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Department of Biology

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Spatial and Temporal Dynamics of Lekking Behavior and Female Mate Choice in the Blue-crowned Manakin (*Lepidothrix coronata*, AVES: Pipridae)

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“Eu quase que nada não sei. Mas desconfio de muita coisa.”

(I don’t know almost anything. But I suspect about an awful lot.)

João Guimarães Rosa, in *Grande Sertão: Veredas*

Dissertation Abstract

Lekking is a rare behavior that has evolved multiple times over several taxa. In species presenting this unusual mating system, males aggregate at display grounds called ‘leks’ that females visit to assess potential mates and to copulate. Lekking systems are not resource-based, to the extent that males do not hold any resources critical to females (besides their own gametes) and females carry out all parental duties unaided. As a result, males are under strong sexual selection pressure and often vary widely in their reproductive output. This dissertation investigates how spatial and temporal factors influence the lekking dynamics and female mate choice of a Neotropical frugivorous bird, the blue-crowned manakin *Lepidothrix coronata*, in eastern Ecuador.

The first chapter is related to the spatial dynamics of lekking behavior, and specifically investigates whether leks are formed by the establishment of territorial males on sites where they maximize their contact with females (the ‘hotspot hypothesis’). We tested this hypothesis by combining field data and GIS modeling to predict the spatial distribution of females on two 100-ha plots, and then contrasting these predictive maps to the distribution and size of existing leks. Contrary to the expectations, leks were found to be located not in female “hotspots”, but rather in “coldspots”, i.e., in sites where males may expect to encounter fewer females than expected by chance. A proportion of males were indeed settled at hotspots, but, contrary to predictions of the hypothesis, they belonged to smaller leks than males located outside hotspots. Our results indicate that this lack of spatial correlation between males and females results partly from differences in sex-specific habitat preferences.

The second chapter is related to the temporal aspects of lekking behavior, and specifically investigates how leks are formed and change over time, and how leks, which are very traditional in location, can persist in face of relatively high rates of male turnover. The fate of individual territorial males was followed during 4 years at up to 15 leks, allowing us to estimate rates of persistence at territories, recruitment, and expected tenure times, as well as to investigate the role of lek size, age, and display rate as correlates of persistence time and/or recruitment probabilities. Finally, we used these estimates to simulate changes in lek size and composition over longer periods of time. Our results suggest that leks rapidly converge to a mean size of 3 males, and that rates of male recruitment and disappearance compensate each other such that leks have the potential to persist for several decades after the original males have disappeared from them.

In the third chapter, we used molecular analyses of paternity to investigate the process of female mate choice at two spatial scales, within- and among-leks. First, we tested the hypothesis that females prefer to mate at larger leks, such that costs of mate search would be lowered. Second, we investigated whether female mate choice within leks is driven by genetic benefits, by asking whether females prefer to mate with individuals that are highly heterozygous or less related to them. Third, we investigated the role of vocalization rates as a correlate of male mating success and as an indicator of heterozygosity, a measure of genetic quality. Females moved beyond their regular home ranges to mate, suggesting that they increase travel costs to assess a larger number of potential mates. In particular, females nesting near small leks tended to travel further and mate at larger leks. In the population at large, however, there is not a preference for larger leks, and even solitary males may sire young. Siring males were not less related to females than expected by chance. Vocalization rates were positively correlated to the mean d^2 index (a measure of heterozygosity). In addition, males with higher vocal display within a given lek were more likely to sire young. However, as males adjust their display to lek size, vocalization rates alone are not a reliable indicator of male heterozygosity. A possible exception is for males at larger leks, where males tend to be more heterozygous and have increased display, such that vocalization rates should more honestly reflect the physiological and genetic quality of those males.

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Table of Contents

Chapter 1

Intersexual Spatial Relationships in a Lekking Species: Blue-crowned Manakins and Female Hotspots

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Abstract

Leks offer an intriguing evolutionary problem: why do males aggregate when this apparently leads to fitness costs? Aggregation costs can be balanced if males settle on patches where they are more likely to encounter females ('hotspot hypothesis'). We evaluated whether female hotspots can account for patterns of lek structure in the blue-crowned manakin (*Lepidothrix coronata*) by modeling female distribution patterns relative to lek locations in two 100-ha plots. Individual females were mapped based on nest locations and capture points, and had their home ranges modeled based on radio-telemetry data. The number of females that lekking males can be expected to encounter was estimated as the number of individual female home ranges (HRs) overlapping each male territory; hotspots were defined as patches where more females are found than average. We investigated how changes in female HR size and devaluation effects (decrease in female availability due to the presence of neighboring males) influence male access to females. Both factors strongly influenced the expected rates of female encounter, but the hotspot hypothesis was not supported: most male territories consistently overlapped fewer or just as many female HRs as expected by chance. Leks were not closer to hotspots than similar-sized non-lek sites. A proportion of males were indeed settled at hotspots, but, contrary to predictions of the hotspot hypothesis, they belonged to smaller leks than males located outside hotspots. Our results indicate that this lack of spatial correlation between males and females results partly from differences in sex-specific habitat preferences.

Introduction

Patterns of spatial distribution can have a direct role on the reproductive success of individuals and, as a consequence, lead to evolutionary changes in populations (e.g., Formica et al. 2004). For example, the extent to which individuals are clustered in space can affect how strongly sexual selection acts upon populations and, thus, may help shape the evolution of mating systems (Höglund and Alatalo 1995). In this regard, lekking species offer an interesting opportunity to investigate how spatial patterns influence sexual selection, because leks are non-resource-based mating systems where male do not defend critical resources for females (Höglund and Alatalo 1995). Moreover, males do not provide parental care and females visit leks primarily to copulate (Lill 1976; Bradbury and Gibson 1983; Wiley 1991). Thus, male territory quality should have little or no direct influence on female mate choice when compared to species in which males have control over resources. This allows one to investigate how the spatial distribution of individuals influences their access to mates largely in the absence of the confounding variable of territory quality. In this study, we asked the question of whether lekking males settle preferentially in areas where they can maximize access to females.

An apparently pervasive characteristic of lekking systems is a strong skew in male fitness (e.g., Payne 1984; McDonald and Potts 1994; Mackenzie et al. 1995; DuVal 2007; but see Lanctot et al. 1997 and Lank et al. 2002). This leads to the question of why males aggregate when such behavior increases competition for mates and potentially reduces an individual’s chances for reproduction. Although several non-exclusive mechanisms have been proposed to explain why leks evolve despite these obvious costs associated with aggregation (reviewed by Höglund and Alatalo 1995), spatial models that present explicit, empirically testable predictions are especially compelling (e.g., Bradbury 1981; Bradbury and Gibson 1983; Beehler and Foster 1988; Westcott 1997).

As originally formulated, the hotspot model (Bradbury and Gibson 1983; Bradbury et al. 1986, 1989) applied the concept of ideal free distribution (Fretwell and Lucas 1970) to a situation where females constitute a patchily distributed resource upon which males settle independently in ways that maximize their rates of female encounter. Assuming that males have enough information about female distribution, patches should be occupied in decreasing order of suitability, where suitability is defined as the number of females expected to be encountered in given patch. Moreover, females are mobile resources, and, thus, when a female copulates with a male at a given patch, this may depress the fertilization expectation of males at all other patches this female visits. In this case, the presence of neighboring males would lead to patch devaluation (patch suitability < number of females encountered). Alternatively, if males do not take into account or are not affected by competition with other settled males, male distribution should mimic directly female distribution (patch suitability = number of females encountered).

The hotspot model is a spatially explicit model that does not necessarily make assumptions about the ultimate causes of lek evolution. Female encounter rates will modulate the balance between the opposing selective forces promoting male clustering (e.g., female preference for clustered males, distribution of females over clustered resources) or male dispersion (e.g., increased mating disruption and reproductive skew at leks) and, thus, hotspot mechanisms may subsequently shape lek structure even if they are not involved in the evolution of lekking systems in the first place. Consequently, given a constant number of female home ranges to be distributed in space, the average patch value, defined as the operational number of females a male may expect to encounter at any given patch, will depend minimally on: 1) the size of female home ranges (HR) – everything else being equal, female overlap will increase with HR size; 2) female dispersion – the more clustered females are in space, the higher the variance among patches; and, 3) whether or not a given patch is devalued by the presence of other males.

Lekking is the predominant mating system among manakins (family Pipridae), small-bodied frugivorous birds dwelling in Neotropical forests and woodlands. In the blue-crowned manakin *Lepidothrix coronata*, males display solitarily or form exploded (dispersed) leks, in which males hold individual, contiguous territories. Females have independent home ranges and visit male territories to mate. Here, we evaluate whether hotspot settlement rules can account for the observed patterns of lek structure in populations of *L. coronata*. Specifically, we test the hypothesis that leks are located in areas of high female density or in their proximity, where males would be likely to encounter more females than expected by chance. We examine this hypothesis using a spatially explicit approach that models female distributions in two 100-ha plots in the Ecuadorian Amazon and contrasts these distributions to the observed spatial structure of leks. Second, we assess the effects of female HR size and patch devaluation on hotspot formation and access to females. Although devaluation is an intrinsic feature of the hotspot model as originally proposed by Bradbury et al. (1986), we consider it possible that, in our study system, a copulation may not significantly decrease the average fertilization expectation for other males within a female's range. Rates of nest failure, mainly due to predation, are extremely high in our study site (>80%, Tori et al. 2006; Durães et al. unpubl. data) and females make repeated nesting attempts during the relatively long (≥ 5 months) breeding season (Durães pers. obs.). Thus, as long as females do not always mate with the same male, a copulation could depress the value of a patch momentarily but not for the entirety of the breeding season. Finally, we investigate how sex-specific patterns of habitat use may influence the distribution and spatial correlation between males and females.

Methods

Study site

Tiputini Biodiversity Station (TBS, 0^{o} 38' S, 76^{o} 08' W, 190-270 m a.s.l.) is a 650-ha biological station located along the Tiputini River in the Orellana Province of eastern Ecuador, within the larger 1.2 million ha Yasuní Biosphere Reserve. The vegetation is lowland, wet-evergreen forest comprised primarily of unflooded *terra firme* and flooded *várzea* forest. Average annual rainfall and temperature are 2,740 mm/year and 28˚C; for more detailed descriptions see Karubian et al. (2005) and Loiselle et al. (2007). Research was conducted on two 100-ha gridded study plots (~1 x 1 km each, 100 x 200 m grid lines) established ~1.5 km apart at nearest edges. GIS databases exist for permanent grid markers, streams, elevation, slope, and aspect for both plots. Harpia plot ranges from 201 to 233 m a.s.l. in elevation and is primarily characterized by more dissected upland forests; Puma plot is overall flatter, ranging from 209 to 235 m a.s.l., and much of it is seasonally flooded.

Study species

Lepidothrix c. coronata is widespread in humid mature forests below 1000 m in eastern Ecuador, northeast Peru and extreme western Brazil (Ridgely and Tudor 1994; Snow 2004; Cheviron et al. 2005). Females and juveniles are bright green whereas males are sooty black with bright blue crowns. Females build nests, incubate eggs and care for the young alone. Nests consist of small open cups lined internally with vegetal fibers and externally with dry leaves and bark, suspended in horizontal forks usually within 1 m off the ground; clutch size is two, or less frequently one egg (Durães pers. obs., J. Hidalgo et al. unpubl. data). Nests of *L. coronata* could be 100% diagnosable and differentiated from those of any other species in our study area based on particular characteristics such as height, size, internal and external lining (J. Hidalgo et al., unpubl. data).

Population survey: captures, nests and leks

The distribution and abundance of adult and juvenile *L. coronata* were assessed on the two plots over several periods between 2001 and 2006 (Feb-Mar 2001; Jan-Mar and Jun-Aug 2002; Jan-Mar 2003; Dec 2003 to Apr 2004; Nov 2004 to Apr 2005; Nov 2005 to Apr 2006). Most population sampling was done during the dry season (late November to early April), which coincides with the main breeding season. Ground-level mist nets (12 x 2.8 m; 36 mm mesh) were operated each year on one day in January (2002-2006) and one day in March (2001-2006) at 96 fixed locations on each plot (12 nets spaced at ca. 50-m intervals and opened each day for ~ 7 hrs; Blake and Loiselle 2008). Additional nets were operated as necessary to target unbanded territorial males (nets set on territories, with or without the aid of song playbacks) and unbanded nesting females (nets set on the proximity of their nests). A total of 435 *L. coronata* individuals were captured during 694 capture events on the two plots and vicinities. Each individual was marked with uniquely-numbered aluminum bands and combinations of color bands, scored for reproductive and molt conditions, sexed and aged when possible, and bled for genetic sampling. Birds in green plumage with signs of reproductive condition (presence of brood patch, egg in oviduct) were classified as adult females. Sex of green birds with no signs of reproductive condition at time of capture was inferred by recapture history or patterns of molt limits on wing coverts, and was later confirmed with molecular techniques (Ryder and Durães 2005).

Nest searching was systematically conducted by a variable number of observers during the breeding seasons of 2004 (Dec 2003 - Apr 2004), 2005 (Nov 2004 - Apr 2005), and 2006 (Nov 2005 - Apr 2006). Attempts were made to search the entire area of each plot at least once a month, but due to logistic limitations, the Harpia plot was more efficiently searched than Puma. Areas known to include female home ranges were sometimes searched more frequently (e.g., every 15 days). When a nest was found, its status was recorded as active or inactive and, in the case of active nests, attempts were made to capture the female for identification (unless her identity was already known) and to obtain a blood sample if necessary. Nest searching was complemented by radio-tracking females with well-developed brood patches and following them to their nests (see details on radio-telemetry procedures below).

Leks were located and mapped each year by systematic searches for displaying males throughout and in the vicinities of the plots. Adult males holding display territories were identified by their color bands; unbanded males were captured and banded. Repeated visits (≥ 3) were made to each individual territory each year to map song perches, and a minimum convex polygon was drawn around these perches to define territories and lek boundaries. Territories were considered to belong to the same lek when males were within auditory contact or when occasional interactions among neighbor territorial males were observed. Locations of most leks were constant over the years, despite relatively high male turnover (see Chapter 2 of this dissertation).

Female capture points, nests, and centroids of male territories and leks were displayed as points in ArcView 3.2 or ArcGIS 9.1 (ESRI$^{\mathrm{TM}}$, Redlands, California). We estimated the degree of spatial dispersion for each of these features using SADIE's Index of Aggregation (I_a) (Perry 1998, Conrad and IACR-Rothamsted 2001), which describes the ratio between the total distance D that points need to move to be spaced as regularly as possible and E_a, the expected average distance to regularity. $I_a = 1$ indicates random distribution; values below or above unity indicate regular or aggregated distribution, respectively; statistical significance was determined after 500 simulations. Spatial patterns of nests, male territories and leks were evaluated with program SADIEM (Perry 1995), which randomizes the data points such that they are free to fall anywhere within a given polygon (in this case, the study plot). Capture points, on the other hand, are spatially constrained to occur in sites where mist nets were set; dispersion of these points were thus estimated with program SADIEShell 1.22, which randomizes points among fixed locations.

Estimation of female home range size (HR)

The spatial distribution of females was modeled by combining information on the occurrence of individual females and average size of female HRs, as estimated by radio-telemetry. Eleven females (five from Harpia, six from Puma) had radio transmitters (model BD-2N, Holohil Systems Ltd., maximum weight 0.5g, <5% body mass) fitted to their backs using a Rappole harness (Rappole and Tipton 1991). Because nesting activities may constrain female movements, we did not radio-tag females with well-developed brood patches or accompanied by fledglings for home range estimation. Two tagged females, however, initiated incubation while being monitored and data collected during incubation were removed from the analyses. Radio-equipped birds were tracked by two observers on foot using hand-held three-element Yagi antennas and portable FM100 Field Master receivers. Bearings were taken every 8 or 15 min for 4 hours/day on average, starting in early morning or early afternoon, over the transmitter's lifetime (2-3 weeks). Radio locations were estimated in Locate II v.1.82 (Nams 2000) and plotted as digital shapefiles in ArcView 3.2. Between 30 and 130 radio locations were gathered for each tagged female, an average of 15 locations/day after excluding fixes with obvious errors.

HRs were estimated as 100% minimum convex polygons (MCP) using Animal Movement v.1.0 (Hooge and Eichenlaub 1997). Of late, kernel estimators have been preferred to MCP because the latter can include considerable expanses of non-utilized area in the estimate of HR (e.g., Worton 1987). Nevertheless, we decided to adopt MCP for two reasons. First, since we are interested in the areas potentially visited by a given female, it was relevant to include areas where females are simply passing. Second, if anything, HR size was likely underestimated rather than overestimated in this study due to the short life of the radio transmitters. Influence of sample size on MCPs was examined by bootstrapping radio locations 50 times, with replacement, in increments of three. Curves of bootstrapped HR sizes against number of locations were visually inspected and reached stabilization for all tagged females; bootstrapped HRs were, on average, 17% smaller than the observed HR. HR size was not correlated either with the number of radio locations obtained per female ($r_s = 0.516$, $p = 0.10$, $n = 11$) or with the number of days the female was monitored ($r_s = 0.350$, $p = 0.29$). Finally, a location-error trial conducted in the study area with fixed radios indicated that precision (a measure of repeatability) and accuracy (a measure of deviation from the true measure) did not differ among observers and that precision was high (repeatability >99% for all observers, following Lessells and Boag 1987; Durães et al. unpubl. data).

Models of female spatial distribution

Two classes of female occurrence data were used to model female distribution: capture and nest locations. These two classes of data were not combined, i.e., each spatial model was built based either on capture or nest points. In each case, only one point was used per female. For analyses based on capture points, only the point of first capture was used in cases when a female was captured more than once within or across years. All adult females captured in the plots between 2001 and 2006 were included in the analyses. Given the long life-spans recorded for manakins (≥ 10-14 years, Snow and Lill 1974), high annual survival rates (58-64% for *L. coronata* in TBS, Blake and Loiselle 2008; see also Blake and Loiselle 2002), high recapture rates (45% of all adult females recaptured at least once in subsequent years) and short recapture distances (90.3 ± 87.0 m, mean ± SD, for *L. coronata* females in TBS, $N = 280$ pairwise distances, Loiselle et al. unpubl. data; see also Snow and Lill 1974), we assume that combining captures over a period of five years does not substantially overestimate population size. In addition, when multiple nests were found for the same female within or across years, they were within a close range of each other (3-145 m, mean ± SD = 53 ± 34 m), indicating a high degree of site fidelity.

For analyses based on nests, when multiple nests were found for the same female (within or across years), only the nest closest to the mean position of all nest points for that female was used for analysis. Because nests of *L. coronata* are distinctive and unlikely to be confounded with those of any other species occurring in the area (J. Hidalgo et al., unpubl. data), both active and inactive nests were included in the analyses. The following conservative assignment approach was adopted when a nest belonged to an unknown female: in cases when the nest was within a known female's home range, the nest was assigned to that female; when it fell in the intersection between two or more known females' home ranges, it was withdrawn from the analyses; and when it was not included in any known female's home range, it was attributed to a novel, unidentified female, and included in the analyses.

To model the spatial distribution of females in each plot, a simulated HR was first drawn in GIS as a circular polygon buffer centered on each occurrence point (nest or capture points). Two sizes of HRs were assumed, representing an average-sized HR and a three-fold larger HR that reflects the upper size limit as estimated by telemetry (see Results). Second, a grid with 30 m x 30 m polygon cells was generated over the area of each plot using the ArcView extension Draw Vector Grid 2.0 (Tchoukanski 2002). This polygon size was adopted to approximate the average size of male territories at leks (see Results). Third, the number of female HR polygons overlapping in each 30 x 30 m polygon cell was counted using the ArcView extension Count Overlapping Polygons (Smith 2004). The resulting grid was then converted to a raster layer where the value of each 30 x 30 m grid cell represented the number of females estimated to overlap in that cell. In models that assumed no patch devaluation, each female HR was assigned a value of 1; in models with devaluation, the value of each female HR was $1/m$, where m = number of male territories intersected by that female's home range. The total number of females overlapping each male territory was estimated for each of the eight models (Table 1) using zonal statistics, where each zone was defined as an individual male territory (ArcGis Spatial Analyst extension). Number of females HRs overlapping male territories was compared across models with non-parametric linear correlations and with two-way repeated-measures ANOVAs, where individual male territories are the subjects, plot is the between-subject factor and HR size (4 or 12 ha) and devaluation (assumed or not) are within-subject factors. Before conducting the repeated-measures ANOVAs, Mauchly's tests were performed with the variances of differences, which, in all cases, were shown not to violate sphericity assumptions (Von Ende 2001). Effect size of each factor, or their interaction, was estimated by partial *eta*-square (η_p^2), a measure of the correlation between the factor and the dependent variable.

