



ENVIRONMENTAL AND SPATIAL SEGREGATION OF LEKS AMONG SIX CO-OCCURRING SPECIES OF MANAKINS (PIPRIDAE) IN EASTERN ECUADOR

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ABSTRACT.—Environmental correlates and geographic spacing of leks were compared for six species of manakins (Pipridae) on two 100-ha study plots in eastern Ecuador. The “hotspot” hypothesis of lek evolution suggests that males should aggregate where females are most likely to be encountered. For ecologically similar species that co-occur at a site, leks are predicted to be clustered in space and, thus, to overlap in macroscale environmental characteristics. The geographic spacing and environmental characteristics of lek sites we observed were inconsistent with the hotspot hypothesis for lek evolution. In general, little geographic overlap occurred among leks, and geographic spacing of leks among heterospecifics more closely fit a regular than a clumped pattern. Further, environmental conditions of leks varied among species with respect to elevation and topography. Leks of some species were more likely to occur on hilltops or ridge tops (e.g., *Machaeropterus regulus*, *Pipra erythrocephala*), whereas others appeared to prefer highly dissected drainages (e.g., *P. pipra*), relatively flat terrain near streams (e.g., *Chiroxiphia pareola*), or seasonally inundated forests (e.g., *P. filicauda*). Using randomly placed leks, we found evidence that certain lek environments may be limited, which is consistent with observed levels of population abundances on the two plots. Such environmental limits may constrain lek placement and size. Further study is needed to determine the reproductive implications of placing leks in apparently suboptimal environments, though such compromises may reflect males making the best of a bad situation. *Received 15 August 2005, accepted 25 March 2006.*

Key words: behavior and ecology, habitat selection, lek mating system, manakins, tropical wet forest.

Segregación Ambiental y Espacial de las Asambleas de Cortejo Entre Seis Especies Simpátricas de Saltarines (Pipridae) en el Oriente de Ecuador

RESUMEN.—Se compararon los correlatos ambientales y el espaciamiento geográfico para seis especies de saltarines (Pipridae) en dos parcelas de estudio de 100 ha en el oriente de Ecuador. La hipótesis de los “sitios calientes” para explicar la evolución de las asambleas de cortejo (“leks”) sugiere que los machos deberían agregarse en lugares en donde es más probable encontrar a las hembras. Para especies ecológicamente similares que coexisten en un lugar, se predice que las asambleas deberían estar agregadas en el espacio, por lo que deberían superponerse en cuanto a sus características ambientales a una escala macro. El espaciamiento geográfico y las características ambientales de los sitios donde se ubicaron las asambleas que observamos fueron inconsistentes con lo esperado de acuerdo a la hipótesis de

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los puntos calientes. En general, existió poca superposición geográfica entre las asambleas, y el espaciamiento geográfico de asambleas heteroespecíficas se ajustó más a un patrón regular que a uno agregado. Además, las condiciones ambientales de los sitios de ubicación de las asambleas variaron entre especies con respecto a la elevación y la topografía. Las asambleas de algunas especies se encontraron más en las cimas de colinas o en los filos (e.g., *Machaeropterus regulus*, *Pipra erythrocephala*), mientras que otras parecieron preferir cuencas fuertemente disectadas (e.g., *P. pipra*), terrenos relativamente planos cerca de quebradas (e.g., *Chiroxiphia pareola*) o bosques estacionalmente inundados (e.g., *P. filicauda*). Utilizando asambleas ubicadas aleatoriamente, encontramos evidencia de que ciertos ambientes usados por las asambleas podrían estar limitados, lo que concuerda con los niveles de abundancia poblacional observados en las dos parcelas. Estas limitaciones ambientales podrían restringir la ubicación y el tamaño de las asambleas. Es necesario realizar más estudios para determinar las implicaciones reproductivas de ubicar las asambleas en ambientes aparentemente subóptimos, aunque dichos compromisos podrían reflejar que los machos sacan el mejor provecho posible de situaciones desfavorables.

