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The Composition, Stability, and Kinship of Reproductive Coalitions in a Lekking Bird

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Post Print

ABSTRACT: Male vertebrates often form reproductive coalitions to gain access to or defend females. One striking example occurs in the wire-tailed manakin (*Pipra filicauda*; Aves: Pipridae), where pairs of males form coalitions to display for females on leks. Here, we use data from a long-term study of the wire-tailed manakin to quantify the composition and stability of display coalitions, to examine how coalitions influence behavioral variation, and to determine if males gain indirect genetic benefits from coalition membership. Our data show that coalitions were most often formed between males of different status and that the presence of coalition partners increased a male's display rate via social facilitation. Display coalitions were nonrandom and varied in stability with male age. Moreover, our data suggest that both floaters and territorial males maintain multiple coalition partnerships through time. Maintenance of fixed partnerships for territorial males is hypothesized to have reproductive fitness benefits by increasing display synchronization and signal intensity. Finally, our data show that although males do not appear to gain indirect inclusive fitness benefits by joining display coalitions with relatives, the kin structuring observed within male social networks is likely a consequence of strong reproductive skew, short dispersal distances, and limited recruitment opportunities.

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Coalitions are formed when individuals, each in their own self-interest, join in cooperative alliances for a common cause. In vertebrate taxa, coalitions among males are formed to gain reproductive access to or defend females but may vary in duration and frequency within a population (Whitehead and Connor 2005). Individual variation in the formation of coalitions has been hypothesized to reflect either fixed strategies in which males form single partnerships (Feh 1999) or dynamic strategies in which males develop multiple social bonds and adjust coalition membership to maximize reproductive success (Noë 1994; Whitehead and Connor 2005). Regardless of how reproductive coalitions are formed, they can serve a variety of functions, including increasing male reproductive success, providing access to otherwise unavailable reproductive opportunities, helping to establish dominance hierarchies, and facilitating the learning of complex social behaviors (Noë 1994).

One well-known example of male–male reproductive coalitions occurs in manakins (family Pipridae) in which 2 or more males join together on leks to display for females (Schwartz and Snow 1978; Foster 1981, 1987; Robbins 1985; Heindl 2002). Display coalitions in manakins appear to have evolved independently at least twice—in *Chiroxiphia* and in the *Pipra aureola* clade (Prum 1994)—and have long been of interest from an evolutionary standpoint because of the paradox arising from apparent cooperative behaviors in a situation characterized by intense sexual competition (DuVal 2007a). Manakin reproductive coalitions are hypothesized to serve either a competitive function to establish dominance in which males express intrasexual aggression as ritualized display behaviors (Snow 1962; Tello 2001) or a reproductive function in which display coalitions may increase male attractiveness and subsequent mating success (Snow 1971a, 1971b; Foster 1981; McDonald 1989).

The wire-tailed manakin, *P. filicauda*, is 1 of 3 species in the *P. aureola* clade that exhibits display coalitions, which form the basis for a complex network of social interactions (Ryder et al. 2008). Specifically, male wire-tailed manakins are spatially aggregated in exploded leks where territory holders may display alone, in a coalition with a nonterritorial partner, or in a coalition with a neighboring territory holder (Schwartz and Snow 1978; Heindl 2002). Coordinated displays among coalition partners contain all the complex elements of solitary displays (e.g., side-to-side, stationary display, twist, and swoop-in-flight; see Schwartz and Snow 1979; Heindl 2002), but partners alternate roles in a highly synchronized display routine. These display coalitions likely play an essential role in establishing dominance hierarchies and teaching the display routines to young males (Ryder 2008; see also McDonald 1989; DuVal 2007b).

Moreover, display relationships are essential as young male manakins transition in social status with age (age-graded queue). Recent work has established that male–male display coalitions have a number of fitness consequences for male manakins. Ryder et al. (2008) found that young males that established and maintained display coalition partnerships were more likely to obtain territories. Likewise, Ryder et al. (2009) showed that wire-tailed manakin leks are characterized by strong reproductive skew and that both territorial tenure and the number of coalition partners predict a male's relative reproductive success.

