the same lek, as we have observed in our system.

Behavioral coordination could be the result of kin-selection if social partnerships form between relatives to maximize indirect fitness for non-territorial partners (Loiselle et al., 2007b). In this type of lekking, system kin selection could work at lek level but would likely have a larger fitness effect at the partnership scale. Loiselle et al. (2007b) found that males within leks of *P. filicauda* were not more related by chance. Similarly, we found that male partners were also not more related than expected by chance allowing us to reject the kin selection hypothesis.

Male tolerance and potential solicitation for social partnerships would be enhanced if joint displays are more stimulating to a female than solitary displays and produce reproductive benefits for territory holders (Snow 1971b; Foster 1981). We have yet to quantify reproductive fitness via molecular paternity for individuals involved in coordinated behavior. We can, however, comment on signal intensity for solitary versus coordinated displays. The finding that coordinated display involves higher rates of display maneuvers suggests that it may be more visually appealing to females. We agree with Heindl (2002) that complex coordinated display is not likely to attract females from further distances but would only affect female choice once at the lek. Males in our study appeared willing to engage in social interactions based on the observations that males clearly solicit display partners and rarely aggressively chase visitors. Moreover, male solicitation of partners suggests an intrinsic benefit to male behavioral coordination. As we begin quantifying male reproductive success, we will examine if this behavior is fitness enhancing and, thus, sexually selected through female mate choice.

Coordinated display in the wire-tailed manakin appears to serve some competitive function that maintains and defines male social status among lek members (see also Heindl 2002, Robbins 1985). Although the behavior does not appear obligatory for female attraction the increased display rates associated with coordinated display do represent an enhanced signal. However, the role that enhanced signal plays in female attraction and stimulation remains undocumented. The stability of male partnerships and the lack of aggression suggests that this behavior does not solely serve a competitive function. We have shown a concrete delayed direct benefit in the form of territorial inheritance for partners, as previously described in *Chiroxiphia* spp. (McDonald 1989; DuVal 2005). Until the fitness increments of this behavior are fully quantified, it remains premature to suggest that coordinated display is a vestigial trait maintained in *P. filicauda* without substantial advantages (Prum, R. pers comm. as cited in Heindl, 2002). Ultimately, the function of coordinated display like so many other traits may have been selected in one context and co-opted for another resulting in a proximate function that is both dynamic and context dependent.

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Table 1 Mean display rate (maneuvers/2 hrs) by the age and social status of wire-tailed manakins at Tiputini Biodiversity Station, Ecuador.

	Pre-definitive Floater (*n* = 16)	**Definitive Floater (*n* = 17)**	**Definitive Territory Visitor (*n* = 19)**	**Definitive Territory Holder (*n* = 25)**
Song	8.81 ± 2.72	12.88 ± 4.36	13.00 ± 3.40	86.63 ± 2.22
Side-side	5.19 ± 1.09	4.64 ± 1.74	5.32 ± 2.10	15.85 ± 2.12
Stationary Display	1.63 ± 0.42	3.18 ± 1.34	2.47 ± 1.60	3.18 ± 0.35
Twist	2.50 ± 1.18	2.35 ± 1.14	0.79 ± 0.28	3.10 ± 0.39
Butterfly Flight	0	0	0	0.57 ± 0.15
Flutter	0.31 ± 0.22	0.12 ± 0.08	0.11 ± 0.07	0.14 ± 0.03
Swoop-in-Flight	1.88 ± 0.63	2.47 ± 1.52	0.95 ± 0.31	1.81 ± 0.28

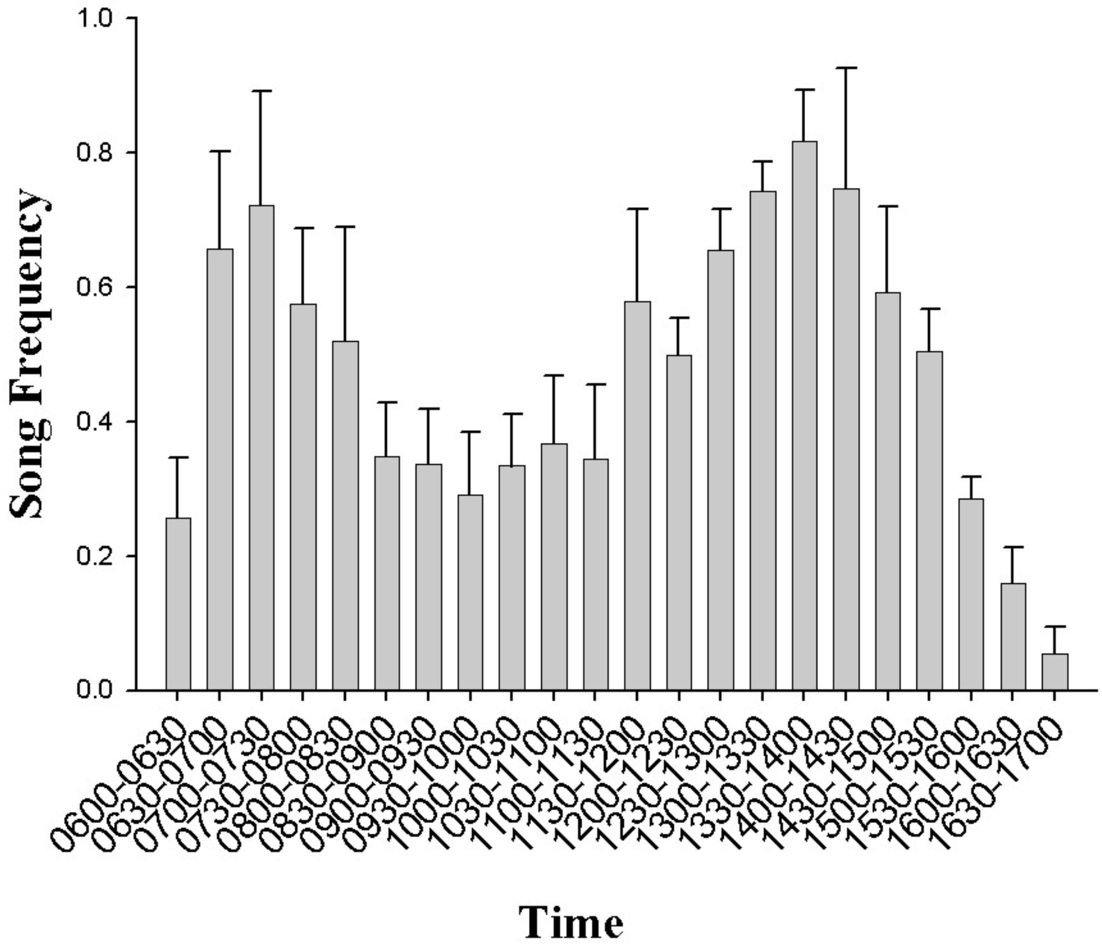

Figure 1 Male activity as measured by song frequency ± SE at five wire-tailed manakin leks at Tiputini Biodiversity Station, Ecuador shows a distinct bimodal distribution with morning and afternoon activity peaks.

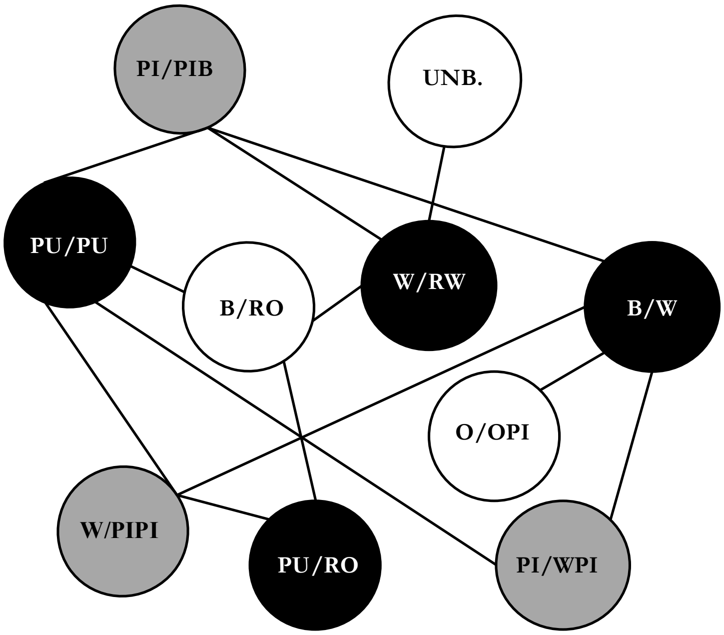

Figure 2 Display affiliations of male wire-tailed manakins within leks form a reticulate network of social interactions. The display partnerships among definitive territory holders (black circles), definitive territorial visitors (white circles) and visiting floaters (gray circles) are shown using lines.

