

Kin selection does not explain male aggregation at leks of 4 manakin species

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In lek-mating systems, males aggregate at display arenas and females visit solely for the purpose of mating. This breeding system is characterized by high variance in male mating success with one male often receiving most copulations. High reproductive skew among males has led to question why males join leks when their chances of reproductive success are so low. Kin selection has been invoked as a mechanism to explain the evolution of lekking behavior, whereby nonreproducing but genetically related males gain indirect inclusive-fitness benefits. Evidence for kin selection among lek-mating birds is, however, mixed. Here, we show that kin selection is unlikely to be an important explanation for evolution of lekking behavior in manakins (Aves: Pipridae). We found that for 4 species chosen from several major clades within Pipridae, males within leks were not significantly more related than expected from random assortment of males in the population. This means that nonreproducing males do not gain indirect inclusive-fitness benefits by joining leks. This result suggests alternative mechanisms must be invoked to explain the evolution of lek-mating systems in manakins. *Key words:* genetic relatedness, kin selection, lek breeding, manakin, pipridae. [*Behav Ecol*]

Lek mating is characteristic of only approximately 6% of bird species (Gill 1995), yet in 2 families—manakins (Pipridae) and birds of paradise (Paradisaeidae)—most species exhibit lekking behavior. In manakins, lek mating is hypothesized to be ancestral (Prum 1994), but characteristics of leks vary substantially among species. In nearly all species, males aggregate on display arenas to attract females, yet whenever documented, male mating success at leks has been highly skewed (Snow 1962; Lill 1974; McDonald and Potts 1994). Variance in male mating success has led to the development of several hypotheses to explain why males should join leks when their chances of reproduction are so low (Bradbury 1981; Beehler and Foster 1988). Recently, kin selection has been proposed as a mechanism by which nonreproducing males gain indirect-fitness benefits by joining leks where the dominant male is a relative (Kokko and Lindström 1996). Supporting the kin selection hypothesis, related males were found together on leks of white-bearded manakins (*Manacus manacus*) (Shorey et al. 2000), peacocks (*Pavo cristatus*) (Petrie et al. 1999), black grouse (*Tetrao tetrix*) (Höglund et al. 1999), and turkeys (*Meleagris galapavo*) (Krakauer 2005). In turkeys, kin selection was further supported by the demonstration that indirect-fitness benefits that subordinate males gain by joining coalitions with dominant males exceed the direct benefits that would be expected if they did not form coalitions (Krakauer 2005). In these species, where aggregating males are close kin, males are hypothesized to be cooperating to attract females (Alatalo et al. 1992; Höglund et al. 1999). In *Chiroxiphia linearis* manakins, however, cooperating males at leks are not closely related, despite very pronounced skew in male mating success (McDonald and Potts 1994). Consequently, kin selection does not provide a mechanism to explain why males join leks in this species (McDonald and Potts 1994).

In eastern Ecuador, 8 species of manakins co-occur in tropical lowland wet forest. Lek characteristics, including inter-male spacing within leks, average number of males at leks, interlek distances, female home range size, and degree of cooperation among males within leks, vary substantially among these 8 species. To examine whether kin selection might explain male aggregation at display arenas in manakins, we used allele frequencies at 6–7 polymorphic microsatellite loci to estimate genetic relatedness of males within leks of 4 species. Given the differences in lek characteristics of our study species and the fact that these species represent 3 genera widely spread throughout the manakin phylogeny (Prum 1994), our analysis is the first test of the general importance of kin selection in explaining the evolution of lekking behavior in manakins.

