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## PATTERNS OF INDIVIDUAL RELATEDNESS AT BLUE MANAKIN (*CHIROXIPHIA CAUDATA*) LEKS

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**ABSTRACT.**—Patterns of relatedness among males attending leks can provide insights into how this reproductive behavior has evolved. Past research on birds has found that lekking males show either elevated levels of relatedness, supporting a mechanism based on kin selection, or a lack of relatedness, supporting a direct-benefits mechanism. We show that males attending Blue Manakin (*Chiroxiphia caudata*) leks exhibit a third pattern, with leks consisting of mixtures of related and unrelated individuals. Kinship analyses of males sampled from 13 leks in three local populations showed that close male relatives ( $r = 0.5$ ) were present, but only at half the leks sampled. Analysis of male relatedness among leks in each local population showed that overall levels of relatedness were not significantly different between males from the same lek and those at different leks and that no isolation-by-distance relationships were present. We argue that these patterns are most parsimoniously explained as a byproduct of limited dispersal rather than as direct selection operating via reproductive behavior to produce specific patterns of relatedness among lek attendees. Received 16 February 2008, accepted 17 June 2008.

Key words: Blue Manakin, Brazilian Atlantic Forest, *Chiroxiphia caudata*, kinship, lek, microsatellite, Pipridae.

### Patrones de Parentesco Individual en Asambleas de Cortejo de *Chiroxiphia caudata*

**RESUMEN.**—Los patrones de parentesco entre machos que se congregan en las asambleas de cortejo pueden ayudar a entender la evolución de este comportamiento reproductivo. Estudios pasados en aves, han encontrado que los machos que se congregan en asambleas de cortejo pueden presentar tanto elevados niveles de parentesco, lo que apoya un mecanismo de selección con base en el parentesco, como la completa ausencia de parentesco, apoyando un mecanismo de beneficio directo. Mostramos que los machos de *Chiroxiphia caudata* que se congregan en asambleas de cortejo exhiben un tercer patrón, en el que las asambleas consisten en una mezcla de individuos emparentados y no emparentados. Los análisis de parentesco realizados con machos provenientes de 13 asambleas en tres poblaciones locales mostraron que en una misma asamblea es posible encontrar machos con el mayor nivel de parentesco ( $r = 0.5$ ), pero sólo en la mitad de las asambleas muestreadas. Los análisis de parentesco de los machos entre asambleas en cada población local mostraron que los niveles generales de parentesco no fueron significativamente diferentes entre machos de la misma asamblea y entre machos de asambleas diferentes, y que no existió una relación entre el aislamiento y la distancia. Argumentamos que estos patrones se explican más parsimoniosamente como producto secundario de una limitación en la dispersión, que por una selección directa que opera a través del comportamiento reproductivo y que produce patrones específicos de parentesco entre los individuos que se congregan en las asambleas.

LEKS ARE AGGREGATIONS of male display territories that females visit primarily for the purpose of mating. This reproductive system is characterized by intense sexual selection, and male mating success is highly skewed, with most “subordinate” males rarely or never reproducing (Höglund and Alatalo 1995). Explaining why subordinate males join leks despite having little or no chance of

breeding is essential to understanding how this form of male mating behavior has evolved. One hypothesis is that subordinate males obtain direct fitness benefits such as access to rare copulations and inheritance of alpha position (McDonald and Potts 1994, DuVal 2007, Loiselle et al. 2007). Several models also provide scenarios in which clustering is advantageous for attracting females (for a