Of additional interest, for reproductive coalitions, is how patterns of genetic relatedness influence the cost and benefits of coalition partnership (e.g., kin selection). Previous work on wire-tailed manakins showed that mean relatedness did not differ from random expectations at the level of the lek (Loiselle, Ryder, et al. 2007). Despite the lack of support for kin selection at the level of the lek, indirect genetic benefits gained from joining in display coalitions with relatives could still explain social partnering in the *P. aureola* clade. Alternatively, strong reproductive skew and short dispersal distances could drive kin structuring within leks and larger social networks. Given that few males sire the majority of offspring in many manakin species (DuVal 2007a; Ryder et al. 2009) and young males have a limited number of leks into which they can recruit, some degree of genetic structure might be expected. The agedifferential hypothesis proposed by McDonald (2009) addresses how demographic factors could influence patterns of relatedness within leks. This hypothesis specifically predicts that strong skew, limited dispersal, and age-graded social queues will generate higher relatedness between recruiting and territorial males than between territory holders themselves (McDonald 2009).

Here, we expand on our previous work that detailed the complex social structure of wire-tailed manakins and the fitness benefits of reproductive coalitions (Ryder et al. 2008, 2009). Specifically, we further investigate wire-tailed manakin reproductive coalitions by quantifying 1) how the composition of coalition partnerships (e.g., age and status) varies among social networks, 2) how display coalitions influence behavioral variation in display rate, and 3) if coalitions are stable or dynamic in nature. Additionally, we further explore the direct and indirect fitness benefits of coalitions by examining patterns of genetic relatedness among display partners and by quantifying patterns of territorial inheritance.

MATERIALS AND METHODS

Field sampling

We conducted our field study from 2003 to 2008 at Tiputini Biodiversity Station (TBS), a 650-ha biological station located at ;200 m above sea level adjacent to Yasun'í National Park yet embedded within the ;1.7 million-ha Yasun'í Biosphere Reserve in Orellana Province, Ecuador (lat 038#S, long 7608#W). The site is not only dominated by upland “terra firme” forest but also includes some “va´rzea” habitat (Ryder et al. 2006). During 2001, 2 100-ha plots (~1 x 1 km each) were established at TBS by J.G.B. and B.A.L. (for description of Harpia and Puma plots; see Loiselle et al. 2007a Loiselle, Blake, et al. 2007; Loiselle, Ryder, et al. 2007).

We located leks of wire-tailed manakins by systematically searching for and mapping locations of 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. Leks average 1 ha in size (Heindl 2002) and are separated by a distance of 300 m or more (Loiselle, Blake, et al. 2007). The number of territorial males per lek at TBS

ranges from 4 to 12, where each male defends a roughly 40 m diameter area; territory borders are typically 10–15 m apart (Ryder 2008). Leks were found in seasonally flooded forests as well as in adjacent terra firme. Leks were typically in low-elevation flat areas near streams (Loiselle, Ryder, et al. 2007). The understory 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 × 2.8 m, 36mm mesh) to capture manakins over the course of the study. Captured manakins were weighed, sexed, aged, and banded with aluminum and individual colorband combinations. Overall, 419 individuals consisting of 133 females, 250 males, and 36 of unknown sex were individually color marked. Blood samples were taken (50 μ l 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 5 leks using song frequency across the day as an indicator of number of males present and active. Male wiretailed manakins sang throughout the day; however, their song frequency varied greatly, and peak activity was bimodally distributed with peak morning activity from 0630 to 0800 and afternoon activity from 1300 to 1500 (Ryder 2008). We then sampled 25 different territorial male manakins from 7 different leks with 2-h continuous focal sampling (Martin and Bateson 1986) from 2003 to 2006 (414 h; mean = 16.2 ± 0.89 h/male, range: 8–20 h/male). Data on male social affiliations were supplemented with scan sampling of each male territory that yielded 1028 resights of 199 different color-banded males.

During observations, we recorded the frequency of all display behaviors, songs, and interactions with other individuals. Cases of male–male social interactions were only included in analyses if the color bands of both individuals were positively identified. Male status was classified by plumage and territoriality over the 5 years of observation. Status classifications follow Ryder et al. (2008) and include “formative plumage floaters,” “predefinitive plumage floaters,” “definitive floaters,” and “definitive territorial.” Here, we additionally split territory holders into “definitive territorial subordinates” who frequently leave their own territory to visit neighboring male territories and “definitive territorial dominants” who always remain in their own territory and did not visit other males’ territories.