METHODS

Study site, species description, and sampling

Populations of 4 species of manakins (*Pipra filicauda*, *Pipra pipra*, *Lepidothrix coronata* and *Chiroxiphia pareola*) were studied from November to April from 2002 to 2005 at the Tiputini Biodiversity Station (TBS), Orellana Province, Ecuador (0°38'S 76°08'W). TBS, a 650-ha biological station located at ~200 m above sea level, was established in 1994 by the Universidad San Francisco de Quito on a tract of undisturbed lowland rain forest within the 1.5-million ha Yasuní Biosphere Reserve, a region noted for its biological diversity. The station is dominated by moist lowland tropical rain forest and is embedded within 1.2 million ha of largely undisturbed forest (Karubian et al. 2005; Ryder et al. 2006). Within TBS, two 100-ha plots (~1 × 1 km each) were established in terra firme forest during 2001 (for description of Harpia and Puma plots, see Ryder et al. 2006; Loiselle, Blake, et al. 2007).

The 4 manakin species studied here differ in certain characteristics of lek behavior and ecology. In all 4 species, males aggregate at leks that are, for the most part, situated in the same location year after year (Snow 2004; personal observations). *Pipra filicauda*, *P. pipra*, and *L. coronata* exhibit “exploded” leks, where territorial males or cooperating males are generally in aural, but not visual, contact. The degree of

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spacing between lek males varies among species but is usually within 10–30 m. Further, leks of *C. pareola* and *L. coronata* have fewer males on average than do leks of *P. filicauda* and *P. pipra* (see below). Unlike the other 2 study species, *P. filicauda* and *C. pareola* males cooperate with coordinated dance displays, although male cooperation appears to be necessary for reproductive success only in the latter species (Schwartz and Snow 1978; McDonald 1989).

Leks of the 4 species were located and mapped throughout, as well as near the vicinity of, the two 100-ha study plots within TBS. Birds were captured with mist nets placed opportunistically at leks and at 96 net sites established on a grid system within each 100-ha study plot. On capture, manakins were weighed, sexed, aged, and banded with aluminum and individual color-band combinations. Blood samples were taken (~50 µl per individual) via puncture of the brachial vein and mixed with 500 µl of lysis buffer (Longmire et al. 1988).

From all leks on the plots, we selected 3 leks per species from one of the 100-ha plots for genetic analysis. Three leks were selected to ensure similar spatial sampling of genotypes among the species; from 3 to 14 leks per species can be found within a 100-ha plot (Loiselle, Blake, et al. 2007). For these analyses, the number of males per lek varied from 3 to 5 in *L. coronata*, 12 to 19 in *P. filicauda*, 9 to 12 in *P. pipra*, and 5 to 8 in *C. pareola*. In the latter species, limited observations at each lek (average 40–50 h observation per lek) identified the likely alpha–beta males. An additional 70, 17, 55, and 17 males were included in genetic analyses from the 4 species, respectively, and represented all territorial and nonterritorial males captured within the same 100-ha study plot on which leks were located.

Genetic analyses

DNA was isolated via phenol–chloroform extraction method followed by a cleaning step of dialysis in $1 \times \text{TNE}_2$ (25). DNA concentration was determined by spectrophotometry. A subset of 12 polymorphic microsatellite loci was selected from a larger set of 25 loci developed for other species of manakins (McDonald and Potts 1994; Piertney et al. 2002; Duval and Nutt 2005; Brumfield R and Braun M, personal communication). Polymerase chain reactions (PCRs) were run in 5 µl volumes and consisted of genomic DNA, 1 mM deoxynucleotide triphosphate's, $10 \times$ reaction buffer, 25 mM MgCl_2 , forward and reverse primer pairs, dimethylsulfoxide additive, and Taq DNA polymerase (Bioline, Randolph, MA). PCR products were tagged using fluorescently labeled forward primers (Applied Biosystems, Inc., Foster City, CA). PCR conditions consisted of an initial denaturation at 94 °C for 2 min, followed by 30–35 cycles of denaturation at 94 °C for 30–45 s, annealing at 50–62 °C for 30–45 s, and extension at 72 °C for 30–60 s, with or without a final extension step of 72 °C for 10 min. PCR products were multiplexed in appropriate dilution ratios and run on an ABI 3100 automated capillary sequencer. Up to 5 positive control individuals were run on every plate. Fragment sizes were determined using a size standard GENESCAN LIZ (500), and genotypes were assigned using Genemapper 4.01 (Applied Biosystems, Inc.). Each species had $\geq 97\%$ of the genotypes determined across loci. Most individuals, and all homozygotes, were run at least twice; any questionable allelic calls were repeated to avoid spurious results and discarded when necessary.