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review, see Isvaran and St. Mary 2003), for reducing predation risks (Gibson et al. 2002), or both. However, it remains unclear whether these direct benefits are sufficiently large to balance the costs of forgoing other reproductive opportunities, such as breeding alone (Höglund et al. 1992). Several other authors have proposed or tested the hypothesis that kin selection could play a role in the evolution of leks or the evolution of cooperative display at leks (McDonald and Potts 1994, Shorey et al. 2000, Höglund and Shorey 2003, Krakauer 2005, DuVal 2007, Loiselle et al. 2007). If kin selection plays a major role, males should establish themselves on leks where successful males are close relatives. If females prefer aggregated males, the increase in lek size will result in an increase in female visits to the lek, leading to higher reproductive success by the dominant male. Kin selection would operate, because the subordinate males would gain indirect reproductive benefits as a result of being related to a successful alpha male. The patterns of relatedness among lek attendees should provide insights into which of these mechanisms could be responsible for the evolution of lek behavior. Past research on birds has found evidence that lekking males can show (1) significant levels of relatedness, which could be related to a mechanism based on kin selection (Höglund et al. 1999, Petrie et al. 1999, Shorey et al. 2000, Höglund and Shorey 2003, Bouzat and Johnson 2004, Krakauer 2005), or (2) a lack of relatedness, which supports a direct-benefits mechanism (McDonald and Potts 1994, Gibson et al. 2005, DuVal 2007, Loiselle et al. 2007).

However, patterns of relatedness can be determined by other factors that influence dispersal and, hence, levels of inbreeding within populations. For instance, population genetic analyses of non-lekking tropical-forest understory birds show evidence for limited dispersal, which may result in high levels of inbreeding within local populations of these birds (Bates et al. 1999, Bates 2000, Brown et al. 2004, Lunardi et al. 2007). Many Neotropical lek-breeding species live in similar habitats. If dispersal is also limited in these lek-breeding birds, patterns of relatedness may not necessarily reflect direct selection on males to choose to display, or not, with relatives, but rather represent a byproduct of high levels of philopatry. This hypothesis (which we term the “philopatry” hypothesis) makes the following predictions, both of which assume that restricted dispersal will result in chance spatial associations among close relatives in local populations. (1) There should be no consistent pattern of relatedness among males attending leks. Some leks should contain relatives, whereas others

should not, reflecting the stochastic nature of dispersal by close relatives within local populations. (2) Levels of relatedness among males at specific leks should not be significantly different from levels of relatedness among males at different leks in the same area. This reflects the idea that under the philopatry hypothesis, relatedness *per se* should not influence whether males join specific leks and close relatives should be randomly distributed among leks in local populations of a species.

We examined these predictions in a tropical-forest understory lek-breeding bird, the Blue Manakin (*Chiroxiphia caudata*), using patterns of relatedness inferred from microsatellite DNA loci. Species belonging to this genus perform highly specialized courtship displays in which males aggregate at the same branch, where they perform a precopulatory dance. Each lek consists of between two and eight males that form a dominance hierarchy with respect to copulations with females but are cooperative with respect to courtship displays (Foster 1981, McDonald and Potts 1994, DuVal 2007, Loiselle et al. 2007). The dominant (alpha) male, with rare exceptions, performs all the copulations, though the participation of at least two males is required to attract females. Lek locations are long-lasting, and the position of the alpha male in the hierarchy persists within and between years (Foster 1981, McDonald 1993, McDonald and Potts 1994, DuVal 2007). Previous work (Francisco et al. 2007) has shown limited dispersal among local populations of *C. caudata* in continuous areas of Brazilian Atlantic forest and found evidence for low levels of inbreeding within these populations that consisted of birds sampled from multiple leks. Here, we refine our analyses and focus on patterns of individual relatedness between males and a small number of females that attended specific leks within three of these previously analyzed populations.

## METHODS

*Study area and bird sampling.*—From 2003 to 2005, we collected blood samples from 93 birds at three sites—Cubatão (CUB; 23°54'S, 46°29'W), Carlos Botelho (CB; 24°04'S, 47°57'W), and Parque Estadual Turístico do Alto Ribeira (PET; 24°32'S, 48°41'W)—within the largest remaining tract of Atlantic forest largely located in São Paulo state, southeastern Brazil. Birds at four to five leks from each local population were sampled (13 total) and used for genetic analyses (see Table 1). All leks were located within 9 km of each other within a given population (Fig. 1).