Molecular techniques

We isolated DNA from blood samples via standard phenol–chloroform extraction (Sambrook et al. 1989) and checked concentration using spectrophotometry and gel electrophoresis. We screened 25 microsatellite loci developed for other species of manakins and chose a subset of 7 markers with sufficient polymorphism (McDonald and Potts 1994; Piortney et al. 2002; DuVal and Nutt 2005; Brumfield R, Braun M, personal communication). Subsequent molecular analyses (polymerase chain reaction, sequencing, and fragment sizing) followed techniques detailed in Ryder et al. (2009, 2010). Most individuals, and all homozygotes, were run at least twice to ensure typing accuracy and repeatability.

Statistical analyses

We examined display variation in 8 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 4 of the most common display elements as predicted by age/social class and display type (social context— solitary vs. coordinated). All variables were tested for normality and homoscedasticity prior to data analysis. We used program DSTLM (Anderson 2004) to analyze our behavioral data because many variables were nonnormally distributed. DSTLM calculates either multivariate analysis of variance (ANOVA) or multivariate regression of any symmetric distance matrix using permutations of the observed data (for theoretical background, see Anderson 2001a, 2001b). This nonparametric statistical tool accommodates more complex statistical designs, including covariates, unbalanced ANOVA designs, and tests of individual terms in a multifactorial 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 2 design matrices were therefore fit sequentially (i.e., Type I sum of squares) as is appropriate for a nested design (Anderson MJ, personal communication). 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 reorderings 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 DSTLM using Euclidean distance as our distance metric.

Following Cairns and Schwager (1987), we calculated the halfweight index (HWI, ranging between 0 and 1) to determine the strength of dyadic associations among male display partners for 25 territorial males (see behavioral sampling above). HWI is an association metric that estimates the proportion of time 2 individuals spent together in social groups. Association indices alone, however, are of little value in describing social structure unless interactions can be differentiated from random (Bejder et al. 1998; Whitehead et al. 2005). To determine if observed HWI indices differed from random, we compared coefficients of variation (hereafter CVs) of observed and random association matrices (Bejder et al. 1998). Specifically, the CV describes variation in the proportion of time dyads (display partners) are seen associating during coordinated display bouts. We tested for preferred/ avoided coalition partnerships among males within each lek using the randomization procedure in SOCPROG v. 2.0 (Bejder et al. 1998; Whitehead 2009). We generated random association matrices by permuting groups (pairs of males in coalitions) within samples (defined as month) to

test for long-term associations among coalition partners (see Whitehead 2009). Given that each permutation creates new association matrices that are not independent, we used an iterative process in which the number of permutations was increased until our P value stabilized (20 000 permutations with 1000 trials per permutation) (Bejder et al. 1998). Given that preferential associations across sampling periods increase the standard deviation (SD) and CV of association indices, we rejected the null hypothesis when the CV and SD of the “true” association indices were significantly higher than the CV of the “random” association indices (Bejder et al. 1998, Whitehead et al. 2005, Whitehead 2009). To determine which coalitions contributed to the high degree of social differentiation (CV) and had significantly stronger associations than expected at random, we ran a 2tailed test in which P values indicate the reliability of our HWI indices (Bejder et al. 1998; Whitehead et al. 2005). Lastly, to ensure that our data had the power to reject the null hypothesis of random interactions, we used the degree of social differentiation (S, a.k.a. CV from above) and the average number of associations per individual (H) to determine if $S^2 \geq 3 H .5$ for each of our social networks (Whitehead 2008).

Descriptive information for each locus (i.e., allele frequencies, richness, linkage, and Hardy–Weinberg [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 H–W equilibrium and showed no significant linkage (Loiselle, Ryder, et al. 2007). We estimated pair-wise, within-lek, and populationbaseline relatedness using RELATEDNESS v. 5.0 (Queller and Goodnight 1989; Goodnight and Queller 1999). 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. Standard error (SE) estimates and 95% confidence intervals were obtained by jackknifing over loci.