Testing the hotspot hypothesis

We tested the hotspot hypothesis by asking whether males establish territories over female hotspots, i.e., areas where they are likely to encounter more females than would be expected if territories were randomly distributed in space. For each model of female distribution, 30 x 30 m non-overlapping cells were randomly selected on each plot, in a number similar to the observed number of real male territories, and the mean number of female HRs overlapping these random territory sites was determined. This operation was repeated 300 times to generate a distribution of expected values, and the one-tailed probability for the null hypothesis of no difference between number of females intercepted at real and random territory sites was estimated as the proportion of simulation means with values more extreme than the observed mean (percentile method, Efron and Tibshirani 1993).

Spatial distribution of males and females may be correlated in a more complex fashion than stated above. For example, it is possible that males establish leks near but not precisely over female hotspot patches. Examples of mechanisms that could account for this pattern are trade-offs between tracking of females and fine-scale, sex-specific habitat requirements or tendency for females not to nest near leks because of increased nest predation risk. To investigate whether leks are more likely to occur near female hotspot patches, we classified each of the 30 x 30 m grid cells in each plot as a lek or a non-lek cell, and correlated the number of female HRs overlapping each cell to the distance to the nearest lek. If lek patches are closer to high female-density patches than non-lek patches, a negative correlation should be observed between number of females per cell and distance to the nearest lek. Statistical significance of the correlation was determined using a procedure implemented in Passage 3.4 (Rosenberg 2001), which adjusts the number of degrees of freedom using Moran's *I* to estimate the degree of spatial autocorrelation in the data set.

Overlap of sexes in environmental space

We examined sex-specific differences in habitat use by comparing the environmental space occupied by display territories and nest sites, which represent critical areas for reproductive success for individual males and females, respectively. Analyses were performed for each plot separately and, to avoid pseudo-replication, only one nest per female was considered. In GIS, a circular buffer zone with a radius of 20 m was created around each nest; this buffer size was chosen to approximate the size of male territories such that comparisons were done at a similar spatial scale. Each male territory or nest site was given a unique numeric identifier. The plots were divided into 1 m x 1 m grid cells, and the environmental characteristics of each territory or nest site were then determined using zonal statistics. Ten environmental variables were extracted, representing mean and range of elevation (in meters), slope (in degrees), distance from streams (in meters), and arcsine and cosine of aspect (i.e., orientation).

Discriminant canonical analyses (DCA) were used to differentiate male territories and nest sites based on the environmental space occupied by each group. To reduce collinearity among the independent variables, non-parametric correlations were performed between each pair of variables; variables showing high pairwise correlations ($r_s > 0.6$) were subjected to one-way ANOVAs with sex as the main effect, and those with the greatest among-group variance were retained for subsequent analyses (McGarigal et al. 2000). Prior probabilities of group membership were weighted by sample sizes and environmental variables were entered together in the model. Variables included in final models fitted normality and homogeneity of variance assumptions or deviated only slightly; transformation of variables did not change results so we used untransformed variables. All statistical analyses were performed in SPSS 11.5 (SPSS 2002); unless indicated, values presented are mean ± SD.

Results

Male spatial distribution and lek structure

Lek structure, defined by lek density, lek size (males/lek), territory size, and inter-lek distance, was very similar between plots. Thirteen to 14 leks were found each year in each plot, encompassing between one and seven individual male territories, with a mean of 2.7 and 3.2 males/lek on Puma and Harpia plots, respectively (Fig. 1). Nearest-neighbor distance between leks, as measured between lek centroids, was 189 ± 63 m for Puma and 224 ± 76 m for Harpia. Estimated territory sizes ranged from 206 to 5045 m^2, averaging 818 ± 451 m^2 on Puma and 1187 ± 917 m^2 on Harpia; thus, the average male territory was approximately equivalent in size to a 30 x 30 m square. As expected, male territories were spatially aggregated in both plots, significantly so on Harpia

(Harpia, $I_a = 1.43$, $p = 0.016$, one-tailed test; Puma, $I_a = 1.18$, $p = 0.09$). Leks, on the other hand, had random-to-regular spatial distribution (Harpia, $I_a = 0.84$, $p = 0.20$; Puma, $I_a = 0.75$, $p = 0.07$).

Female captures and nests

A total of 71 and 78 adult individual females were captured on the Harpia and Puma plots, respectively (Fig. 2). Number of captures per female across the entire study period ranged from one to seven. Females were randomly distributed according to capture points (only one capture point per female; Harpia, $I_a = 0.87$, $p = 0.24$; Puma, $I_a = 0.87$, $p = 0.29$). Nest location data also suggests that females were substantially separated in space. A total of 66 nests (31 active, 35 inactive) were found on Harpia and were assigned to 29 individual females, with one to six nests assigned to each female; 35 nests were found on Puma (18 active, 17 inactive) and were assigned to 18 different females, with one to five nests per female (Fig. 2). Distribution of nest points was random-to-regular (one nest point per female; Harpia, $I_a = 0.66$, $p = 0.002$; Puma, $I_a = 0.93$, $p = 0.41$).

Considering only active nests, average inter-nest distance of an individual female was 49 ± 23 m (range: 20-99 m, $N = 17$ pairwise distances; a single outlier female that had one nest in 2004 and another in 2005 separated by 145 m was removed from this analysis). The distance between an active nest and the nearest active nest of a different female was 189 ± 134 m (range: 61-743 m, $N = 36$; a single outlier point was removed, representing two different females nesting 34 m apart). Thus, nests belonging to a same female were substantially closer to each other than to nests belonging to a different female.

Models of female spatial distribution: effects of HR size and devaluation

Female HRs averaged 4 ha when estimated as 100% MCP (95% CI: 2-6 ha; range: 1.5-12.9 ha). A circular 4-ha range would have a radius of 113 m, which is in close agreement with the mean recapture distances of 90.3 m observed for females. Models of female spatial distribution were built assuming two different HR sizes: (1) 4 ha, or a circular area with a radius of 113 m, representing an average-sized HR, and (2) 12 ha, or a circular area with a radius of 200 m, representing an upper size-limit HR, as estimated with radio-telemetry.

Female home ranges encompassed, on average, just one lek according to models that assume a 4-ha range (Harpia, nests or captures: 1.0 ± 0.8 leks / HR; Puma, nests: 0.8 ± 0.6, captures: 0.8 ± 1.1), or two leks when a 12-ha HR is assumed (Harpia, nests: 2.1 ± 0.7, captures: 2.3 ± 1.0; Puma, nests: 1.9 ± 0.7, captures: 1.8 ± 0.9).

Mean number of female HRs estimated to overlap a male territory varied from 0.4 to 8.9 depending on model and plot (Fig. 3, see also Fig. 4 for examples). Number of females at each male territory was highly correlated across models (Harpia models: $p < 0.05$ for 26 out of 28 pairwise comparisons, r_s values = 0.32-0.85; Puma models: $p < 0.05$ for 28/28 pairwise comparisons, r_s values = 0.42-0.93), demonstrating that the different models produced qualitatively similar outputs.

Quantitatively, however, patch devaluation and HR size, as well as their interaction, had strong effects on the number of females a given male could expect to encounter (Table 2). These effects were similar for models based on nests or captures, and between plots (Fig. 5; notice the lack of a significant plot effect on number of overlapping females, Table 2). As expected, number of female HRs overlapping a male territory increased with female HR size. This increase was, however, slowed down by patch devaluation. When devaluation was assumed, the effect of HR size, although still significant, was reduced to less than one third of its effect in the absence of devaluation (one-way repeated-measures ANOVA assessing the effect of HR size in devaluation models based on nests: $F_{1,72} = 20.047$, $p < 0.001$; η_p^2, the effect size of HR size is 0.22, compared to 0.70 for non-devaluation models; for devaluation models based on captures: $F_{1,72} = 12.351$, $p = 0.001$, HR size $\eta_p^2 = 0.15$, compared to 0.85 for non-devaluation models).

Also, for a given HR size, devaluation significantly decreased the number of females a male may expect to encounter (Fig. 5). This effect was significant for both HR sizes (HR = 4 based on nests: $F_{1,72} = 20.047$, $p < 0.001$; based on captures: $F_{1,72} = 80.565$, $p < 0.001$; much larger differences were observed for 12-ha HR models, so *post-hoc* comparisons were not performed), but it was 25-40% stronger when the larger HR was assumed (models based on nests: η_p^2 is 0.58 vs. 0.77 for HR = 4 and 12 ha, respectively; models based on captures: $\eta_p^2 = 0.53$ vs. 0.88 for HR = 4 and 12 ha, respectively).

In summary, the number of females at male territories increases with female HR size, but this increase is slowed by patch devaluation; this is due to the fact that, for a given size of HR, patch devaluation reduces the number of females a male can expect to encounter.

Testing the hotspot hypothesis

On each plot, mean number of females intercepted at male territories significantly differed from random expectations for five to six of the eight models of female distribution, including all models assuming devaluation (Fig. 3). However, the direction of the differences was opposite to that hypothesized: on average, males at real territories consistently intercepted females in numbers similar to or *lower* than expected if their territories were randomly located in space. Thus, rather than being located at female "hotspots", most territories are actually located at "coldspots", or else in sites where female density is not different from random expectations.

The variance in number of females intercepted per male was, however, large, especially for devaluation models (see above). As a result, for any given model a small proportion of males had territories located at hotspots. In non-devaluation models, on average 24% of the territorial males intercepted more females than expected by chance, whereas in devaluation models this proportion fell to 9% (Fig. 6). However, once more contradicting predictions of the hotspot hypothesis, leks overlapping female hotspots were not larger than those located outside of hotspots. Rather, in a consistent way across models and for both plots, leks located at hotspots were smaller than leks located away from hotspots (Harpia: 2.9 ± 1.0 vs. 3.9 ± 1.4 males/lek, respectively; Puma: 2.1 ± 1.1 vs. 3.2 ± 1.3, respectively; values averaged across models). Leks were also not more likely to be located near hotspot patches (Table 3). Number of female HRs overlapping at a given cell and distance from this cell to the nearest lek were uncorrelated for all non-devaluation models in both plots. For most devaluation models, a strong and significant correlation did exist (r-values: 0.30-0.41) but was positive and therefore opposite to the direction hypothesized by the hotspot model. In sum, increasing the number of females in a patch did not increase the probability that a lek would be located nearby and in some cases (when devaluation was assumed) actually decreased this probability.

Overlap of sexes in environmental space

Male territories and female nest sites were moderately segregated along an environmental axis, significantly so on Puma but not on Harpia (Fig. 7). Based on the environmental variables, the discriminant analysis was able to correctly assign points as being male territories in 81.4% of the cases on Harpia and in 84.4% of the cases on Puma. Efficiency of assignment of nest sites was lower on both Harpia (50%) and Puma (55.6%). In both plots, nest sites were closer to streams than were male territories. On Harpia, nests were located in steeper areas than were male territories, while on Puma nests were in flatter sites. This reflects the topographic differences between the plots: Harpia is dominated by unflooded upland forest, and streams are concentrated in areas dissected by ravines; on Puma, the larger concentration of streams are in flat areas dominated by seasonally inundated forest.

Discussion

The hotspot model is arguably the most influential hypothesis for the formation of leks, yet it has received mixed support. Some species form leks in areas of high female traffic (sage grouse *Centrocercus urophasianus*, Gibson 1996; ochre-bellied flycatchers *Mionectes oleagineus*, Westcott 1997), near nesting sites (greater prairie chicken *Tympanuchus cupido*, Schroeder and White 1993) or near feeding patches used by females (four species of manakins, Théry 1992). For other species, however, hotspots are only partially important in explaining male aggregation patterns. For example, there is evidence that leks of the topi *Damaliscus lunatus* are initiated in areas where females concentrate, but other mechanisms are subsequently important in modulating lek structure, such as clustering of satellite males around successful, 'hotshot' males and/or a positive feedback caused by female preference for clustered males (Gosling and Petrie 1990; Bro-Jørgensen 2003).

For other species, the hotspot model has been dismissed because leks were not located in areas of high female concentration (cappercaillie *Tetrao urogallus*, Wegge and Rolstad 1986; three species of ungulates, Balmford et al. 1993; small heath butterfly *Coenonympha pamphilus*, Wickman et al. 1995) or because female decoys failed to attract wild males (little bustard *Tetrax tetrax*, Jiguet and Bretagnolle 2006). We did not find evidence that *L. coronata* leks are located on female hotspots (defined as areas where a large number of females' home ranges overlap) or in their proximity. To the contrary, we found that most territorial males settle on areas where they intercept *fewer* or as many females as expected if they were distributed randomly in space. These results held for both plots, across models assuming different HR sizes and devaluation conditions, and for two independent data sets of female occurrence (captures and nests).

It seems counter-intuitive that lekking males would settle in areas of low female concentration. Is it possible that males do not have enough information about female distribution to make better settlement decisions? We find this explanation unlikely: the strong site-fidelity and long life-span observed for this species should result in a high degree of spatial predictability in female distribution that favors optimal male settlement. Rather, the lack of spatial correlation between males and females may be due to differences in the habitat selected by lekking males and nesting females: in particular, nest sites were located closer to streams than leks in both plots. Similarly, location of *T. urogallus* leks did not coincide with areas of high female overlap but was strongly influenced by habitat quality (Wegge and Rolstad 1986). In addition, whereas *C. urophasianus* leks seem to follow hotspot settlement rules at a coarse spatial scale, sex-specific habitat requirements disassociate distributions of males and females at a finer scale (Bradbury et al. 1989). Habitat selection by lekking males also seems to be important for niche partitioning among the several manakin species coexisting in the study area (Loiselle et al. 2007). From the female perspective, selection of optimal nest habitat and positioning of nests away from noisy display sites may be favored due to the extremely high rates of nest predation observed (Tori et al. 2006; Durães et al. unpubl. data).

It is possible that hotspots play a role in modulating lek structure in *L. coronata*, but that other mechanisms are further involved. Variance among males in number of females intercepted was high for all models, and some males were always settled at hotspots, particularly for non-devaluation models. Mechanisms that could explain why high-quality patches remain unoccupied are, for example, unequal competition in male settlement (Sutherland 1996), in which patches are occupied according to competitive ability of males, coupled with patch limitations set by habitat selection and/or territorial behavior of males setting minimum inter-lek distances (see below). In addition, we can not rule out the possibility that the hotspot model might hold if female concentration had been characterized differently, e.g., based on foraging areas (e.g., Théry 1992) or corridors of female movements (e.g., Westcott 1997), rather than based on overlapping female home ranges. This is conceivable because females can make rapid visits to key foraging sites that are difficult to detect with radio-telemetry.

However, we consider it more likely that hotspot settlement strategies are not advantageous for *L. coronata*. Despite the spatial predictability in female distribution, the long breeding season with low synchrony in mating receptivity of females may render high-quality patches temporally unpredictable. Also, females may not be concentrated enough to warrant hotspot patterns of settlement. Female *L. coronata* have small home ranges (4 ha, on average) with relatively little overlap and distributed in a random-to-regular, rather than aggregated, pattern. Further, there was evidence for moderate sex-specific habitat selection, which suggests that patches preferred by females may be unsuitable for lek establishment and vice-versa. Finally, the uniform dispersion of leks and the regularity in their structure – very similar lek density, size, and inter-lek distances in both plots – suggests that a settlement pattern that minimizes competition among leks may be more important than one that tracks female distribution. Likewise, Wegge and Rolstad (1986) suggested that the remarkably regular spacing of *T. urogallus* leks seems to be regulated by the territorial behavior of males.

In summary, we suggest that territorial behavior and habitat selection may be more influential than hotspot mechanisms in shaping lek distribution and structure in *L. coronata*. Limited female aggregation, temporal unpredictability in the distribution of receptive females, and sex-specific habitat requirements may reduce the potential benefits gained by males settling at hotspots. When both males and females are long-lived and site-faithful, as in this species, there may be little need for individuals of opposite sexes to be spatially correlated: females know where leks are and can leave their usual home ranges to mate. This has been confirmed by molecular analyses of paternity showing that females do not necessarily mate with males at the closest leks and that sires may have territories located well outside a female's home range (see Chapter 3 of this dissertation). We can therefore predict that traditional lek territories would receive more female visits than newly established territories, a hypothesis to be tested when more data accumulate. In keeping with this prediction, lek locations of this (see Chapter 2 of this dissertation) and other species (Westcott and Smith 1994; Hovi et al. 1996) tend to be consistent across years despite sometimes considerably high rates of turnover in male ownership. In addition, mating histories of territories are correlated across years in some lekking species, because females tend to go back to the same territories to mate, regardless of changes in male ownership (Gibson et al. 1991).

HR size and devaluation effects on patch suitability

Regardless of the overall lack of support for hotspot settlement rules in *L. coronata*, the fact that our models showed strong effects of HR size and devaluation – and the interaction of the two – deserves further attention. Not surprisingly, increasing the size of female HRs increased the average number of females intercepted at a territory; more interesting, though, was how HR size interacted with devaluation. Without devaluation, a three-fold increase in HR size caused an increase of the same magnitude in numbers of females intercepted, but when devaluation was taken into account, these numbers increased half as fast. Everything else being equal, the larger the HR of a female, the more males she will visit and the stronger the effect of devaluation is expected to be. In fact, the effect of devaluation on patch suitability was more pronounced with the larger HR: on average, devaluation caused a 56% reduction in number of females intercepted in models with a 4-ha HR, compared to a 77% reduction with a 12-ha HR. Devaluation also had a stronger effect than HR size in determining patch suitability, as demonstrated by the estimates of effect size (Table 2). This last observation is in general agreement with the computer simulations performed by Bradbury et al. (1986), in which devaluation had a stronger effect on hotspot topography than changes in HR size.

Given its overriding influence in the outcome of our models, how important is devaluation in our study system? Because females often nest several times within a breeding season due to high nest failure rates, a fertilization does not necessarily deplete a patch for other males over the course of the entire breeding season. Yet, this assertion depends on a simplistic scenario in which females do not always mate with the same male, an assumption that at present we are unable to verify. However, strong skew in male mating success has been reported for other species of manakins and, although this is mostly based on field observations (Lill 1976; McDonald and Potts 1994), at least in one case, strong male reproductive skew was substantiated by genetic analyses of paternity (DuVal 2007), suggesting that patch devaluation may in fact be important in manakin populations.

Concluding remarks

Spatial models such as the hotspot model and its variants remain at the core of lek-evolution theory, yet few studies have attempted to test them empirically. Moreover, the idea of patch devaluation by neighboring males is often ignored, although this is one of the main assumptions of the model. While strong evidence supporting the hotspot model was found for *Mionectes oleagineus* (Westcott 1997), another lekking member of the Tyrannoidea clade (which includes flycatchers and manakins), and more indirectly for *L. coronata* and red-capped manakin *Pipra mentalis* (Westcott 1994), its rejection in this study renews the debate on how leks evolve and are shaped. So far, the only firm conclusion we can reach is that spatial considerations are an important issue for lek evolution that likely involve multiple interacting mechanisms.

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Table 1 – Parameters of the eight models of spatial distribution of *L. coronata* females built for each of two 100-ha study plots.

Class of occurrence point	Female home range size (ha)	Devaluation assumed?	Model
Captures	4	No	(1) 4C
		Yes	(2) 4C-dev
	12	No	(3) 12C
		Yes	(4) 12C-dev
Nests	4	No	(5) 4N
		Yes	(6) 4N-dev
	12	No	(7) 12N
		Yes	(8) 12N-dev

Table 2 – Two-way repeated-measures ANOVAs testing for the effect of female HR size (4 or 12 ha) and patch devaluation (assumed or not) on number of females intercepted at male territories on Harpia (n = 43 territories[a]) and Puma plots (n = 31 territories[a]), according to models of female spatial distribution based on either nests or capture points; effect size is given by partial *eta*-square (η_p^2).

	Models based on nests				Models based on captures			
Source	DF	F	p	η_p^2	DF	F	p	η_p^2
Between-subjects								
Plot	1, 72	2.836	0.096	0.038	1, 72	0.387	0.536	0.005
Within-subjects								
Devaluation	1, 72	250.875	**<0.001**	0.777	1, 72	397.992	**<0.001**	0.847
HR size	1, 72	145.926	**<0.001**	0.670	1, 72	285.862	**<0.001**	0.799
Devaluation x HR	1, 72	163.262	**<0.001**	0.694	1, 72	390.335	**<0.001**	0.844

[a] To avoid spatial biases in the analyses, only territories located inside the plot boundaries were considered.

Table 3 – Correlations between the number of female HRs overlapping at a given grid cell and the distance from this cell to the nearest lek, on (a) Harpia and (b) Puma plots. *P*-values and sample sizes were corrected for spatial autocorrelation among cells.

Model	*r*	Effective *n*	Corrected *p-value*
(a) Harpia plot			
C4	0.11	56	0.426
C4-dev	0.37	53	**0.006**
C12	0.07	54	0.598
C12-dev	0.38	45	**0.009**
N4	0.15	76	0.189
N4-dev	0.39	77	**0.001**
N12	0.16	58	0.245
N12-dev	0.41	48	**0.004**
(b) Puma plot			
C4	0.09	57	0.487
C4-dev	0.30	49	**0.034**
C12	0.08	61	0.516
C12-dev	0.38	47	**0.008**
N4	-0.12	58	0.388
N4-dev	0.05	60	0.704
N12	-0.12	51	0.396
N12-dev	-0.09	67	0.450

Figure Legends

Figure 1 – Location of leks and individual male *L. coronata* territories in two 100-ha study plots, Harpia and Puma, in Tiputini, Ecuador.

