Intersexual spatial relationships in a lekking species: blue-crowned manakins and female hot spots

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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 (hot-spot hypothesis). We evaluated whether female hot spots 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 (HRs) modeled based on radiotelemetry data. The number of females that lekking males can be expected to encounter was estimated as the number of individual female HRs overlapping each male territory; hot spots 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 hot-spot 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 hot spots than similar-sized nonlek sites. A proportion of males were, indeed, settled at hot spots, but, contrary to predictions of the hot-spot hypothesis, they belonged to smaller leks than males located outside hot spots. Our results indicate that this lack of spatial correlation between males and females results partly from differences in sex-specific habitat preferences. *Key words:* Amazon, blue-crowned manakin, Ecuador, female spatial distribution, habitat selection, hot-spot hypothesis, lek, *Lepidothrix coronata*, Pipridae. *[Behav Ecol 18:1029–1039 (2007)]*

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 on 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 nonresource-based mating systems where males 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 with 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 nonexclusive mechanisms

have been proposed to explain why leks evolve despite these obvious costs associated with aggregating (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 hot-spot 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 on 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 a 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 hot-spot 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, hot-spot 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 (HRs) 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 HRs—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 HRs and visit male territories to mate. Here, we evaluate whether hot-spot 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 2 100-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 hot-spot formation and access to females. Although devaluation is an intrinsic feature of the hot-spot 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. 2007; Ryder TB, Durães R, Tori WP, Hidalgo JR, Loiselle BA, Blake JG, unpublished data), and females make repeated nesting attempts during the relatively long (≥5 months) breeding season (Durães R, personal observation). 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°38′S, 76°08′W, 190–270 m above sea level [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 2740 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 × 1 km each, 100 × 200 m grid lines) established ~1.5 km apart at nearest edges. Geographic Information Systems (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 ex-

treme 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 2 or less frequently 1 egg (Durães R, personal observation). 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 (Hidalgo JR, Ryder TB, Tori WP, Durães R, Blake JG, Loiselle BA, unpublished data).

Population survey: captures, nests, and leks

The distribution and abundance of adult and juvenile *L. coronata* were assessed on the 2 plots over several periods between 2001 and 2006 (February–March 2001; January–March and June–August 2002; January–March 2003; December 2003–April 2004; November 2004–April 2005; November 2005–April 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 × 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 h; Blake JG, Loiselle BA, unpublished data). 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 2 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 (December 2003–April 2004), 2005 (November 2004–April 2005), and 2006 (November 2005–April 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 HRs 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 radiotelemetry 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 (MCP) 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 neighboring territorial males were observed. Locations of most leks were constant over the years despite relatively high male turnover (Durães R, in preparation).

Female capture points, nests, and centroids of male territories and leks were displayed as points in ArcView 3.2 or ArcGIS 9.1 (ESRI, Redlands, CA). We estimated the degree of spatial dispersion for each of these features using the index of aggregation I_a (Perry 1998), 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 the program SADIEM (Perry 1995) that 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 the program SADIEShell 1.22 that randomizes points among fixed locations.

Estimation of female HR size

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 radiotelemetry. Eleven females (5 from Harpia, 6 from Puma) had radio transmitters (model BD-2N, Holohil Systems Ltd, maximum weight 0.5 g, <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 HR 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 2 observers on foot using handheld 3-element Yagi antennas and portable FM100 Fieldmaster receivers. Bearings were taken every 8 or 15 min for 4 h/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 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% MCP using Animal Movement 1.0 (Hooge and Eichenlaub 1997). Of late, kernel estimators have been preferred to MCP because the latter can include considerable expanses of nonutilized area in the estimate of HR (e.g., Worton 1987). Nevertheless, we decided to adopt MCP for 2 reasons. First, because 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 3. 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 R et al., unpublished data).