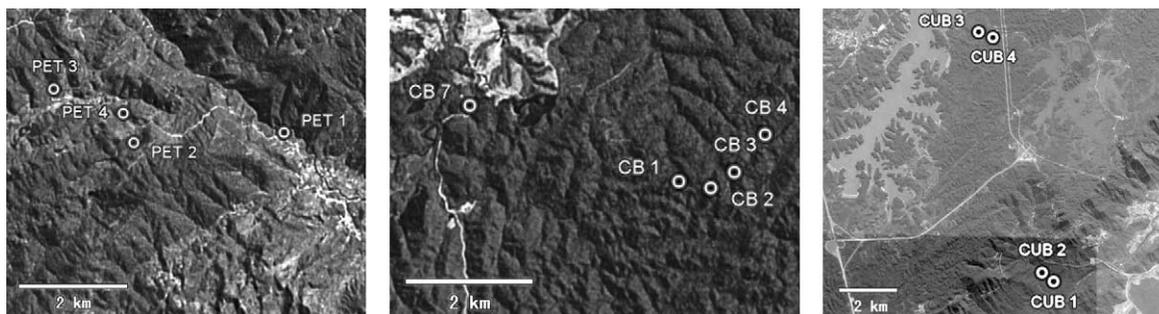


FIG. 1. Spatial distribution of Blue Manakin leks within three study sites: Parque Estadual Turístico do Alto Ribeira (PET), Carlos Botelho (CB), and Cubatão (CUB) (modified from Google Earth). These three study sites, separated by distances ranging from 90 to 230 km, are embedded in continuous forest and constitute part of the last large Atlantic forest corridor, mostly located in São Paulo state, southeastern Brazil. For a larger-scale view of the study areas, see figure 1 in Francisco et al. (2007).

TABLE 1. Characteristics of leks in three populations of Blue Manakins: Carlos Botelho (CB), Cubatão (CUB), and Parque Estadual Turístico do Alto Ribeira (PET).

Lek	CB 1	CB 2	CB 3	CB 4	CB 7
Number of males	5	3	3	4	6
Number of significant relatedness comparisons/total comparisons	0/10 (0.0%)	0/3 (0.0%)	0/3 (0.0%)	2/6 (33.3%)	0/15 (0.0%)
Proportion of males in kin groups <sup>a</sup>	0.0%	0.0%	0.0%	100% ( <i>n</i> = 2)	0.0%
Lek	CUB 1	CUB 2	CUB 3	CUB 4	
Number of males	7	8	3	3	
Number of significant relatedness comparisons/total comparisons	2/21 (9.5%)	2/28 (7.1%)	0/3 (0.0%)	0/3 (0.0%)	
Proportion of males in kin groups <sup>a</sup>	57.1% ( <i>n</i> = 1)	37.5% ( <i>n</i> = 1)	0.0%	0.0%	
Lek	PET 1	PET 2	PET 3	PET 4	
Number of males	9	7	9	7	
Number of significant relatedness comparisons/total comparisons	5/36 (13.8%)	2/21 (9.5%)	3/36 (8.3%)	2/21 (9.5%)	
Proportion of males in kin groups <sup>a</sup>	62.5% ( <i>n</i> = 2)	66.7% ( <i>n</i> = 2)	66.7% ( <i>n</i> = 2)	57.1% ( <i>n</i> = 2)	

<sup>a</sup>See Appendix for details of kin-group membership.

At each site, leks were located by first identifying call sites for sets of displaying males. We then carefully observed male behavior to determine the precise location where cooperative displays occurred. Once this was established, we captured individual birds using two to four 12 × 2.5 m mist nets. Sampled birds were banded with metal rings for permanent identification. Although birds captured at specific display sites were not color-banded for subsequent confirmation of their participation in the leks, we are confident that they were members of the target leks, given that mist nets were set up directly in front of these display sites and netting at a given site was conducted for no more than two consecutive days, reducing the possibility of catching other birds from nearby leks by chance. On the basis of visual estimates of the number of displaying individuals, we estimate that we were able to sample most of the birds present at a given lek. We sampled only leks that were ≥500 m from another lek to avoid sampling birds from multiple leks. However, we do not discount the possibility that small numbers of floaters (males that are not consistently present in only a single display area) were present, as previously detected in Lance-tailed Manakins (*C. lanceolata*; DuVal 2007). At CB, we captured 15 additional birds (12 males and 3 females) that, because of the proximity of various displaying sites, we could not assign to specific leks. We excluded these birds from analyses that required birds from known leks but used them for estimating background allele frequencies in this population (see below).