Figure 2 – Distribution of *L. coronata* females on Harpia and Puma plots based on location of nests (asterisks) and capture points (circles). Each nest or capture point represents an individual female, but any individual female may be depicted by both a nest and a capture point. Captures were performed between 2001 and 2006; each circle represents 1-3 (Harpia) or 1-4 (Puma) individual females. Nests were located in the breeding seasons of 2004, 2005, and 2006.

Figure 3 – Mean number (and SE) of female home ranges overlapping at male territories (gray bars) and at an equal number of random sites (white bars) on (a) Harpia and (b) Puma plots, as estimated by eight models of female distribution (see Table 1). For most models, males intercepted less females at their territories than expected by chance; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; *a* = statistical significance disappears when applying a sequential Bonferroni procedure (Rice 1989) across tests based on either nests or captures.

Figure 4 – Modeled patterns of female distribution for the Harpia plot, assuming an average female HR size of 4 ha; the four different models were based either on capture or nest points, with or without patch devaluation. Values are number of females per cell; cells are 30 x 30 m in size; white crosses indicate centers of male territories.

Figure 5 – Effect of female home range (HR) size and patch devaluation on number of females HRs overlapping at *L. coronata* male territories on Harpia plot, according to models based on (a)

nests or (b) capture points. Vertical bars indicate 1 SE. Patterns for Puma plot were identical and are not shown.

Figure 6 – Proportion of lekking males intercepting fewer (in white), same number (light gray), or more (dark gray) females than expected if territories were located randomly in space, according to eight models of female distribution (see Table 1), on (a) Harpia plot ($n = 43$ territorial males) and (b) Puma plot ($n = 31$). Asterisks indicate models for which males intercepted on average significantly less females than expected (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; see also Figure 3).

Figure 7 – Discrimination of *L. coronata* male territories (open circles) and nest sites (closed circles) along an environmental axis, on (A) Harpia and (B) Puma plots; centroids ± 1 SE bars are shown above or below points. Variables more strongly correlated with the axis are specified, along with the correlation coefficient between the variable and the discriminant function. Harpia plot: number of variables included in model = 7; eigenvalue = 0.203; canonical correlation = 0.41; χ^2 = 12.09; $p = 0.10$. Puma plot: number of variables = 6; eigenvalue = 0.341; canonical correlation = 0.51; χ^2 = 13.22; $p = 0.04$.

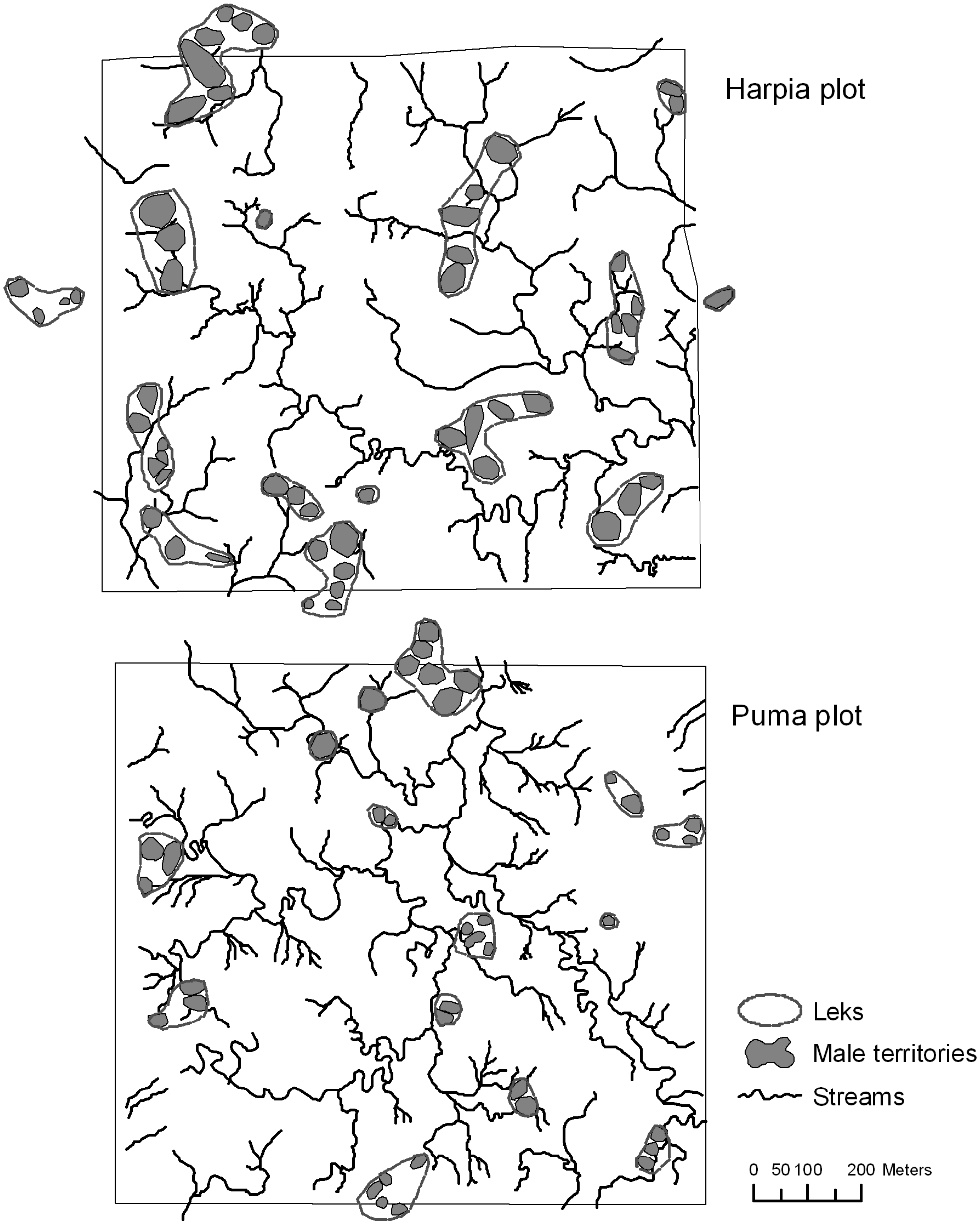

Harpia plot
Puma plot
Leks
Male territories
Streams
0 50 100 200 Meters

Figure 1

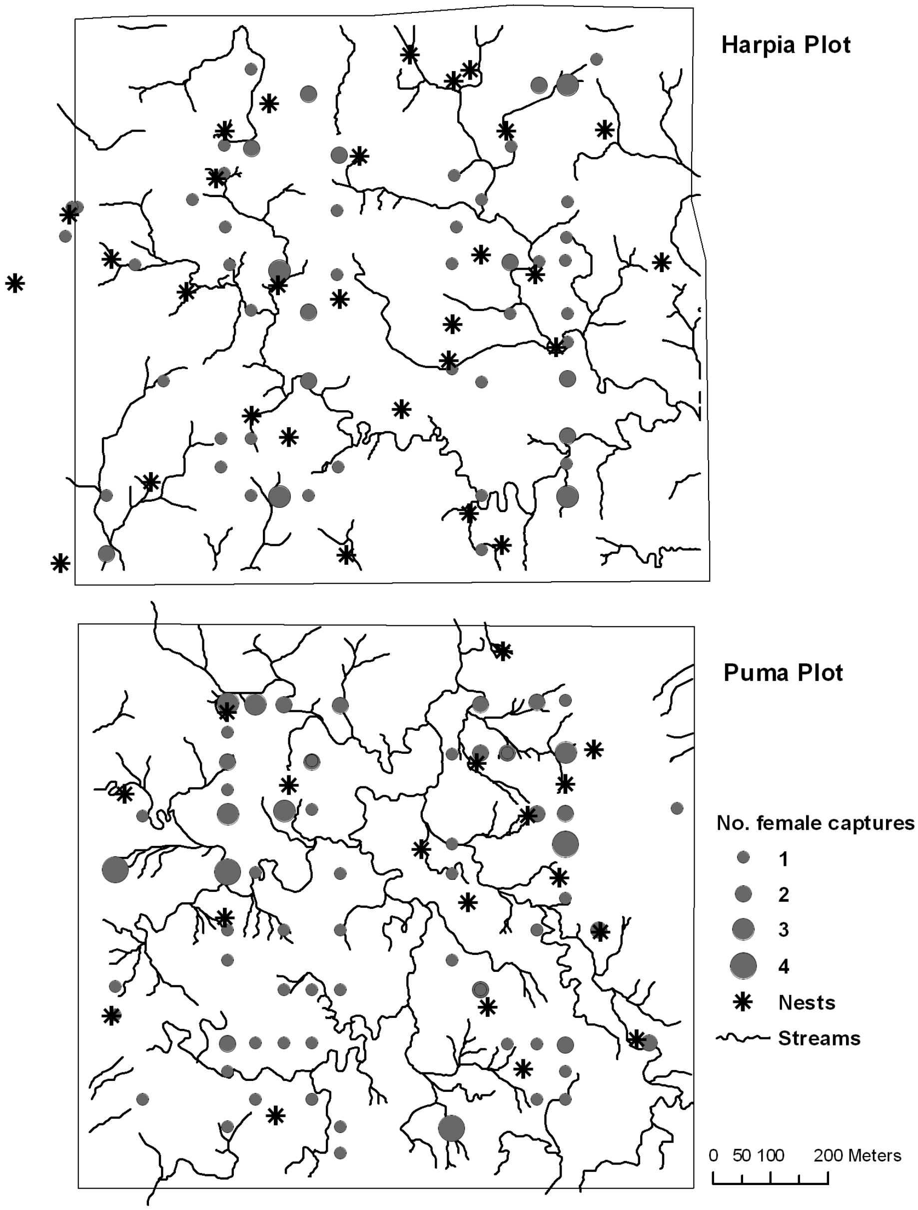
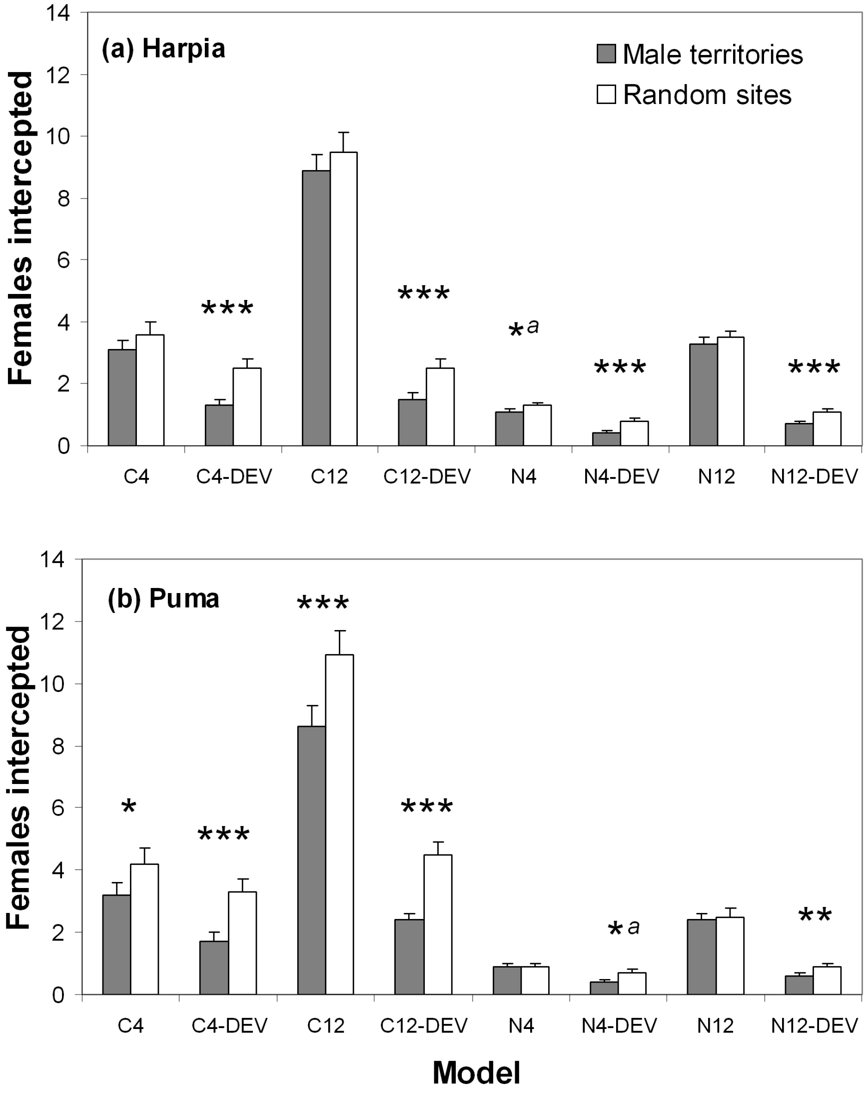

Harpia Plot
Puma Plot
No. female captures
1
2
3
4
Nests
Streams
0 50 100 200 Meters

Figure 2



(a) Harpia
Male territories
Random sites
Females intercepted
14
12
10
8
6
4
2
0
***
***
*a
***
***
C4
C4-DEV
C12
C12-DEV
N4
N4-DEV
N12
N12-DEV
(b) Puma
Females intercepted
*
***
***
***
*a
**
C4
C4-DEV
C12
C12-DEV
N4
N4-DEV
N12
N12-DEV
Model

Figure 3

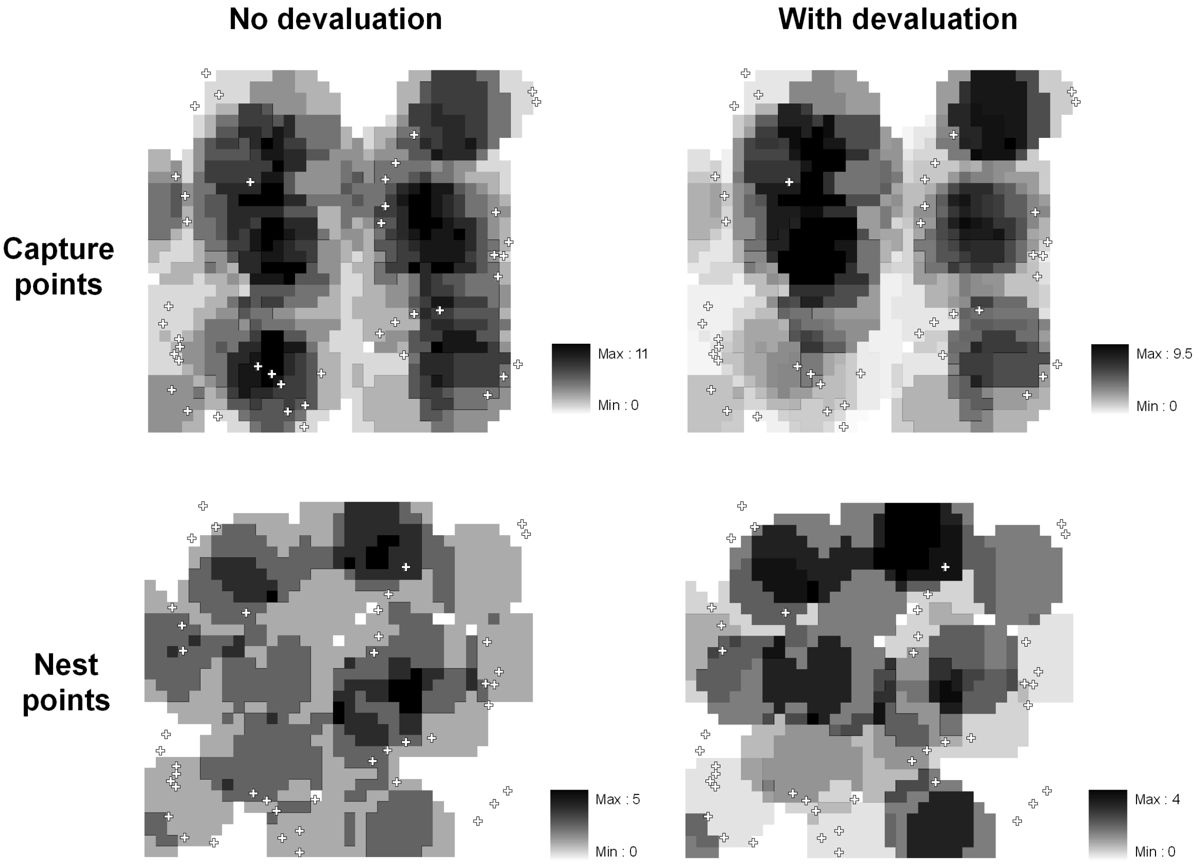
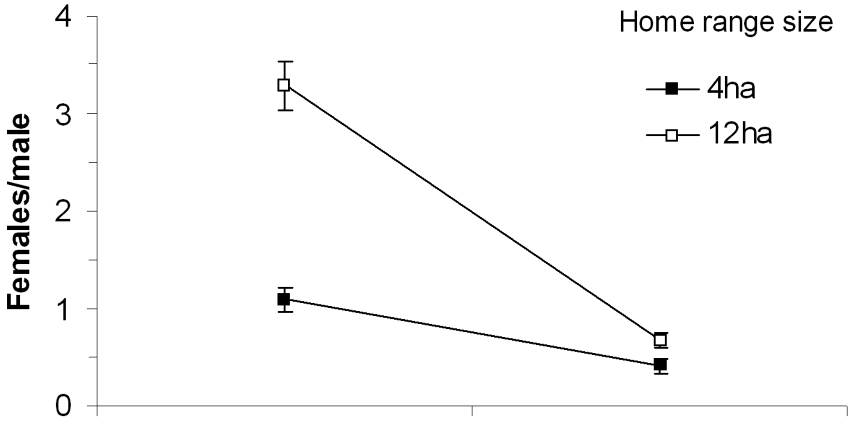

No devaluation
With devaluation
Capture points
Nest points
Max : 11
Min : 0
Max : 9.5
Min : 0
Max : 5
Min : 0
Max : 4
Min : 0

Figure 4

(a) Models based on nests



(b) Models based on captures

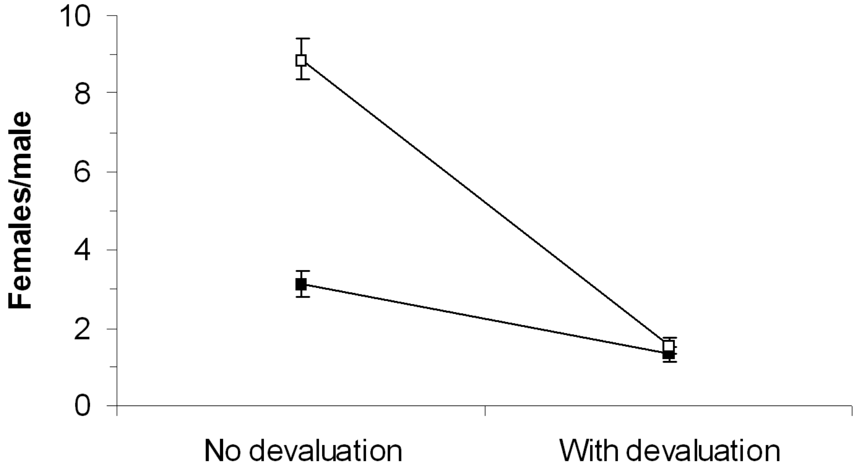
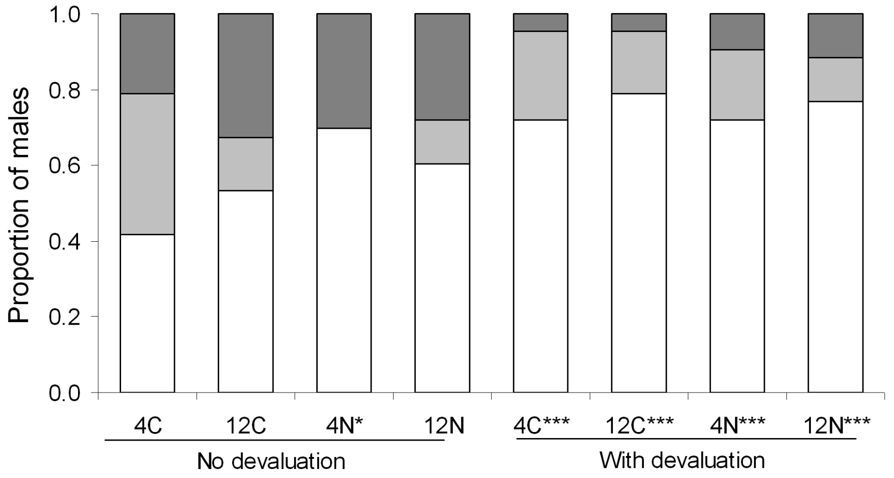