Models of female spatial distribution

Two classes of female occurrence data were used to model female distribution: capture and nest locations. These 2 classes of data were not combined, that is, each spatial model was built based on either 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 (64–89% for *L. coronata* in TBS, Loiselle BA, Blake JG, Durães R, unpublished data; 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 ± standard deviation [SD], for *L. coronata* females in TBS, $N = 280$ pairwise distances, Loiselle et al., unpublished data; see also Snow and Lill 1974), we assume that combining captures over a period of 5 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 (Hidalgo JR, Ryder TB, Tori WP, Durães R, Loiselle BA, unpublished 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 HR, the nest was assigned to that female; when it fell in the intersection between 2 or more known females' HRs, it was withdrawn from the analyses; and when it was not included in any known female's HR, it was attributed to a novel, unidentified female and was 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 3-fold larger HR that reflects the upper size limit as estimated by telemetry (see Results). Second, a grid with 30 × 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 × 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 × 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 HR. The total number of females overlapping each male territory was estimated for

Table 1

Parameters of the 8 models of spatial distribution of *Lepidothrix coronata* females built for each of two 100-ha study plots

Class of occurrence point	Female HR size (ha)	Devaluation assumed	Model
Captures	4	No	4C
		Yes	4C-dev
	12	No	12C
		Yes	12C-dev
Nests	4	No	4N
		Yes	4N-dev
	12	No	12N
		Yes	12N-dev

each of the 8 models (Table 1) using zonal statistics, where each zone was defined as an individual male territory (ArcGis Spatial Analyst extension). Number of female HRs overlapping male territories was compared across models with nonparametric linear correlations and 2-way repeated-measures analyses of variance (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 that, 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 hot-spot hypothesis

We tested the hot-spot hypothesis by asking whether males establish territories over female hot spots, that is, 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, 30×30 m nonoverlapping 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 1-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 hot-spot 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 to not nest near leks because of increased nest predation risk. To investigate whether leks are more likely to occur near female hot-spot patches, we classified each of the 30×30 m grid cells in each plot as a lek or a nonlek 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 nonlek 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) that 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 pseudoreplication, only 1 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 1×1 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 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, nonparametric correlations were performed between each pair of variables; variables showing high pairwise correlations ($r_s > 0.6$) were subjected to 1-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 interlek distance, was very similar between plots. In all, 13–14 leks were found each year in each plot, encompassing between 1 and 7 individual male territories, with a mean of 2.7 and 3.2 males/lek on Puma and Harpia plots, respectively (Figure 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 m², averaging 818 ± 451 m² on Puma and 1187 ± 917 m² on Harpia; thus, the average male territory was approximately equivalent in size to a 30×30 m square. As expected, male territories were spatially aggregated in both plots, significantly so on Harpia (Harpia, $I_a = 1.43$, $P = 0.016$, 1-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 (Figure 2). Number of captures per female across the entire study period ranged from 1 to 7. Females were randomly distributed according to
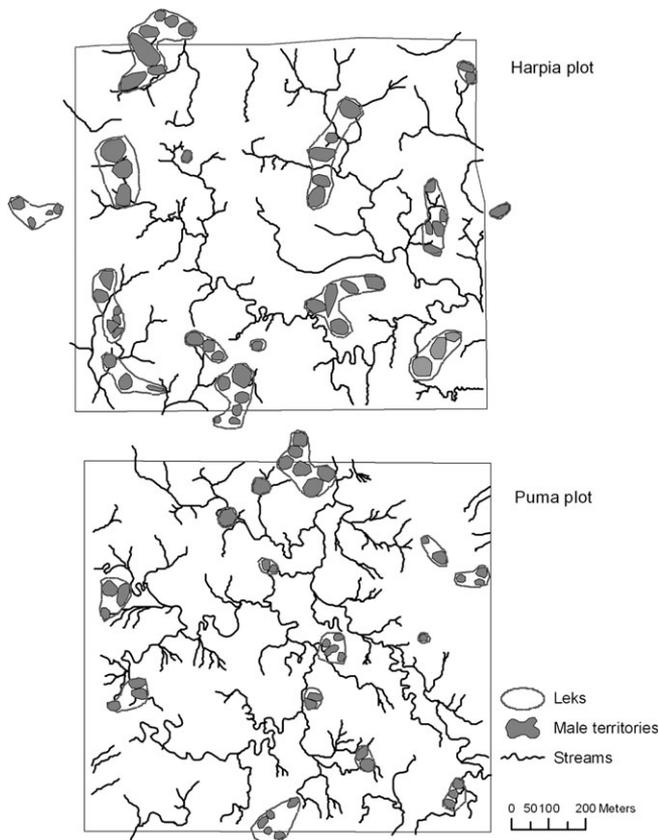
Figure 1
Location of leks and individual male *Lepidothrix coronata* territories in two 2100-ha study plots, Harpia and Puma, in Tiputini, Ecuador.