Data analysis

We determined allele frequencies per locus, allelic richness, and ran tests for linkage disequilibrium and Hardy–Weinberg equilibrium using FSTAT version 2.9.3.2 (Goudet 2001). Departure from equilibrium was assessed via randomization pro-

Table 1

Microsatellite loci, number of individuals sampled (*n*), and number of alleles (alleles) used in calculating pairwise-relatedness values for 4 species of manakins, *Lepidothrix coronata* (LEPCOR), *Pipra filicauda* (PIPFIL), *Pipra pipra* (PIPPIP), and *Chiroxiphia pareola* (CHIPAR) (Aves: Pipridae)

Locus	LEPCOR		PIPFIL		PIPPIP		CHIPAR	
	<i>n</i>	alleles	<i>n</i>	alleles	<i>n</i>	alleles	<i>n</i>	alleles
Lan10	—	—	60	11	82	6	30	3
Lan20	82	30	62	19	79	14	35	20
Lan22	81	20	—	—	85	20	35	12
LTMR8	79	8	—	—	—	—	—	—
LTMR15	—	—	—	—	—	—	35	14
Man3	80	25	60	15	—	—	33	15
Man6	—	—	61	5	85	9	—	—
Man7	—	—	60	17	—	—	—	—
Man13	80	25	60	15	—	—	33	15
Maniac3	—	—	—	—	80	16	—	—
Maniac5	79	10	—	—	—	—	—	—
Maniac13	—	—	59	7	84	23	—	—

cedures, and Bonferroni corrections were applied when appropriate. We included only the loci that were in Hardy–Weinberg equilibrium and showed no significant linkage. Under these criteria, 6 loci were included for genetic analysis of *L. coronata* and *C. pareola*, whereas 7 loci were used for *P. filicauda* and *P. pipra* (Table 1).

We used RELATEDNESS version 5.0 (Queller and Goodnight 1989) to estimate average and pairwise genetic relatedness among males within leks and within the male population at large. Patterns of relatedness among males in 3 leks per species were compared with background levels of relatedness among a larger set of males that included both adult and young males captured at leks and outside leks within a given 100-ha study plot or its near vicinity. The spatial extent sampled and the distances separating focal leks were similar for all manakin species. We calculated relatedness using a bias-corrected value for population allele frequencies. The correction excludes the focal individual and all other individuals within the same lek from contributing to the calculation of population allele frequencies. The bias correction is recommended for small sample sizes as genetic similarity of relatives could bias population allele frequencies and result in an underestimate of true relatedness (Queller and Goodnight 1989). We jackknifed over loci to obtain estimates of standard errors and 95% confidence intervals.

RESULTS

We found that average relatedness of males within leks varied between -0.0138 and 0.0266 in the 4 species of manakins; in no case were males within leks more related than expected by chance (Figure 1). In *C. pareola*, leks consist of an alpha–beta pair of males and other associated males. The pairwise genetic relatedness of the alpha–beta pairs in the 3 leks were -0.0133 , -0.1017 , and 0.3521 , respectively. As for the alpha–beta pair in *C. pareola* lek 3, pairwise genetic-relatedness values of males within leks do show that some males are close kin (Figure 2). In one 3-male *L. coronata* lek, pairwise *r* values varied between 0.14 and 0.36, suggesting male relatedness on this lek was equivalent to that of second-order relatives. Yet, negative *r* values were as likely as positive *r* values between male pairs on a lek (9 vs. 10 in *L. coronata*, 153 vs. 176 in *P. filicauda*, 67 vs. 70 in *P. pipra*, 31 vs. 17 in *C. pareola*). If kin selection was operating, one would expect positive relationships between males to predominate (McDonald and Potts 1994).