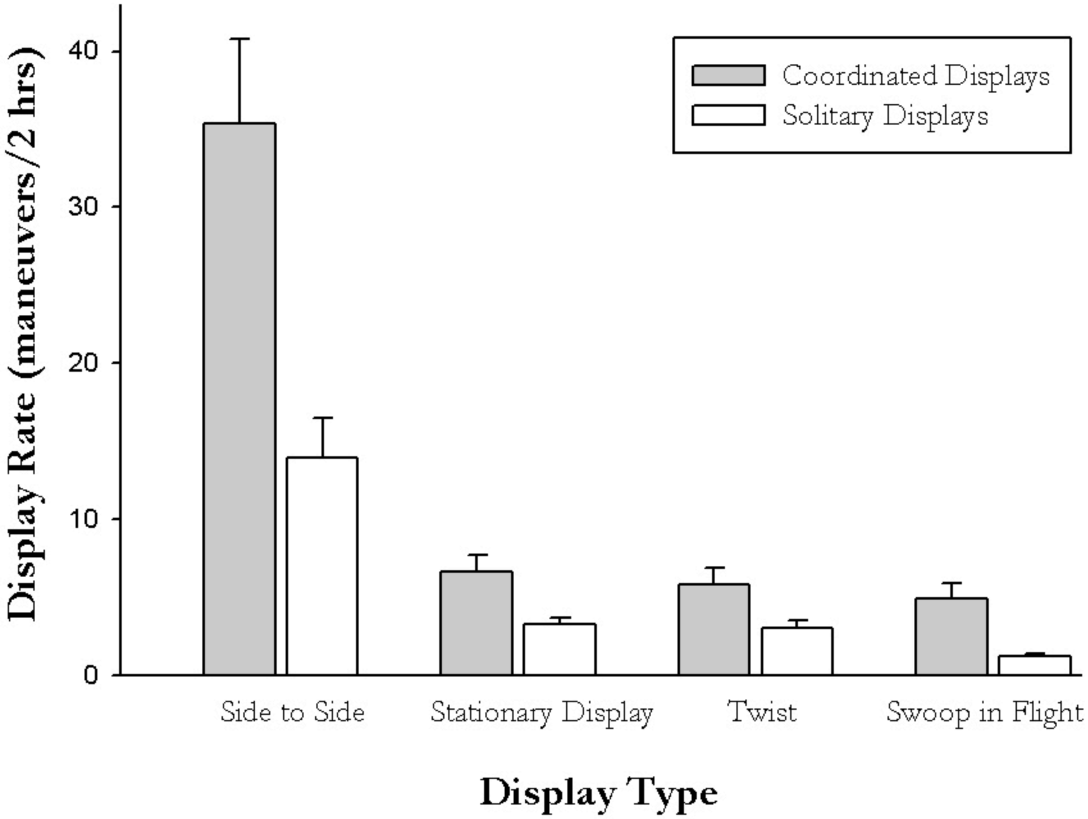

Figure 3 Rates of four common display maneuvers in the wire-tailed manakin are higher during coordinated display than solitary display as evidenced by average frequency ± SE.

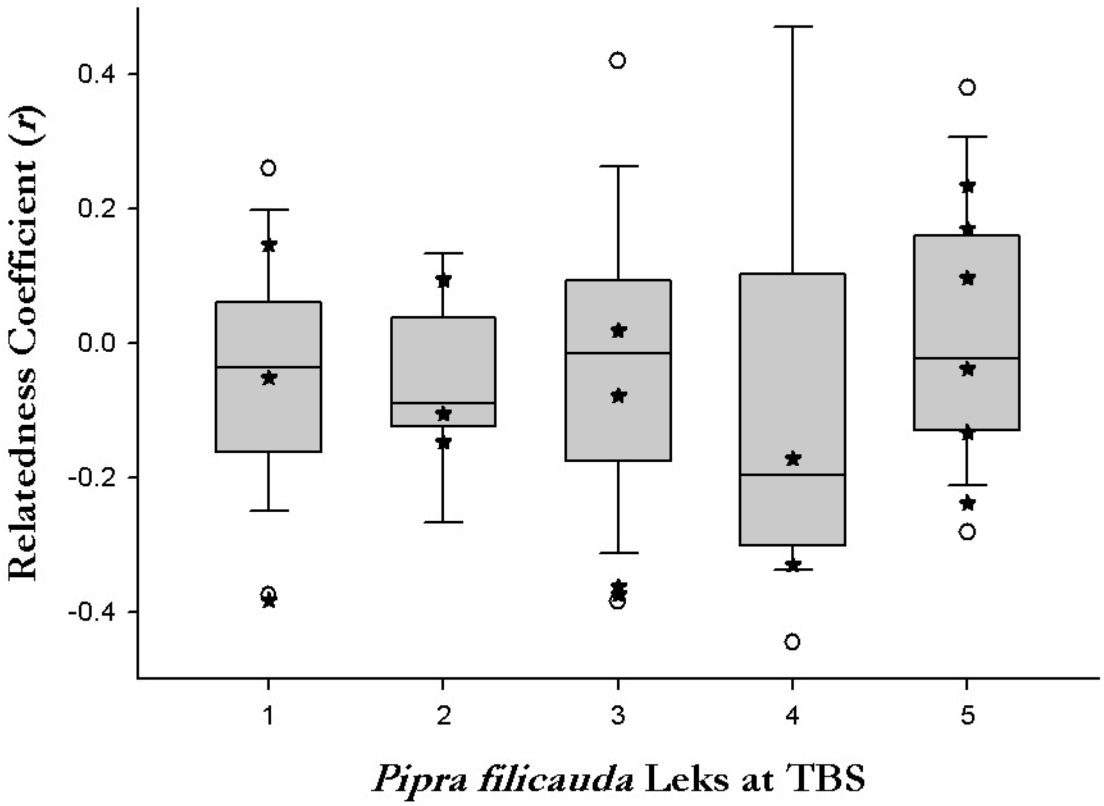

Figure 4 Wire-tailed manakin coordinated display partners are not more related than expected by chance as depicted in this box-plot showing 5th and 95th percentiles around average relatedness for 5 wire-tailed manakin leks. Circles show pair-wise relatedness value outliers for males within the lek and stars show pair-wise values for known male display partners (both territorial and floaters included).

CHAPTER 2- SOCIAL NETWORKS IN THE LEK-MATING WIRE-TAILED MANAKIN (*Pipra filicauda*)

ABSTRACT

How social structure interacts with individual behavior and fitness remains understudied despite its potential importance to the evolution of cooperation. Recent applications of network theory to social behavior advance our understanding of the role of social affiliations in various contexts. Here we applied network theory to the social system of lek-mating wire-tailed manakins (*Pipra filicauda,* Pipridae, Aves). We analyzed the network of interactions among males in order to examine the position of the coordinated displays and affiliative behaviors of this species along the spectrum that ranges 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 theory for the evolution of cooperation within social networks. The manakin networks had a "small-world" topology, with high node clustering and short mean path length among individuals. 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 shortest (geodesic) paths of male connectivity, predicted male social rise. The duration of a male's territorial tenure during the four 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 behavior, is incomplete. Recently, social network theory, developed for the study and analysis of human social behavior (Wasserman & Faust 1994), has been applied to vertebrate animal systems (Croft et al. 2004; Lusseau 2003; 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 behavior, 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 (Newman 2003; Wasserman & Faust 1994). In its simplest form, a social network is a graph consisting of *nodes* (individual actors) connected by *links* (social interactions) (Newman 2003; Wasserman & Faust 1994). 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 one; individuals separated by one intermediate individual are connected by a path of length two, and so forth. 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, 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, etc.) 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. 2005; Santos et al. 2006b). 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. The topologies of real-world networks are often compared to mathematically well-studied random and ordered networks. Real-world networks often exhibit the "small-world effect" (Newman 2003; Watts & Strogatz 1998), with high clustering (characteristic of ordered networks) and short average geodesic paths (characteristic of random networks).

Recently, evolutionary game and network theories have been applied jointly to investigate the evolution of cooperation, altruism, and indirect reciprocity (Nowak & Sigmund 2005; Ohtsuki et al. 2006; Santos & Pacheco 2005; Santos & Pacheco 2006; Santos et al. 2006a; Santos et al. 2005). These models have shown that certain network structural components can drive selection gradients that affect behavioral outcomes. Networks exhibiting low average degree (*k*) and preferential attachment, where new actors tend to attach to nodes of high degree, provide sufficient conditions for the evolution of cooperation (Ohtsuki et al. 2006; Santos et al. 2005). Similarly, the architecture of relations in "small-world" networks (high clustering and short geodesic path lengths among nodes) facilitates behavioral coordination among nodes (Cassar 2007).

Following Hamilton (1964), Ohtsuki et al. (2006) derived an elegant rule for the evolution of cooperation within social networks: the ratio of benefit to cost must exceed average degree (*k*). Scale-free networks (those 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 behaviors. The lack of evidence for this relationship, however, likely reflects the recent origin of the models rather than a lack of the necessary conditions, especially 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 behaviors from non-cooperative to strongly cooperative. Manakins (Pipridae) provide a useful opportunity to examine how network structure and social behavior interact given the continuum from solitary to obligate cooperative male display behaviors across the roughly 40 species in the family.

Lek-mating manakins (Pipridae) are Neotropical birds well known for their exaggerated courtship displays, which involve complex movements by, and sometimes interactions between, males. These displays have been described as the most complex behaviors 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 (DuVal 2007b; Foster 1987; Heindl 2002; McDonald 1989b; Robbins 1983; Robbins 1985; Schwartz & Snow 1978) and are thought to have evolved independently on two occasions (Prum 1994). The *Chiroxiphia* species can range from frequent but not obligate cooperation (*C. lanceolata*, Duval 2007a,b) to strict obligate cooperation (*C. linearis*, McDonald 1989a,b). 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 behaviors (Schwartz and 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; Foster 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 (DuVal 2007a; McDonald 1989a; McDonald & Potts 1994).

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 four 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., low average degree, high variance in degree distribution and extent of clustering) relate to the incipient cooperation involved in the intermittent phenomenon of coordinated courtship displays. Further, 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 coordinated display behavior 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. 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 (0º 38´ S 76º 08´ W). TBS is a 650-ha biological station operated by the Universidad San Francisco de Quito; the site has ~ 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 and fitted with aluminum leg bands and unique color combinations to aid in individual recognition. Blood was taken from the brachial vein of all individuals for genetic analyses (see below). Leks range from seven to ten territorial males and to quantify male-male affiliations we employed two sampling techniques: 1) observations of 27 territory holding male manakins at six leks during two-hour focal observation periods totaling 414 hours of observation, and 2) systematic scan samples at all other male territories within those leks. The two techniques over four years yielded 818 color-band resightings from which we quantified male social affiliations. Social interactions among males were restricted to the cases where the color combinations of both males were positively identified. Male social affiliations often occurred between males of differing status. Male plumage categories included *formative plumage* males characterized by green plumage with molt-limits showing them to be less than one 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, who are approximately two years of age, and *definitive plumage* males characterized by adult plumage and who were at least three years of age (see Ryder & Durães 2005). Female-male affiliations (almost exclusively for mating) were excluded from the analyses because of their brevity and rarity and because our goal was to assess the dynamics of male-male social structure.