Figure 2
Distribution of *Lepidothrix 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.

capture points (only 1 capture point per female; Harpia, I_a = 0.87, P = 0.24; Puma, I_a = 0.87, P = 0.29). Nest location data also suggest 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 1–6 nests assigned to each female; 35 nests were found on Puma (18 active, 17 inactive) and were assigned to 18 different females, with 1–5 nests per female (Figure 2). Distribution of nest points was random-to-regular (1 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 internest 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 2 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% confidence interval: 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 2 different HR sizes: 1) 4 ha or a circular area with a radius of 113 m, representing an average-sized HR and
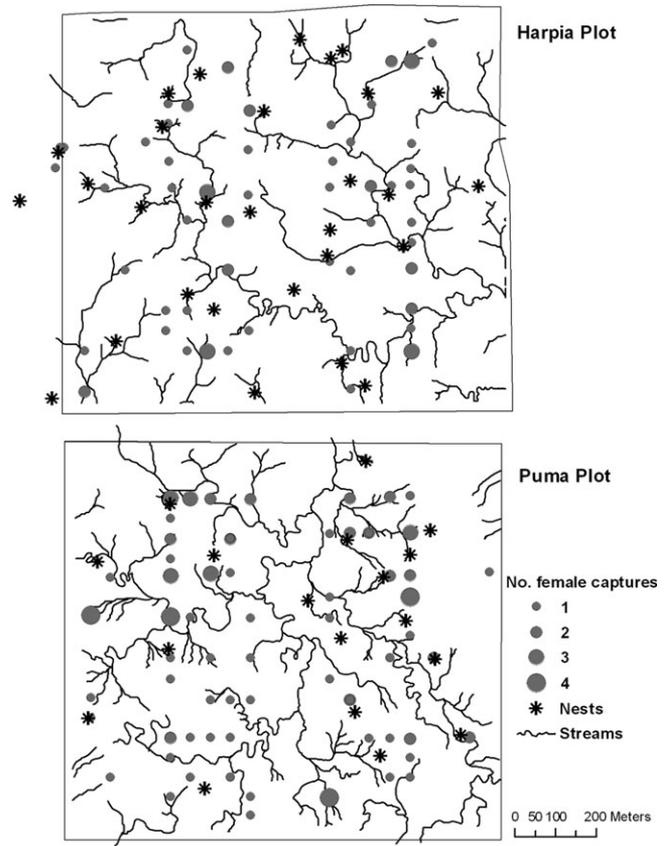
2) 12 ha or a circular area with a radius of 200 m, representing an upper size-limit HR, as estimated with radiotelemetry.