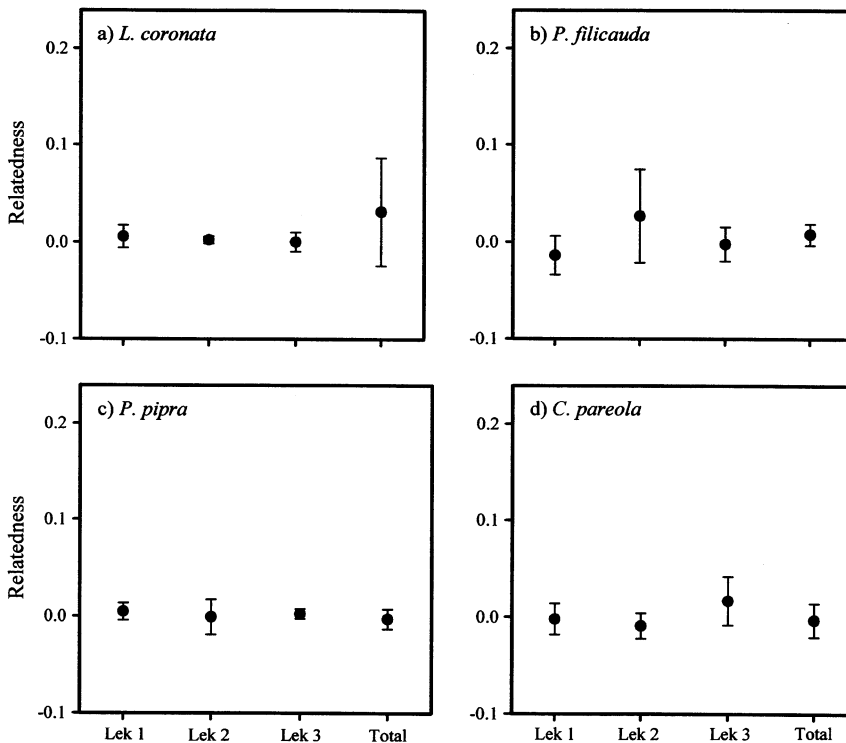


Figure 1
Average pairwise-relatedness values ($\pm 95\%$ confidence interval) for males at 3 leks and in the total population for each of 4 manakin species: (a) *L. coronata*, (b) *P. filicauda*, (c) *P. pipra*, and (d) *C. pareola*. In no case were males within leks significantly more related than expected.

DISCUSSION

The close match between relatedness values within a lek and those of the background population suggests that males join leks at random with respect to relatedness, and kin selection need not be implicated in explaining patterns of male aggregation. Nevertheless, kin selection might still partially explain the lekking behavior patterns observed here if the following conditions held. In general, theory and empirical evidence have demonstrated that larger male aggregations receive more female visits than do smaller aggregations (Alatalo et al. 1992; Widemo and Owens 1995; Shorey et al. 2000), although we do not have the data to say if this holds in any of our study species. In “exploded” leks where males are generally within aural, but not visual contact, variance in male reproductive success is expected to be lower either because of reduced male–male competition or because of inefficiency of female choice (Shuster and Wade 2003). As a result, more males are expected to receive direct-fitness benefits and strategies for joining leks may differ between males as a function of their dominance rank. For example, higher ranking males that join leks are likely to mate with females, especially in larger leks, and their decision to join may be based only on acquisition of direct benefits. On the other hand, the strategy for lower ranking males who have little or no chance of copulating is likely to be different, and these males might be expected to join leks where the dominant male is a close relative. Therefore, males on leks might consist of lower ranking, nonreproducing males that are related to a dominant male and that receive indirect inclusive-fitness benefits and higher ranking males that may or may not be related to the dominant male and that receive direct- (and possibly indirect) fitness benefits. Alternative explanations for why related males might join leks include the possibility of encountering females that are more likely to prefer the phenotype of a related male or the reduced costs (lowered aggression from related dominant male) of joining leks (Saether 2002; see also Greenwood et al. 1979; Lacy and Sherman 1983). Except in the case of limited