(b) *Male Social and Reproductive Success*

Male status was classified by plumage and territoriality as follows: *Formative floaters* were all-green males, less than one year old, who did not hold territories, but who were seen visiting other males on leks; *Predefinitive-plumage floaters* were males with some red head feathers and black back feathers, who did not hold territories, but who were seen visiting lek territory holders; *Definitive floaters* were definitively-plumaged males without territories who 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 social and plumage status were determined across the four years of the study by subsequent resightings and affiliative behavior with other males. Males were considered to rise in social hierarchy when they changed from floater status and inherited a territory. Male status was coded as 0 if a male failed to change status and 1 if he inherited a territory during the four 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 binary fashion 0/1, where any male that sired an offspring with at least 80% confidence was coded 1, and any male who could not be assigned at least one offspring with 80% was coded 0 (see 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 versus unsuccessful territory holders as they relate to network metrics. We view this as a first step towards later investigating more fine-grained variation in success.

(c) *Network Metrics*

We constructed social network models based on four years of behavioral observations of color-banded individuals. Network links (1 vs 0 in the corresponding *adjacency matrix*; Wasserman and Faust 1994) represented social affiliations among males and were unweighted and undirected (0/1), so that frequency of interactions was not incorporated. Several applications of social network theory have applied filtering to data for co-occurrence in groups in fission-fusion type societies (see Rubenstein et al. 2007; Sundaresan et al. 2007). Such filtering reduces the likelihood of over-emphasizing random or chance co-occurrence that do not represent any real affiliation 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 behaviors in the context of courtship displays. The minimum requirement for a link (1 vs 0 in the corresponding adjacency matrix) was joint perching within 20 centimeters for several minutes. Our observational data indicate that this behavior is frequently the precursor to coordinated male displays and that males rarely perch close to males with whom they do not engage in coordinated displays. Moreover, the vast majority of links (~90%) among males represent joint coordinated display events in which males engaged in ritualized coordinated displays (for a detailed description see Schwartz and Snow 1978). We also explicitly examined the relationship between observer effort and social connectivity to make sure our results were not biased towards certain males. Our investigation of these patterns yielded no relationship between number of hours observed and the number of male affiliations ($r^2 = 0.0081$) or time in the network and number of male affiliations ($r^2 = 0.069$).

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. That is, each network comprised a distinct pair of leks and had a non-overlapping set of individuals, making each a statistically independent replicate. A few floaters males, with affiliations to territory holders in each of the paired leks within a network, formed the links between spatially adjacent leks. We used the cumulative interactions over the entire four-year study period to compute all network metrics and statistical measures, because individual-year sub-networks were not fully connected.

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 focal node influence over adjacent nodes of lesser degree; *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 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 paths connecting other pairs of nodes, including paths longer than the geodesic (Stephenson & Zelen 1989); *nBetweenness* is a measure of the number of geodesic paths between pairs of nodes that run through the focal node (see Albert & Barabasi 2004; Newman 2003; Wasserman & Faust 1994). We also used *UCINET*™ to generate constrained random networks (same number of nodes and links, which yields a network of equal density) for comparison to our observed networks. The random graph generator randomly reattaches links with the constraint of equal density, and is the procedure routinely used for comparing real-world graphs to the well-developed theory of random graphs (e.g., Watts and Strogatz 1998). Average network degree ($\bar{k}$) was calculated following (Albert & Barabasi 2004). D. B. McDonald programmed *Mathematica*™ routines following algorithms in Wasserman and Faust (1994) and Newman (2003) to generate ordered networks and to calculate network diameter, global clustering and mean geodesics (shortest path lengths). Network diagrams were created using *Netdraw* 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 1) male social rise or 2) 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 to 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). We used random and ordered networks of equal density (same number of links and nodes) as comparators for the degree distribution, network statistics and topology of the observed manakin networks. Best-subsets analyses were done using *Minitab*™; all other statistical tests were done 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 (Fig. 1A). Within-lek connectivity (Fig. 1A) 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 observed networks were topologically intermediate between the random and ordered networks of equal density (same number of nodes and links; Fig. 1). That is, they were "small-world" networks, with short mean geodesic path lengths among nodes (like the random network of Fig. 1B; Table 1) and high clustering of nodes (like the ordered network of Fig. 1C).

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 $n = 31$, $\bar{k} = 2.83 \pm 0.29$). When compared to the random and ordered networks (Fig. 1), the manakin networks had intermediate average degree yet the highest variance in number of links (Manakin $\bar{k} = 3.34$, $\sigma_k^2 = 4.17$; Random $\bar{k} = 3.60$, $\sigma_k^2 = 3.32$; Ordered $\bar{k} = 2.66$, $\sigma_k^2 = 0.33$). The variance in degree was further evident in the cumulative degree distribution of the three observed manakin networks, each of which showed a strong positive skew (Fig. 2A), with a few nodes of high degree linking many nodes of lower degree. In contrast, the cumulative degree distributions of the random and ordered networks were homogeneous, with low skew (Fig. 2B & C).

(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 2). Predictors incorporated into the model varied in their explanatory power, with degree ($P = 0.001$, odds ratio = 7.31, 95% CI 2.36 to 22.62) having the largest effect. That is, each additional degree increased a male's odds of inheriting a territory by a factor of seven. 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 3).

(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 to 8.02; Table 2). That is, a male's odds of siring offspring increased by a factor of about four for each additional year he was a territory holder (Fig. 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 within 2). None of the other network metrics contributed to best-fit models for reproductive success.

4. DISCUSSION

Our major results were to show that social network connectivity explained a male's ability to become a territory holder and that the network topologies were consistent with 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. Topologically, the manakin networks had a high clustering coefficient and short geodesic path lengths among nodes, key characteristics of "small-world" networks. Cassar (2007) showed that a small-world effect increases the likelihood of behavioral coordination among nodes. The manakin networks also met other theoretical criteria favoring the evolution of cooperation. Although we did not measure 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 behavior 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 characterize scale-free networks, although demonstrating a power-law distribution (versus alternative distributions) is virtually impossible in small networks (Keller 2005).

(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. 2006b). Graph-theoretical modeling of both static and dynamic networks has shown that selection can favor the evolution of non-selfish behavior in the context of heterogeneous social ties (Cassar 2007; Santos & Pacheco 2005; Santos et al. 2006a).

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 (Foster 1981; McDonald 1989a; Snow 1971a; Snow 1971b). Wire-tailed manakins show such intermediacy, with behavioral 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 favoring the evolution of cooperation suggest that cooperative benefits, at least as much as aggressive, dominance-establishing benefits, may be important in wire-tailed manakin social interactions.

The ingredients needed for the evolution of cooperation are present in the complex networks of social affiliations among male wire-tailed manakins. Establishing that the social networks meet some of the necessary criteria specified by theoretical models is a first step toward 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. 2006; McDonald 2007) have shown that investigating social contacts can improve our understanding of complex behaviors. 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, as encapsulated 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, *Chiroxiphia 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 wire-tailed manakins requires them to build social affiliations over time 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 the relative number of links determines the speed of male social ascendancy. Although de novo establishment of new territories does occur, most males acquire territories by inheritance, for which social partnership with the previous territory holder is an essential prerequisite (Ryder, unpubl. data).

(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 1989b). However, understanding the sources of variation in male mating success continues to be a major challenge for behavioral 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 2007a). The wire-tailed manakin also exhibits reproductive skew, but with a more equitable distribution across males (Ryder, unpubl data). This lower variance in mating success in wire-tailed manakins as compared to *Chiroxiphia* spp. means males have more options for mating success in the short term. The high variance in *Chiroxiphia*, skewed toward the oldest males, and hence fewer reproductive options for young males, may have helped drive evolution toward the extreme of obligate cooperation.

Male reproductive success was best predicted by the duration of a male's 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, males 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 (Doucet et al. 2007; DuVal 2007b; McDonald 1989a).

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, requiring the multi-actor formalism of network models.

Previous network studies of animal social behavior have focused largely on the emergent properties of networks, particularly classifications based on degree distributions. These studies have shown that affiliation 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 behavioral 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 behavioral patterns of young males.

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Table 1. Average network metrics for three different network topologies, each with the same density (same number of nodes and links). The manakin network has short mean geodesic path lengths among nodes (like a random graph) and high clustering coefficient (like an ordered graph), two characteristics of “small world” networks.

	Manakin	Random	Ordered
Diameter	8.33 ± 0.33	7.33 ± 0.58	10.67 ± 1.20
Mean Geodesic	3.92 ± 0.28	3.27 ± 0.14	5.60 ± 0.47
Local Clustering	0.39 ± 0.03	0.06 ± 0.01	0.58 ± 0.04

Table 2. Akaike Information Criteria (AIC) used to predict the best-fit models for male social rise and reproductive success in male wire-tailed manakins at Tiputini Biodiversity Station, 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 Akaike's Information Criterion used in model selection

Table 3. Measures of male network connectivity predict fitness components in male wire-tailed manakins at Tiputini Biodiversity Station, 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 ± SE are shown.