Upon capture, a 10- to 20-μL blood sample was obtained from each bird by cutting the tip of the inner toe's nail. Blood was then mixed with an amount of 0.5 M EDTA that was 3× the blood volume, and the blood-EDTA mixture was immediately added to a 1.5-mL tube containing 1 mL of 100% ethanol. After returning from the field, samples were placed in a -20°C freezer for long-term storage.

*Genetic analyses.*—DNA was extracted using a standard phenol-chloroform protocol (Sambrook et al. 1989) for subsequent genetic analyses. As described previously (Francisco et al. 2004, 2007), DNA samples from all individuals were amplified at 10 species-specific microsatellite loci (*CHIR1-16*, *CHIR1-18*, *CHIR2-9*, *CHIR3-2*, *CHIR3-15*, *CHIR3-22*, *CHIR3-27*, *CHIR4-21*, *CHIR4-33*, and *CHIR4-34*) using fluorescently labeled primers. Details on isolation of loci and polymerase chain reaction (PCR) conditions used to amplify individual loci are given in Francisco et al. (2004). Amplified products were run on an ABI 377 sequencer, and allele sizes were scored using GENESCAN, version 3.0, and GENOTYPYPER, version 2.5 (Applied Biosystems, Foster City, California).

Most individuals that were captured were clearly males, having the characteristic male-specific blue plumage (see Foster 1987, Willis and Oniki 1988). However, a small number of green-plumaged birds were also captured. Because juvenile males retain a female-like plumage (Foster 1987), all green-plumaged individuals were sexed using the primers P2/P8, as described by Griffiths et al. (1996, 1998). These primers amplify the homologous copies of the CHD (chromo-helicase-DNA-binding) genes, located in the Z and W sex chromosomes. In birds, the CHDZ and CHDW sequences differ in length because of a variation found in an intronic region, such that amplification products result in one band for males and two bands for females. The PCR reactions were performed according to Anciães and Del Lama (2002), and the amplification products run on 3% agarose gels. As a control, PCR products of 15 males identified by the definitive blue plumage were examined and all were conclusively identified as males.

*Relatedness analyses.*—We analyzed relatedness among individuals using KINSHIP (Goodnight and Queller 1999). This program estimates relatedness for given dyads of individuals in terms of *r* (Queller and Goodnight 1989), which is a measure of the average proportion of

alleles shared by a given pair of individuals across all loci corrected for background allele frequencies in a reference population. This measure has been widely used to estimate relatedness among lek-breeding birds (McDonald and Potts 1994, Krakauer 2005, Regnaut et al. 2006). The expected value of  $r$  is 0 for unrelated individuals, 0.25 for half siblings, and 0.5 for full siblings or parent–offspring pairs, though there is a large variance around these expected values depending on the levels of variation of the loci used (cf. Alderson et al. 1999).

We used the microsatellite data to perform two sets of relatedness analyses on birds from leks in each local population. For all analyses, the reference population used to estimate background allele frequencies consisted of all individuals genotyped from the local population in which specific birds were sampled. In two populations (CUB and PET), this consisted of all individuals captured at leks that were the focus of our analyses. For the CB population, we also included the 15 additional birds that could not be assigned to specific leks (see above). Most previous analyses focused on identifying sets of close kin ( $r \geq 0.25$ ) within leks. Therefore, for the first set of analyses, we used likelihood-based tests of specific hypotheses about relatedness ( $r = 0.25$  and  $r = 0.5$ ) against a null hypothesis of no relatedness ( $r = 0$ ) to identify pairs of related individuals that had  $r$  values significantly greater than zero. To minimize type 1 error resulting from the large number of pairwise comparisons, we set the critical value for statistical significance for a given comparison at  $P \leq 0.01$ . In the course of our analyses, we found almost complete overlap in the dyads that were classified as showing significant relatedness under hypotheses of expected  $r$  values of 0.25 and 0.5. Therefore, in the results presented below, we define “closely related” individuals as dyads of birds with statistically significant  $r$  values of 0.5.