Figure 5


(a) Harpia

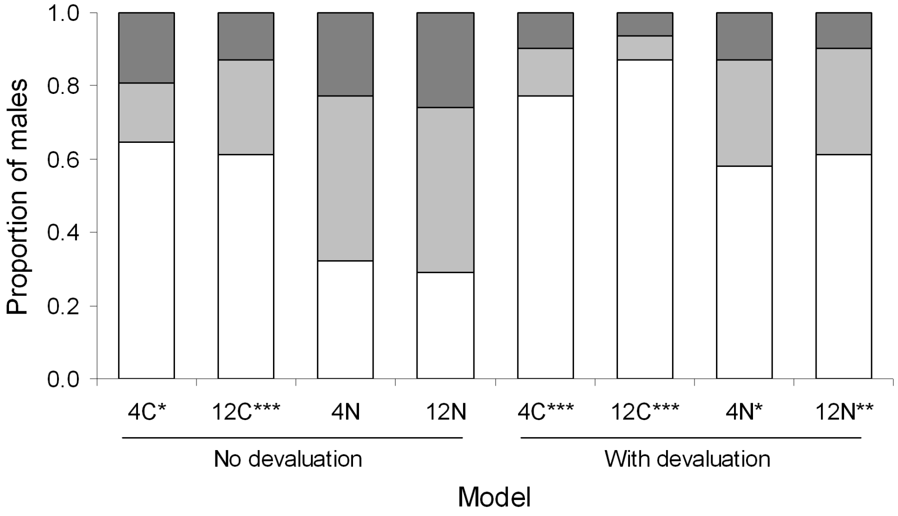

(b) Puma

Figure 6

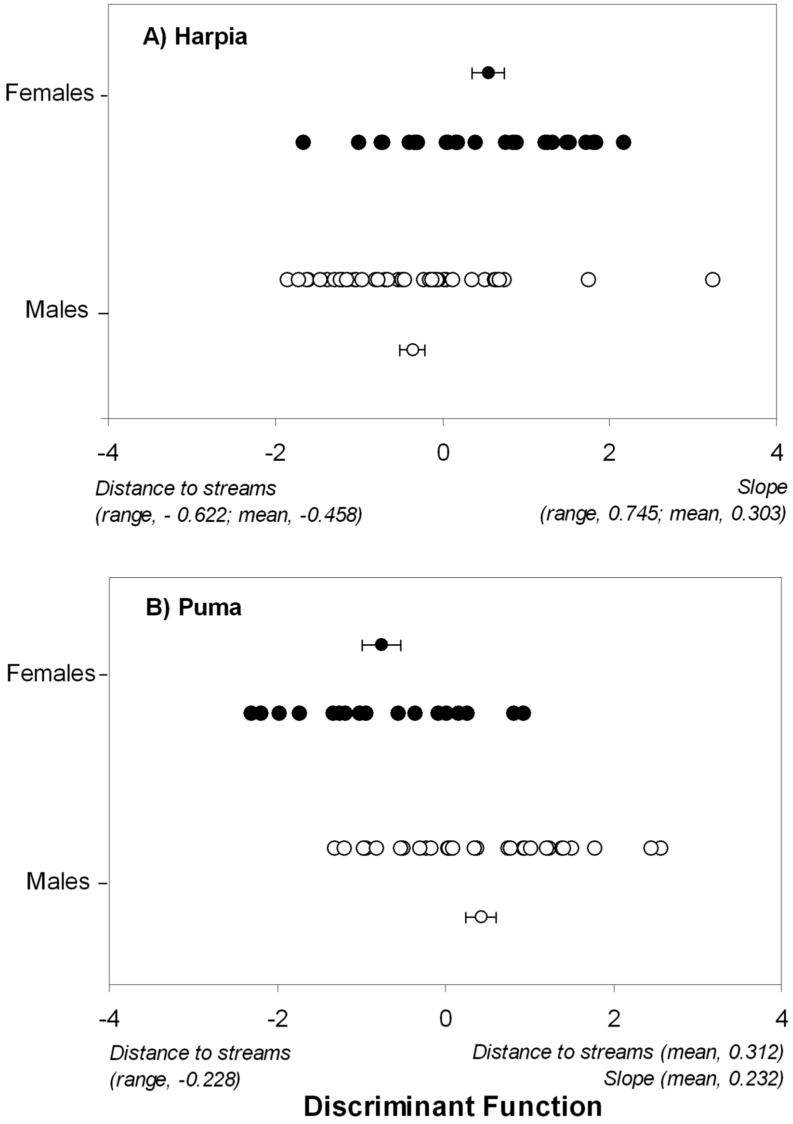

A) Harpia
Females
Males
-4
-2
0
2
4
Distance to streams
(range, - 0.622; mean, -0.458)
Slope
(range, 0.745; mean, 0.303)
B) Puma
Females
Males
-4
-2
0
2
4
Distance to streams
(range, -0.228)
Distance to streams (mean, 0.312)
Slope (mean, 0.232)
Discriminant Function

Figure 7

Chapter 2

Spatial and Temporal Dynamics at Manakin Leks: Reconciling Lek Traditionality with Male Turnover

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Abstract

Leks, display grounds where males congregate and females visit to copulate, are typically traditional in location, despite often high turnover of individual males. How leks can persist in face of male turnover is not well understood, in part due to a lack of detailed field data allowing for a clear understanding of lek dynamics. We followed the fate of individual males at 11 to 15 leks of the blue-crowned manakin *Lepidothrix coronata* across 4 breeding seasons to gain insights on how leks are formed and change in space and time. Between years, leks were traditional in location despite changes in territory ownership due to male disappearance and recruitment. New males were equally likely to recruit by taking over existing territories or by establishing new territories. Recruitment was influenced by age, as recruits were more likely to be adults than sub-adults. Lek size did not affect the probabilities of a male recruiting or persisting at a territory, and vocalization rate, a correlate of mating success in this population, did not affect male persistence. We used our field data to model changes in lek size and composition over longer periods of time (100 yrs) to understand how lek traditionality can be reconciled with high male turnover. Our simulations showed that leks in our population rapidly stabilize in size despite changes in territory ownership,

and that rates of male recruitment and disappearance compensate each other, such that leks have the potential to persist for several decades after the original males have disappeared from them.

Introduction

Lekking is a type of promiscuous mating system in which males aggregate at display grounds, the 'leks', to attract females for copulation (Bradbury and Gibson 1983, Wiley 1991). Leks of birds and mammals typically are traditional in location over time, as males congregate at the same sites in successive years and recruiting males tend to join existing leks rather than establish new, isolated territories (Lill 1976, Hovi et al. 1996, Wiley 1991). Yet, turnover of individual males via disappearance and recruitment at leks can be high (Höglund and Robertson 1990a, Gibson 1992, Westcott and Smith 1994). Leks can thus be viewed as dynamic mating foci where individual males are replaced over time.

Mechanisms maintaining lek traditionality in the face of high male turnover are not fully understood. Site traditionality suggests that there are spatial limitations for the establishment of leks, that males benefit by settling in pre-established leks, or both. In relation to the first alternative, there is evidence that creation of new leks may be limited to some extent by availability of suitable habitat, constraints on optimal spacing among males, or niche partitioning between the sexes or with other lekking species (Wegge and Rolstad 1986, Bradbury et al. 1989b, Gosling and Petrie 1990, Westcott 1993, Durães et al. 2007, Loiselle et al. 2007). In relation to the second alternative, two main hypotheses address how males that occupy traditional lek sites would have increased fitness. First, if the species is long-lived and females tend to return to familiar sites to mate, new male recruits that occupy territories vacated by successful males, or that join leks that receive a large number of female visits, would 'inherit' the mating history of these sites, a phenomenon known as 'temporal spillover effect' (Apollonio et al. 1989, Gosling and Petrie 1990, Gibson et al.

1991, Gibson 1992, Jiguet and Bretagnolle 2006). Alternatively, traditionality could be maintained if successful males tend to hold the same territories across years, but there is turnover of lower-rank males that cluster around these 'hotshot' males in an attempt to intercept copulations (the 'hotshot' or 'spatial spillover effect', Höglund and Robertson 1990b, Rintamäki et al. 1995, Lanctot et al. 1998).

All these are mechanisms by which lek site traditionality could be sustained with high turnover of individual males, at least up to some threshold level. Several factors may influence rates of male turnover at leks. The first and most obvious of these are the intrinsic rates of recruitment and mortality in the population (e.g., Bradbury et al. 1989a, Alatalo et al. 1992). However, male behavioral strategies may also play a role in modulating turnover at leks. For example, males may recruit into some leks at a higher rate due to female preferences for leks in a given size range (Lank and Smith 1992, Höglund et al. 1993, Hovi et al. 1996, Jiguet and Bretagnolle 2006, but see Lanctot et al. 1998). Individual competitive abilities of males may also affect turnover rates at leks because the optimal lek size and tenure time may differ in relation to relative competitive ability, affecting the probability that a given individual would recruit into or remain at a given lek (Alatalo et al. 1992, Widemo and Owens 1995, Westcott and Smith 1997, Hernandez et al. 1999, Apollonio et al. 2003). Finally, previous individual mating history may affect turnover at leks when successful males tend to return to the same territories between breeding seasons, and unsuccessful males are more likely to change territories (Höglund and Robertson 1990a, Gibson 1992, Westcott and Smith 1994, Rintamäki et al. 1995, Apollonio et al. 2003).

Although hypotheses have been proposed to reconcile individual turnover at leks with their long-term spatial stability, we currently lack a clear understanding of what drives this pattern. In part, this is due to a paucity of data from natural populations on rates of male turnover and lek stability: most reports are anecdotal and there have been few attempts to quantify turnover across years. Here, we provide such information based on observations at leks of the blue-crowned manakin *Lepidothrix coronata* in eastern Ecuador. Manakins (Pipridae) are lek-breeding, Neotropical birds generally characterized by marked sexual dimorphism and elaborate male courtship displays (Sick 1967, Prum 1990, Snow 2004). Leks of manakins are typically traditional in location, and there are anecdotal reports of leks persisting on the same sites for several years, and even decades (Sick 1967, Lill 1976, McDonald 1989, Tello 2001). In these long-lived species (at least 10-14 years, Snow and Lill 1974, McDonald 1993), spatial traditionality would suggest that individual males keep the same territories for several years, but too few studies have followed marked individuals across time to corroborate this. In this study, we first estimated rates of male recruitment and disappearance from leks by following the fate of banded territorial males over the course of four breeding seasons. Second, we tested for the influence of lek size, male age (a typical correlate of individual competitive ability), and vocalization rate (a correlate of mating success in the blue-crowned manakin, see Chapter 3 of this dissertation) on these rates. Third, we used the estimated rates of male recruitment and persistence at territories to model changes in lek size and composition over longer periods of time, in an attempt to understand how traditionality in lek location can be reconciled with high male turnover rates.

Methods

Study species

The blue-crowned manakin is widespread in humid and unflooded forests below 1000 m in northwestern Amazonia, the Chocó region west of the Andes, and southern Central America (Ridgely and Tudor 1994, Snow 2004). As in most manakins, males exhibit delayed plumage maturation; females and juveniles (<1 yr-old) are bright green, younger males (‘sub-adults’) have a predefinitive plumage with varying degrees of black and blue feathers mingled with green, and males >2 years of age (‘adults’) are sooty black with bright blue crowns (Ryder and Durães 2005). Adult and sub-adult males, but not green-plumaged juveniles, establish territories at leks or display solitarily (R. Durães, in prep.; for the sake of simplicity, the term ‘lek’ will be used in this paper to describe both group and individual display sites). Leks are ‘dispersed’ (*sensu* Prum 1994), being formed by individual, contiguous male territories, each ~1000 m^2 in size (Durães et al. 2007). During the breeding season, territories are actively defended against other adult and sub-adult males, although juvenile males are usually tolerated and may form temporary coalitions with territorial males (R. Durães, in prep.). Females make short visits to leks, usually alone, to observe male displays and to mate. As in all lekking species, nest building and parental care is completely maternal.

Study site and mapping of male territories

Research was conducted at Tiputini Biodiversity Station (TBS), Orellana Province, Ecuador (00°38' S, 76°08' W, 190-270 m a.s.l.). TBS covers 650 ha of virtually undisturbed lowland, wet-evergreen forests comprised primarily of unflooded *terra firme* and flooded *várzea* habitats (more details in Loiselle et al. 2007). Over the course of four breeding seasons (from December of the previous year to April/2004, 2005, 2006 and 2007), we systematically searched for and mapped leks within and immediately surrounding a 100-ha permanent study plot (Harpia plot). Harpia ranges in elevation from 201 to 233 m a.s.l., contains a grid at 100 x 200 m intervals, and is primarily characterized by upland forest (Loiselle et al. 2007). Each year, we attempted to capture all territorial males and to mark them with unique numbered aluminum bands and color band combinations. Individual territories were delimited by mapping song perches used by the resident male during repeated visits (≥ 3 visits/year). Territories were considered to belong to the same lek when males were within auditory contact and/or if interactions among neighboring males were observed. Territory ownership was confirmed each year and several times over the course of each breeding season by re-sighting of color bands; territory ownership was never observed to change within a breeding season. The same procedures were used to map all leks in a second 100-ha plot (Puma plot, 209-235 m a.s.l.) located ~1.5 km from Harpia. Puma leks were not included in the estimation of territory transitions (see below), and data from this plot are presented here mostly as a comparison with the size distribution of Harpia leks.

To test whether the distribution of lek sizes departs from random (e.g., if there is an excess of smaller or larger leks), we did simulations in which we reshuffled males holding territories on a plot in a given year at random among the existing leks, with the constraint that each lek should receive at least 1 male. We repeated this procedure 100 times and computed the average number of leks that should fall in each size class as expected by chance. We then compared the expected and observed distribution of leks per size class with two-sample Kolmogorov-Smirnov tests.

Ownership transitions at territories

We established the transition in ownership status for each male territory in Harpia, from one breeding season to the next, for the three inter-annual periods studied (i.e., 2004-2005, 2005-2006, 2006-2007; in 2007, although we could establish the number of males at all leks, we were unable to determine confidently the identity of four territorial males and therefore we excluded these individuals when estimating rates of persistence or turnover at territories). For each territory, one of four transition classes were noted: (1) *maintained*, when the same male held the territory in one year (t_x) and also in the following year (t_{x+1}); if the initial male was not present at that territory in year t_{x+1}, the territory could either be (2) *vacated*, if it was unoccupied, or (3) *taken-over*, if a different male occupied that territory in the second year (takeovers could potentially happen by passive occupation of vacated territories or by aggressive displacement of the resident male; we were unable to ascertain the frequency of these alternatives, although we have anecdotal evidence that aggressive takeovers do occur; R. Durães, in prep). In addition, territories could be (4) *new*, if a male occupied a site at the lek that was vacant the previous year. Each male/territory/year was treated as a unit and we estimated the probability that each of these transitions would occur. Given that S (for 'survival') is the probability that a male will persist at the same territory from time t_x to time t_{x+1}, and 1- S is the probability that it will not, TO ('takeover') is the probability that a new male will recruit into the lek by occupying that territory at t_{x+1}, and B ('birth') is the probability that a male will recruit by establishing a new territory, the probabilities for each of the four transition classes can be described as:

(1) $P_{maintained} = S$;

(2) $P_{vacated} = (1\text{-}S) * (1\text{-} TO)$;

(3) $P_{taken\text{-}over} = (1\text{-}S) * (TO)$;

(4) $P_{new} = B$

The takeover rate, TO, was estimated empirically as: (number of territories taken-over) / ((number of territories taken-over) + (number of territories vacated)), averaged across time intervals. Because 1-B, the probability that a suitable, unoccupied lek site will remain unoccupied from time t_x to time t_{x+1}, can not be estimated accurately, B could only be estimated at a *per* lek basis, as: (number of new territories established) / (number of observed leks). Therefore, in order to make the rate at which new territories arise comparable to the estimates of territory persistence, vacancy and takeover for use in the simulations (see below), we assumed that males could recruit into leks via takeover or by establishing new territories with similar probabilities (i.e., $B = TO$; thus, equation (4) becomes $P_{new} = TO$). Although this may not always be true (e.g., if males establishing new territories face less resistance than males taking over pre-existing territories), we did confirm with a Chi-square test that the frequencies of recruitment by either mechanism do not differ (see Results). Chi-square tests were also used to assess whether age (sub-adult vs. adult) influenced the way a male recruits into a lek (i.e., via takeover vs. establishment of new territory), with data combined across all years, and to test whether the probability that a male recruits into a lek was influenced by lek size, for each year separately.

S, the rate of male persistence at territories, was estimated using the 'known fate' model implemented in program MARK (White and Burnham 1999). The sample unit was a male/territory association; thus, a territory that underwent a takeover, being occupied by a male at year t_x and by a different male at year t_{x+1}, corresponded to two independent data points according to the different males that came to occupy that territory. For each of the four sampled breeding seasons, an entry of 1 was given if the territory was occupied by the focal male, and an entry of 0 was given if the territory was not occupied by the focal male. Lek sizes at year t_x, the first year of each time interval, were included a unstandardized covariates. Four competing models were evaluated, which included a general model assuming a constant *S* rate irrespective of year or lek size, plus three models incorporating year and/or lek size at year t_x (Table 1). Logit or sine link options were used to build models with or without covariates, respectively. When lek size was included in a model, the real persistence parameters were estimated assuming the mean lek size in the population for that year. The relative likelihood of each model in the candidate set was estimated based on second-order Akaike's information criterion values, or AIC$_c$ (Burnham and Anderson 2002). Models with AIC$_c$ values differing by ≤ 2.00 units were considered equally supported, in which case *S* estimates were averaged across all models to account for uncertainty in model selection, with the contribution of each model to the final average being proportional to their AIC$_c$ weight (Burnham and Anderson 2002, Johnson and Omland 2004).

Lacking sufficient data to test directly for the effect of previous mating history on the probability of a male persisting at a territory, we used vocalization rates as a correlate of mating success. Display rate has been repeatedly shown as an important correlate of male mating success in lekking species (reviewed in Fiske et al. 1998), and we have data showing that this is also the case for vocal display rates in our study population (see chapter 3 of this dissertation). Vocalization rates were estimated for a sub-set of the territorial males during 30-min sessions (in 2005, 32 males observed) or 120-min sessions (in 2006, 25 males observed) conducted during early morning (0630-0830) or mid-afternoon (1400-1600), which are periods of peak lek activity. Identity of the focal male was confirmed by resighting of color bands during each observation session. Each individual was observed for a total of 132 (± 39, 1 SD) minutes in 2005 and 713 (± 271) minutes in 2006. A sitting observer recorded the number of calls given by a focal male during 5 (2005) or 10-min (2006) intervals. Calls included advertisement songs, which are produced only by males and are used for territory defense and long-distance attraction of females, and whistle calls, which are uttered by both sexes and by birds of all ages, are much softer and propagate to shorter distances than songs (R. Durães, in prep.). Data collection was halted while females or other males were present at the territory or when the focal male was displaying at his dance court. Vocalization rates were estimated as mean number of calls/min, and compared for males persisting vs. disappearing from a territory between years using a non-parametric Mann-Whitney test. Because individuals increase vocalization rates according to lek size (see Chapter 3 of this dissertation), we repeated this analysis after controlling for lek size with residual analysis, and obtained similar qualitative results (recently, the use of residual analysis in ecology has come under criticism, e.g. Darlington and Smulders 2001, but visual inspection of scatterplots confirmed a lack of consistent direction in the differences in vocalization rates between persisting and non-persisting males across lek size class). Due to the small number of males that were observed in 2006 and disappeared from territories in

2007, we combined data across years; qualitative results did not change when only data from 2005 were considered.

Simulations of lek dynamics

Estimated probabilities of male recruitment and persistence at territories were combined to model lek dynamics over periods of time longer than the four year span of this study, with the objective to understand how lek size and composition are modulated by these parameters and how long leks can remain traditional in location in the face of male turnover. A simulation started at time $t_x = 0$ with a lek whose size was chosen at random from the natural range observed in our population (i.e., 1-7 males). Each male in the lek had a probability S of persisting in its territory until t_{x+1} and S-1 of disappearing, in which case that territory had a probability TO of being re-occupied by a different male and 1- TO of remaining unoccupied at t_{x+1}. In addition, during each time interval t_x to t_{x+1}, one male could establish a new territory at the lek with probability $B = TO$. This process was iterated 1000 times for 100 years. Leks that disappeared (i.e., reached a size of 0 males) were not allowed to be re-colonized; although recolonization may potentially happen in nature, we made this assumption because we never observed it in our population. Output measures were lek size at time t_x, proportion of original males still present at time t_x, and probability that a lek will persist up to x years, which is given by the proportion of the initial 1000 leks remaining at that time period. Statistical analyses were performed in SPSS 11.5 (SPSS 2002); unless stated otherwise, values are means ± 1 SD.