Network Metrics	**Social Rise**[a]		**Reproductive Success**[b]	
	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

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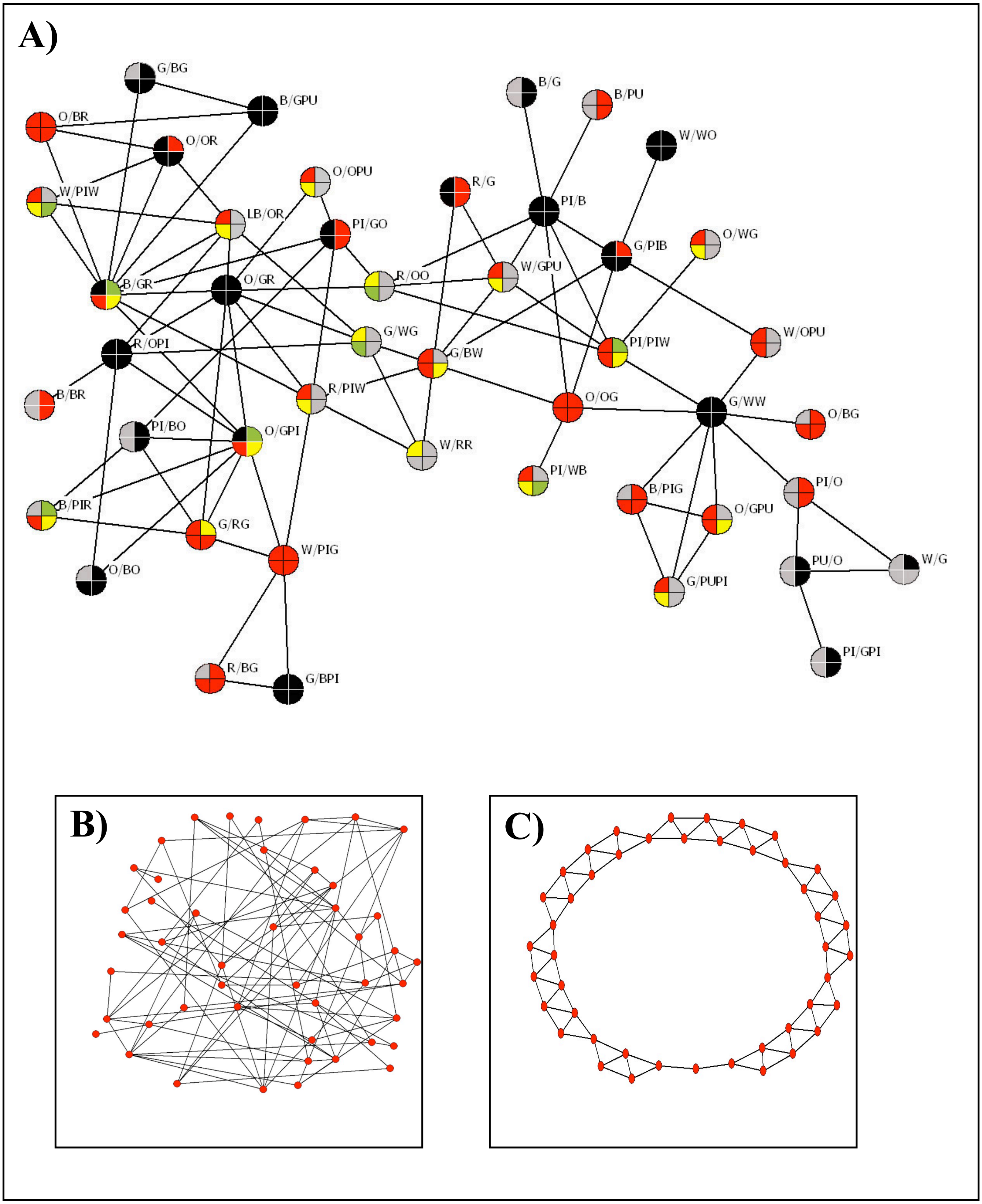
a Male social status coded 0 (no social rise) and 1 (social rise)

b Male reproductive success coded as 0 (zero offspring sired) and 1 (at least 1 offspring sired)

Figure 1. A) A representative social network for male wire-tailed manakins during a four-year period at Tiputini Biodiversity Station, Ecuador. Each node represents a male, and the links represent social affiliations 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. Gray: not present in the network; green: formative-plumage floater; yellow: pre-definitive-plumage floater; red: definitive-plumage floater; and 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. B) A random network with the same number of nodes and links as the observed network, for comparison. Relatively short path lengths connect any two nodes in the random network (as well as the manakin network). C) An ordered network with the same number of nodes and links as the observed network, for comparison. Many paths across the network are long (unlike the manakin network) but distinct clusters of nodes exist (like the manakin network but unlike the random network).

Figure 2. A) The cumulative degree distribution, averaged across the three manakin social networks, shows low average degree (dashed vertical line), high variance, strong positive skew and a long tail. A few highly connected males (degree > 7) connected many males of lower degree. B) The cumulative degree distribution of random social networks also shows low average degree, yet it differs from the observed in having low variance and negative skew. C) The cumulative degree distribution for ordered social networks shows low average degree, very low variance and negative skew. The most striking difference was the high variance and positive skew of the observed manakin network.

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


A)
G/BG
B/GPU
O/BR
O/OR
W/PIW
O/OPU
LB/OR
PI/GO
R/G
B/G
B/PU
W/WO
PI/B
G/PIB
O/WG
R/OO
W/GPU
B/GR
O/GR
G/WG
G/BW
PI/PIW
W/OPU
R/OPI
B/BR
R/PIW
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PI/WB
B/PIG
PI/O
O/GPU
B/PIR
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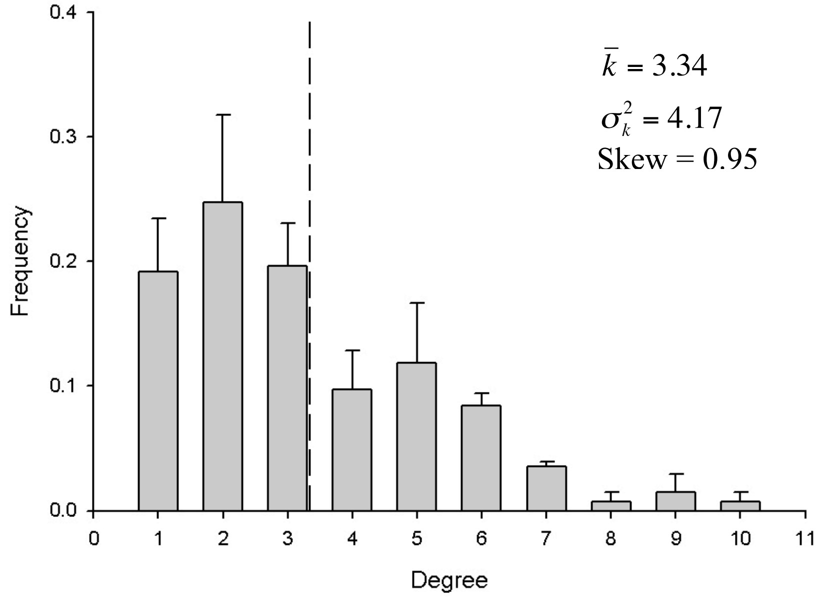
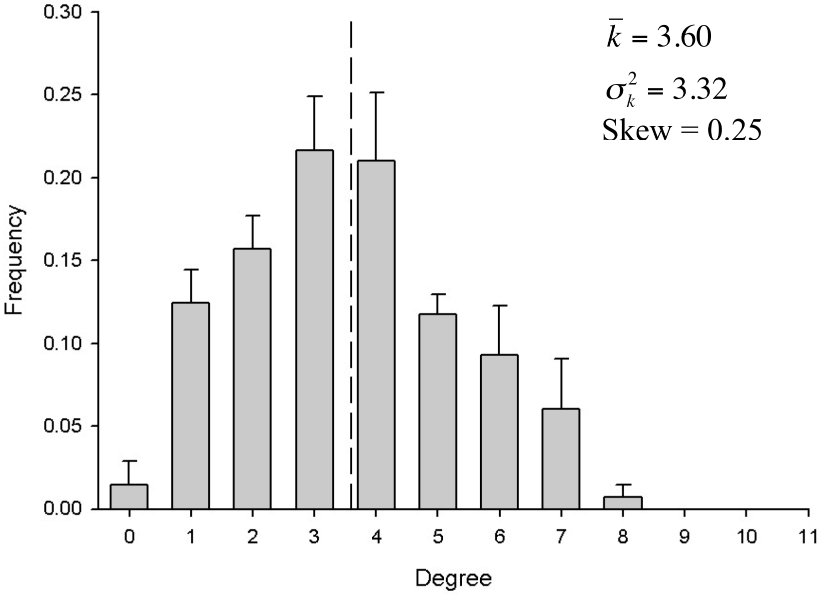
PU/O
W/G
PI/GPI
R/BG
G/BPI
B)
C)

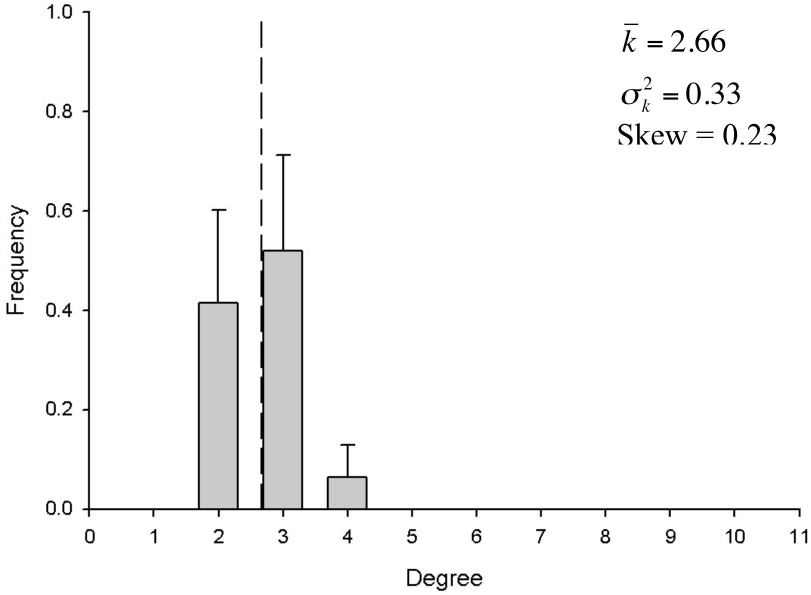
A)