natal dispersal where related males may aggregate by chance, the explanations given above require that males be able to recognize kin; phenotype matching has been one mechanism proposed for kin recognition (e.g., van der Jeugd et al. 2002). Phenotype matching has been demonstrated in mice (Yamasaki et al. 2000; Hurst et al. 2001) and salamanders (Pfenning et al. 1994), which use olfactory cues to recognize relatives, but has yet to be demonstrated in birds (Komdeur and Hatchwell 1999; van der Jeugd et al. 2002). Thus, it appears unlikely that kin selection is operating in our system, but a real test of these ideas requires specific information on male status and reproductive success within leks, as well as evidence that males can recognize related but, likely, unfamiliar males. We do not yet have this information for our species.

If kin selection is not important in the evolution of lek behavior in manakins, then what alternative hypotheses might explain why males join leks when their chances of reproduction are so low? Three prevalent hypotheses are the “hot-spot” (Bradbury and Gibson 1983), “hotshot” (Beehler and Foster 1988), and “delayed benefits” (McDonald and Potts 1994; Kokko and Johnstone 1999) hypotheses for lek evolution. In the former, males are hypothesized to sequentially cluster in areas of high female density or movement. In the hotshot hypothesis, subordinate males settle near dominant males with high reproductive success; in this hypothesis, female mate choice is considered relatively unimportant when compared with male–male dominance interactions. In the delayed benefits hypothesis, subordinate males receive direct-fitness benefits later in life when they replace higher ranking males on the leks. In our system, evidence supporting the hot-spot hypothesis is mixed. Areas around leks have been shown to contain significantly more fruit resources than do control areas (Ryder et al. 2006), and previous work with manakins has shown that capture rates of manakins are higher in fruit-rich patches (Loiselle and Blake 1993). However, given the high overlap in fruit diet among manakin species (Loiselle, Blendinger, et al. 2007), the hot-spot hypothesis would predict