Results

Lek sizes and ownership changes at territories

We located 11-15 leks each year on each study plot, though the true number of leks per study plot probably ranged from 13-15 (11 leks were located on the Harpia plot in 2004, but this number is almost certainly underestimated, as additional leks were located, with greater effort, in subsequent years). Leks were traditional in location, and lek centroids changed little in position between years (21 ± 26 m, range: 0-89 m; $n = 26$ inter-annual observations of 13 leks). The few exceptions were due to the disappearance of two leks (with 1 and 3 males in the previous year) and the establishment of a new lek by a solitary male. Leks held between 1 and 7 territorial males, with an average of 3.0 ± 1.6 males/lek (Fig. 1). Mean size of leks was similar between plots (plots compared during 2006, $t_{26} = 0.16$, $p = 0.91$) and, in the Harpia plot, among years ($F_{3,49} = 0.08$, $p = 0.97$). There was no indication that the number of leks in each size class departed from random for Harpia in any given year or for Puma in 2006 (Kolmogorov-Smirnov tests, all p-values > 0.99).

Although leks were stable both in location and in mean size within the population, individual leks changed as a result of relatively high male turnover rates. Ownership status was unambiguously established each year for 34-47 territories in 12-15 leks, for a total of 117 observed territory transitions involving 65 different individual males over four seasons (Fig. 2a). In 68% of these cases ($n = 80$), the territory was maintained by the same male between years, in 15% ($n = 17$) the territory became vacant, in 9% ($n = 11$) it was taken-over by a different male, and in 8% of the cases ($n = 9$) a new territory was established. During the observed period, 29% of the males ($n = 19$) held a territory for 1 year, 28% ($n = 18$) for 2, 26% ($n = 17$) for 3 and 17% ($n = 11$) for 4 years; because most of these histories were incomplete, however, it was not possible to make inferences about the average male tenure time in the population. Between consecutive years, leks changed in size in 32% of the cases ($n = 44$ inter-annual lek comparisons) as a result of males disappearing and/or recruiting into the lek. These changes in size ranged from a gain of 2 to a loss of 3 males per lek (Fig. 2b), with an average net change of +0.4, -0.4, and –0.3 males/lek for the inter-annual periods of 2004-2005, 2005-2006, and 2006-2007, respectively. Among the males disappearing from their territories, only one was later resighted; this male held a territory for at least two years (2004-2005), and in 2006 he had taken over another male's territory on a neighboring lek.

Recruitment of males at leks

Each year, between zero and two new males were recruited at each lek, either via takeovers (n = 11 events) or by establishing new territories (n = 9). Combining data across years, recruitment by each of these mechanisms happened at similar frequencies ($\chi^2_1 = 0.20$, $p = 0.66$). The average rate of takeovers, *TO*, was 0.39 (2004-2005: 0.33; 2005-2006: 0.40; 2006-2007: 0.43). The average rate of establishment of new territories *per* lek was 0.23 new territories/lek/year, but it was highly variable across time intervals (0.50, 0.20, and 0). Males recruiting into leks were more likely to be adults (n = 15) than sub-adults (n = 5; $\chi^2_1 = 5.00$, $p = 0.025$). This does not seem to be due to an excess of adult floaters in the population, as roughly similar proportions of unbanded adults and subadults not known to hold territories were captured each year during systematic mist-netting sampling at the plots (J. G. Blake and B. A. Loiselle, unpubl. data; see Blake and Loiselle 2008 for details on the systematic mist-netting sampling). While age seems to influence the probability of a male to recruit into a lek, it did not influence the mode of recruitment: both adults and sub-adults recruited via takeovers or by establishing new territories with similar probabilities ($\chi^2_1 = 1.68$, $p = 0.19$). The number of males recruiting into leks of a given size was proportional to the frequency of leks in that size class (2004: $\chi^2_3 = 1.37$, $p = 0.71$; 2005: $\chi^2_6 = 7.71$, $p = 0.26$; too few recruitments were observed in 2006 to allow for tests), indicating that the size of a lek does not affect the probability that a male will recruit into it.

Male persistence at territories

The model incorporating lek size but not year had the lowest AIC_c value amongst the four models being compared (Table 1). However, three of the four screened models, including the general model *S*(.), were equally supported based on AIC_c values (i.e., Δ AIC_c values < 2), indicating that lek size or year are not good predictors of theprobability that a male will persist at a territory between two breeding seasons. We thus averaged survival estimates across all models; the weighted average probability of male persistence at territories was 0.76 when averaged across years (Table 1). Vocalization rates did not differ between males persisting (n = 40) or disappearing from a territory (n = 13) in the next year (U = 182.0, p = 0.13). This same result held after controlling vocalization rate for lek size in that year (U = 192.0, p = 0.24).

Modeling lek dynamics

Temporal changes in size and composition of leks were modeled assuming S = 0.76 and both TO and B = 0.39. Each lek from the initial pool of 1000 started with 1 to 7 males and was allowed to undergo changes in size and composition according to these rates. Each year, a fraction of leks disappeared; persisting leks rapidly converged to a mean size of 3 males (Fig. 3). Male turnover rates, i.e., the rate at which individuals present at t_0 disappear from a lek, show that on average 21% of the original males are expected to have disappeared from the lek after 1 year, 39% after 2 years, and 53% after 3 years (Fig. 4a). These rates are in general agreement with the rates of territory turnover observed on the Harpia plot: on average, 23% males disappeared within a year (19%, 33%, and 17% for 2004-2005, 2005-2006, and 2006-2007, respectively), 46% disappeared within 2 years (52% and 39% for 2004-2006 and 2005-2007), and 61% within 3 years (2004-2007). Estimated tenure times (i.e., number of years an individual male is expected to retain a given territory) had a distribution strongly skewed towards short tenure times, and a long right-side tail indicating that a small proportion of the males may hold territories for a long time (median = 3 yrs; 56% males expected to have tenures of ≤ 3 yrs, and 9% of ≥ 10 yrs; Fig. 4b). This small proportion of long-tenure males is also reflected by the long time taken, on average, for a complete turnover of males at leks (Fig. 4a, solid symbols). Due to the presence of these “anchor” males, and to the recruitment of new ones, leks are expected to persist for very long times; assuming that all the initial conditions remain unchanged, the average probability that a lek would persist for 100 years according to our simulation was 9% (Fig. 4b, open symbols).

Discussion

Territoriality has a critical influence on male fitness in lek-breeding populations (e.g., Kokko et al. 1998). Floater males that are not able to secure a lek arena are expected to have reduced or nil mating success, as females are unlikely to mate away from leks; in the blue-crowned manakin, molecular analyses of paternity suggest that only territorial males sire young (see Chapter 3 of this dissertation). As such, attendance and display rates at leks are important correlates of male mating success across species (Mackenzie et al. 1995, Fiske et al. 1998). Holding territories for extended periods may also be important for securing copulations, as male mating success can increase with age or tenure time in some lekking birds (e.g., Tsuji et al. 1994, Lanctot et al. 1998), including manakins (McDonald 1993, Ryder et al. 2008). Manakin males show strong territory fidelity and at least some individuals exhibit long tenure times (Lill 1976, McDonald 1993, Castro-Astor et al. 2004, Ryder et al. 2008). On the other hand, there is at least anecdotal evidence suggesting that male turnover rates at leks can also be high (e.g., Foster 1981). Here, we provide what is, to our knowledge, the first detailed information on the temporal dynamics and male turnover at manakin leks, and show that leks of the blue-crowned manakin are spatially traditional yet fairly dynamic in composition.

Our observations show that, on average, one fourth of the males present at a lek in any given year is not present in the following year, yet simulations suggest that individual leks can persist for many decades. The fate of most males observed disappearing from leks is unknown, with the exception of a single individual re-sighted holding a territory at a different lek in the subsequent year. However, the fact that this observed movement was very limited (the centroids of the first and the second territories held by that male were only 80 m apart) and that we surveyed systematically a large area (two 100-ha plots located ~1.5 km apart and their immediate surroundings) without recording other post-juvenile dispersal events suggests that most cases of male disappearance from leks are likely due to mortality. This is further supported by observations that adult manakins have small home ranges, with males being more sedentary than females (Graves et al. 1983, Blake and Loiselle 2002). In five years of systematic mist-netting capture-recapture studies at the two plots at TBS, long-distance dispersal was virtually unrecorded for adult blue-crowned males (recapture distances: 121.4 ± 97.5 m, range: 0-281 m; J. G. Blake and B. A. Loiselle, unpubl. data).

Our estimates of annual male persistence at territories (0.76 on average) were higher than estimates of survival based on capture-recapture. Blake and Loiselle (2008) report an average annual survival rate of 0.59 (range: 0.58-0.64 depending on the model) for blue-crowned manakins in TBS, but their analyses included individuals of all ages and both sexes. When sexes were considered separately, survival rates were ~11% lower for males than for females (0.54 vs. 0.61, respectively; J. G. Blake and B. A. Loiselle, pers. comm.), and still below our estimates. Because our analyses considered only lekking individuals, they might have overestimated male survival, e.g., if floaters survive less than territorial males. On the other hand, due to the pronounced sedentarism of territorial males, direct resighting at leks may provide more accurate survival figures for this class of birds than recapture events. For example, fairly similar survival rates were recorded for males (0.78 ± 0.03) and females (0.75 ± 0.04) of the long-tailed manakin (*Chiroxiphia linearis*) when a combination of resightings at leks and systematic netting was applied (McDonald 1993).

At the same time that males disappear, new males recruit into the leks. Competitive ability for territory acquisition often increases with male age (Apollonio et al. 1989, McDonald 1993, Tsuji et al. 1994, Kokko et al. 1998), and our data suggest that this may be the case with blue-crowned manakins as well. For each three recruiting males in definitive plumage (adults), only one in predefinitive plumage (sub-adults) was observed recruiting into a lek. Green-plumaged juvenile males do not establish stable territories but may form loose associations with territorial males during which they practice display elements together (R. Durães, in prep.). This suggests that older males have an advantage over younger males when acquiring lek territories, or that males delay establishment of stable territories and initiation of costly courtship displays until an age when they are more likely to successfully secure copulations.

We did not find evidence that the probability of a male recruiting into a lek or persisting in a given territory is influenced by lek size. An effect of lek size could be expected in at least two situations. First, larger leks could be more effective as recruiting foci due to the increased display activity levels. Second, if females prefer to mate at leks of a given size, as has been observed for other species (Lank and Smith 1992, Höglund et al. 1993, Hovi et al. 1996, Jiguet and Bretagnolle 2006, but see Lanctot et al. 1998), males could attempt to recruit preferentially into these leks. Likewise, if territories at larger leks are preferred, the pressure of takeover attempts could be higher at these leks. However, we have data showing that, although some females seem to favor larger leks over small ones, in the population at large, males at leks of all sizes, including individuals displaying solitarily, obtain copulations (see Chapter 3 of this dissertation).

Song rate is a strong correlate of male mating success in many lekking species (Fiske et al. 1998), including the blue-crowned manakin (see Chapter 3 of this dissertation). Males that are unsuccessful in acquiring mates in one season have been shown to change territories more often than successful ones for several lekking species (Höglund and Robertson 1990a, Gibson 1992, Westcott and Smith 1994, Rintamäki et al. 1995, Apollonio et al. 2003), and thus we hypothesized that blue-crowned males with higher vocal display rates would persist longer at their territories. As an alternative, it is also conceivable that a high energetic investment in costly lekking displays (e.g., Vehrencamp et al. 1989, Höglund et al. 1992) could reduce male survival, leading to a negative relationship between vocalization rate and persistence at leks. We, however, failed to detect an effect of vocalization rate on persistence probabilities at territories of the blue-crowned manakin, suggesting that previous mating history does not affect territoriality in this species, and/or that vocal display is not costly enough to reduce survival (e.g., Dearborn et al. 2005).

Stability in lek sizes and locations

The distribution of lek sizes in this population was constant both in time (across the four years of study) and space (between two study plots). In addition, the results of our model indicate that, regardless of their initial size, persisting leks converge rapidly to a mean size of 3 males, similar to what we observed in the field. At a first look, this might suggest that there is an “optimal” lek size that maximizes male fitness, perhaps due to a non-random female preference for leks of particular sizes (Lank and Smith 1992, Höglund et al. 1993, Hovi et al. 1996, Jiguet and Bretagnolle 2006). However, there are three lines of evidence that refute this idea: first, the distributions of observed lek sizes were not different from basic random expectations; second, males recruited into leks irrespective of their size; third, lek size did not affect the survival probabilities of males at territories. Thus, lek size seems to be more likely a by-product of the observed rates of recruitment and survival in this population, rather than a selective force modulating lek structure.

Leks were also extremely traditional in location. Although our study had a short timeframe, our model of lek dynamics showed that leks could persist for much long periods (>100 yrs) even in the face of turnover of individual males. By projecting lek changes over time, we were thus able to show that despite their dynamic nature, leks of the blue-crowned manakin seem to be at a balance where rates of male disappearance are compensated by male recruitment. How long leks will actually persist in nature will certainly be affected by other factors, such as changes in the forest structure, but our simulations show that, assuming that the initial conditions observed during this study are maintained, leks have the potential to persist long after all the original males have been replaced.

One possible mechanism allowing for the persistence of leks on the same locations is limitation of suitable lekking habitat or some other type of spatial constraint on lek establishment. We have previously shown that male settlement is not bounded by female spatial distribution (i.e., leks are not located at female 'hotspots', Durães et al. 2007), and that, although location of leks seems to be influenced by male habitat selection and by niche partitioning with other manakins, suitable lekking habitat is not limited for blue-crowned manakin in the study area (Durães et al. 2007, Loiselle et al. 2007). On the other hand, leks are spatially distributed in an extremely regular pattern, which suggests that a settlement pattern that minimizes competition among leks may be favored (Durães et al. 2007; see also Wegge and Rolstad 1986). In addition, fruit availability is higher at manakin lek sites than at non-lek control sites (Ryder et al. 2006). Whether leks have been settled at those sites precisely because of their high fruit availability, or whether seed deposition underneath display perches have created these patterns, the fact is that the presence of territorial males creates a positive feedback in resource levels that would promote traditionality in lek location. Thus, it is possible that increased availability of food resources and reduced competition with males from other leks play a part in maintaining lek locations.

An alternative explanation for lek traditionality is an increased fitness for males occupying traditional sites. The 'spatial spillover' or 'hotshot' model proposes that leks are formed when less successful males cluster around more successful males in an attempt to intercept copulations (Beehler and Foster 1988, Höglund and Robertson 1990b, Rintamäki et al. 1995, Lanctot et al. 1998). This model predicts that mating females are faithful to males, not to sites, and that at least the more successful males should hold territories for long periods of time. In contrast, the 'temporal spillover' model proposes that leks are maintained because females tend to go back to familiar places to mate and, as a result, males tend to settle at traditional sites, where they would enjoy increased mating success (Apollonio et al. 1989, Gosling and Petrie 1990, Gibson et al. 1991, Gibson 1992, Jiguet and Bretagnolle 2006). This model predicts that females are faithful to sites, not males, and that males settled at more traditional sites would have higher mating success than males settled at more recently formed leks. At present, we lack sufficient data to tease apart these two possibilities, but we suggest that male recruitment at leks of the blue-crowned manakin is unlikely to be modulated in the long term by the presence of specific "hotshot" males. Our simulations suggest that, although most males have short tenure times (≤ 3 yrs), a small fraction can retain territories for long periods of time (9% of males expected to have tenures of ≥ 10 yrs). However, we did not find evidence that these 'anchor' males are 'hotshot' males, to the extent that persistence at territories was not higher for males with higher vocal display rates. We also have anecdotal data showing that females can mate repeatedly at the same leks within and between breeding seasons, but not necessarily with the same individual males (R. Durães, unpubl. data), lending circumstantial evidence for the temporal spillover hypothesis.

In conclusion, leks of the blue-crowned manakin are stable in relation to the distribution of lek sizes in the population and to their location. Stability of lek sizes seem to be a by-product of the intrinsic rates of mortality and recruitment of territorial males, which, coupled with the presence of a small fraction of males that have long-tenure times and act as 'anchors', would allow leks to persist in the same locations for very long periods of time. That males tend to recruit into established leks rather than initiate new leks at unoccupied sites may be due, at least in part, to the increased food availability at leks, to a spatial pattern that minimizes competition among leks, and to a tendency of females to mate at familiar sites.

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Table 1 – Candidate models describing *S*, the probability that a male holding a territory in year t_x will persist at this same territory at year t_{x+1} at leks of the blue-crowned manakin *Lepidothrix coronata*, during 2004-2007, at TBS, Ecuador. Model 1 allows *S* to vary with lek size, model 3 with year and lek size, and model 4 only with year, while model 2 assumes a constant persistence rate. Models are sorted in decreasing order of AIC_c values; Δ AIC_c is the difference between the AIC_c value for the current model and the model with the lowest AIC_c, and AIC_c weight is a relative measure of model support, given the model set. Mean estimates of *S* (and SE, between parentheses) for each inter-annual interval are presented for each model, as well as the weighted average across models.

Model	AIC_c	Δ AIC_c	AIC_c weight	No. parameters	Persistence estimates per period		
					2004-2005	***2005-2006***	***2006-2007***
(1) *S* (*lek size*)	128.194	0.00	0.371	2	0.769 (0.042)	0.746 (0.042)	0.772 (0.042)
(2) *S* (.)	128.572	0.38	0.307	1	0.752 (0.041)	0.752 (0.041)	0.752 (0.041)
(3) *S* (*lek size*year*)	129.561	1.37	0.187	4	0.817 (0.063)	0.669 (0.067)	0.816 (0.061)
(4) *S* (*year*)	130.236	2.04	0.134	3	0.806 (0.071)	0.674 (0.069)	0.806 (0.066)
Weighted average					**0.778 (0.057)**	**0.724 (0.063)**	**0.779 (0.055)**

Figure Legends

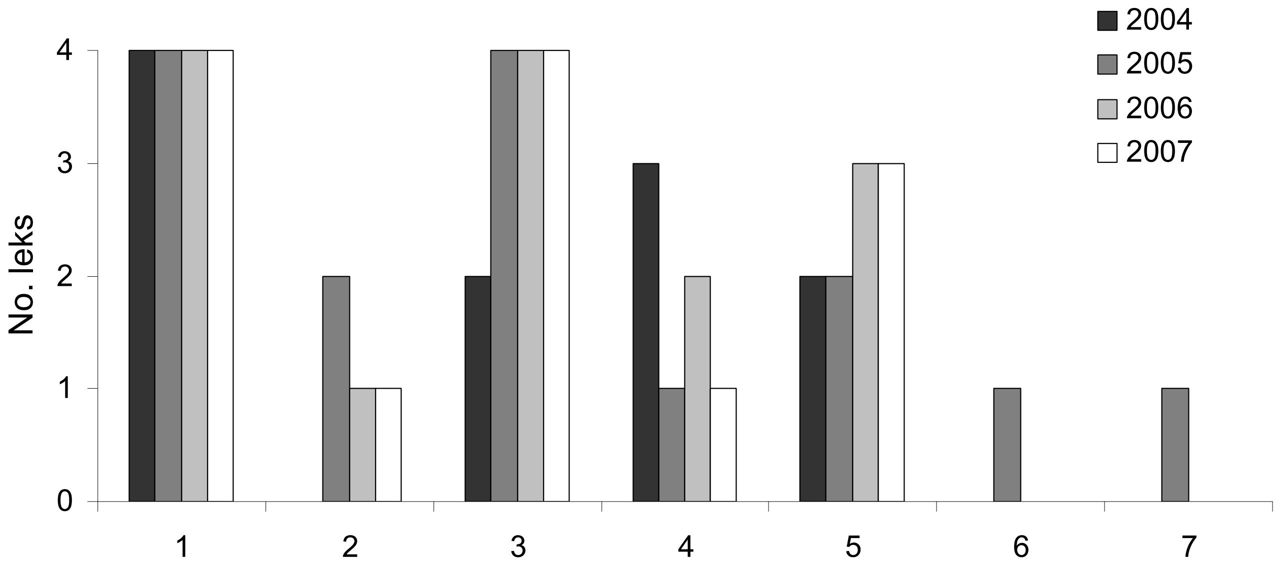
Figure 1 – Distribution of lek sizes (in number of male territories) for the blue-crowned manakin, in (a) Harpia plot, 2004 (2.9 ± 1.6 males; *n* = 11 leks), 2005 (3.1 ± 1.9; *n* = 15), 2006 (2.9 ± 1.5; *n* = 14), and 2007 (2.9 ± 1.7; *n* = 13), and in (b) Puma plot, 2006 (2.9 ± 1.7; *n* = 14). Harpia and Puma are two 100-ha study plots located ~1.5 km apart between closest edges.

Figure 2 – Changes in territory ownership and lek size observed between 2004 and 2007. In (a), the frequency of each type of transition observed at territories between consecutive years is depicted; existing territories could be maintained by the same male, be taken-over by a different male, or vacated; in addition, new territories could be established in previously unoccupied sites. Thirty-four transitions were recorded in 2004-2005, 47 in 2005-2006, and 36 in 2006-2007, for a total of 117 territory transitions observed in 54 territories belonging to 15 leks. In (b), net changes observed between consecutive years in lek size are shown; observations were recorded between 2004 and 2007 for up to 15 leks each year, for a total of 44 inter-annual observations.