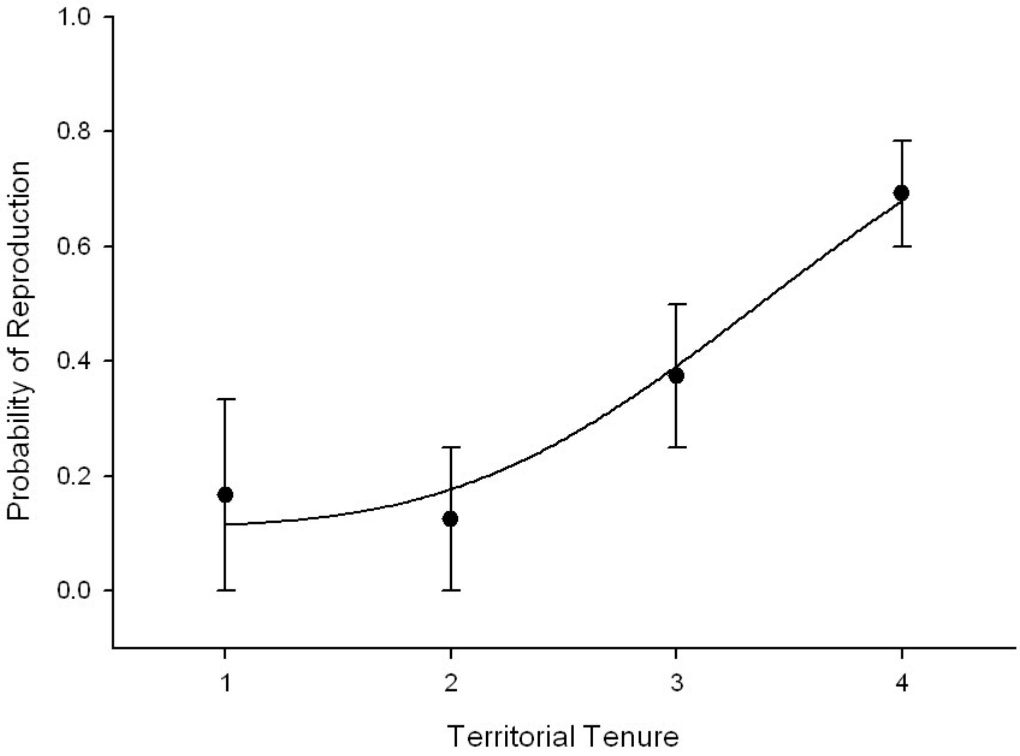

$\bar{k}$ = 3.34
σ_k^2 = 4.17
Skew = 0.95
Frequency
0.0
0.1
0.2
0.3
0.4
Degree
0 1 2 3 4 5 6 7 8 9 10 11

B)


$\bar{k}$ = 3.60
σ_k^2 = 3.32
Skew = 0.25
Frequency
0.00
0.05
0.10
0.15
0.20
0.25
0.30
Degree
0 1 2 3 4 5 6 7 8 9 10 11

C)


$\bar{k}$ = 2.66
σ_k^2 = 0.33
Skew = 0.23
Frequency
0.0
0.2
0.4
0.6
0.8
1.0
Degree
0 1 2 3 4 5 6 7 8 9 10 11


1.0
0.8
0.6
0.4
0.2
0.0
Probability of Reproduction
1
2
3
4
Territorial Tenure

CHAPTER 3- MOLECULAR ESTIMATES OF REPRODUCTIVE SKEW AND SOCIAL CORRELATES OF MALE MATING SUCCESS IN A LEK BREEDING BIRD

ABSTRACT

Variance in reproductive success among individuals has become a defining characteristic of many highly social vertebrates. Our understanding of what factors drive high variance in reproductive success (i.e., intra vs. inter-sexual selection) and which male attributes contribute is still fragmentary in most cases. Here the joint application of molecular tools and a novel analytical methodology (network analysis) have enhanced our ability to measure reproductive variance as well as to better understand the role of sociality in a lek breeding bird. We examine the complex social and reproductive dynamics of the wire-tailed manakin (*Pipra filicauda*) from a four-year study in the Amazon basin of Ecuador. More specifically, we present reproductive skew estimates generated from molecular paternity analyses and explain the variation in male reproductive success in the context of complex male social affiliations via the application of social network theory. Our data show that four of six leks examined have significant reproductive skew with the majority of success apportioned to very few individuals in each lek. Metrics of male social affiliations derived from our networking analysis, specifically, male connectivity, as measured by the number of other males with whom the focal male has extended interactions explained a large portion of the variance in male reproductive success. Not surprisingly, number of both male-female and male-male affiliations explained a portion of the variance in male reproductive success. Female selectivity of highly connected males may explain the selective regime, which promoted the evolution of the complex male-male display behavior in this species.

1. INTRODUCTION

The unequal 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 (Cant & Johnstone 1999; Kokko & Johnstone 1999; Magrath & Heinsohn 2000; Reeve et al. 1998). Moreover, such indices provide an important framework for understanding the evolution and maintenance of social behavior because they assess the immediate fitness costs and benefits that are associated with group living and cooperation (Clutton-Brock 1998; Griffin et al. 2003; Keller & Reeve 1994).

At the center of much of skew research are lekking taxa in which males are spatially aggregated presumably due to their inability to profitably control or monopolize resources essential for the acquisition of females (Emlen & Oring 1977). Lekking as a reproductive strategy is of primary interest because leks are characterized by high reproductive variance among males, an essential fitness component of the lek social system (Hoglund & Alatalo 1995; Mackenzie et al. 1995; McDonald 1989; Wiley 1991). Leks are also of interest because female choice is assumed to be the major determinant of non-random mating and that those choices are not related to immediate fitness gains (Hoglund & Alatalo 1995). Recently, however, the paradigm that female choice is the only determinant of variance in male mating success has been challenged (Kirkpatrick & Ryan 1991). Although female choice clearly operates in many lekking systems (Hoglund and Alatalo 1995), the relative contributions of intra- and inter-sexual forces to variance in mating success remain largely unknown. The importance of male-male competition as a factor driving high variance in male reproductive success also merits attention and is suggested to be important in lekking taxa where males share perches or engage in coordinated display. In a broader context, adaptive female mate choice for elaborate male traits also remains an enigmatic problem in evolutionary biology because female preferences are predicted to exhaust genetic variation in male traits (the paradox of the lek) (Kirkpatrick & Ryan 1991).

Male reproductive coalitions, where two or more males join together to display for females are of particular interest among lekking taxa. Such coalitions represent an evolutionary paradox because one individual often accrues all the reproductive benefits while the other individual appears to sacrifice their own reproductive potential to assist the social partner. Males in several species of manakins, in the family Pipridae, engage in social partnerships for the attraction of females (e.g., *Chiroxiphia* and *Pipra aureola* clade). Previous work has revealed strong reproductive skew among male *Chiroxiphia* partners (DuVal 2007; McDonald 1989), yet no work has addressed the cost or benefits of coalitions in the *Pipra aureola* clade. Ultimately, the study of species which engage in facultative social behavior , such as those in the *P. aureola* clade, can begin to elucidate the relationship between variable social traits and fitness trade-offs (Wey et al. 2008).

In the past, our understanding of variance in reproductive success was often limited by the techniques applied (e.g., incongruities between observationally-derived and true molecular estimates of reproductive success). The relatively recent integration of molecular techniques into behavioral studies, however, has revolutionized our understanding of reproductive variance and mating systems (Hughes 1998). Specifically, microsatellite loci have reunited theory and practice to provide a powerful molecular tool for parentage analysis in most biological systems (Jones & Arden 2003). Ultimately, coupling paternity analysis with a mathematical framework, will provide a starting point for the examination of selective forces in social evolution, and reproductive skew in hierarchically structured populations (Ross 2001).

In addition to molecular tools, recent analytical tools, such as the mathematical framework of networking analysis, have begun to advance our understanding of the fitness implications of social structure at the individual level (Ryder et al. 2008) (Krause et al. 2007; McDonald 2007). 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 (Newman 2003; Wasserman & Faust 1994). 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). This mathematical framework, coupled with molecular assessments of reproductive success, may provide the exact kind of coupling Ross (2001) had envisioned. Despite the enormous potential of network applications in animal behavior it has received relatively little attention (reviewed in Krause et al. 2007, Wey et al. 2008), especially in birds (but see McDonald 2007, Ryder et al. 2008). Of particular value would be an examination of how quantitative measures of male network connectivity relate to variation in reproductive success (Krause et al. 2007).

Here, we investigate the strength of reproductive skew as measured using molecular markers and examine the social correlates of variance in male reproductive success using metrics derived from a social network analysis of a lek breeding bird. More specifically, we use data from a four-year study of the wire-tailed manakin (*Pipra filicauda*), a member of the *P. aureola* clade that engages in coordinated male-male partnerships, to investigate the costs associated with group living and the roles of social partnerships in determining reproductive success.

2. METHODS

(a) Field Methods

We studied a population of wire-tailed manakins from 2003 to 2007 at the 650 ha Tiputini Biodiversity Station located in Orellana province of eastern Ecuador (0º 38´ S 76º 08´ W) (for a detailed site description see (Loiselle et al. 2007a). 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. Blake and B. A. Loiselle. Over the four years of the study, we captured 424 individuals, consisting of 133 females, 250 males and 36 of unknown sex, using mistnets. Captured manakins were weighed, sexed, aged, and banded with aluminum and individual color-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. Two-hour focal behavioral observations and half-hour territorial scans were conducted in male territories to assess male behavior and quantify social affiliations through time (for details see Ryder et al BES).

Over the course of the four years, we searched for manakin nests between November and March. 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 the previous years. Systematic nest searching was supplemented by following radio-tagged females to their nests. Radio transmitters (Holohil Systems Ltd.) weighed 0.54 -0.70 grams (i.e., <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. There was no evidence that radio transmitters affected the mating behavior of females, as tagged females were able to build nests, copulate, incubate eggs and raise young (pers. obs.). Once the nest was located, nets were placed strategically around the nest for recapture of the female and radio removal.