Female HRs encompassed, on average, just 1 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 2 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 (Figure 3, see also Figure 4 for examples). Number of females at each male territory was highly correlated across models (Harpia models: P < 0.05 for 26 of 28 pairwise comparisons, r_s values = 0.32–0.85; Puma models: P < 0.05 for 28 of 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 (Figure 5; note 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 be less than one-third of its effect in the absence of devaluation (1-way repeated-measures ANOVA
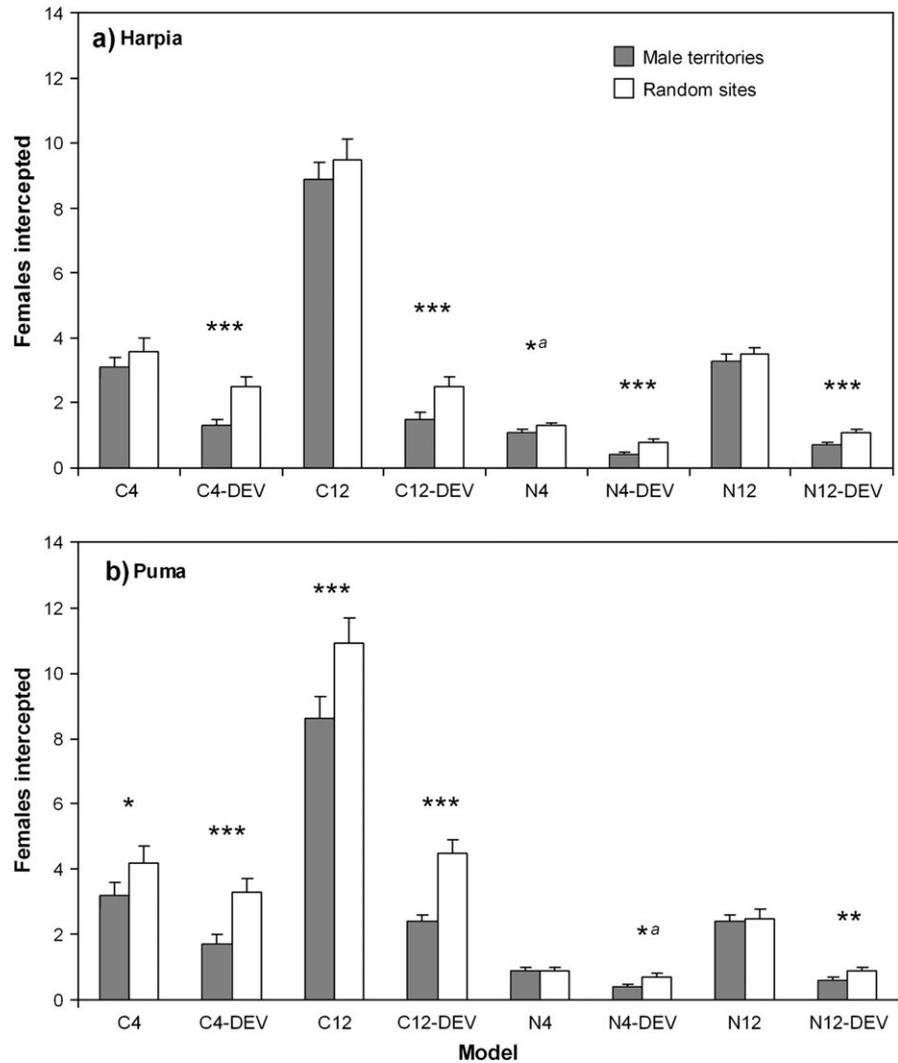
Figure 3
Mean number (and standard error) of female HRs overlapping at male territories (gray bars) and at an equal number of random sites (white bars) on (a) Harpia and (b) Puma plots, as estimated by 8 models of female distribution (see Table 1). For most models, males intercepted less females at their 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.

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 with 0.70 for nondevaluation models; for devaluation models based on captures: $F_{1, 72} = 12.351$, $P = 0.001$, HR size $\eta_p^2 = 0.15$ compared with 0.85 for nondevaluation models).

Also, for a given HR size, devaluation significantly decreased the number of females a male may expect to encounter (Figure 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 hot-spot hypothesis