Figure 3 – Predicted changes in lek size (in number of males) over time. Leks starting with 1 to 7 males rapidly converge to a mean size of ~3 males; solid and hatched lines represent average and 95% confidence intervals, respectively.

Figure 4 – In (a), proportion of leks (open symbols) present in the population at time = t_0 that are expected to persist (i.e., retain ≥ 1 male) after t years, or proportion of males (solid symbols) initially present and that are expected to persist at those leks after t years. In (b), expected tenure times for lekking males; no males were observed to hold a lek territory for more than 30 years during simulations; the median (3 years) is shown in black.

(a) Harpia plot



(b) Puma plot, year 2006

Figure 1

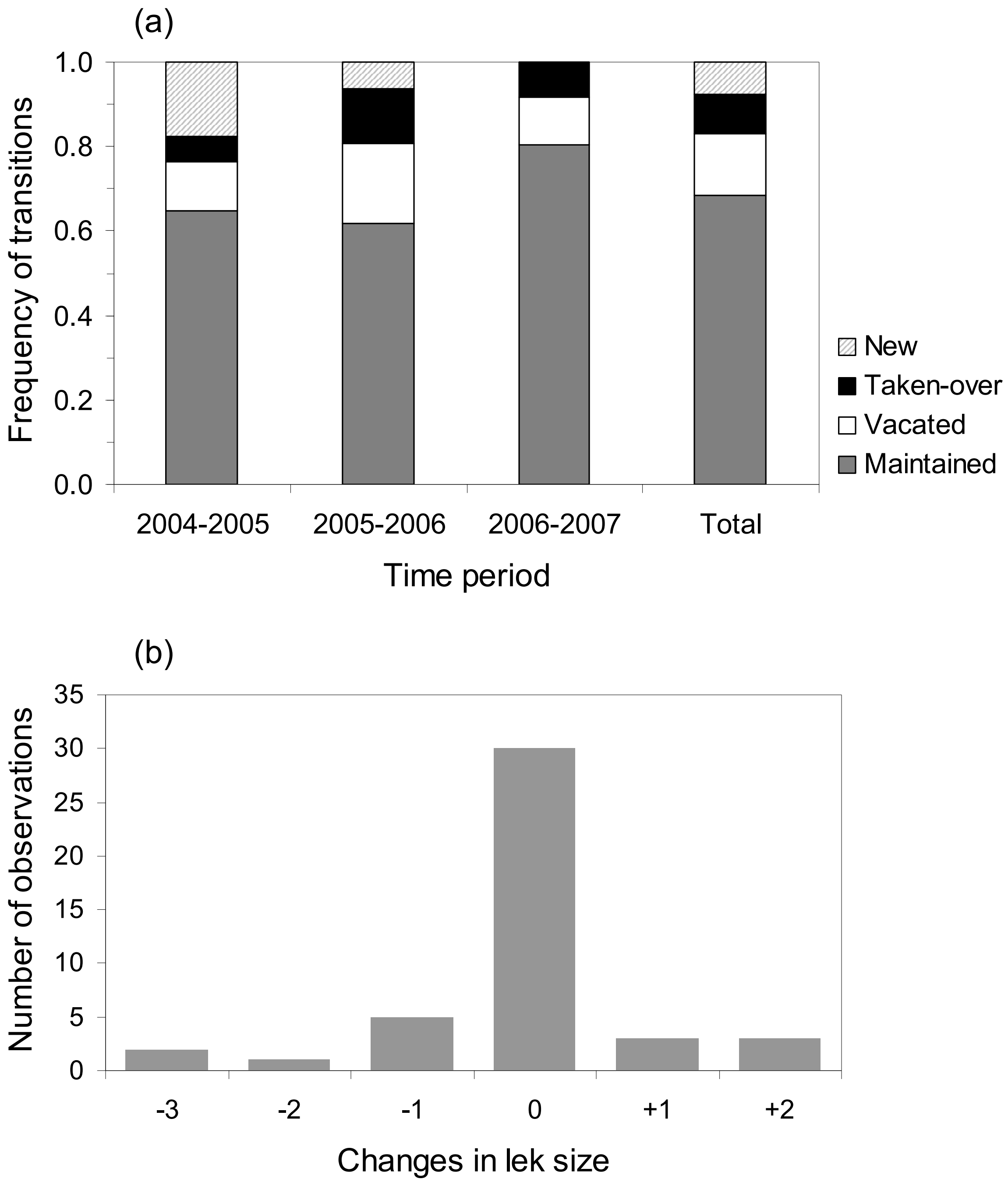
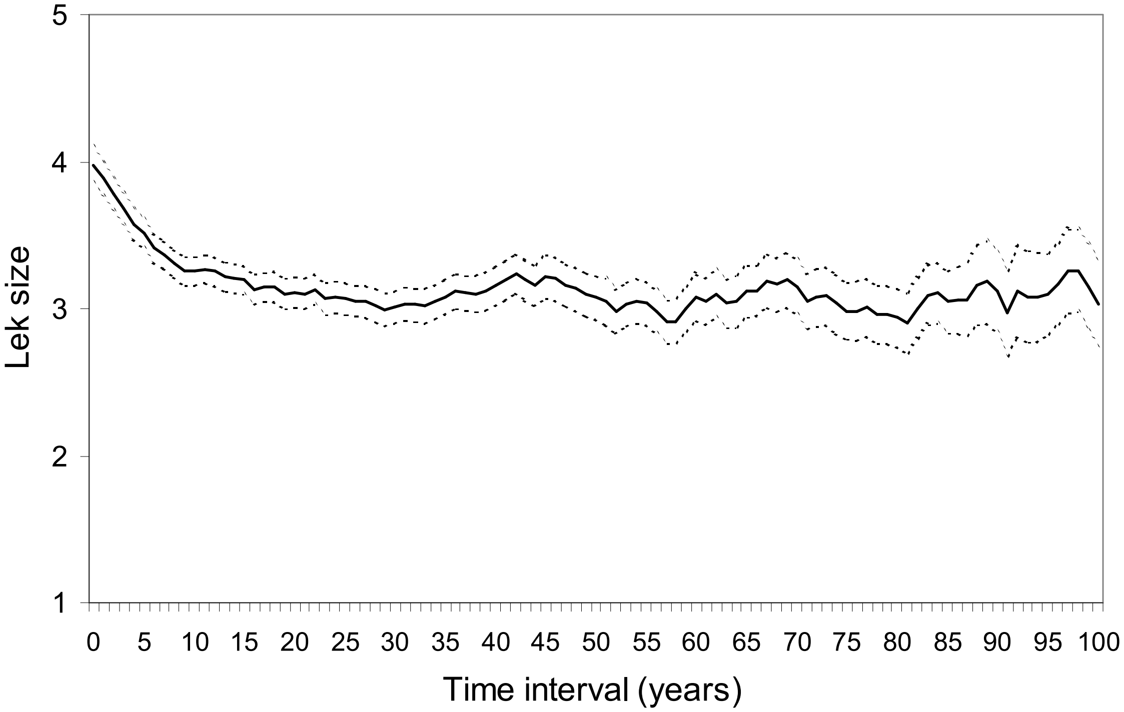

(a)
1.0
0.8
0.6
0.4
0.2
0.0
Frequency of transitions
2004-2005
2005-2006
2006-2007
Total
Time period
▨ New
■ Taken-over
□ Vacated
■ Maintained
(b)
35
30
25
20
15
10
5
0
Number of observations
-3
-2
-1
0
+1
+2
Changes in lek size

Figure 2



Lek size
5
4
3
2
1
0
5
10
15
20
25
30
35
40
45
50
55
60
65
70
75
80
85
90
95
100
Time interval (years)

Figure 3

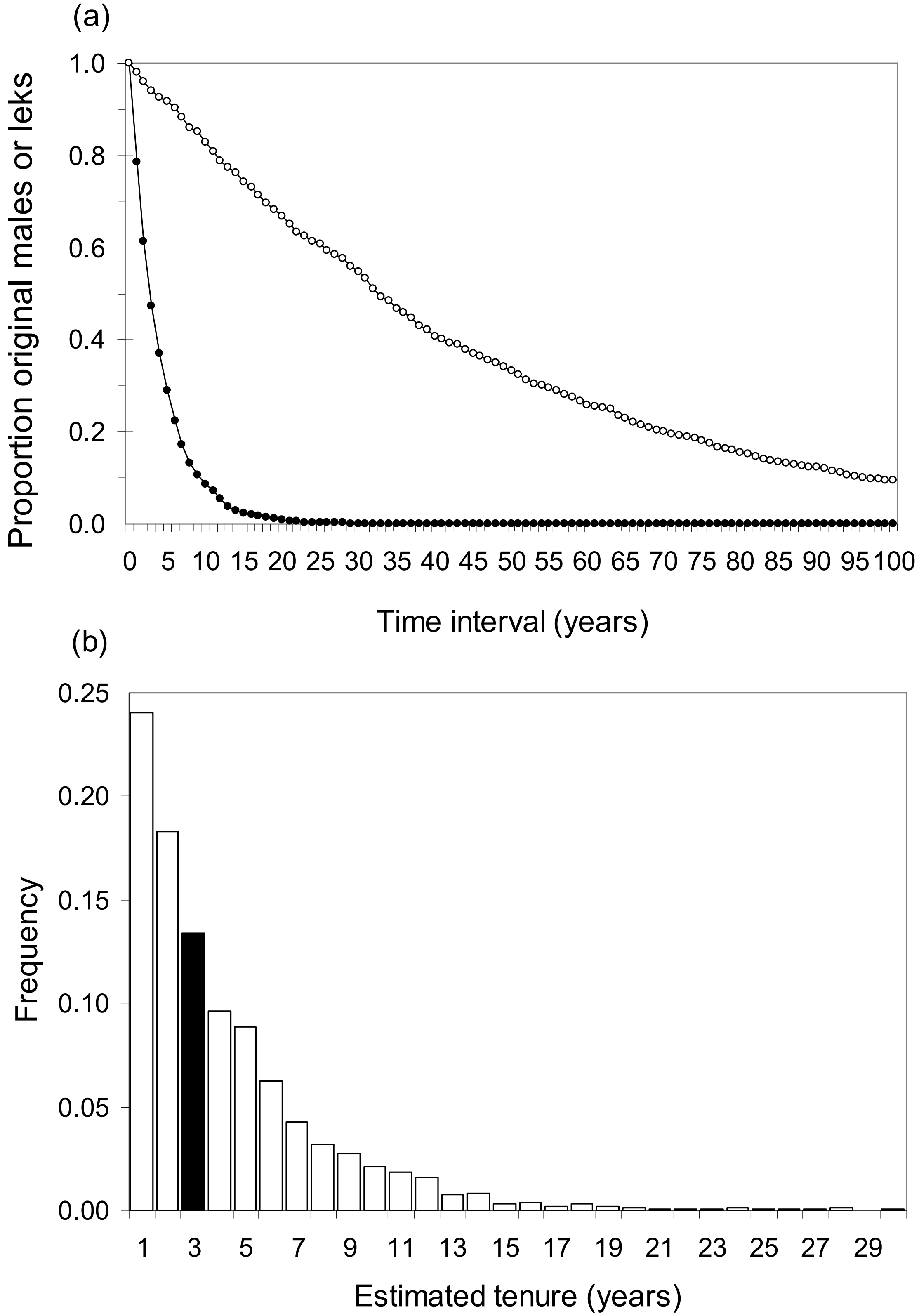

(a)
Proportion original males or leks
1.0
0.8
0.6
0.4
0.2
0.0
0
5
10
15
20
25
30
35
40
45
50
55
60
65
70
75
80
85
90
95
100
Time interval (years)
(b)
Frequency
0.25
0.20
0.15
0.10
0.05
0.00
1
3
5
7
9
11
13
15
17
19
21
23
25
27
29
Estimated tenure (years)

Figure 4

Chapter 3

Female mate choice across spatial scales: influences of lek or male attributes on mating success of blue-crowned manakins

Unsubmitted manuscript

Abstract

In lekking species, mate choice is primarily female-driven and often results in strong mating skew within and/or among leks, yet female choice is likely influenced by different factors at these two spatial scales. We used molecular analyses of paternity to examine male mating success in the blue-crowned manakin (*Lepidothrix coronata*) and to investigate patterns of female choice at the within-lek and among-lek spatial scales. First, we tested the hypothesis that females prefer to mate at larger leks, such that costs of mate search would be lowered. Second, we investigated whether female mate choice within leks is driven by genetic benefits, by asking whether females prefer to mate with individuals that are highly heterozygous or less related to them. Finally, we investigated the role of vocalization rate as a correlate of male mating success and as an indicator of male heterozygosity, a measure of genetic quality. Although females travel much beyond their home ranges to mate, they do not show preference for larger leks in the population at large, and even solitary males are successful in siring young. Females nesting close to small leks, however, tend to mate at larger leks located further from the nest. Siring males were not less related to their mates than expected by chance, nor were they more heterozygous than non-siring males. Within a given lek, males who vocalize more were more successful in siring young. Vocalization rates were correlated to mean d^2 heterozygosity, but this seems to be an indirect result of the fact that males increase vocalization rates in proportion to lek size, and that males at larger leks tend to be more heterozygous. This

implies that display rate would serve as a reliable indicator of male genetic quality only at large leks, and that males may recruit at leks of different sizes according to their perceived competitive abilities.

Introduction

Lekking systems are characterized by aggregations of males in display arenas (‘leks’) that females visit to assess potential mates and copulate; parental care is completely maternal and males do not provide females with any critical material resources (Bradbury 1981). Mate choice in lekking species is primarily female-driven and often leads to a strong skew in male mating success among lek-mates (Mackenzie et al. 1995). In addition to within-lek mating skew, some studies also demonstrated mating skew among leks, usually caused by female mating biases according to lek size (Lank and Smith 1992, Höglund et al. 1993, Jiguet and Bretagnolle 2006). Males thus have to compete for females both with lek-mates and with males from different leks, but the process of female mate choice is likely influenced by different factors at these two distinct spatial scales. For example, females may be drawn to large leks, either by active preference or passive attraction, resulting in increased overall copulation rates at these leks; on the other hand, increased competition for visiting females at larger leks can change patterns of mating skew, with males having decreased or increased success depending on their competitive abilities (Widemo and Owens 1995, Hernandez et al. 1999).

Given that females do not obtain direct material benefits from lekking males, such non-random mating patterns have been taken as indirect evidence that choosy behavior in females is promoted primarily by indirect (genetic) benefits (e.g., Miller and Moore 2007). The existence of genetic benefits implies that females are able to discriminate among males of different genetic quality and that mating with high-quality males results in the production of fitter offspring. Indeed, research on both lekking and non-lekking species suggests that females can effectively discriminate among potential mates of differing quality by using one or a combination of phenotypic indicator traits (Welch et al. 1998, Doucet and Montgomerie 2003, Chaine and Lyon 2008), and that highly successful males also produce offspring that are more viable (Houtman 1992, Petrie 1994, Welch et al. 1998, Johnsen et al. 2000) or more successful in mating (Wedell and Tregenza 1999, Head et al. 2005). The more contentious implication that genetic benefits are enough to compensate for the direct costs of mate search (e.g., Kirkpatrick 1987) has also received empirical support in recent years (e.g., Head et al. 2005). In addition, genetic benefits should be especially compensating in situations when mate sampling costs are low, e.g., because males are aggregated in space, as in colonial (Gwinner and Schwabl 2005) or lek-breeding species (Reynolds and Gross 1990, Alatalo et al. 1998). Yet, it is perhaps ironic that most empirical evidence for genetic benefits come from extra-pair copulatory behavior in socially monogamous species (Houtman 1992, Petrie et al. 1998, Johnsen et al. 2000, Foerster et al. 2003, Tarvin et al. 2005, Fossøy et al. 2007, Suter et al. 2007), with relatively few examples on lekking or other socially promiscuous species for which benefits of mate choice are expected to be predominantly genetic. Among these exceptions are studies that showed that black grouse males (*Tetrao tetrix*) with higher mating success are also more vigorous and survive longer (Alatalo et al. 1991), and that lifetime reproductive success increases with individual heterozygosity in this lekking species (Höglund et al. 2002). Another study showed that male peacocks (*Pavo cristatus*) with the most elaborate trains were more successful in copulating and produced offspring that were more viable, even after controlling for rearing environment and maternal effects (Petrie 1994). Finally, in the lekking sandfly (*Lutzomyia longipalpis*), females mating with more attractive males did not increase their fitness directly via increased survival or fecundity, but benefited indirectly by producing more attractive sons (Jones et al. 1998).

One mechanism by which genetic benefits could be obtained is by increasing the genetic variability (i.e., heterozygosity) of the offspring. While the adaptive value of particular 'good genes' is likely to be strongly dependent on the environment (Hunt et al. 2004b), high heterozygosity is generally beneficial to individuals because it reduces the expression of lethal or deleterious recessive alleles, increases the general adaptability of the organism, and confers heterozygote advantage at certain loci (Brown 1997). Across a wide range of species, including wild and non-isolated populations, individual heterozygosity has been positively correlated with several measures of fitness such as developmental homeostasis, condition, immuno-competence, growth rate, survival, attractiveness, and reproductive output (reviews in Brown 1997, Coltman and Slate 2003, and Mitton and Grant 1984). Females can effectively increase the genetic variability of offspring by mating with males that are less related to them (Bull and Cooper 1999, Amos et al. 2001, Suter et al. 2007) or that are more heterozygous themselves (Höglund et al. 2002, Hoffman et al. 2007). While in the first case the 'best mate' should vary from female to female and consistent mating biases are not expected, in the second case preference for more heterozygous males could lead to mating skew without loss of genetic diversity within the population, thus providing a potential solution for the 'lek paradox' (Borgia 1979).

Manakins (Pipridae) are small, forest-dwelling frugivorous birds restricted to the Neotropics (Prum 1994). Most manakin species are lek-breeders, and skewed mating success among lek-mates was observed for the five species studied to date (long-tailed manakin *Chiroxiphia linearis*, McDonald 1989; golden-headed manakin *Pipra erythrocephala*, Lill 1976; white-bearded manakin *Manacus manacus*, Lill 1974; golden-collared manakin *Manacus vitellinus*, Stein and Uy 2006; white-throated manakin *Corapipo gutturalis*, Théry and Vehrencamp 1995). In addition, the single study to date to assess mating success in manakins with molecular analyses of paternity revealed a strong skew within alpha/beta male dyads in the lance-tailed manakin (*Chiroxiphia lanceolata*, DuVal 2007). Yet, the degree of male reproductive skew can be expected to vary with social and spatial factors such as the degree of dominance hierarchies among males and inter-male spacing within leks (Foster 1983, Loiselle et al. in prep.), and five of the six species studied to date represent a limited sample of the alternative social behaviors and types of lek structure found within the clade (Prum 1994). These species have 'concentrated' leks (*sensu* Prum 1994, *P. erythrocephala* and *Manacus*) or well-structured male hierarchies (*Chiroxiphia* spp.), two cases in which a strong variance in male mating success can be expected. It is less clear whether species with 'dispersed' leks (where males are within aural but not visual contact) and with less well-defined male hierarchies, in which lek mates are expected to be under more relaxed competition for mates, will be characterized by such strong variance in mating success. In addition, no study has investigated patterns of mating skew among manakin leks.

In this study, we applied molecular analyses of paternity to investigate patterns of female mate choice in the blue-crowned manakin (*Lepidothrix coronata*) among and within leks. Males in this species form dispersed leks and do not show well-defined dominance hierarchies within leks. We first test the hypothesis that females should prefer to mate at large leks, either because large leks passively attract a larger number of females, or because females actively prefer to mate at these leks in order to lower the costs of mate search and maximize sampling of potential mates. As a result, males at large leks should be more likely to sire young than males at small leks. Alternatively, if females are not selective in relation to the lek where they mate, we should observe a tendency for females to mate at the lek nearest to their nest, and males at larger leks should not necessarily be more successful in siring young. Second, we investigated the hypothesis that females prefer mates that can maximize the genetic variability of the offspring, which are either individuals less related to them than expected by chance, or highly heterozygous individuals. Finally, we investigated the role of vocalization rate as a correlate of male mating success and as an indicator of the genetic quality of males. Sustained display rate can be energetically challenging for males (Vehrencamp et al. 1989, Höglund et al. 1992, Hunt et al. 2004a) and it is a typical correlate of mating success in lekking species (reviewed in Fiske et al. 1998), making this behavioral trait a good candidate as an honest signal of male quality that can be readily assessed by females. We thus tested the hypothesis that, within a given lek, females mate with males presenting more vigorous vocal displays, and that vocalization rate is correlated to heterozygosity.