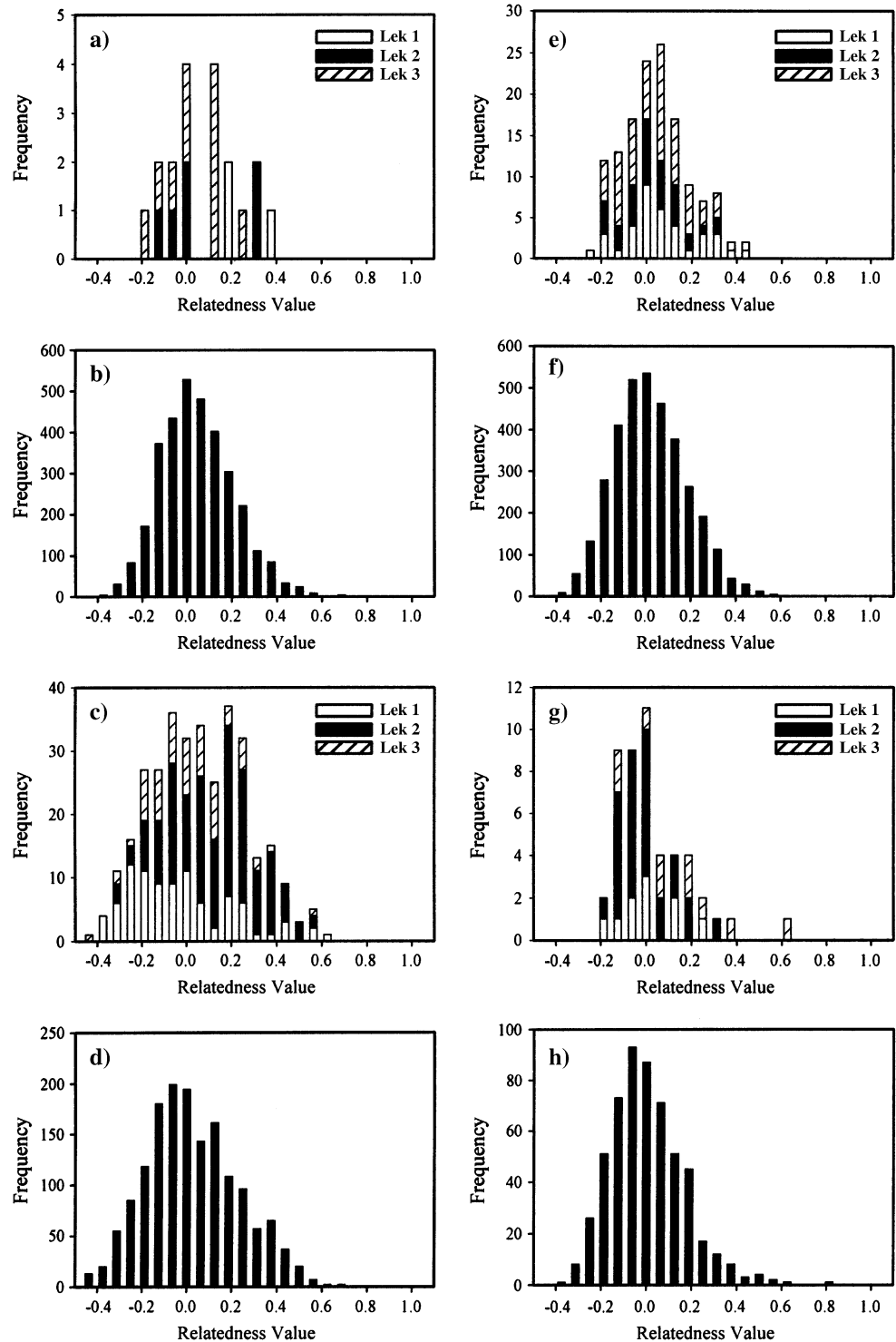


Figure 2

Frequency histogram of pairwise-relatedness values for males at 3 leks and for males in the background population. Lek and background panels, respectively, are (a) and (b) *L. coronata*, (c) and (d) *P. filicauda*, (e) and (f) *P. pipra*, (g) and (h) *C. pareola*. Notice that in all cases, the values center fairly evenly on zero relatedness and that lek values appear to be representative subsamples of the population distributions.

that leks of different species should be aggregated in space (Westcott 1994). In our system, we found that leks are not aggregated in space (unpublished data) but appear to be associated with interspecific selection of particular forest environments (Loiselle, Blake, et al. 2007). We do not yet have the data to test all predictions of the hotshot hypothesis, but there is considerable variation in attendance and singing and display rates among males within a lek, which would be consistent with inequalities in male reproductive success and would likely provide cues to other males. In all 4 species, male–male

interactions or associations may occur, but differences in internal spacing of males within leks likely result in more or less opportunities for the formation of dominance hierarchies. We cannot yet evaluate the importance of delayed benefits, but as manakins are long lived and many show site fidelity to leks (Snow 2004), the basic foundation for this hypothesis is supported. Data on male reproductive success and turnover dynamics and movement patterns of females are key to further evaluations of the importance of the hot-spot, hotshot, and delayed benefits hypotheses in our system.