The formation of male–male display coalitions and the reticulate interaction history of males is the basis of a complex social structure. Previous work has detailed both the emergent (population)-level and node (individual)-level properties of 3 male social networks (Ryder et al. 2008, 2009). Each social network was composed of 2 contiguous leks; hereafter, the social networks are referred to as Tower, Huaira, and Puma. To quantify the composition of display coalitions, we examined all links between territory holders and their coalition partners for each social network. To determine if the frequency of coalitions differed between networks, we used contingency table chi-square tests. To examine if males formed coalitions with relatives (kin selection) and the extent to which social structure was related to genetic structure, we conducted 4 analyses. First, we examined the potential for kin selection by comparing the distributions of relatedness for coalition partners to the distribution of nonpartners in the same network using Komolgorov–Smirnov tests. Relatedness distributions represent all possible dyads of coalition partners and nonpartners with the social network. If males were selecting relatives as coalition partners, we expected the coalition distribution to have a positive mean ($r > 0.1$),

whereas the distribution of nonpartners within the same network should be centered on zero.

Second, we calculated a male's average relatedness to his coalition partners (all those he was directly connected to in the network) and asked if relatedness predicts a male's social connectivity (degree) (i.e., more related males have more social partners). Degree is a direct measure of male social connectivity (i.e., number of coalition partners) and was calculated using program UCINET v. 6.0 (Borgatti et al. 2002). In addition, we graphically examined relatedness patterns by overlaying dyadic relatedness onto network links formed among male display partners using program NETDRAW v. 2.504 (Borgatti 2002). Third, we asked if a male's relatedness to all individuals within his social network would predict his relatedness to his coalition partners. That is, could coalitions of relatives be a byproduct of kin structure resulting from other processes (limited dispersal and strong reproductive variance). Because a male's mean relatedness to his coalition partners and his mean relatedness to all males within the social network were not independent, we used the Spatial Analysis in Macroecology program v. 3.03 (Rangel et al. 2006) to conduct a Mantel test with 1000 permutations. To follow up on this analysis, we asked if patterns of kin structuring among coalition partners were related to an age differential (age-differential hypothesis; McDonald 2009). We sorted dyadic relatedness values of partners into 2 categories, territorial-floater versus territorial-territorial coalitions, and compared the mean relatedness of the coalition types using a t-test. Because coalitions can be maintained after transitions in male status (i.e., floaters becoming territory holders), several values had to be placed in both categories to ensure unbiased means. All parametric statistics were conducted with program JMP v. 8.0. Means and SE are reported unless otherwise noted.

RESULTS

Display rate variation

During the observations, we observed 145 displays bouts of sufficient duration to quantify behavior of which 31% (45/145) were coordinated and 69% (100/145) were solitary. The frequency with which individual males engaged in coordinated display \pm ranged from 0% to 100% ($31.3 \pm 5.50\%$, $n = 25$; mean \pm SE). Territorial males varied greatly in the number of visiting display partners as derived from our cumulative network analyses (focal observations and resights) (4.0 ± 0.37 , range = 1–10, $n = 41$). Likewise, nonterritorial males (predefinitive and definitive floaters combined) varied in the number of territories \pm they visited (3.25 ± 0.28 , range = 1–7, $n = 44$). Quantifying the composition of display coalitions showed that display partnerships were by far the most frequent between territorial males and definitive plumage floaters (Table 1). The frequency of coalition types did not vary among social networks ($\chi^2 = 7.35$, degrees of freedom (df) = 6, $P = 0.29$).

We found that display 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- $F_{17,159} = 2.12$, $P = 0.001$). Territorial male behavior within leks varied significantly in twist (pseudo- $F_{17,165} = 2.68$, $P = 0.001$), swoop-in-flight (pseudo- $F_{17,165} = 2.60$, $P = 0.001$), hover flight (pseudo- $F_{17,165} = 2.45$, $P = 0.002$), and stationary display maneuvers (pseudo- $F_{17,165} = 1.65$, $P = 0.043$) but not in frequency of side-to-side (pseudo- $F_{17,165} = 1.34$, $P = 0.161$), flutter (pseudo- $F_{17,165} = 1.25$, $P = 0.237$), or butterfly flight displays (pseudo- $F_{17,165} = 1.19$, $P = 0.256$).

All age classes of visitors, except for formative plumage floaters, engaged in active coordinated display routines and some singing while on the territory of another male (Table 2). Individual display rates of visiting males in all age and status categories were on average lower than those of territorial dominant males during coordinated display bouts (Table 2). Overall, display rate among male visitors was predicted by social status in which the 4 most common display maneuvers differed significantly between predefinitive, definitive floaters, and definitive territorial subordinates (pseudo- $F_{2,49} = 2.76$, $P = 0.020$).