Methods

Study site and study species

Research was conducted at Tiputini Biodiversity Station (TBS, 0^o 38' S, 76^o 08' W, 190-270 m a.s.l.), Orellana province, eastern Ecuador. TBS covers 650 ha of virtually undisturbed habitat and is located within the 1.2 million-ha Yasuní Biosphere Reserve. The vegetation is lowland, wet-evergreen forest comprised primarily of unflooded *terra firme* and flooded *várzea* forest; average annual rainfall and temperature are 2,740 mm/year and 28°C. Data were collected at two permanent study plots (Harpia and Puma plots) established ~1.5 km apart at nearest edges; each plot is 100-ha (~1 x 1 km) in size and has grid lines every 100 or 200 m (for more details, see Loiselle et al. 2007).

The blue-crowned manakin occurs in humid, mature unflooded forests below 1000 m in northwestern Amazonia, the Chocó region west of the Andes, and southern Central America (Snow 2004). Females and hatching-year males ('juveniles') are bright green, while adult males are sooty black with bright blue crowns. Males have delayed plumage maturation, and 2-yr old, 'sub-adult' males present a pre-definitive plumage with variable degrees of green before reaching full adult plumage around their third year (Ryder and Durães 2005). In our study population, adult and sub-adult males, but not juveniles, display solitarily or establish territories at leks with up to seven contiguous individual territories, each averaging 1000 m^2 in size (Durães et al. 2007; for sake of simplicity, we will refer to both solitary and group display sites as ‘leks’). During the breeding season, males spend most daylight hours vocalizing and displaying at leks (R. Durães, unpubl. data). Females observed visiting leks were always unaccompanied, whether the visit resulted in copulation or not. Nest building and parental care are carried out solely by females. Nests are small open cups suspended in horizontal forks usually within 1 m of the ground, and clutch size is two, or less frequently one egg (Hidalgo et al. 2008). Incubation lasts 16-17 days, followed by a nestling period of about 14 days (Ryder et al. 2008). Nest success is low at TBS due to high rates of predation (81-84% daily survival rate, DSR, Tori et al. 2006, Ryder et al. 2008).

General field methods

Field work was conducted between 2001 and 2006, during the dry season (late November to early April each year), coinciding with the main manakin breeding season in the region; here, we shall refer to a given breeding season by the year of the last sampled month (e.g., season of Nov 2005-Apr 2006 will be referred as ‘2006’). Individuals were captured each year with ground-level mist nets (12 x 2.8 m; 36 mm mesh) operated on one day in January (2002-2006) and one day in March (2001-2006) at 96 fixed locations on each study plot (12 nets spaced at ca. 50-m intervals and opened each day for ~ 7 hrs, Blake and Loiselle 2008). Additional nets were operated as necessary on the two plots and vicinities to target unbanded territorial males (nets set on territories, with or without the aid of song playbacks) and nesting females (nets set near their nests). A total of 435 post-fledging individuals were captured during 694 capture events. Each individual received uniquely-numbered aluminum bands and combinations of color bands, was weighed, sexed and aged (for sexing and aging procedures, see Durães et al. 2007), and had a blood sample (~ 25-50 µl) taken via puncture of the brachial vein and stored in 500 µl of lysis buffer (Longmire et al. 1988).

Leks were located and mapped each year by systematic searches for displaying males within and in the vicinities of each plot. Territories were considered to belong to the same lek when males were within auditory contact or when occasional interactions among neighbor territorial males were observed. Territorial males were identified each year by their color bands; unbanded males were captured and banded. Leks are very traditional in location across years, despite relatively high levels of male turnover at territories (see Chapter 2 of this dissertation).

Nests were systematically searched for by a variable number of observers during the breeding seasons of 2004-2006. Attempts were made to search the entire area of each plot at least once a month, but due to logistic limitations, the Harpia plot was more efficiently searched than Puma; because of sample size issues, some of the analyses presented here are limited to nests found at Harpia in 2005 and 2006. To improve genetic sampling of offspring in face of the high rates of nest predation observed in our study area, we replaced most of the natural eggs with plaster replicas and completed the incubation of real eggs in the laboratory (Tori et al. 2006). Immediately upon hatching in incubator, chicks were sampled for blood and returned to the nest if this was still active, or collected if the nest had already failed.

Vocalization rates were estimated in behavioral observations conducted during the breeding season at a sub-set of leks in the Harpia plot in 2005 and 2006. Males were observed during 30-min sessions (in 2005, 32 males observed at 11 leks) or 120-min sessions (in 2006, 25 males at 10 leks) conducted during early morning (0630-0830) or mid-afternoon (1400-1600), which are periods of peak lek activity (R. Durães, unpubl. data). Each male was observed for a total of 132 ± 39 (SD) minutes in 2005 and 713 ± 271 minutes in 2006. Focal males were rotated among sessions to avoid seasonal biases during behavioral observations. Data collection was halted when females or other males were present at the territory or when the focal male was displaying ("dancing") at the courtship court, during which males are mostly silent (R. Durães, in prep.). While sitting at a strategic point within a male's territory, an observer recorded how many times the male uttered advertisement songs or whistle calls during every 5-min (in 2005) or 10-min (in 2006) interval. Advertisement songs are produced only by males and are used for territory defense and long-distance attraction of females; whistles are uttered by both sexes and by birds of all ages, are much softer and propagate to shorter distances than songs (R. Durães, in prep.). When a female is present in their territories, males change vocalization patterns from mostly advertisement songs to mostly whistles. Vocalization rates were estimated as the mean number of songs or total calls (i.e., songs plus whistles) given per minute, averaged through all observation sessions for each male. These two measures of vocalization rate were strongly correlated ($r = 0.88$, $p < 0.001$, $n = 55$) and produced qualitatively similar results in subsequent analyses, and thus we only present results based on total calls (calls, hereafter). Vocalization rates were constant throughout the season for most males (correlations between vocalization rates and date, n = 3-8 observation days/male each year; 23 in 28 comparisons in 2005 and 18 in 20 comparisons in 2006 with p-values > 0.09; significant positive or negative trends in 4 and 3 comparisons, respectively). Nineteen individuals were observed both in 2005 and 2006 and their vocalization rates were correlated between years ($r = 0.55$, $p = 0.015$ and $r = 0.73$, $p < 0.001$ for song and calls, respectively); we thus averaged vocalization rates between years for these males for subsequent analyses in order to avoid pseudo-replication; analyses yielded similar results if rates were not averaged between years.

Molecular analyses: microsatellite DNA genotyping and analyses of paternity

DNA was isolated from blood samples via standard phenol–chloroform extraction followed by a cleaning step of dialysis in 13 TNE_2 (Sambrook et al. 1989), or from tissue samples (eggs and chicks) via ethanol extraction (DNeasy® Tissue Kit, Qiagen). Individuals were genotyped at six hypervariable microsatellite loci previously developed for other manakin species (Table 1).

Polymerase chain reactions (PCRs) were run in 5 μl volumes and consisted of genomic DNA, 1 mM deoxynucleotide triphosphate's (DNTPs), 10X reaction buffer, 25 mM $MgCl_2$, forward and reverse primer pairs, dimethylsulfoxide additive (DMSO), and *Taq* DNA polymerase (Bioline, Randolph, MA). 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 50–60° C for 30–45 s, and extension at 72° C for 60 s, with a final extension step of 72° C for 10 min. PCR products were tagged using fluorescent-labeled forward primers (Applied Biosystems, Inc., Foster City, CA) and visualized on an ABI 3100 automated capillary sequencer. Fragment sizes were determined against a size standard Genescan LIZ (500), and genotypes were analyzed with Genemapper 3.7 (Applied Biosystems, Inc.). Most individuals, and all homozygotes, were run in at least two separate PCR reactions. Ninety-four percent of the individuals were genotyped at all six loci (5.9 ± 0.3 (SD) genotypes/individual). We used the program FSTAT 2.9.3 (Goudet 2001) to estimate allelic richness and for tests of per locus departure of Hardy-Weinberg and genotypic equilibria, with statistical significance assessed by randomization procedures and Bonferroni-adjusted. We used the program CERVUS 3.0.3 (Marshall et al. 1998, Kalinowski et al. 2007) to estimate frequencies of null alleles. All loci showed no significant departure from equilibria, but two loci showed evidence for the presence of null alleles (Man3 and Mani(AC)5, Table 1), although with frequencies that are not expected to introduce serious bias in exclusion probabilities for parentage analyses (Dakin and Avise 2004).

A total of 83 offspring from 48 broods was sampled for genetic material. Nests were assigned to the attending female. To assign paternity, we used CERVUS 3.0.3, which employs a maximum-likelihood approach to assign parents to an individual with a known level of statistical confidence, while accommodating a user-entered rate of genotyping error. This last point is important given the indication for null alleles in some of the loci. In absence of genotyping errors and combining the six loci, the probability of excluding a single unrelated male as the father was estimated as >99.9% if the mother was known or >99.7% if the mother was unknown. We used genotyping inconsistencies within 64 known offspring-mother dyads to estimate genotyping error for each locus, and used the average of 0.06 across loci as the estimated rate of genotyping error. When we were not able to confidently identify the female attending a nest in the field, we often had a 'candidate mother' based on our knowledge of the location of home ranges of individual females, which overlap little in space (Durães et al. 2007). In these cases, we first ran a maternity assignment analysis in CERVUS and in all instances the female assigned with the highest likelihood was the one we had previously suspected, upon which we included this female as the known mother during subsequent paternity analyses. Strict (95%) and relaxed (80%) confidence levels were attributed to the assignments produced by the paternity analyses based on 10,000 simulations with 160 sampled candidate fathers (mean number of post-fledging males sampled in the population each year), which were assumed to represent 90% of all possible candidate fathers based on recapture rates. CERVUS assignments were accepted if done at the 95% level of confidence when the mother was known or not, or at the 80% level of confidence if the mother was known and the trio (mother-offspring-father) was assigned with 95% of confidence.

Based on the paternity assignments, we classified lekking males as siring or non-siring individuals. Despite our intensive searches for nests, it is always possible that some of the males were incorrectly classified as non-siring. To reduce bias when comparing vocalization rates and heterozygosity levels between these two classes of males, we limited our comparisons to males belonging to leks located in well-sampled areas within the Harpia plot. For this reason, sample sizes may differ slightly between some of the analyses.

Choosing a lek: distances to mate and lek size

Male territories, lek boundaries, and nests were displayed as shapefiles in ArcView 3.2 or ArcGIS 9.1 (ESRI^{TM}, Redlands, California). We measured the distance between each nest and the centroid of the siring male's territory, which should represent the minimum distance females travel in order to mate. We simulated the area of influence of nesting females by creating circular buffers around each nest with a radius equal to the average distance observed between nests and the centroids of the siring males' territory, and determined how many male territories and leks a female moving this average distance away from her nest is expected to have contact with before mating, as well as the size (in terms of number of male territories) of all leks included in this area of influence. For this analysis, only one nest was included for each individual female.

To test the hypothesis that females mate at the nearest lek, we used a paired *t*-test to compare the distance between each nest and the edge of the nearest lek to the distance between nests and the edge of the lek where the females actually mated. To test the hypothesis that females prefer to mate at larger leks, we drew individuals at random and with replacement from the pool of territorial males present in a plot in a given year, in a number similar to the number of paternity assignments done for that year, and computed the mean size of the lek to which those males belonged. We iterated this procedure 1000 times to build a distribution of expected values, and computed the one-tailed probability that the mean lek size of siring males was larger than the mean lek size expected by chance (percentile method, Efron and Tibshirani 1993). To avoid pseudo-replication due to the fact that siblings in almost all nests were sired by the same male (see Results), in this analysis we considered each nest as a single assignment, except in cases when multiple paternity was observed. Due to sample size limitations, this analysis was carried out just for the Harpia plot and the years of 2005 and 2006. In addition, we tested whether females prefer to mate at larger leks when the pool of potential mates was restricted to those present within the area of influence around each nest; we tested if the proportion of times females mate at the larger lek within its area of influence is different from 0.5 with a Binomial test.

Choosing a male: relatedness between mates, male heterozygosity, and call rate

We estimated the genetic relatedness between nesting females and their mates with the program ML-Relate (Kalinowski et al. 2006), which calculates maximum likelihood estimates of relatedness based on microsatellite data and which can accommodate the presence of null alleles. To test the hypothesis that females are less related to their mates than expected by chance, we conducted a permutation test in which we paired each female nesting in the Harpia plot in a given year (years 2005 and 2006) with a randomly chosen male among those holding territories in that plot in that same year, and recorded the relatedness between those two individuals. We repeated this procedure 1000 times to build a distribution of average relatedness values expected under the assumption of random mating. The one-tailed probability that the average relatedness observed between nesting females and their mates is lower than expected by chance was estimated as the proportion of simulation means with lower values than the observed mean.

We used two measures of multilocus heterozygosity, mean d^2 (Coulson et al. 1998) and standardized observed heterozygosity, H_s (Coltman et al. 1999), as estimates of genome-wide individual genetic diversity of males. Mean d^2 uses the difference in the length of alleles in a genotype as an indication of the time since their coalescence, and it is thus supposed to reflect inbreeding due to longer-term processes in the past history of the population. H_s is a measure of the proportion of heterozygous loci that corrects for incomplete genotyping, and should reflect genetic diversity due to more recent events, such as parental inbreeding. We adopted both indices because they carry potentially different and relevant information about the inbreeding history of the population. Other heterozygosity indices proposed in the literature are largely variants of the H_s index (*IR*, Amos et al. 2001; H_s_Obs, Amos 2005; *HL*, Aparicio et al. 2006); when compared across 429 individuals, these other three indices were highly correlated among themselves and with H_s (absolute r_s-values ≥ 0.94, all *p*-values < 0.001) and yielded similar results to that index, so we did not include them in further analyses.

Vocalization rates and heterozygosity levels were compared between siring males and non-siring males with two-tailed *t*-tests. Parametric or non-parametric bivariate correlations and multiple linear regressions were used to assess whether heterozygosity or lek size could explain a significant proportion of the variance in vocalization rates.

Analyses were conducted using SPSS 15.0.0 (SPSS Inc., Chicago, IL). Variables that violated normality or heteroscedasticity assumptions were transformed when possible, otherwise non-parametric tests were adopted. Unless stated, values represent means ± SE.

Results

Paternity analyses

We were able to confidently assign paternity to 57 offspring belonging to 37 broods, resulting in an assignment success of 69%. Failure to assign paternity was due to inability to match a father with high confidence (50% of the failure cases, $n = 13$), to genotyping problems usually due to poor DNA quality (38%, $n = 10$), or a combination of both (12%, $n = 3$). Among 20 broods containing two offspring for which both could be assigned a father, only one indicated mixed paternity. Paternity was assigned to a total of 25 males, all known to hold lek territories with exception of two males; the first had been captured at a lek where he did not hold a stable territory but could have potentially intercepted copulations from other territorial males, while the second sired young at two nests in the outer edge of the Harpia plot and could potentially hold a territory in an undetected lek located outside the plot. All siring males were at least 2 yr-old (i.e., adults or sub-adults), and none was a green-plumaged juvenile male. To check for spatial biases on the probability of assigning a father, we tested for correlations between the distance from a nest to the center of the sire's territory and the LOD score (the log-likelihood of the parentage assignment) of both the offspring-father pairs and the mother-offspring-father trios. A lack of significant correlations suggests that, given that the true fathers had been sampled, they were equally likely to be assigned independently of how far they were from the sired nests (offspring-father pairs, one offspring included per nest: $r = 0.24$, $p = 0.19$, $n = 30$; mother-offspring-father trios: $r = 0.22$, $p = 0.26$, $n = 28$).

Choosing a lek: distances to mate and lek size

The average distance between a nest and the center of the territory of the siring male was 265 ± 19.7 m (range: 94-592 m, $n = 30$). Females mated at leks located significantly further than the nearest one to their nest (distance to closest edge of the nearest lek: 101 ± 9.6 m; distance to closest edge of lek to which siring male belonged: 208 ± 21.0 m; paired *t*-test, $t_{29} = -4.788$, $p < 0.001$). In fact, in only 33% of the cases ($n = 10$) did females mate at the nearest lek, while in the other 67% of the cases, siring males belonged to leks located on average 160 ± 26.2 m beyond the nearest lek (Fig. 1). By assuming that the area of influence of females around their nests is a circle with 265 m of radius (i.e., the average distance females traveled to mate), the average female is expected to come into contact with 8.5 ± 0.5 males belonging to 3.1 ± 0.1 leks.

Males in leks of all sizes sired young, from solitary males to males in the largest leks (i.e., leks with seven male territories, in our population). Mean lek size of siring males was 3.6 ± 0.3 and 3.4 ± 0.5 for the Harpia and Puma plots, respectively (years combined). Siring males did not belong to leks larger than expected by chance in the Harpia plot in 2005 (observed lek size of siring males: 3.6 ± 0.4; expected lek size after 1000 permutations: 3.7 ± 0.3, $p = 0.41$) or 2006 (observed: 3.9 ±

0.6; expected: 4.2 ± 0.6; $p = 0.32$). This result did not change when we restricted the pool of potential mates to the males included in the expected area of influence of a nest (i.e., a circle of r = 265 m or equal to the distance to the siring male in cases when that distance was > 265 m). Females mated at the larger lek in the area of influence of their nests in 40% of the cases ($n = 12$ out of 30), not significantly different from a 50% proportion expected by chance (Binomial test, $p = 0.36$).

Other lines of evidence do suggest, however, that females increase travel costs in order to mate at larger leks when the nearest leks are small. First, there was a non-significant tendency for the nearest lek to be smaller in cases when females mated elsewhere (size of nearest lek when females mated at that lek: 3.5 ± 0.4 males, $n = 10$; when females mated at a different lek: 2.7 ± 0.4, $n = 20$; Mann-Whitney test, $U = 66.50$, $p = 0.13$; Fig. 1). More importantly, for the subset of females that did travel beyond the nearest lek to mate ($n = 20$), the nearest lek was significantly smaller (2.7 ± 0.4 males) than the lek where they actually mated (3.9 ± 0.4 males, paired t-test, $t_{19} = 2.397$, $p = 0.03$).

Choosing a male: relatedness between mates, male heterozygosity, and call rate

Females nesting in the Harpia plot were not less related to their mates than expected under the assumption of random mating, either in 2005 (observed relatedness: 0.072 ± 0.052, range: 0.000 – 0.363, $n = 7$ pairs; expected average relatedness after 1000 permutations: 0.049 ± 0.030, $p = 0.80$) or 2006 (observed: 0.062 ± 0.034, range: 0.000 – 0.249, $n = 11$ pairs; expected: 0.041 ± 0.024, $p = 0.82$). Our sample sizes for these analyses were small, and a retrospective power analysis (Zar 1991, Thomas 1997) indicated that a minimum absolute difference of 0.19 (in 2005) or 0.10 (in 2006) between the average relatedness of nesting females to their true mates and the average relatedness of nesting females to all potential mates (i.e., males holding territories in a given year) would be necessary for a significant departure from the population mean to be detected with 75% of confidence. While it is clear that our analyses lack statistical power, the average relatedness between males and females in the population was low, such that genetic inbreeding should not be likely even if females mate randomly.

Next, we examined the potential role of call rates as an indicator of male heterozygosity, a measure of genetic quality. Mean d^2 heterozygosity was significantly correlated with call rate (mean d^2 ln-transformed for normality, $r = 0.37$, $p = 0.03$, $n = 35$), but H_s heterozygosity was not ($r_s = -0.14$, $p = 0.41$). In addition, an effect of lek size was observed, as males at larger leks had higher mean d^2 (ln-transformed mean d^2, $r = 0.38$, $p = 0.023$, Fig. 2A) and higher call rates ($r = 0.51$, $p = 0.001$, Fig. 3), although not higher H_s ($r_s = 0.005$, $p = 0.98$, Fig. 2B). We thus used a multiple regression to evaluate the independent effects of lek size and mean d^2 heterozygosity on call rates. The model explained a significant proportion of the total variance in call rates ($r^2_{adj} = 0.20$, $F_{2,34} = 5.232$, $p = 0.011$), but this was primarily due to the effect of lek size ($\beta = 0.363$, $p = 0.037$), and not to heterozygosity (ln-transformed, $p = 0.18$). This suggests that males at larger leks tend to have higher mean d^2 heterozygosity and also to vocalize more, but if we control by lek size, call rates do not reflect heterozygosity.

Lastly, we examined if call rates and/or heterozygosity influence male mating success. Males siring or not siring young did not differ in vocalization rates (7.9 ± 1.3 *vs.* 7.5 ± 0.6 calls/min, respectively; $t_{29} = -0.385$, $p = 0.70$; $n = 10$ siring and 21 non-siring males). Males siring or not siring young also did not differ in heterozygosity (mean d^2, ln-transformed: 4.91 ± 0.33 *vs.* 5.11 ± 0.18, respectively, $t_{29} = 0.570$, $p = 0.57$; H_s, 0.90 ± 0.04 *vs.* 0.96 ± 0.04, $t_{29} = 0.880$, $p = 0.39$). These comparisons were, however, confounded by the fact that both call rates and mean d^2 values increased with lek size, so we regressed each one of these variables on lek size and used the residuals to compare the two groups of males. Because the size of some leks changed slightly between years and it is possible that males adjust their vocalization rates (but not heterozygosities) accordingly, for regressions involving vocalization rates we did not average data between years. After controlling for lek size, vocalization rates were higher for siring males than for non-siring males (1.61 ± 0.745 for siring, -0.59 ± 0.55 for non-siring, $t_{31} = -2.266$, $p = 0.031$, Fig. 3), but mean d^2 was not ($t_{29} = 0.404$, $p = 0.69$). This suggests that, although males at leks of all sizes, including solitary males, sire young, within a given lek sires tend to be those males that vocalize more vigorously, but not necessarily those males that are more heterozygous.