On each plot, mean number of females intercepted at male territories significantly differed from random expectations for 5 to 6 of the 8 models of female distribution, including all models assuming devaluation (Figure 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 "hot spots," most territories are actually located at "cold spots" 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 hot spots. In nondevaluation models, on average, 24% of the territorial males intercepted more females than expected by chance, whereas in devaluation models this proportion fell to 9% (Figure 6). However, once more contradicting predictions of the hot-spot hypothesis, leks overlapping female hot spots were not larger than those located outside hot spots. Rather, in a consistent way across models and for both plots, leks located at hot spots were smaller than leks located away from hot spots (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 hot-spot patches (Table 3). Number of female HRs overlapping at a given cell and distance from this cell to the nearest lek were
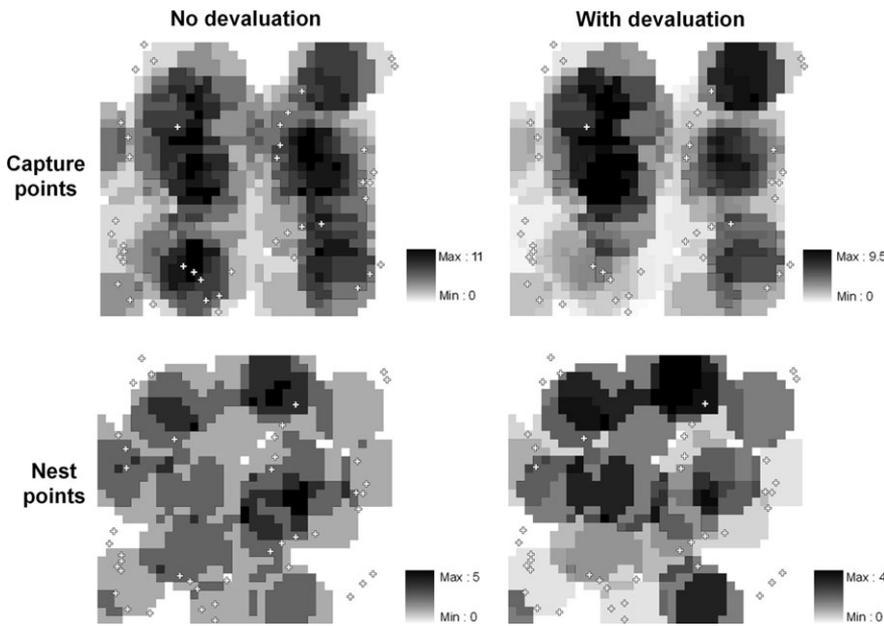
Figure 4
Modeled patterns of female distribution for the Harpia plot, assuming an average female HR size of 4 ha; the 4 different models were based on either capture or nest points, with or without patch devaluation. Values are number of females per cell; cells are 30 × 30 m in size; white crosses indicate centers of male territories.

uncorrelated for all nondevaluation 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 hot-spot 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 (Figure 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, whereas 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 hot-spot 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 flycatcher *Mionectes oleagineus*, Westcott 1997), near nesting sites (greater prairie chicken *Tympanuchus cupido*, Schroeder and White 1993), or near feeding patches used by females (4 species of manakins, Théry 1992). For other species, however, hot spots 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, "hot-shot" males and/or a positive feedback caused by female preference for clustered males (Gosling and Petrie 1990; Bro-Jørgensen 2003).

For other species, the hot-spot model has been dismissed because leks were not located in areas of high female concentration (capercaillie *Tetrao urogallus*, Wegge and Rolstad 1986;

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)

Source	Models based on nests				Models based on captures			
	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 × HR	1, 72	163.262	**<0.001**	0.694	1, 72	390.335	**<0.001**	0.844

Significant *P* values are shown in bold. df, degrees of freedom.