We further tested for differences in the display rate of territorial males when they were displaying alone or with a coalition partner for the 4 most common display maneuvers. We found that coordinated displays had significantly higher maneuver frequencies than did solitary displays (pseudo- $F_{1,144} = 9.36$, $P = 0.001$; Figure 1). During coordinated displays, males performed side-to-side (pseudo- $F_{1,144} = 40.11$, $P = 0.001$), stationary (pseudo- $F_{1,144} = 15.69$, $P = 0.001$), twist (pseudo- $F_{1,144} = 12.92$, $P = 0.002$), and swoopin-flight displays (pseudo- $F_{1,144} = 29.28$, $P = 0.001$) at higher rates than did those same individuals when engaged in solitary display bouts (Figure 1).

Display coalitions

Display coalitions of males represented nonrandom partnerships as evidenced by significantly higher CV (Tower $CV_{true} = 3.85$, $CV_{random} = 2.58$, $P < 0.001$; Huaira $CV_{true} = 3.62$, $CV_{random} = 2.27$, $P < 0.001$; and Puma $CV_{true} = 3.78$, $CV_{random} = 2.60$, $P < 0.001$) and SD in all 3 of our social networks (Tower $SD_{true} = 0.15$, $SD_{random} = 0.11$, $P < 0.001$; Huaira $SD_{true} = 0.16$, $SD_{random} = 0.12$, $P < 0.001$; and Puma $SD_{true} = 0.18$, $SD_{random} = 0.12$, $P < 0.001$). Additionally, association data from all 3 of our networks showed a strong degree of social differentiation and sufficient power to reject the null hypothesis (S^2 3 H; Tower = 3.85^2 3 $3.58 = 53.02$; Huaira = 3.62^2 3 $3.61 = 47.32$; and Puma = 3.78^2 3 $3.46 = 49.46$). The number of coalitions (dyads) that had stronger associations than expected at random varied by network (Table 3). Moreover, a number of those territorial males that had strong coalitions (significant dyads) maintained more than one fixed coalition partnership (35%, 9/26). Finally, coalition partnerships appear to strengthen with the age and status because significant coalitions were only formed between definitive plumage floaters and territorial males (73%, 22/30) and between territory holders within the same lek (27%, 8/30).

Table 1

Coalition partnerships formed among males of different social status occurred in similar frequencies within 3 wiretailed manakin social networks at TBS, Ecuador

Coalition type Total	Tower (n = 78)	Puma (n = 47)	Huaira (n = 42)
DT–DT	11 (14.1)	11 (23.4)	13 (31.0)
DT–DF	38 (48.7)	25 (53.2)	16 (38.1)
DT–PDF	20 (25.6)	9 (19.1)	9 (21.4)
DT–FF	9 (11.5)	2 (4.3)	4 (9.5)

Partners of territorial males included other definitive territorial males (DT–DT), definitive plumage floaters (DT–DF), predefinitive plumage floaters (DT–PDF), and formative plumage floaters (DT–FF). The number of display coalitions per network (n), frequencies, and (percentages) are presented for 3 social networks.

Network relatedness

Our comparison of dyadic relatedness distributions for coalitions versus potential partners within a male's social network suggests that males are not displaying with their relatives on average (Kolmogorov–Smirnov $Z = 21.76$, $P = 0.08$; Figure 2a). Moreover, the marginal significance of the test was in the opposite direction than predicted by the kin selection hypothesis, with coalition partners being less related than social network members on average. Although males were not, on average, displaying with relatives, the mean relatedness of males and their coalition partners varied greatly in the context of the social network (range = 0.29–0.51; Figure 2b). Although some males were highly related to their coalition partners, these males were not more well connected as measured by degree (number of coalition partners) ($F_{1,101} = 0.86$, $r^2 = 0.01$, $P = 0.36$). In contrast, males that had higher average relatedness to their coalition partners also had more relatives within the network as a whole (Mantel test, Pearson's $r = 0.232$, $P = 0.001$; Figure 3a). Lastly, territorial–floater coalitions (0.03 ± 0.02) had significantly higher relatedness than did territorial–territorial coalitions (0.12 ± 0.03 ; $t = 24.50$, $df = 140$, $P < 0.0001$; Figure 3b).