(b) Male Classification and Status

Male wire-tailed manakins undergo a series of plumage and social transitions (age graded social queue) from when they leave the nest until they become eventual territory holders. 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; predifinitive plumage floaters have mixed formative and definitive plumage who have established social relationships with territory holders but lack territories; definitive plumage floaters are the same as predifinitive plumage floaters except they have attained definitive adult plumage; and definitive plumage territory holders have attained the apex of social and plumage status (see Ryder et al. 2008)

(c) Molecular Analyses and Paternity Assignments

DNA was isolated using standard phenol-chloroform extraction followed by dialysis in TNE_2. Once DNA was extracted and concentrations were checked we screened 25 microsatellite primers (DuVal & Nutt 2005; McDonald & Potts 1994; Piertney et al. 2002)(Brumfield R and Braun M, personal communication) and isolated seven polymorphic markers for the genotyping analyses of individual wire-tailed manakins. PCR reagents and reaction conditions are detailed in (Loiselle et al. 2007b). We tagged our PCR products using fluorescently labeled 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 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 low proportion of typing error (Table 1). We assessed departures from H-W equilibrium and linkage using FSTAT version 2.9.3.2 (Goudet 2002). None of the loci examined showed linkage and only one of the seven failed to meet Hardy-Weinberg expectations (e.g., MAN 7) likely 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, 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 v3.03, (Kalinowski et al. 2007; Marshall et al. 1998). 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 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.

Due to small sample sizes in some years, we performed paternity analyses on the cumulative data across the four 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 molecular markers. The number of candidate males was 250 and given our complete sampling of territorial individuals at leks of interest we assumed we had sampled 95% of candidates across our four-year study. High male survival (see Blake and Loiselle in press) and strong male site fidelity also contribute to confidence in our sampling assumptions. In addition to nestlings sampled, post-fledging individuals can be aged as less than a year old using molt limits within their greater-coverts (Ryder & Durães 2005). We also attempted to assign paternity to any post-fledging individual that was born during the four 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: (1) 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; (2) if two males with the same number of mismatches had similar LOD scores but the assigned male was compared to the offspring at fewer loci; (3) 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 Newman 2003; Wasserman & Faust 1994). We constructed social networks based on data for four years of behavioral observations and scan sampling. Network links among males represent male-male social affiliations and male-female affiliations as determined by paternity. All links were undirected and unweighted so that the frequency of male interactions was not incorporated. Frequency was not used in the analyses because some males received multiple two-hour focal observations while other males only received scan sampling resulting in an uneven sampling effort. Detail on the explicit behavior criterion used to create male links can be found in Ryder et al. (2008).

Cumulative male interactions at six leks yielded three social networks that are described in detail in Ryder et al. (2008). We used the cumulative social network to calculate all network metrics because individual-year sub-networks were not fully connected. 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*) as explanatory variables for variance in reproductive success. *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 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 paths connecting other pairs of nodes, including paths longer than the geodesic

(Stephenson & Zelen 1989); *nBetweenness* is a measure of the number of geodesic paths between pairs of nodes that run through the focal node (see Albert & Barabasi 2004; Newman 2003; Wasserman & Faust 1994).Network diagrams were created using Netdraw 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). While 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 use the binomial skew index, in which observed group variance is corrected by expected variance if each member has an equal probability of gaining reproductive opportunity (Nonacs 2000). We used the skew calculator v1.2 to calculate indices and present the binomial index because it has the fewest statistical limitations, corrects differing lengths of group membership and calculates confidence intervals (Nonacs 2003).

To examine the social correlates of male reproductive success, we used step-wise multiple regression. We used 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. We carried out these analyses in two steps, first using network metrics calculated with both males and females present in the networks and second with females removed from the networks. We felt inclusion of females was biologically important because they are a strong component of the system, yet we wanted to see whether patterns based on male-male interactions remain after removal of females. Variables were entered into the model in a step-wise fashion to find the best-fit overall model. All analyses were run in JMP v5.0.1; means and standard errors are reported unless otherwise noted.

3. RESULTS

(a) Molecular Paternity and Reproductive Skew

Over four years, we sampled 125 offspring from 63 broods and 76 post-fledging individuals and typed them at seven polymorphic microsatellite loci for paternity analyses (Table 1). Mother-offspring relationships were known for 101/125 (81%) of the nestlings and 0/76 (0%) of the individuals less than one year of age. Of the total 201 offspring we successfully assigned paternity to 114 (57%) with varying degrees of confidence. More specifically, 16/99 (16%) were assigned using the “total evidence” approach, 31/99 (31%) were assigned at relaxed 80% confidence, 52/99 (53%) were assigned at 95% confidence for the nestlings. Of the young individuals, where neither mother nor father was known, all 15 individuals were assigned at the relaxed 80% confidence.

We assessed detailed paternity patterns for 52 broods and found that within broods, only 7/38 (18%) females had mixed paternity in their nests while a single male sired each the remaining clutches. Within a single year, we observed six females that made repeated nesting attempts, each being represented by two broods. In three of these instances, females switched mates between broods and in three they did not. Between years, females were more likely to switch mates 6/8 (75%) than to remain with the same partner from the previous year 2/8 (25%).

Of the 114 offspring for which we assigned paternity, 112/114 (98%) were sired by territorial males whereas only 2/114 (2%) were sired by definitive plumage floaters (i.e., non-territorial individuals). In both instances the non-territorial floater sired a single chick and in one case was the partner of more successful male territory holder. 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 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 3-11 with an average of 5.3 ± 1.1 successful individuals per 10 territories. Although in some leks multiple males sired offspring, on average only three top-ranked males per lek sired more than 80% of the total offspring. We further examined the relationship between male rank and proportion of offspring sired at a larger spatial scale by combining males from spatially contiguous leks linked by floater individuals. In all three instances, these pairs of contiguous leks defined our social networks and again we found that only the three top ranked males sired 70-90% of the offspring (Figure 2). In a step-wise multiple regression analysis we found that *degree, eigenvector centrality, information centrality, distance weighted reach* and *power* were predictive of number of offspring sired ($F_{5,24} = 21.6$, $p = 0.0001$, $r^2 = 0.82$) (Table 3). We repeated the analysis to remove the effect of females in the social network and found that the two strongest predictors, *degree* and *eigenvector centrality*, predicted number offspring a male sired but with lower explanatory power ($F_{2,25} = 9.1$, $p = 0.0011$, $r^2 = 0.42$) (Table 3). In both analyses, *degree*, which is a direct measure of a male's social connectivity, was the best predictor of number of offspring sired (Figure 2 & Figure 3).

4. DISCUSSION

Here we have presented data on wire-tailed manakins, which begins elucidating the importance of reproductive and social dynamics in a lek mating system with male-male coordinated displays. Four of the six leks we studied showed significant reproductive skew with only a few territorial males receiving the vast majority of the reproductive benefits. Overall our data show that territoriality is a fairly strong prerequisite for access to reproduction in this system. Two social partners of reproductively successful males, however, did sire one offspring each but they both appear to be exceptions to the rule (i.e., 2% of matings) rather than common occurrences. Here we have also documented a previously unrecognized social component (i.e., number of male affiliations) important for understanding variation in male reproductive success. Metrics derived from a social networking analysis predicted the number of offspring a male was likely to sire. Moreover, variation in male reproductive success was explained by social affiliations that included both a female and male component.

(a) Molecular Paternity and Reproductive Skew

Previously documented strong skew in lekking systems (Hoglund and Alatalo 1995; Mackenzie et al. 1995; Wiley 1991) suggests that females primarily make unanimous mate choices (Bradbury et al. 1985). Mate choice unanimity has two components that contribute to variance in male reproductive success, one unanimous mate choice among different females and two the unanimous consecutive within brood choices of a single female. Mate choice unanimity is evidenced in our data for both components. Strong skew within four of our six leks in which few individuals received the majority of the reproductive benefits suggests unanimity among females (e.g. in one lek a single male sired 20 0f 24 total offspring). Likewise, consecutive within brood choices of females showed that 82% of females make unanimous mate choices. Female mate choice unanimity can be achieved via utilization of the same mate-choice cues to assess and select males or via females copying their own or other female choices to consistently mate with particular males (reviewed in Balmford 1991). Information about the acuity and accuracy of females in assessing mating cues, however, is still lacking (Bradbury et al. 1985).

Although mate-choice unanimity represents the general trend in our data, we did find some females that mated multiple times resulting in offspring with mixed paternity. Moreover, between-brood and among-year female choice suggest that females do mate with more than one male. This contrasts 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). Female polyandrous behavior, however, has been previously documented in other lekking taxa (e.g. peacocks, *Pavo cristatus*, (Petrie et al. 1992); buff-breasted sandpipers, *Tryngites subruficollis*, (Lanctot et al. 1997) yet clearly does not play as important a role in the reproductive strategies of female wire-tailed manakins. Regardless, such observations on female choice in a lekking system support the supposition that females are free to choose respective partners (Balmford 1991). Female choice of males at leks in wire-tailed manakins, however, does appear to be limited to a few top individuals, with the majority of mate changes being to other successful individuals.

The existence of reproductive skew in the majority of wire-tailed manakin leks we studied further adds to the number of documented behavioral and molecular skew estimates for manakin species that engage in male-male display (e.g., *Chiroxiphia linearis* and *lanceolata*) (Duval 2007; McDonald 1989). Skew at the lek level is an inevitable consequence of lek membership because solitary display or not joining a lek yields no fitness benefits. The costs of engaging in joint male coordinated display, however, likely vary by age class and social status. Engaging in male-male coordinated displays does provide access to reproduction yet the frequency of offspring sired by partners does not appear to produce a significant benefit. However, measurable delayed direct fitness benefits are associated with coordinated displays, where participation in a social network is an essential precursor for social ascendancy and territory acquisition (Ryder et al. 2008).

Our results show that territoriality is a fairly strong prerequisite for male reproductive success because territorial males sired nearly all offspring. In addition, our previous work showed that the length of a male’s tenure as a territory holder was also a strong determinant of a male’s likelihood of siring offspring (Ryder et al. 2008). Thus, it appears that males must build social affiliations via coordinated displays to accrue social capital essential for territory acquisition and then maintain that territory to increase their chances for reproductive success.