MANAKINS (PIPRIDAE) ARE generally characterized by strong sexual dimorphism, elaborate courtship displays, and a lek mating system in which males cluster together to attract females and females rear their young without assistance from males (Snow 1962a, Sick 1967, Bradbury 1981, Prum 1990, Wiley 1991). Most studies of lek mating systems have found large variance in reproductive success, with few males obtaining most copulations (e.g., McDonald 1989, Wiley 1991, Alatalo et al. 1992, Höglund and Alatalo 1995, Mackenzie et al. 1995). The total number of copulations observed at a lek has been linked to lek size (i.e., number of males at a lek; e.g., Lank and Smith 1992). Yet the benefits and costs of joining leks differ among males depending on their reproductive potential as mediated by total number of offspring that result from the lek, genetic relatedness among males at leks, and the ability of males to "control" access to females. As lek size increases, the probability that disruptive behaviors will occur also increases, which may help explain observed reductions in reproductive skew in larger leks (Kokko 1997; but see Robbins 1985, Johnstone and Earn 1999). Disruptive behavior can be reduced if clear dominance hierarchies exist among males or if displaying males are farther apart (Foster 1983, Kokko 1997).

Likely as a result of these conflicting selection pressures, social organization and spatial structure of leks vary markedly among species of Pipridae (e.g., Foster 1983, Prum 1990). In general, Prum has defined four types of leks—concentrated, dispersed, solitary, and cooperative—in which the number of males,

their dispersion, and participation in cooperative behaviors differ. Evidence for the importance of selection and evolutionary history in shaping lek behaviors and spatial structure exists (e.g., Prum 1997, Tello 2001, Castro-Astor et al. 2004), yet little attention has been given to the ecological factors that influence and constrain lek placement and spatial dispersion (but see Foster 1983; Westcott 1994, 1997). Several hypotheses have been proposed to explain lek evolution with different expected outcomes on the patterns of lek placement and structure. In the "hotshot" hypothesis, particular males are especially "attractive" to females, and other males tend to cluster near these highly successful males (Beehler and Foster 1988, Hovi et al. 1997). Lek structure and placement under this hypothesis are driven by male–male interactions, and one would expect little or no interspecific overlap or clustering in lek locations. The "hotspot" hypothesis, by contrast, states that certain sites are particularly attractive to females (e.g., near resource patches), or environmental features channel movements of females into similar areas, and males tend to aggregate near areas where there are more females (Bradbury and Gibson 1983). Thus, female distribution and movement are the primary driving forces in lek structure and placement under this hypothesis. Westcott (1994) extended the hotspot hypothesis to interspecific patterns of male aggregations and predicted that leks of ecologically similar, sympatric species should form clusters and that the degree of clustering should reflect the similarity in diets among species. Geographic clustering of

leks might also be expected to lead to interspecific similarities in macroscale environmental conditions found at lek sites.

In lowland forests of eastern Ecuador, six species of manakins locally co-occur and establish leks (e.g., English 1998, J. Blake and B. Loiselle unpubl. data). These six species represent the different lek types described by Prum (1990), and diet data from four species indicate that manakins overlap substantially (range: 0.79–0.98; mean overlap = 0.91) in species of fruit consumed (B. Loiselle et al. unpubl. data). Thus, this system offers a unique opportunity to test Westcott's (1994) predictions of the hotspot hypothesis as it is applied to heterospecific patterns of lek placement. Specifically, we tested whether leks of these six manakin species are clustered and whether the degree of clustering reflects the similarity in diets between species. Assuming that leks formed tight clusters, like those shown by Westcott (1994), we tested a second prediction that leks should overlap in macro-environmental space. In light of these findings, we discuss the implications of lek-site selection for manakin populations and ecology.

METHODS

The spatial and environmental dispersion of leks of six syntopic species of Pipridae were studied in lowland wet forest of eastern Ecuador. These six species include "classical" or "concentrated" lek species (*Pipra erythrocephala*), where males are in visual contact with each other, and "exploded" or "dispersed" lek species (*Chiroxiphia pareola*, *Lepidothrix coronata*, *Machaeropterus regulus*, *P. filicauda*, *P. pipra*), where most of the males are in auditory but not necessarily visual contact (Snow 1962b, Sick 1967, Lill 1976, Prum 1990, Théry 1992). In some species, males have obligate cooperative behaviors and coordinated displays (*C. pareola*; Snow 1976); in others, males regularly cooperate, but such cooperation is not necessary for reproductive success (e.g., *P. filicauda*; Schwartz and Snow 1978, Heindl 2002). Average lek size, as defined by number of territorial males, varied from 1.6 to 12.3 males per lek; in some species, we occasionally found a male displaying alone, but most leks had two or more territorial males.