In conclusion, our study does not support recent findings that implicate kin selection as an explanation for male aggregation in lekking birds. To date, genetic-relatedness patterns among male manakins show that in only 1 of 7 species are males closely related ($r > 0.25$) within leks (*M. manacus*) (Shorey et al. 2000). Yet, even in this species, some spatially structured groups of males within the lek are closely related, whereas others are not. Further, Shorey et al. (2000) failed to show any benefits accruing from relatedness. Although relatedness is a necessary precondition for kin selection, it does not guarantee cooperative behavior (West et al. 2002). In addition to the 4 species studied here, cooperative display partners in leks of *C. linearis* and *C. lanceolata* are not closely related (McDonald and Potts 1994; Duval E, personal communication). Thus, alternative mechanisms, such as delayed benefits, aggregation around hotshot males, or female hotspots, likely prevail to explain the evolution of lekking behavior in manakins.

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REFERENCES

- Alatalo RV, Höglund J, Lundberg A, Sutherland WJ. 1992. Evolution of black grouse leks—female preferences benefit males in larger leks. *Behav Ecol*. 3:53–59.
- Beehler BM, Foster MS. 1988. Hotshots, hotspots, and female preference in the organization of female mating preference. *Am Nat*. 131:203–219.
- Bradbury JW. 1981. The evolution of leks. In: Alexander RD, Tinkle DW, editors. *Natural selection and social behavior: research and new theory*. New York: Chiron Press. p. 138–169.
- Bradbury JW, Gibson RM. 1983. Leaks and mate choice. In: Bateson P, editor. *Mate choice*. Cambridge (UK): Cambridge University Press. p. 109–138.
- Duval EH, Nutt KJ. 2005. Isolation and characterization of polymorphic microsatellite loci in the lance-tailed manakin (*Chiroxiphia lanceolata*). *Mol Ecol Notes*. 2:112–114.
- Gill FB. 1995. *Ornithology*. New York: WH Freeman and Co.
- Goudet J. 2001. FSTAT, a program to estimate and test gene diversities and fixation indices (version 2.9.3) [Internet]. [Cited 2002 Feb]. Available from: <http://www2.unil.ch/popgen/softwares/fstat.htm>.
- Greenwood PJ, Harvey PH, Perrins CM. 1979. Kin selection and territoriality in birds: a test. *Anim Behav*. 27:645–651.
- Höglund J, Alatalo RV, Lundberg A, Rintamäki PT, Lindell J. 1999. Microsatellite markers reveal the potential for kin selection on black grouse leks. *Proc R Soc Lond B Biol Sci*. 266:813–816.
- Hurst JL, Payne CE, Nevison CM, Marie AD, Humphries RE, Robertson DHL, Cavagioni A, Beynon RJ. 2001. Individual recognition in mice mediated by major urinary proteins. *Nature*. 414:631–634.
- Karubian J, Fabara J, Yunes D, Jorgenson JP, Romo D, Smith TB. 2005. Temporal and spatial patterns of macaw abundance in the Ecuadorian Amazon. *Condor*. 107:617–626.
- Kokko H, Johnstone RA. 1999. Social queuing in animal societies: a dynamic model of reproductive skew. *Proc R Soc Lond B Biol Sci*. 266:571–578.
- Kokko H, Lindström J. 1996. Kin selection and the evolution of leks: whose success do young males maximize? *Proc R Soc Lond B Biol Sci*. 263:919–923.
- Komdeur J, Hatchwell BJ. 1999. Kin recognition: function and mechanism in avian societies. *Trends Ecol Evol*. 14:237–241.
- Krakauer AH. 2005. Kin selection and cooperative courtship in wild turkeys. *Nature*. 434:69–72.
- Lacy RC, Sherman PW. 1983. Kin recognition by phenotype matching. *Am Nat*. 121:489–512.
- Lill A. 1974. Social organization and space utilization in the lek-forming white-bearded manakin, *M. manacus trinitatis* Hartert. *Z Tierpsychol*. 36:513–530.