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

a) Models based on nests
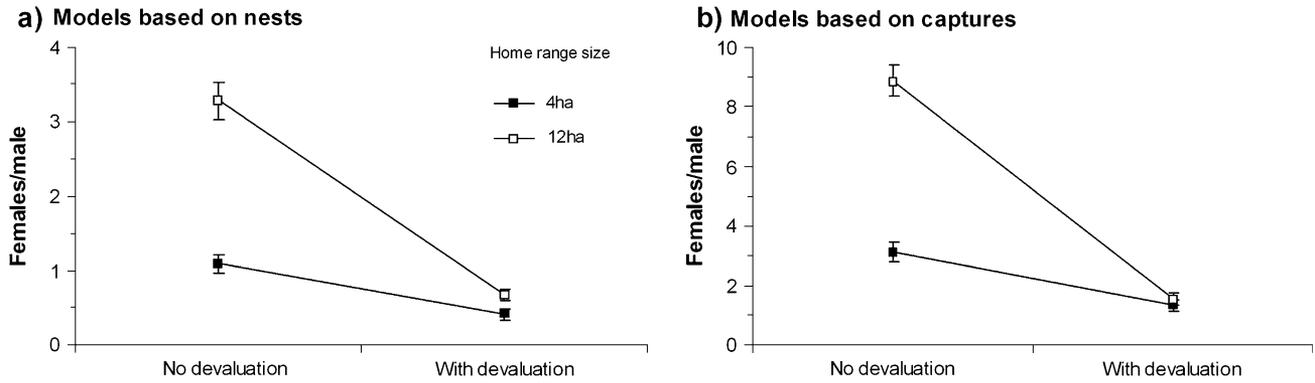
b) Models based on captures

Figure 5
Effect of female HR size and patch devaluation on number of females' HRs overlapping at *Lepidothrix coronata* male territories on Harpia plot, according to models based on (a) nests or (b) capture points. Vertical bars indicate 1 standard error. Patterns for Puma plot were identical and are not shown.

3 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). In this study, we did not find evidence that *L. coronata* leks are located on female hot spots (defined as areas where a large number of females' HRs 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 2 independent data sets of female occurrence (captures and nests).

It seems counterintuitive 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
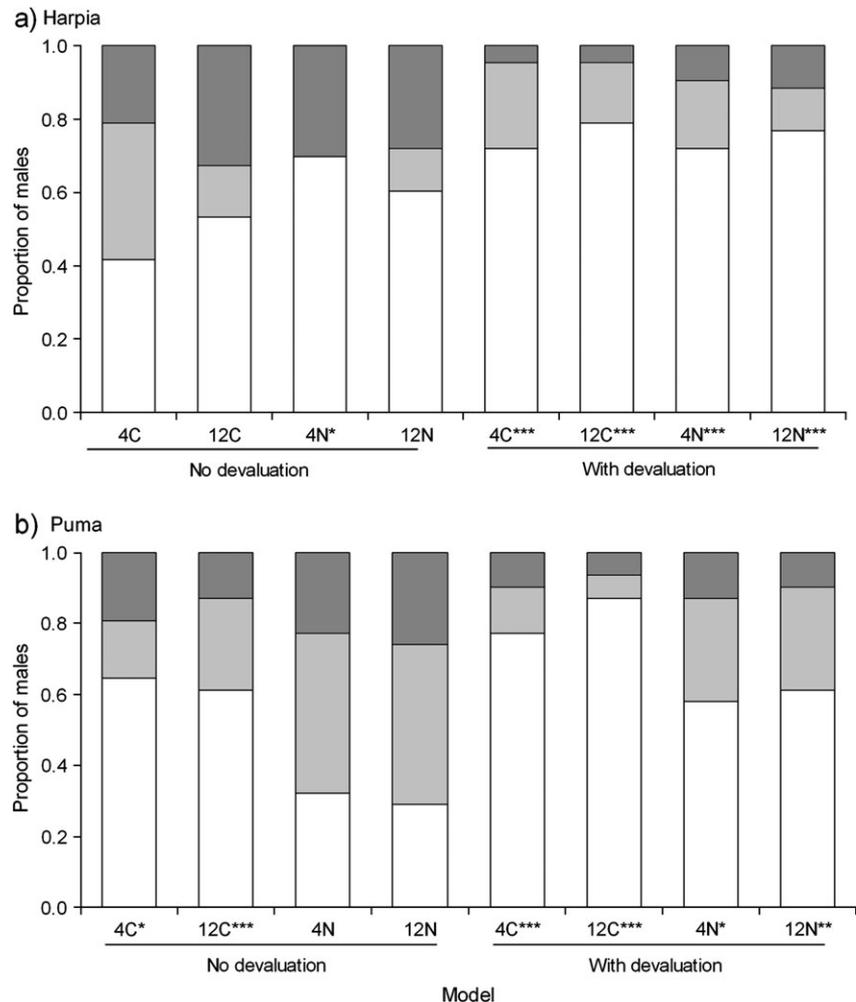
a) Harpia

b) Puma

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 8 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).