Leks of the six study species were mapped during a four-year period at Tiputini Biodiversity Station (TBS), Orellana Province, Ecuador

(~0°38'S, 76°08'W). Tiputini Biodiversity Station was established in 1995 by the Universidad San Francisco de Quito (USFQ) on a tract of undisturbed lowland rainforest within the 1.5-million-ha Yasuní Biosphere Reserve, a region noted for its biodiversity. There are >300 species of trees (>10 cm diameter at breast height) per hectare (Kreft et al. 2004), >525 species of birds, including 12 species within the family Pipridae, and >150 species of mammals. The station and nearby areas contain a variety of habitats, including *terra firme* and *várzea* forest, palm swamps and other wetlands, as well as numerous areas of natural regrowth (i.e., blow-down areas in various stages of succession). Geographic-information-system (GIS) databases exist for trails and trail markers, the Tiputini River and some tributaries, and elevation (at 20-m intervals). In addition, a 10 × 10 km, high-resolution (2.4-m pixel size), multispectral image centered on TBS was taken on 4 January 2003. Within TBS, two 100-ha plots (about 1 × 1 km each) were established in *terra firme* forest during 2001. Both plots are gridded (100 × 200 m grid lines) and marked. We have produced GIS databases for permanent grid markers, mist-net locations, streams, elevation, slope, and aspect. The Harpia plot ranges from 201 to 233 m in elevation and is characterized by more dissected upland forests. The Puma plot is flatter overall; elevation ranges from 209 to 235 m.

Between 2001 and 2004 (February–March 2001; December–April 2002–2004), the distribution and abundance of manakins have been studied on the two plots using mist nets, spot-mapping, and intensive observations. Mist nets (12 × 2.8 m; 36-mm mesh) were operated on one day in January (2002–2004) and one day in March (2001–2004) at 96 locations on each plot (12 nets were opened per day from dawn to ~7 h later). In total, 440 individual manakins have been captured and banded with uniquely numbered aluminum leg bands and combinations of color bands (Table 1). In addition, locations of manakins have been mapped throughout each plot during 10- to 12-day periods in February and April 2002–2004 during systematic spot-mapping activities.

Locations of manakins obtained from mist netting and spot-mapping were plotted in GIS to generate preliminary maps of manakin abundance and concentration (i.e., potential lek sites). We used these maps to facilitate additional focal

TABLE 1. Number of manakin individuals captured in mist nets (recaptures not included) or observed during spot-mapping censuses on the Harpia and Puma study plots, 2001–2004.

Species	Harpia		Puma	
	Captured (<i>n</i>)	Observed (<i>n</i>)	Captured (<i>n</i>)	Observed (<i>n</i>)
<i>Chiroxiphia pareola</i>	22	189	19	198
<i>Lepidothrix coronata</i>	94	314	104	250
<i>Machaeropterus regulus</i>	8	43	18	17
<i>Pipra erythrocephala</i>	23	158	11	53
<i>P. filicauda</i>	16	2	62	42
<i>P. pipra</i>	46	112	17	38

observations at leks of all six study species during 2002–2004. Each potential lek site was visited more than five times to map positions of displaying males; visits lasted 1–4 h. All such locations were mapped using the existing grid system, compass, and laser rangefinder. In most cases, male display perches (i.e., perches where males were observed singing) were mapped only if the male was observed on the same perch multiple times. Color combinations of bands were noted (when possible) and, if unbanded males were present at leks, target netting was used to capture and band those males at lek sites in 2004. Nonetheless, there remain a few unbanded males at leks, especially for *P. erythrocephala* and *M. regulus*.

Mapped locations of males were used to determine lek area. Male display perches were displayed as points in ARCVIEW 3.2 or ARCGIS 8.3. A minimum convex polygon was then drawn around display perches that were clustered within an area to define lek locations. In some cases, aggregations of males within a lek were drawn as two to four disjunct polygons because of distinct separation among male clusters. These clusters were given the same lek identification when males were within auditory contact, and occasional interactions among disjunct males were observed. Use of disjunct polygons to define some leks means that the environmental space of leks described here only reflects “active” sections of the lek.