Discussion

Female mate choice is an important mechanism of sexual selection that, in lekking systems, can lead to remarkable levels of mating skew among males (Mackenzie et al. 1995). The aggregated distribution of males at leks, unusual in other mating systems, implies that males have to compete for females at distinct spatial scales, among and within leks. Female mate choice in lekking systems has often been investigated in relation to phenotypic correlates of mating success (examples from manakins: McDonald 1989, Théry and Vehrencamp 1995, Trainer and McDonald 1995, Shorey 2002, Stein and Uy 2006), which are likely more important at the within-lek scale, or attributes of lek structure, such size (e.g, Lank and Smith 1992, Höglund et al. 1993, Jiguet and Bretagnolle 2006), which are likely more important at the among-lek scale. Few studies have attempted to integrate these two aspects of female choice. In this study, we investigated the patterns of mate choice by female blue-crowned manakins among and within leks, with the expectations that females should prefer to mate at large leks and thus reduce costs associated with mate search and assessment, and that within a given lek females should prefer males that display more vigorously and/or that can increase the genetic quality of their offspring.

In relation to mate choice among leks, we found evidence that most females mated at leks located further than the one nearest to their nests. In fact, we found that females often travel considerably beyond their usual home ranges in order to mate. Blue-crowned females have small home ranges that cover on average 4 ha, which would correspond to a circle of 113 m of radius (Durães et al. 2007), less than half of the average distance observed between nests and the territories of sires (265 m). A 4-ha home range encompasses, on average, a single lek, and often no leks at all (Durães et al. 2007), and it is likely that females travel further in order to encounter and more effectively assess potential mates. Contrary to observations for other lekking species (Lank and Smith 1992, Höglund et al. 1993, Jiguet and Bretagnolle 2006), we did not find mating biases toward the larger leks within the population at large. However, a sub-set of females nesting close to small leks tended to mate at larger leks located further away. This supports the idea that females may actively increase traveling costs in order to find better mates, as has also been shown, for example, for Antarctic fur seals (*Arctocephalus gazella*, Hoffman et al. 2007).

Because lekking is a non-resource based mating system where females are largely unconstrained to choose their mates, mating skew among males has been taken as evidence that females select mates according to their genetic quality. We investigated two mechanisms by which females could increase the genetic variability of their offspring through mate choice, but found that nesting females were not less related to their mates than expected under the assumption of random mating, and that siring males were not more heterozygous than non-siring males. On the other hand, we found evidence that females use vocalization rates as a cue for mate selection, such that, within a given lek, males that sing more vigorously are more likely to sire young. Although we observed a correlation between call rates and heterozygosity, this seems to be an indirect result of the fact that males increase vocalization rates in proportion to lek size and that males at larger leks tend to be more heterozygous.

Individual vocalization rates, which were shown to affect male mating success, were thus influenced by the social environment (i.e., lek size), and this effect could be explained by behavioral plasticity or by differential recruitment according to male quality. Behavior could be changed, e.g., by social facilitation, which occurs when males stimulate each other during display, such that males in larger groups sing more than males displaying solitarily or in smaller groups (Clayton 1978, Brooke et al. 2000); the same pattern can result if males elevate display rates due to the increased competition with other males at larger leks (Greenfield 1994). This would imply that individual vocalization rates are determined primarily by the social environment rather than by the quality of the male, and therefore mate choice based on vocalization rates should not have adaptive value. Differential recruitment, on the other hand, would imply that high-quality males are inherently able to display more vigorously than low-quality males, and that males recruit into leks of different sizes according to their competitive abilities (Sutherland 1996, Hernandez et al. 1999). In this case, vocalization rates would be an honest signal of male quality and female choice for more vigorous males could have an adaptive value. For example, heterozygosity has been positively correlated to male song structure (Seddon et al. 2004) or song repertoire size in birds (Marshall et al. 2003), but to our knowledge this is the first study to investigate the relationship between vocal rate and heterozygosity.

These two possibilities (i.e., socially vs. genetically determined song rates) are not completely mutually exclusive, and we found evidence that a combination of both act in blue-crowned manakins. On one hand, lek size was important in explaining vocalization rates, while heterozygosity, a measure of genetic quality, was not. Within the scope of this study, this finding does not support the idea that vocalization rates are a reliable signal of male genetic quality. On the other hand, the fact that only the more vigorous males can expect to successfully mate within a given lek suggests that males are constrained to some extent by how much they can increase their vocalization rates and that male-male competition in large leks can drive males to increase display within their capabilities. This is further supported by the fact that individual vocalization rates were consistent across years and throughout the breeding season, and that males in larger leks tended to be more heterozygous, suggesting that males recruit into leks according to their perceived competitive abilities and that, once established in a lek, they further adjust their display rates according to that of their lek mates.

Sustained display can be costly (Vehrencamp et al. 1989, Höglund et al. 1992, Hunt et al. 2004a), and has been shown to honestly signal phenotypic quality such as body condition and immune-competence in other species, such as the song sparrow *Melospiza melodia* (Reid et al. 2005, Pfaff et al. 2007). In addition, vocal display attributes such as rate, duration and repertoire size are often sexually selected in birds and other vertebrates (Fiske et al. 1998, Burke and Murphy 2007) and can be genetically transmitted to offspring (Houtman 1992, Gwinner and Schwabl 2005). Females mating with males that display more vigorously could thus enhance offspring quality by other means than increased heterozygosity, such as by transmission of genes conferring attractiveness (reviewed by Kokko et al. 2003). Still, the role of vocalization rates as an indicator of heterozygosity should not be completely ruled out, at least for females mating at larger leks, where they would find sets of males that are both more genetically diverse and whose vocalization rates reflect more honestly this heterozygosity. Given the evidence that some females increase their travel costs to mate at larger leks when the nearest lek is small, these females may, by selecting highly vocal males, indirectly select more heterozygous males.

On the other hand, if mate choice at larger leks is more efficient, we should expect most females to prefer mating at these leks, a prediction that did not hold. A possibility is that mate search by blue-crowned females is too costly to be ideal. Strong male mating skew has been observed in other species of manakins, but most of these are species for which mate choice can be expected to be relatively “cheaper”, given that males are more tightly clustered in space (species with classical leks or with larger leks, Lill 1974, 1976, Stein and Uy 2006) or present strong dominance hierarchies that facilitate assessment during male-male interactions (McDonald 1989, DuVal 2007). In support of this, when compared to two other manakin species that co-occur at Tiputini but have larger leks and stronger dominance hierachies, blue-crowned manakins had lower mating skew among leks (Loiselle et al. in prep.). In this species, females have small home ranges that encompass few or no leks and, thus, have to travel relatively large distances to be able to increase the number of males and leks assessed, which should increase significantly the costs of mate choice.

The process of female mate choice operates at multiple scales, but most studies to date have concentrated on either the among-lek scale (e.g., by assessing how females choose among leks of different sizes) or the within-lek scale (e.g., by estimating mating skew among lek mates). By considering both of these spatial scales, we were able to have a better understanding of how female mate choice happens at the population level in the blue-crowned manakin. Our observations suggest that females travel move their regular home ranges to mate, indicating that they increase their travel costs to assess a larger number of potential mates. This is especially true for females nesting near small leks, which tend to mate at larger, further leks. At the population at large, however, there is not a preference for larger leks, and even solitary males may sire young; we suggest that this is due in part to the the high costs of mate search in this species. Male mating skew is more pronounced at the within-lek scale, where females prefer males with higher vocalization output. Female mate choice should be more effective for females mating at larger leks, where vocalization output is expected to be a more honest signal of male phenotypic quality (i.e., vigor) and genetic quality (as measured by mean d^2 heterozygosity). An untested prediction that follows from these observations is that females mating at larger leks should produce fitter offspring than females mating at smaller leks.

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Table 1 – Microsatellite loci for which blue-crowned manakins (*Lepidothrix coronata*) were genotyped, with number of detected alleles, size range (in base pairs, with size of repeat units between parentheses), adopted annealing temperature (in °C), observed and expected heterozygosities, and estimated frequencies of null alleles.

	No. alleles	Size range (repeat unit size)	T_a	Heterozygosity		Null allele frequency
				H_o	H_e	
Man3[a]	33	190-344 (4)	54	0.749	0.927	+0.1047
Mani(AC)5[b]	13	204-232 (2)	50	0.668	0.765	+0.0647
Man13[a]	31	124-194 (2)	55	0.891	0.935	+0.0237
LTR8[c]	10	140-156 (2)	60	0.566	0.535	-0.0391
Lan20[d]	32	86-158 (2)	56	0.855	0.919	+0.0369
Lan22 [d]	26	154-204 (2)	56	0.912	0.921	+0.0045

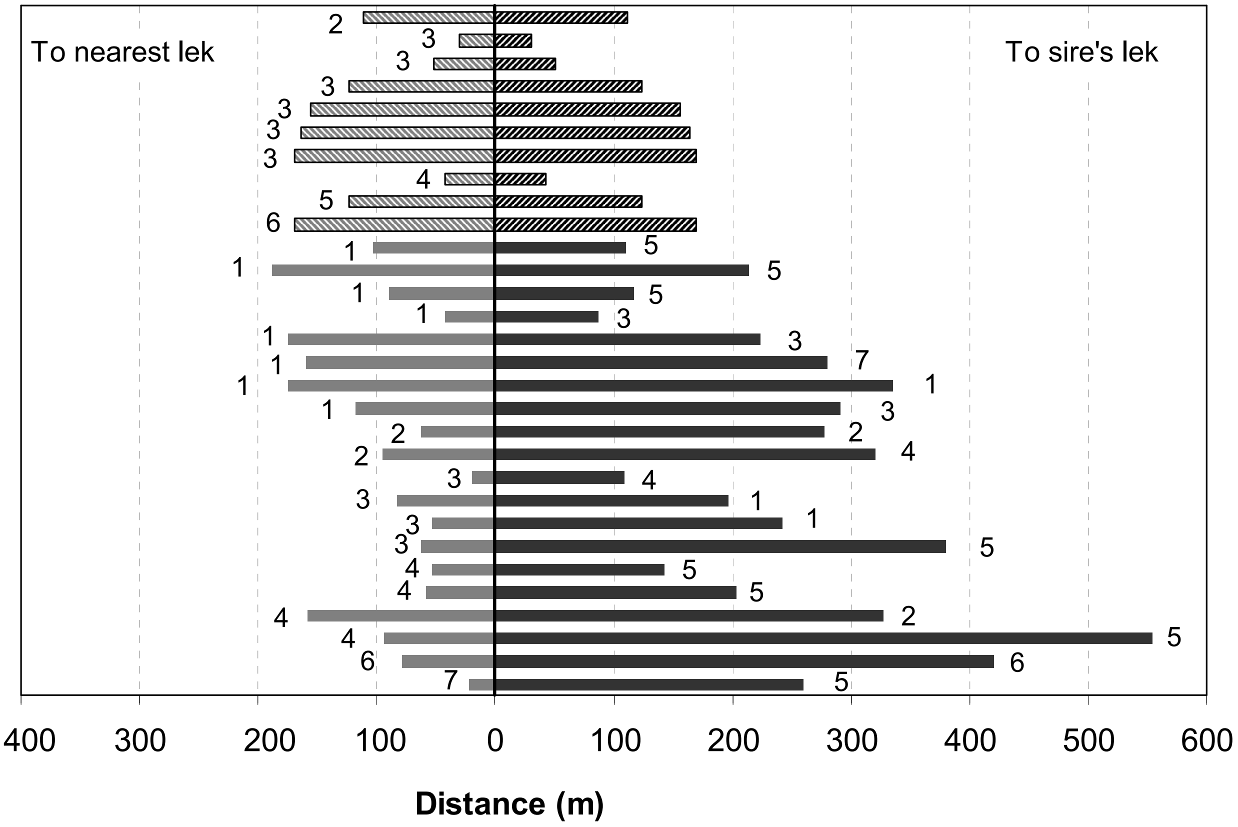
References: [a]Piertney et al. (2002); [b]R. T. Brumfield and M. J. Braun, pers. comm., Brumfield (1999); [c]McDonald and Potts (1994); [d]Duval and Nutt (2005).

Figure Legends

Figure 1 – Distance between blue-crowned manakin nests and the closest edge of the nearest lek (left panel, in gray) or the lek to which the siring male belongs (right panel, in black); each row represents a nest; hatched bars represent cases in which the nesting female mated at the nearest lek (*n* = 10), solid bars represent cases in which the nesting female mated at a lek located further than the nearest one (*n* = 20); numbers associated with bars indicate the size of the lek (i.e., number of territorial males).

Figure 2 – Relationship between individual heterozygosity and lek size (in terms of number of male territories) among blue-crowned manakin males; (A) mean d^2 heterozygosity (ln-transformed) increases with lek size, (B) but H_s heterozygosity does not.

Figure 3 – Male blue-crowned manakins increase call rates according to lek size. Tendency lines are fitted separately for males that sired young (black circles, solid line) and males that did not sire young (gray circles, hatched line); open circles represent males for which no information is available on reproductive success.



To nearest lek
To sire's lek
400
300
200
100
0
100
200
300
400
500
600
Distance (m)

Figure 1

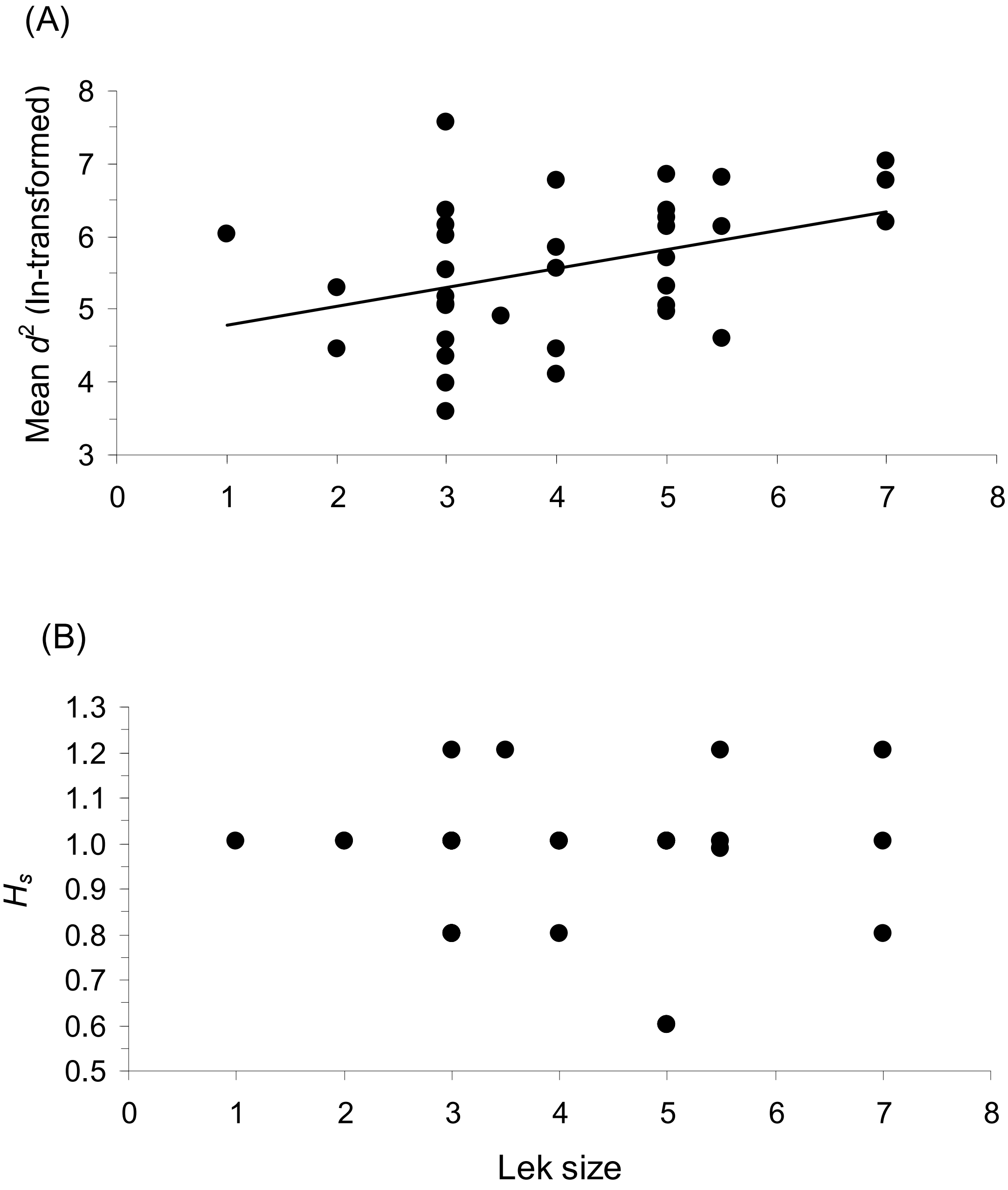

(A)
Mean d^2 (ln-transformed)
8
7
6
5
4
3
0
1
2
3
4
5
6
7
8
(B)
H_s
1.3
1.2
1.1
1.0
0.9
0.8
0.7
0.6
0.5
0
1
2
3
4
5
6
7
8
Lek size

Figure 2

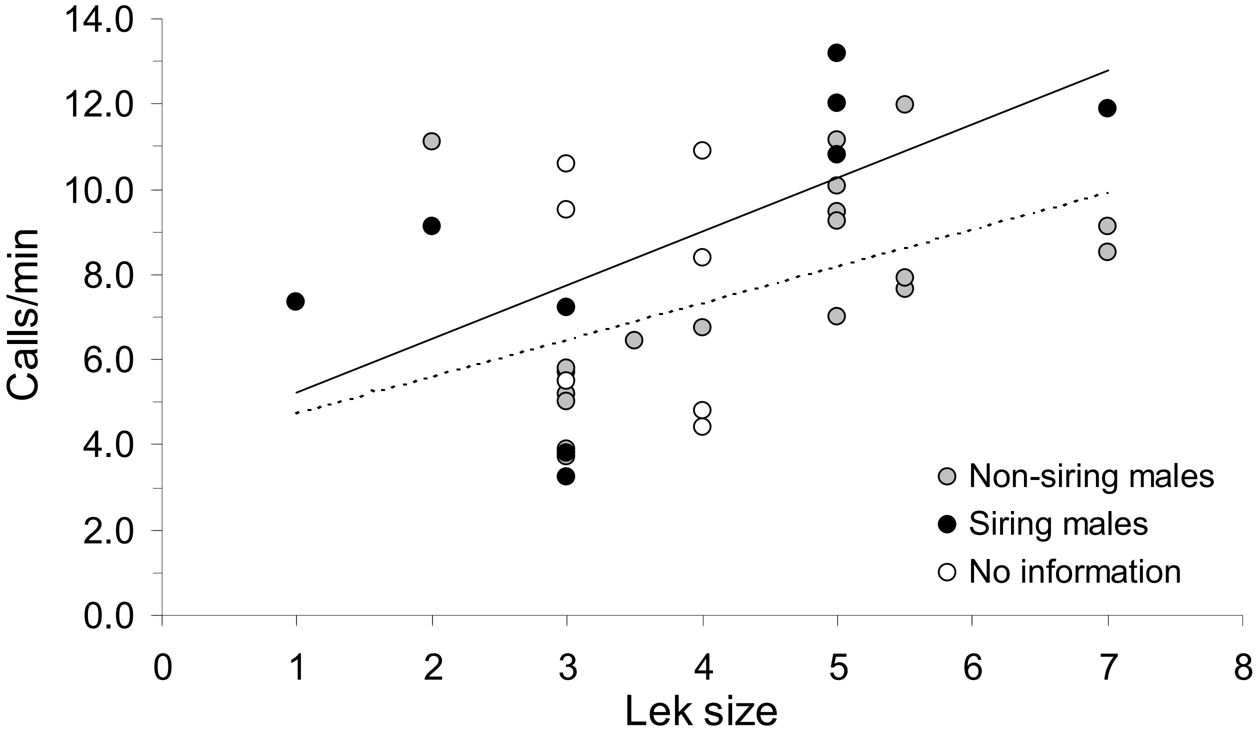

14.0
12.0
10.0
8.0
6.0
4.0
2.0
0.0
Calls/min
0
1
2
3
4
5
6
7
8
Lek size
Non-siring males
Siring males
No information

Figure 3