Territorial turnovers

Between 2003 and 2008, we observed 35 territorial turnover events. The majority of transitions, 60% (21/35), were characterized by floaters, who had been part of a

previously established display coalition, inheriting the territory. Less common, 23% (8/35), were instances of territorial inheritance by floaters who were part of display coalitions with neighboring territory holders within the same lek as the vacancy. Least common, 17% (6/35), were instances when the new territorial holder was not part of any previously observed display coalitions within the lek.

DISCUSSION

The coordinated displays and the resulting reproductive coalitions formed among male wire-tailed manakins represent a rare example of apparent male–male cooperation within a lek social system. In general, these male–male display coalitions form the foundation for a complex social structure in which males of different social status have varied social contacts. Differences in display rates of males during coordinated display bouts were largely explained by status in the agegraded queue, with territorial males having higher rates of display. Additionally, our results show that social facilitation via coalition partnerships increased display rates for 4 common maneuvers. Our randomization tests show clearly that males form long-term preferred associations and that display coalition formation strategies may differ with male age/social status. Although male partnerships are nonrandom, our relatedness analysis showed that males are not displaying with relatives, despite the occurrence of relatives within their social networks. Moreover, a male's mean relatedness to his social partners appears to follow from his overall relatedness to males within his social network. Our patterns of relatedness among coalition types suggest that demographic factors (e.g., reproductive skew and limited dispersal) rather than kin selection per se may underlie our observed variability in a male's relatedness to his social partners (see also McDonald 2009). Lastly, our data on male territorial turnover further corroborate previous work showing that social affiliations are important for territory acquisition (see also Ryder et al. 2008).

Behavioral variation

Table 2
Mean display rate (maneuvers/2 h) by age and social status for male wire-tailed manakins during coordinated display bouts at TBS, Ecuador

Display element	Predefinitive floater (n = 16)	Definitive floater (n = 17)	Definitive territorial subordinate (n = 19)	Definitive territorial dominant (n = 25)
Song	8.81 ± 2.72	12.88 ± 4.36	13.00 ± 3.40	86.63 ± 2.22
Side-to-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

Our data show that display rates did not differ among leks but that males within those leks differed substantially. This finding suggests that leks are indeed composed of individuals that vary in quality and display vigor as has been shown recently for blue-crowned manakins (*Lepidothrix coronata*) (Durães et al.

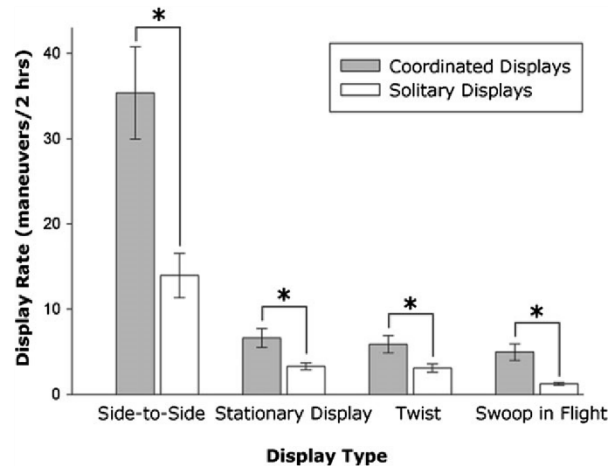


Figure 1

Paired comparisons of males displaying alone and with coalition partners showed significantly higher frequencies of 4 common display maneuvers during coordinated display bouts. Bars represent average frequency \pm SE, and asterisks denote significance of $P < 0.01$.

2009). One possible explanation for variability in male display rate is the notion of age-dependent sexual advertisement, which is a characteristic of many lekking social systems (Kokko 1997). Although, our current data do not enable us to decouple the effects of age and status, the existence of age-graded queues suggests that the 2 are closely linked. Specifically, most manakin social systems are characterized by age-graded social queues in which predefinitive plumages are accurate indicators of both male age and status (Schwartz and Snow 1978; Robbins 1985; McDonald 1989; Doucet et al. 2007). If age and status are indeed closely linked, then our data support the supposition that sexual advertisement is age dependent, with older males of higher status displaying at higher rates than either younger territorial males or individuals in predefinitive plumage and status classes.