Second, we compared patterns of relatedness among birds captured at the same or at different leks within a given population. To do this, we first used KINSHIP to estimate  $r$  values between all pairs of birds (including females) in a population. We then compared mean  $r$  values for pairs of males ( $M \times M$  comparisons) from the same lek versus  $r$  values between males captured at different leks but within the same local population. If males preferentially choose to join leks containing relatives, within-lek  $M \times M$   $r$  values should be significantly higher than between-lek values. We also repeated this analysis for pairs of males and females ( $M \times F$  comparisons) from the same versus different leks. Where sample sizes were sufficiently large (the  $M \times M$  comparisons only), we used a Mantel matrix randomization test as implemented in the program

ZT (Bonnet and Van de Peer 2002) to test whether within-lek  $r$  values were significantly greater than between-lek  $r$  values.

Finally, we tested whether there was an isolation-by-distance relationship in relatedness between males at the same versus different leks within each local population, as would be predicted if there was male-based kin structuring (cf. Höglund and Shorey 2003). Specifically, we used the ZT program to determine whether there was a significant positive relationship between  $r$  values for all males and the distances between leks where specific males were trapped.

## RESULTS

We genotyped an average of  $5.7 \pm 2.3$  (SD) males per lek from 13 leks in the three populations (Table 1). Results from the KINSHIP analyses show that just over half the leks (7 of 13, or 54%) contained one or more pairs of males that were close relatives. The proportion of leks with relatives varied among local populations: at CB, only 20% (1 of 5) of all leks contained kin, whereas at CUB this value was 50% (2 of 4) and at PET all leks (100%; 4 of 4) contained closely related males.

Leks with relatives contained either one or two groups of kin that consisted of pairs or trios of related males (see Appendix) and, in 6 of 7 leks, additional unrelated birds. Across all leks, males with at least one close relative present made up an average of  $63.9 \pm 18.8\%$  of all birds genotyped in a given site, though on a per-lek basis the proportion of all pairwise comparisons made up by related males was much lower ( $7.23 \pm 9.20\%$ ) (Table 1).

Despite the presence of close relatives at half of the leks, there was no evidence that male kin preferentially associated with each other; substantial numbers of relatives of a given male were also found at other leks in a local population. As a consequence, the levels of relatedness among males at a given lek are not significantly different from that among males at different leks in a particular population: there was no significant difference in the magnitude of  $r$  values for comparisons among males from the same lek (mean = 0.0077) versus among males at different leks (mean =  $-0.0057$ ) in all three populations (Mantel matrix randomization tests; all  $P > 0.1$ ; Table 2). Likewise, comparisons between males and the small number of females that were captured and genotyped showed  $r$  values of similar magnitude to the male–male comparisons, though statistical tests were not done because of the small numbers of females captured ( $n = 1$  to 6 in each population) (Table 2). This implies that the

TABLE 2. Mean  $r$  values ( $\pm$ SD) for pairwise comparisons between individual males (M) and females (F) within the same lek and between different leks found in each of three populations (CB = Carlos Botelho, CUB = Cubatão, and PET = Parque Estadual Turístico do Alto Ribeira;  $n$  = number of pairwise comparisons;  $P$  = result of Mantel test comparing  $r$  values for within and between lek comparisons; NA = nonavailable).

Population	M × M		M × F	
	Within	Between	Within	Between
CB	0.002 ± 0.136	0.001 ± 0.136	0.115 ± 0.137	0.002 ± 0.130
<i>n</i>	37	413	9	163
<i>P</i>		0.400		NA
CUB	0.000 ± 0.149	−0.008 ± 0.146	0.003 ± 0.039	0.012 ± 0.098
<i>n</i>	55	158	3	21
<i>P</i>		0.219		NA
PET	0.021 ± 0.146	−0.01 ± 0.138	0.095 ± 0.138	0.017 ± 0.149
<i>n</i>	106	359	8	23
<i>P</i>		0.103		NA

observed pattern of relatedness in males is attributable to factors that influence dispersal patterns of both sexes, and not males only.