- Loiselle BA, Blake JG. 1993. Spatial dynamics of understory fruit eating birds in a lowland wet forest. *Vegetatio*. 107/108:177–189.
- Loiselle BA, Blake JG, Durães R, Ryder TB, Tori W. Forthcoming 2007. Environmental segregation in lek sites among six co-occurring species of manakins (Aves: Pipridae) in eastern Ecuador. *Auk*. 124.
- Loiselle BA, Blendinger PG, Blake JG, Ryder TB. 2007. Ecological redundancy in seed dispersal systems: a comparison between manakins (Pipridae) in two tropical forests. In: Dennis AJ, Schupp EW, Green R, Westcott DW, editors. *Seed dispersal: theory and its applications in a changing world*. Wallingford, Oxfordshire (UK): CABI Publishing.
- Longmire JL, Lewis AW, Brown NC, Buckingham JM, Clark LM, Jones MO, Meinke LJ, Meyne J, Ratliff RL, Ray FA, et al. 1988. Isolation and molecular characterization of a highly polymorphic centromeric tandem repeat in the family Falconidae. *Genomics*. 2:14–24.
- McDonald DB. 1989. Correlates of male mating success in a lekking bird with male-male cooperation. *Anim Behav*. 37:1007–1022.
- McDonald DB, Potts WK. 1994. Cooperative display and relatedness among males in a lek-mating bird. *Science*. 266:1030–1032.
- Petrie M, Krupa A, Burke T. 1999. Peacocks lek with relatives even in the absence of social and environmental cues. *Nature*. 401:155–157.
- Pfennig DW, Sherman PW, Collins JP. 1994. Kin recognition and cannibalism in polyphonic salamanders. *Behav Ecol*. 5:225–232.
- Piertney SB, Shorey L, Höglund J. 2002. Characterization of microsatellite DNA markers in the white-bearded manakin (*Manacus manacus*). *Mol Ecol Notes*. 2:504–505.
- Prum RO. 1994. Phylogenetic analysis of the evolution of alternative social behavior in the manakins (Aves: Pipridae). *Evolution*. 48:1657–1675.
- Queller DC, Goodnight KF. 1989. Estimating relatedness using genetic markers. *Evolution*. 43:258–275.
- Ryder TB, Blake JG, Loiselle BA. 2006. A test of the environmental hotspot hypothesis for lek placement in three species of manakins (Pipridae) in Ecuador. *Auk*. 123:247–258.
- Saether SA. 2002. Kin selection, female preferences and the evolution of leks: direct benefits may explain kin structuring. *Anim Behav*. 63:1017–1019.
- Schwartz P, Snow DW. 1978. Display and related behavior of the wire-tailed manakin. *Living Bird*. 17:51–78.
- Shorey L, Piertney S, Stone J, Höglund J. 2000. Fine-scale genetic structuring on *Manacus manacus* leks. *Nature*. 408:352–353.
- Shuster SM, Wade MJ. 2003. *Mating systems and strategies*. Princeton (NJ): Princeton University Press.
- Snow DW. 1962. A field study of the black and white manakin, *Manacus manacus*, in Trinidad. *Zoologica*. 47:65–104.
- Snow DW. 2004. Family Pipridae (Manakins). In: Del Hoyo J, Elliot A, Christie D, editors. *Handbook of the birds of the world. Volume 9: Cotingids to Pipits and Wagtails*. Barcelona (Spain): Lynx Editions. p. 110–169.
- van der Jeugd HP, van der Veen IT, Larsson K. 2002. Kin clustering in barnacle geese: familiarity or phenotype-matching? *Behav Ecol*. 13:786–790.
- West SA, Pen I, Griffin AS. 2002. Cooperation and competition between relatives. *Science*. 296:72–75.
- Westcott DA. 1994. Leaks of leks: a role for hotspots in lek evolution? *Proc R Soc Lond B Biol Sci*. 258:281–286.
- Widemo F, Owens IPF. 1995. Lek size, male mating skew and the evolution of lekking. *Nature*. 373:148–151.
- Yamasaki K, Beauchamp GK, Curran M, Bard J, Boyse EA. 2000. Parent-progeny recognition as a function of MHC odor identity. *Proc Natl Acad Sci USA*. 97:10500–10502.