(b) Social Correlates of Male Success

Understanding the adaptive significance of female mate choice in lekking taxa has remained a prominent goal of behavioral ecologists because of the apparent lack of fitness benefits for choosy females. Mate choice decisions in wire-tailed manakins appear hierarchical, in which females use territoriality and length of male tenure as the primary criteria (see Ryder et al. 2008). Once a female has narrowed the pool of potential candidate males, it is likely she uses multiple cues (e.g., behavioral, phenotypic, social and genetic) to assess mates and choose among territory holders. Evidence from other lekking taxa support the supposition that male mating success is determined by a multitude of potentially interacting traits (Hoglund & Alatalo 1995). Fiske et al. (1998) reviewed the importance of traits in a meta-analysis of male mating success on leks and found that behavioral (male attendance), territorial (territory centrality), and morphological (extravagant traits) cues all played important roles.

Studies of mating success in male manakins have also found numerous factors to be determinants of male success. Predictors of male mating success in manakins have varied widely and include song and display rate in *Chiroxiphia linearis* (McDonald 1989), male size, condition, territory position, and levels of aggression in *Manacus manacus* (Shorey 2002) and female preferences for male plumage brightness also in *Manacus manacus* (Stein & Uy 2005). To date, however, no studies have documented the importance of social structure or male affiliations for reproductive success. Moreover, the direct fitness consequences of social relationships are rarely documented

(Wey et al. 2008). Social affiliations are likely not important in all manakin mating systems but are particularly pertinent for those where males engage in joint displays. The importance of network metrics, such as degree, that measure connectivity, have only recently been recognized to have bearing on both male social status and reproductive opportunities (see Krause et al. 2007, McDonald 2007, Ryder et al. 2008).

We found that male degree, a direct measure of a male's social connectivity, was the strongest positive predictor of variation in male reproductive success. Degree, as used in our analyses included both male and female components, where male links represented social display partnerships and female links represented copulations and successfully sired offspring. In a second analysis, we removed female links because of the known positive association between number of offspring and number of females a male mated with. Removal of female links did reduce the explanatory power of the model yet degree was still strongly predictive of number of offspring sired.

We viewed the female contribution to degree as biologically important because of the potential role of female copying in lekking taxa. Female copying is known to increase the variance in male mating success (Pruett-Jones 1992; Wade & Pruett-Jones 1990) and is characterized by groups of females at the lek, multiple visitation before mating and the existence of few males achieving the majority of the reproductive success (reviewed in (Losey et al. 1986). The existence of multiple female visitation and strong reproductive skew in our system and previous studies of other manakins (Lill 1974; Lill 1976) do not prove the existence of copying in manakin mating systems but rather are compelling indication that it remains a biologically real possibility.

Although the potential for female copying might explain a portion of the strong variance in male reproductive success, it would not explain how females make mate choices in the absence of other females. This begs the question of how male-male connectivity (degree) might be assessed by females in our system. Degree quantifies male social affiliations and, thus, is a direct measure of the number of social display partners each male has. As such, males with higher degree (more social partners) were more likely to engage in coordinated displays. Currently, we do not have direct evidence that coordinated display frequency and the numbers of offspring sired are correlated because not all males were monitored with detailed observation techniques. Previous work, however, did show a significant per male increase in the frequency of display maneuvers when social partners were present (Ryder et al. BES). Females could indirectly assess male connectivity by this measured increase in display activity. Moreover, if females were selecting males based on coordinated display frequency, it would explain the fitness advantage of male partnerships and how selective pressures via female choice may have driven these elaborate behaviors to an evolutionary equilibrium.

In addition to degree, we found that eigenvector centrality and information centrality also predicted male reproductive success. These centrality measures contrast with degree because they are negatively correlated with the number of offspring a male sired (see Table 3 beta parameters). Unlike degree, these measures credit indirect network paths and, therefore, incorporate the importance of weak social ties (need citation). More specifically, the centrality measure of each male is determined by the centrality of those males to whom he is connected. Why then might these measures be negatively correlated with reproductive success? Successful males have high connectivity yet those connections are dominated by males of lower or equal degree but rarely to those with a higher degree than themselves. It is rather the young, typically floater, individuals who create links among these highly successful males territorial males. As a result, a young male who is connected to many individuals of higher degree will have a higher centrality measure than a territorial male with the same number of links. A male's centrality during his years as a floater has previously been shown to predict his probability of social rise in both *Chiroxiphia linearis* and *Pipra filicauda* (see McDonald 2007, Ryder et al. 2008).

Lekking social systems have long been at the center of empirical and theoretical reproductive-skew research. Here, we have coupled molecular and novel analytical tools to better understand the fitness implications associated with these complex social systems. Specifically, an examination of dynamic social interactions has begun clarifying behavioral strategies that were previously thought to lack demonstrable fitness benefits (see McDonald 2007, Ryder et al. 2008). Duval (2007) recently noted that selection for complex male behaviors requires long-term male social affiliations, which in turn reinforces the evolution of complex social structure. Here, we emphasize that understanding the evolution of behavioral strategies necessitates investigating the existence of social connectivity as well as measures of individual variation associated with those metrics. Undoubtedly, future research utilizing social network theory will continue to underscore the broader importance of social relationships in a fitness context.

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Table 1. Details of the seven polymorphic microsatellite markers used in the paternity analysis of wire-tailed manakins at Tiputini Biodiversity Station.

Locus	**K**[a]	**N**[b]	**Ho**	**He**	**PIC**[c]	**Exc**[d]	**H-W**	**Fnull**[e]	**Error**
LAN10	15	508	0.797	0.801	0.779	0.454	NS	0.002	0.000
LAN20	24	505	0.828	0.849	0.837	0.562	NS	0.012	0.000
MAN13	8	495	0.521	0.550	0.471	0.156	NS	0.029	0.000
MAN3	18	494	0.858	0.890	0.879	0.634	NS	0.017	0.049
MAN6	5	479	0.526	0.506	0.460	0.132	NS	-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	NS	0.031	0.018

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a) number of independently assorting alleles
b) number of individuals typed
c) polymorphic information content
d) average exclusion probability of first parent
e) frequency of null alleles

Table 2. Distribution of reproductive benefits among group members at wire-tailed manakin leks of different size at Tiputini Biodiversity Station, Ecuador. Binomial index for actual reproductive skew (B), equal distribution (equal) and monopolized distribution (monopoly) of benefits among group members are shown. Note that index values for equitable distribution of reproductive benefits are all negative.

LEK	**N**[a]	**Nb**[b]	**B**	**Equal**[c]	**Monopoly**[d]
Tower	17	3	0.552	-0.038	0.836
Chichico	19	6	0.127	-0.052	0.901
Puma 2.5-800	16	6	0.080	-0.085	0.844
Puma 2-200	15	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

a) Number of males, both court-holders and their floater affiliates

b) Number of males which sired offspring

c) B index assuming equally apportioned reproductive benefits among group members

d) B index assuming total monopoly by a single group member

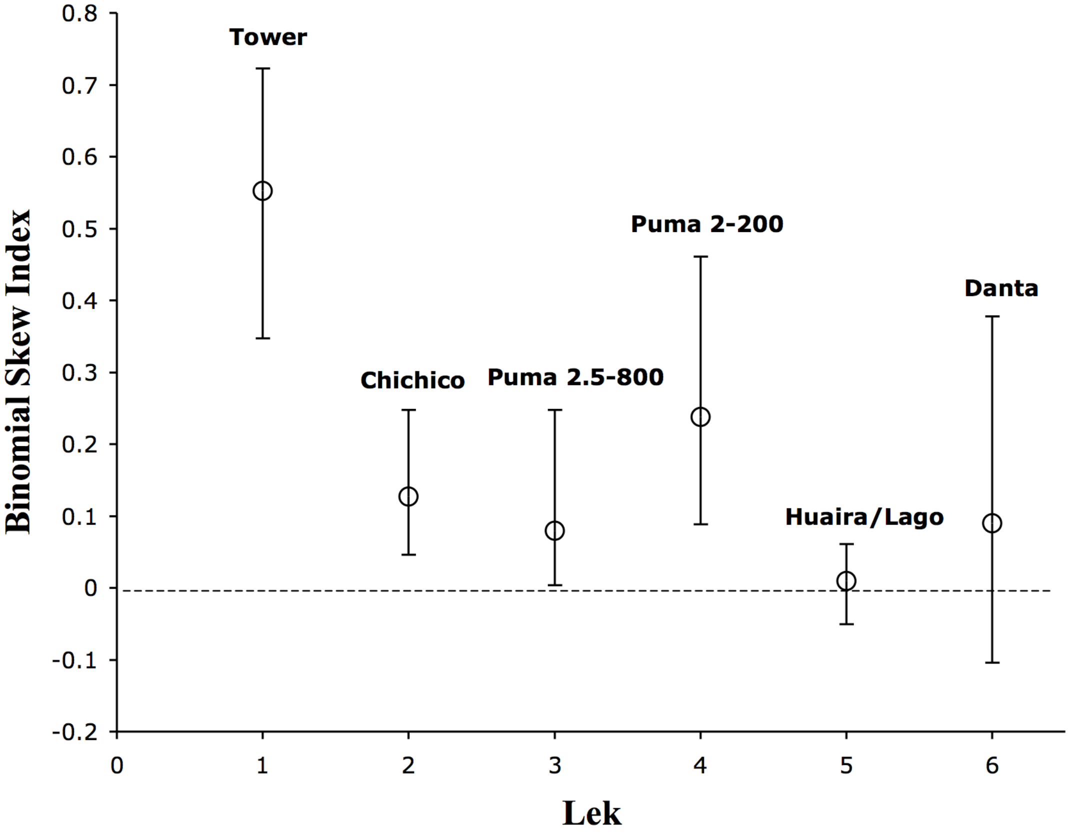
Table 3. Results of a step-wise multiple regression between social network metrics and molecular estimates of male reproductive success for male wire-tailed manakins at Tiputini Biodiversity Station, Ecuador.