Finally, if male relatives were clustering together at specific leks, a negative isolation-by-distance relationship should exist between the magnitude of pairwise  $r$  values for males and distances between the leks where males were displaying (cf. Höglund and Shorey 2003, Regnaut et al. 2006). However, Mantel matrix randomization tests showed that no significant relationship exists between individual relatedness of males and distance between leks in any of the three populations (correlation between  $r$  values and distance [ $P$  value]: CB,  $r = 0.067$ ,  $P = 0.179$ ; CUB,  $r = 0.0438$ ,  $P = 0.316$ ; PET,  $r = 0.0075$ ,  $P = 0.453$ ). Overall, these results argue that although close male kin are present in Blue Manakin populations, kinship *per se* has little influence on how individual birds associate in space.

### DISCUSSION

Our main result is that there is no evidence that male kin preferentially associate with one another at leks within local populations of the Blue Manakin. Rather, our results show that close male relatives are present at some leks, as found in other species (Höglund et al. 1999, Petrie et al. 1999, Shorey et al. 2000, Höglund and Shorey 2003, Bouzat and Johnson 2004, Krakauer 2005), but are absent at others. Further, contrary to the patterns expected in kin-structured populations, there is no isolation-by-distance relationship between male relatedness and lek proximity, nor are males at a given lek more closely related to one another than to males at other leks. These patterns are most similar to those described for six other manakin species, including the previously studied congeners Blue-backed Manakin (*C. pareola*), Lance-tailed Manakin, and Long-tailed Manakin (*C. linearis*) (McDonald and Potts 1994, DuVal 2007, Loiselle et al. 2007), and indicate that fine-scale genetic structure in Blue Manakin populations may be unrelated to kin selection acting on males to maximize their reproductive success and may be better explained as an incidental byproduct of limited dispersal. They also contribute to the increasing recognition that birds that lek may show a diverse set of patterns with respect to kin relationships among lek attendees.

At face value, our results suggest a very limited role, if any, for kin selection as a determinant of lek attendance by males. We are surprised by this result because conceptually it would seem that the need for males to display cooperatively would lead to strong kin selection acting on males to display with relatives. In particular, because male Blue Manakins must participate in a cooperative display to attract females (Foster 1981, McDonald 1993, McDonald and Potts 1994), the opportunity for subordinate males to gain reproductive success by displaying alone must be nonexistent. As such, there would be strong selection to display with even a distantly related dominant male. Using the framework described by Krakauer (2005), our argument is that Hamilton's rule provides a way of evaluating the costs and benefits faced by subordinate males in terms of deciding whether to participate in a cooperative lekking display with a dominant male. Under this rule, kin selection should occur when  $rB - C > 0$ , where  $r$  = relatedness among the dominant and subordinate males at a lek,  $B$  is the benefit to the dominant male in terms of reproductive success, and  $C$  is the cost of subordination in terms of forfeited reproductive success that accrues to solitary males. In Blue Manakins,  $C$  is likely close to or

equal to zero for subordinate males because males must display in leks consisting of more than one bird to gain any success. This means that even if  $r$  is very small, the  $rB$  term will always be positive and favor subordinates that display with even distantly related dominant males. This conclusion is tentative in that these conceptual arguments may be overly simplistic. In particular, it does not take into account the facts that (1) joining a lek may be a joint decision between a dominant and subordinate male, (2) the outcome favored by the parties may not coincide, and (3) a subordinate may have other behavioral options (e.g., displaying with an unrelated male) that are not considered here.