To determine environmental space occupied by each lek, the plots were first divided into 1 × 1 m grid cells and assigned unique numbers to each lek. Thus, grid cells within a lek were identified by the same value. The environmental characteristics of each lek were then determined using zonal statistics in GIS (SPATIAL ANALYST, ESRI, Redlands, California). Zonal

statistics provide minimum, maximum, mean, and standard deviation of values for each environmental variable; lek identification values defined the zones. Environmental variables used here included elevation (m), slope (degrees), distance from stream (m), and band values for the Quickbird multispectral image (blue, green, red, near-infrared bands). Preliminary analyses revealed that data from the multispectral image did not help explain location of leks in environmental space, so final analyses contained only slope, elevation, and distance-to-stream variables.

STATISTICAL ANALYSES

To determine whether leks were clustered heterospecifically, we plotted lek centers using GIS. Following Westcott (1994), we then used a Donnelly modification of the Clarke and Evans test (Krebs 1999) to describe the spatial pattern of lek distribution. The test compares observed and expected nearest-neighbor distances in populations whose densities (i.e., number of leks) are known and determines whether or not deviations exist from a random distribution. If the index of aggregation $R = 1.0$, then a random distribution is indicated; aggregation scores approaching 0 indicate increasingly clumped distribution, whereas those above 1.0 indicate increasingly uniform distribution.

Discriminant function analysis was used to examine whether manakin leks occurred in similar environmental space. Manakin species were the *a priori* groups in the analysis. Data were tested for assumptions of normality and homogeneity of variances before analysis. All variables fit normality and homogeneity of variance assumptions or deviated only slightly. Standardization of these variables did

not change qualitative results presented here; thus, we report the results using data in their original form.

Discriminant function analysis builds a predictive model of group membership based on observed characteristics of each lek. Six predictor variables were used in the analysis: means and standard deviations of elevation, slope, and distance to stream; individual leks were the replicate unit. A set of discriminant functions are constructed on the basis of linear combinations of the predictor variables that provided the best separation among the groups. Here, discriminant functions were generated for each study plot separately; these functions were then applied to an equal number of randomly generated "leks" within each plot to determine the relative environmental space available for each manakin species (i.e., random leks were assigned to a group [manakin species] on the basis of their discriminant function scores). The average size of leks varied from 707 m² to 8,229 m² among the six manakin species; overall mean (\pm SD) lek area was 2,647 \pm 1,828 m². Therefore, average lek area (~2,700 m²) was used to construct a set of random leks. Random leks were generated such that they did not overlap with known leks or other random leks, because we wanted to determine the relative availability of unoccupied sites that had the same environmental characteristics as active leks. Further, if random leks overlapped real leks, the data would not be independent. Thirty-seven random leks were generated for the Harpia plot and 33 for Puma; the number of random leks matches the number of observed leks on each plot.

For each discriminant function analysis, eigenvalues, percentage of variance explained by each canonical discriminant function, and overall significance of the model are reported. Leks are plotted along the first two discriminant functions to visualize separation among manakin species.

RESULTS

GENERAL DESCRIPTION OF LEKS

Over the four-year study period, we individually banded 209 and 231 manakins at the 96 net locations on Harpia and Puma, respectively (Table 1). All six species were captured on each

plot, but distribution of captured individuals differed among species ($\chi^2 = 48.3$, $df = 5$, $P < 0.0001$). *Lepidothrix coronata* was the most frequently captured and observed manakin on both plots, and its abundance was relatively equal between plots. In general, significantly more *P. erythrocephala* and *P. pipra* individuals were captured on Harpia than on Puma, whereas more *P. filicauda* and *M. regulus* were captured on Puma. Spot-mapping produced 818 manakin records on Harpia and 598 on Puma (Table 1). The distribution of records among species differed between plots ($\chi^2 = 112.4$, $df = 5$, $P < 0.0001$). In general, we observed more *C. pareola* and *P. filicauda* on Puma, and more *P. erythrocephala* and *P. pipra* on Harpia.