Behavioral variation in display rates can be caused by social facilitation when males are stimulated by the presence of other males during display bouts (Brooke et al. 2000). Social stimulation has been previously reported for male blue-crowned manakins, where individual call rate increased with lek size (Durães et al. 2009). Here, we have shown that males display at significantly higher rates when a social partner is present during coordinated display bouts. Thus, male display coalitions seem to increase signal intensity, making them a potential target of female choice. Previous work has documented the importance of male partnerships in a fitness context in which males of higher connectivity (more display partners) had higher relative reproductive success (Ryder et al. 2008, 2009). Ultimately, the greater signal intensity

of coordinated displays may be the mechanism that links connectivity to male reproductive success and explains the fitness advantage of display coalitions for male wire-tailed manakins.

Table 3
HWI indices indicate the strength of display coalition partnerships among male wire-tailed manakins from 6 leks at TBS, Ecuador

Network	N ^a	Total ^b	Mean _{HWI} ± SD ^c	Range HWI ^d	P value ^e
Tower	14	23	0.53 ± 0.19	0.44–1.00	<0.03
Huaira	6	14	0.55 ± 0.22	0.57–1.00	<0.02
Puma	10	14	0.70 ± 0.14	0.57–0.89	<0.02

Note that each social network consisted of 2 spatially contiguous leks.

^a The number of dyadic associations that were stronger than expected at random.

^b The total number of coalitions observed for 25 focal males.

^c Mean HWI indices ± SD.

^d The range of HWI indices among coalition partners.

^e All P values for significant dyads where less than or equal to the P value presented.

Display coalitions

The social organization of wire-tailed manakins in this study is similar to that of band-tailed manakins (*P. fasciicauda*) (Robbins 1983, 1985) and has many similarities to that described by Heindl (2002) for wiretailed manakins in Venezuela. Display coalitions were composed of males of different status with the most common partnerships being formed between territorial and definitive plumage floaters. Unlike other species in the *P. aureola* clade, however, territorial wire-tailed manakins maintain multiple beta partners of different social status. Moreover, whereas Robbins (1985) found that *P. fasciicauda* males regularly excluded contiguous territory owners, male wire-tailed manakins often partner with other territory holders.

Our data on territorial turnover presented here, and previously published data on the impact of social connectivity on territory acquisition, clearly show that display coalitions are important in determining which young males inherit territories (Ryder et al. 2008). More specifically, floater males that maintained more display coalition partners (higher degree) were more likely to transition to territorial status (social rise: 4.47 ± 0.6 , no social rise: 3.03 ± 0.2 ; Ryder et al. 2008). If floater males employed a dynamic switching strategy, they would be expected to adjust partnerships in such a way as to maximize the probability of inheriting a territory. Although this is conceptually appealing, our current data are limited to documenting the maintenance of multiple coalition partnerships. As such, future work should aim to document if and how floaters partition their time among social partners to influence their social trajectory.

Given that male wire-tailed manakins follow agegraded queues, it is likely that age and social experience play an important role in the formation of coalitions and their subsequent stability. Previous work on lance-tailed manakins (*Chiroxiphia lanceolata*) suggests that changes in social experience may explain variability in coalition formation strategies (DuVal 2007b). Our association index data and randomizations show that the display coalitions of territorial males are temporally stable (i.e., long-term preferred associations), with many associations being stronger than what would be expected at random. These patterns suggest that as a male moves up in the aged-graded queue, these social relationships may increase in stability and eventually reflect the “fixed” partnerships of territorial individuals. Likewise, although lance-tailed manakin alpha–beta alliances showed variability, alpha males tended to converge toward a single beta alliance over time (DuVal 2007b). Wire-tailed manakins often maintained partnerships with more than one beta male and whereas this strategy differs subtly from previously described fixed coalition strategies (Whitehead and Connor 2005), the maintenance of multiple social bonds may have fitness benefits. For example, the maintenance of preexisting display coalitions has been shown to influence the synchronization of behaviors (Trainer and McDonald 1995; Trainer et al. 2002). The benefits of behavioral coordination, increased signal intensity, and overall partner number (male connectivity) may select for coalition maintenance through time in some species of manakins.

Network relatedness

Kin selection has been proposed as one plausible mechanism by which nonreproducing males could gain indirect fitness benefits by joining leks and/or display coalitions with their relatives (Kokko and Lindström 1996). Support for kin selection in manakins has been mixed, with 5 species showing no support for aggregations of relatives (McDonald and Potts 1994; Francisco et al. 2007; Loiselle, Ryder, et al. 2007; McDonald 2009) and 1 species showing kin structure among territorial males (Shorey et al. 2000). Although leks may represent a mix of related and unrelated individuals, resulting in low average relatedness among lek members, what should matter for species that form display coalitions is the relatedness of display partners. Our data for male wire-tailed manakins suggest that males are not more likely to join in display coalitions with relatives than with unrelated males within their social network. Although males were not, on average, displaying with relatives, we observed significant variability in the mean relatedness of males and their coalition partners. Moreover, males that showed a tendency to display with kin were more likely to be related to all males within their social network.