However, if our logic is sound, we are uncertain why this situation has not led to greater kin structuring in Blue Manakin leks. A possible reason may be a lack of kin-recognition mechanisms that would preclude the ability to choose to display with kin at leks (cf. Loiselle et al. 2007). Sustained contact with male relatives, necessary for kin imprinting to occur, is likely rare, because young manakin males are raised in the absence of any contact with their fathers, brood sizes are small ( $n = 2$ ), and nestling sex ratios are equal (Foster 1981, Willis and Oniki 1988, Sick 1997, DuVal 2007). This argues that, for kin recognition to occur, some sort of innate kin-recognition system must exist, yet evidence for such a mechanism in birds is lacking (cf. Komdeur and Hatchwell 1999). Other birds, such as Wild Turkeys (*Meleagris gallopavo*) (Krakauer 2005), may show evidence of kin selection because coalitions of related males may consist of males that have been raised in the same large brood and, hence, are able to recognize each other through some form of kin imprinting. Another possible explanation for the limited kin structuring observed here is that, although lower levels of dispersal can favor the evolution of altruistic behaviors because of the increased relatedness among individuals, recent models have demonstrated that this effect can be offset by increased competition between relatives. Therefore, limited dispersal may not always promote the evolution of altruistic behavior (for review, see West et al. 2002).

Limited dispersal by both sexes seems the most likely primary mechanism in determining patterns of fine-scale relatedness between males at Blue Manakin leks. Recent work by us (Francisco et al. 2007) has shown that genetically effective dispersal is limited (for unknown ecological or evolutionary reasons) between populations of these birds over relatively small distances. As a result, we suggest that high levels of philopatry lead to closely related males (e.g., siblings) remaining within local populations, dispersal within which then leads to a more-or-less random distribution of close kin among leks. Thus, as has been argued by Loiselle et al. (2007), we suggest that close kin end up recruiting to some leks and not others by chance, which accounts for the existence of some leks with kin and others without. Random distribution of kin among leks can also explain the lack of an isolation-by-distance relationship with respect to relatedness in these birds.

Others have suggested that philopatry is a significant cause of co-occurrence of kin at leks (Höglund et al. 1999, Bouzat and Johnson 2004). However, they have focused on birds that show male-limited dispersal and have argued that philopatry will tend to produce increased structuring of leks. Manakins are different in that all evidence suggests that there is no sex-biased dispersal in *Chiroxiphia* (McDonald 2003, Francisco et al. 2007), and we hypothesize that the effects of philopatry are realized at the level of the local population rather than the level of the lek, because the distribution of

kin at leks is a byproduct of dispersal in local populations rather than a result of kin associating with each other. If our explanation is true, it predicts that relatedness should also be high in female Blue Manakins in local populations because of limited dispersal. In support of this claim, we found that six females captured at specific leks across all populations had close male relatives in each population, including one female that was significantly related to one of the displaying males at the lek where it was captured.

Because kin selection is improbable, it seems likely that subordinate males join leks for direct fitness benefits such as access to rare copulations and inheritance of alpha position, as previously pointed out for the other species in this genus (McDonald and Potts 1994, DuVal 2007, Loiselle et al. 2007). In other words, in *Chiroxiphia* spp., subordinate males participate in leks because although their chances to copulate are rare, if they did not display with other males they would have no opportunity, given that, as previously shown by Foster (1981), McDonald (1993), and McDonald and Potts (1994), at least two males are necessary to excite the females for copulation. This leaves subordinate males no other choice than to cooperate.

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APPENDIX. Details of kin relations among Blue Manakin males at leks with at least one related pair of males. "Groups" are defined as sets of individuals with  $r$  values of 0.5 that are significantly different from zero at the 0.01 level of significance (see text; CB = Carlos Botelho, CUB = Cubatão, and PET = Parque Estadual Turístico do Alto Ribeira).

Lek	Kin groups
CB 4	Group 1: 481, 482 Group 2: 483, 487
CUB 1	Group 1: 449, 453, 454 Plus four unrelated birds
CUB 2	Group 1: 455, 456, 469 Plus five unrelated birds
PET 1	Group 1: 509, 510, 511 Group 2: 514, 516 Plus three unrelated birds
PET 2	Group 1: 518, 520 Group 2: 522, 523 Plus two unrelated birds
PET 3 <sup>a</sup>	Group 1: 525, 529, 531 Group 2: 526, 527, 533 Plus three unrelated birds
PET 4	Group 1: 538, 539 Group 2: 537, 540 Plus three unrelated birds

<sup>a</sup>Note that birds 531 and 533 are also related to each other.