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 Harpia and Puma plots

Model	r	Effective N	Corrected P
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**
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

Significant *P* values are shown in bold. *P* values and sample sizes were corrected for spatial autocorrelation among cells.

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 hot-spot 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. 2007).

It is possible that hot spots 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 hot spots, particularly for nondevaluation 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 interlek distances (see below). In addition, we cannot rule out the possibility that the hot-spot model might hold if female concentration had been characterized differently, for example, based on foraging areas (e.g., Théry 1992) or corridors of female movements (e.g., Westcott 1997), rather than based on overlapping female HRs. This is conceivable because females can make rapid visits to key foraging sites that are difficult to detect with radiotelemetry.

However, we consider it more likely that hot-spot 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 hot-spot patterns of settlement. Female *L. coronata* have small HRs (4 ha, on average) with relatively little overlap and are 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 interlek distances in both plots—suggest 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
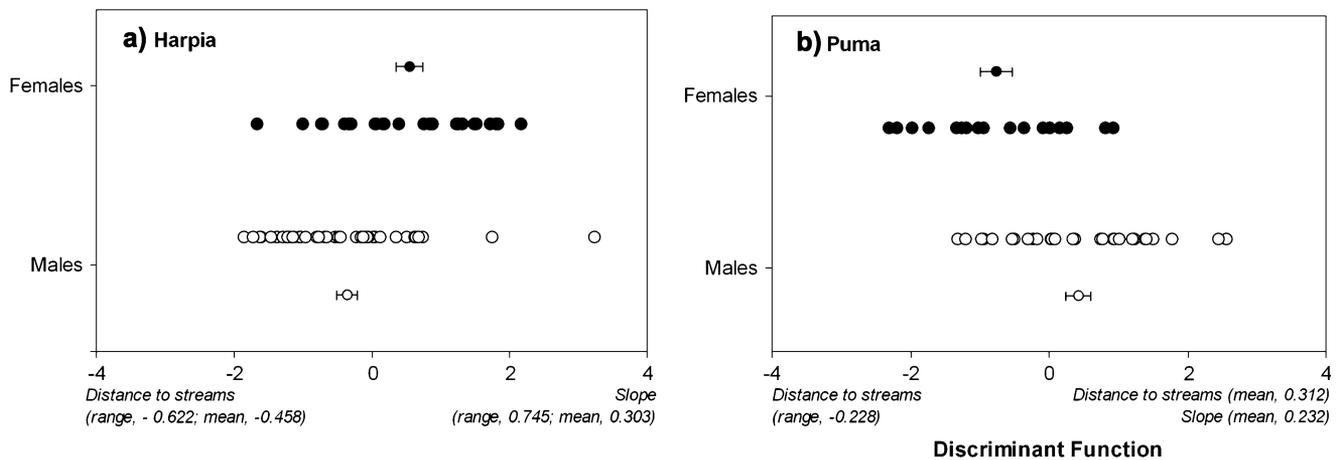

Figure 7
Discrimination of *Lepidothrix coronata* male territories (open circles) and nest sites (closed circles) along an environmental axis on (a) Harpia and (b) Puma plots; centroids ± 1 standard error bars are shown above or below points. Variables more strongly correlated with the axis are specified 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.

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 hot-spot 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 hot spots. 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 HRs 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 HR (Durães R, in preparation). 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 (Durães R, in preparation) 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 hot-spot settlement rules in *L. coronata*, the fact that our models showed strong effects of HR size and devaluation—and the interaction of the 2—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 3-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 with 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 hot-spot 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 hot-spot 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. Although strong evidence supporting the hot-spot model was found for *M. 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 refutation 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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