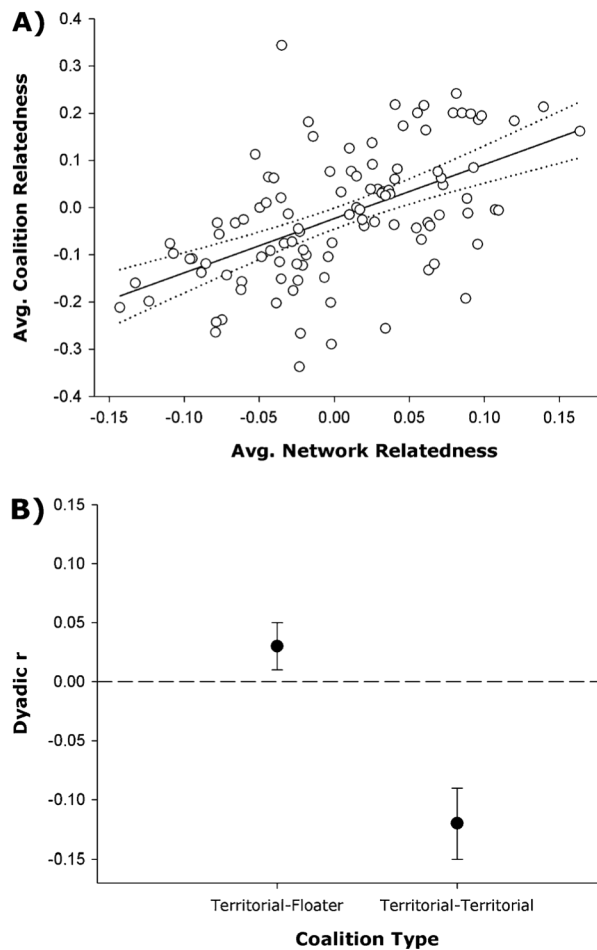


Figure 3

Patterns of relatedness at 2 levels of wire-tailed manakin social organization show that (A) at the level of the social network, a males average relatedness to all males in his network predicted his relatedness to his coalition partners and (B) at the level of the coalition, the relatedness of partnerships formed between males of different age and status was significantly higher than those of similar age and status.

This intriguing pattern could be explained by the underlying genetic architecture created by both demographic and reproductive consequences (e.g., age-differential relatedness; McDonald 2009). Strong variance in reproductive success as has been shown in our study system (Ryder et al. 2009) coupled with short dispersal and eventually recruitment distances (Ryder et al. 2010) can have a strong impact on genetic population structure (Francisco et al. 2007). Thus, if few males sire the majority of offspring and those male offspring are limited in lek-recruitment opportunities, then recruiting males may by chance end up in display coalitions with relatives. Alternatively, the likelihood of close kin display coalitions among territorial males is likely diminished by both the long queue for territorial status and the dominance hierarchy among territory holders. This combination of factors predicts that coalitions formed between territorial and floater individuals (i.e., those with a larger age differential) would have higher relatedness than territorial–territorial males (McDonald

2009). Our data indeed show this pattern with territorial–floater coalitions having significantly higher relatedness than territorial–territorial coalitions. Moreover, although our analysis fails to control for absolute age, the nature of male age-graded queues for status and our observed patterns of male social ascension support the assumption that age differentials between territory–floater are greater than those between 2 territorial males.

Our broader patterns of mean relatedness among coalition partners and males within the network further suggest that strong skew and limited dispersal make successful males more prone to interact with kin, even in the absence of kin selection. Although our data suggest that the formation of display coalitions between sons and successful sires may drive agedifferential kin structure, the mean relatedness of territorial–floater coalitions was still only slightly above zero. Likewise, the limited number of territorial–territorial display coalitions among relatives does not appear frequent enough to provide substantial inclusive fitness benefits to the partners. Ultimately, demography, rather than kin selection, is likely the best explanation for the observed patterns.

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