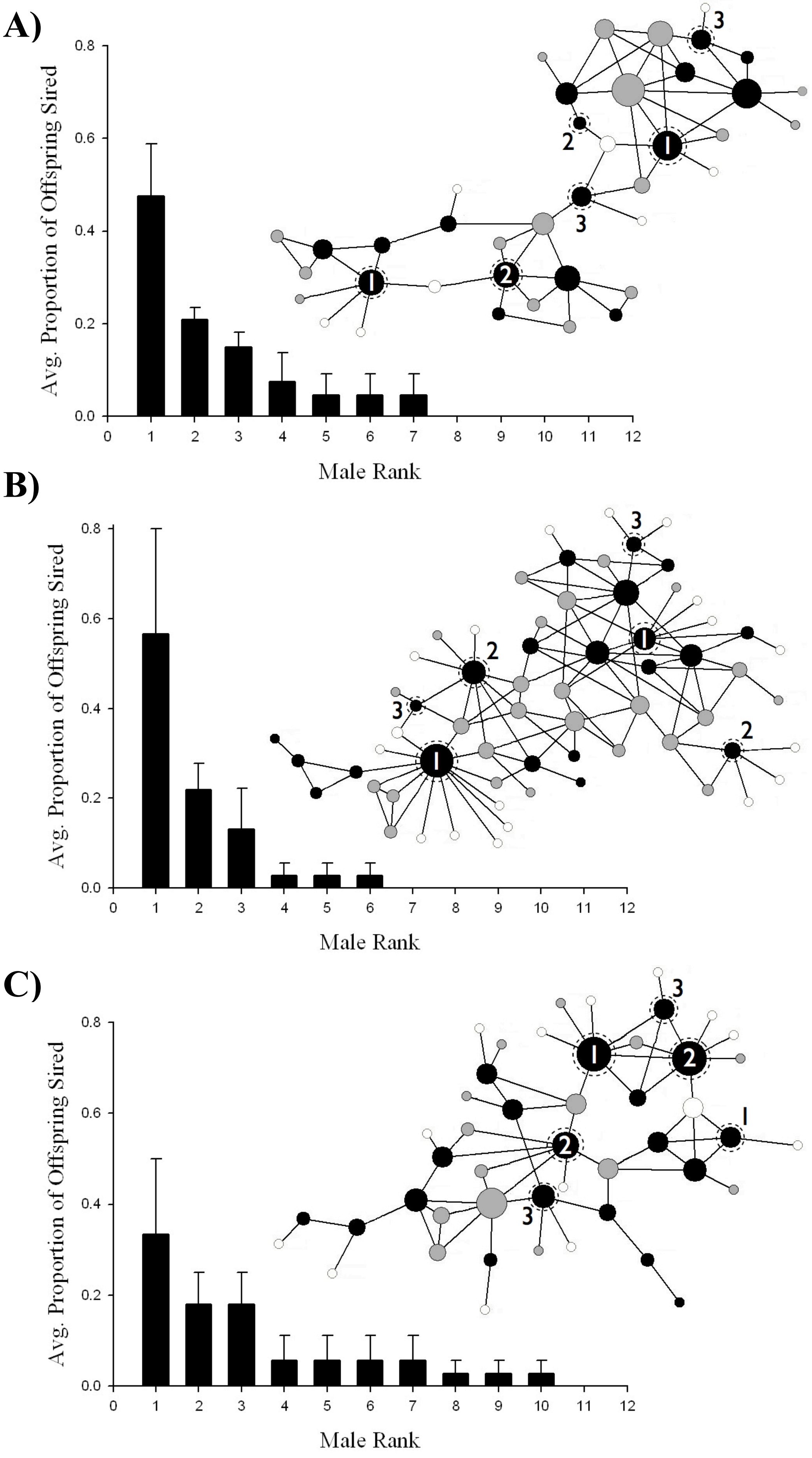
Model Parameters	**ß**	**F-Ratio**	***P***
w/ Females			
Degree	1.150	24.086	<0.001
dwReach	0.552	4.183	0.051
Eigenvector Centrality	-0.089	17.532	<0.001
Information Centrality	-25.198	7.773	0.010
Power	0.241	3.925	0.059
w/out Females			
Degree	1.182	15.534	<0.001
Eigenvector Centrality	-0.152	11.456	0.002

Figure 1 Binomial skew index with 95% confidence intervals for six wire-tailed manakin leks of varying sizes at Tiputini Biodiversity Station, Ecuador. Indices not overlapping zero are considered statistically different from random.

Figure 2 Male ranks as a function of average proportion of offspring sired for spatially contiguous leks within a social network of male wire-tailed manakins. Inset within each graph is the corresponding social network. The top three ranked males in each lek are designated with numerical labeling 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 gray 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 gray nodes that create the connections among territory holders and between leks. A) Puma network, B) Tower-Chichico network, and C) Huaira-Lago network.

Figure 3 The relationship between degree and proportion of offspring sired in a social network of male wire-tailed manakins. A) Puma network, B) Tower-Chichico network, and C) Huaira-Lago network.


0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
-0.1
-0.2
Binomial Skew Index
0
1
2
3
4
5
6
Lek
Tower
Chichico
Puma 2.5-800
Puma 2-200
Huaira/Lago
Danta


A)
Avg. Proportion of Offspring Sired
0.0
0.2
0.4
0.6
0.8
Male Rank
0
1
2
3
4
5
6
7
8
9
10
11
12
1
2
3
1
2
3
B)
Avg. Proportion of Offspring Sired
0.0
0.2
0.4
0.6
0.8
Male Rank
0
1
2
3
4
5
6
7
8
9
10
11
12
1
2
3
1
2
3
C)
Avg. Proportion of Offspring Sired
0.0
0.2
0.4
0.6
0.8
Male Rank
0
1
2
3
4
5
6
7
8
9
10
11
12
1
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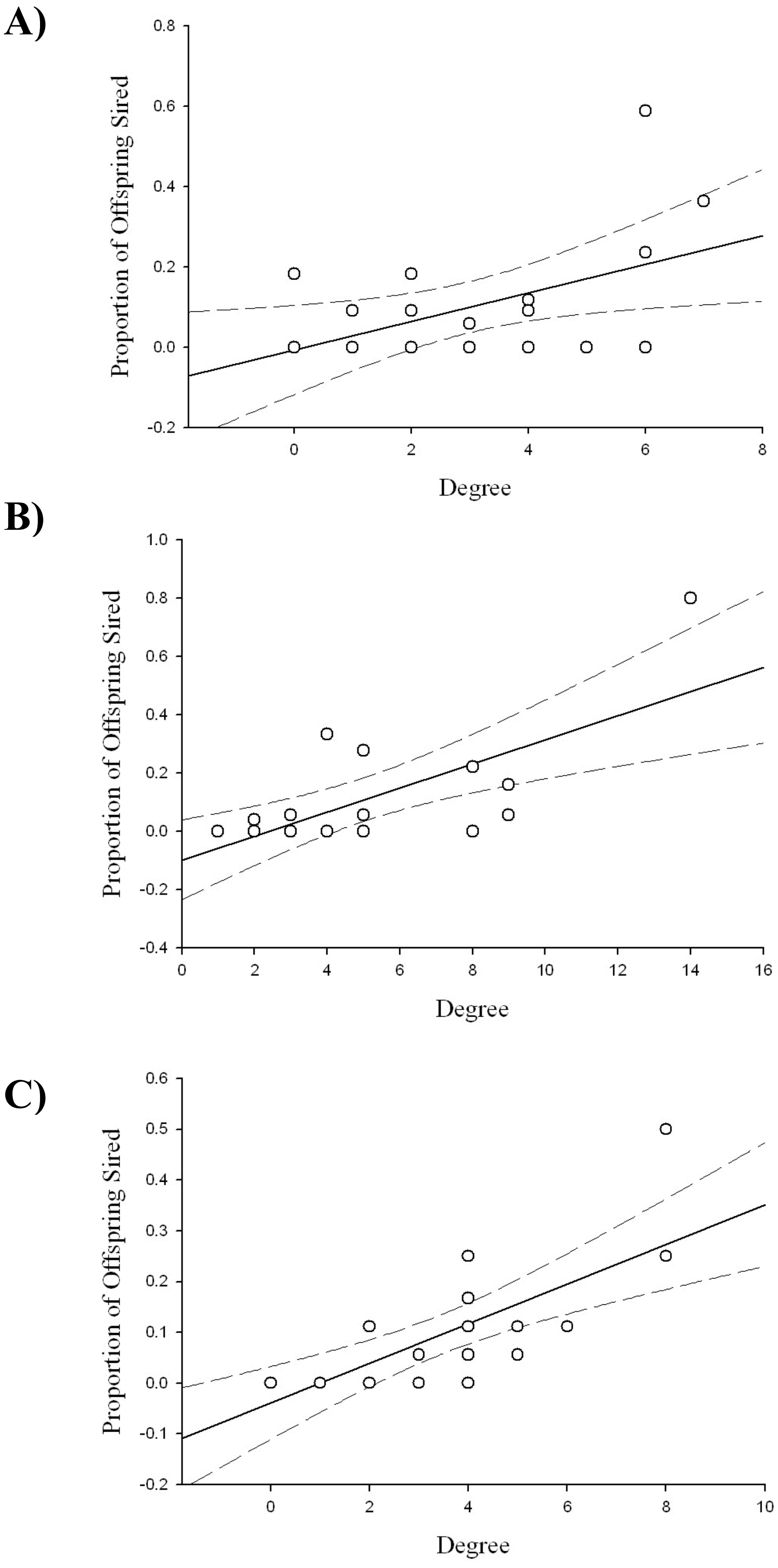
1
2
3


A)
Proportion of Offspring Sired
0.8
0.6
0.4
0.2
0.0
-0.2
0
2
4
6
8
Degree
B)
Proportion of Offspring Sired
1.0
0.8
0.6
0.4
0.2
0.0
-0.2
-0.4
0
2
4
6
8
10
12
14
16
Degree
C)
Proportion of Offspring Sired
0.6
0.5
0.4
0.3
0.2
0.1
0.0
-0.1
-0.2
0
2
4
6
8
10
Degree