We mapped 38 and 34 manakin leks on or immediately adjacent to Harpia and Puma, respectively; leks outside the study plots were not included in discriminant function analysis, because GIS databases for streams and topography are restricted to within the boundaries of the plot (Fig. 1). Lek locations were stable across years, as has been reported for manakins elsewhere (e.g., Snow 1962a, Tello 2001, Blake and Loiselle 2002). We found leks of all six species on Puma, but only five of the six species on Harpia. Although results may change somewhat with additional mapping effort in subsequent years, currently there is little direct overlap in geographic space of manakin leks. When spatial overlap occurred, it was almost always between *C. pareola* and *L. coronata*; one *P. erythrocephala* lek with one displaying male was nested within an *L. coronata* lek. Manakin lek size (in terms of both number of males and area) varied within and among species. Overall, the number of males displaying on leks varied from 1 to 12, with leks of *Pipra* species generally being larger than those of other manakin species (Table 2). Number of males, however, represents a minimum estimate of males at a lek, because not all males have been individually banded; number of males on a lek was scored in the most conservative manner. The most notable differences between plots were the relatively large leks of *P. filicauda* on Puma and the relatively small leks (both in area and number of males) of *P. erythrocephala* and *M. regulus* on Puma (Table 2 and Fig. 2). With additional mapping effort, we expect that the leks of the latter two species may increase somewhat in size, but in no cases are they expected to approach the largest lek sizes found on Harpia.

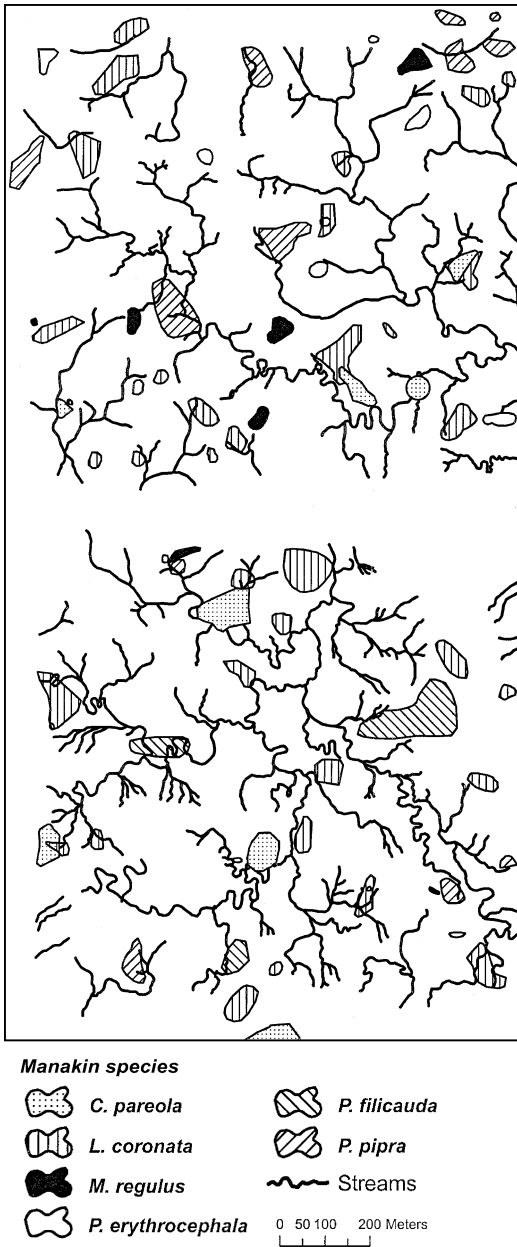


FIG. 1. Location of manakin leks on two 100-ha study plots, Harpia (top) and Puma (bottom), within the Tiputini Biodiversity Station.

SPATIAL CLUSTERING OF LEKS

We found that leks were significantly more uniformly distributed than expected by chance on both Harpia ($R = 1.24, z = 2.74, P < 0.01$) and

Puma plots ($R = 1.22, z = 2.67, P < 0.05$). The mean distance to nearest-neighbor heterospecific lek was 110 m and 104 m on the Puma and Harpia plots, respectively. Consequently, manakin leks were not clustered on either plot, and our results do not support either prediction of the hotspot hypothesis. Because manakin leks were not clustered, we can also reject the prediction that species with similar diets are more clustered.

ENVIRONMENTAL CORRELATES OF LEKS

If leks were clustered, as predicted by the hotspot hypothesis, leks might be expected to be found in similar environments at the macroscale. By contrast, we found significant or nearly significant separation of leks in environmental space among species on both Harpia and Puma (Figs. 2 and 3). The first two discriminant functions explained 87.7% of variance in environmental location of leks on Harpia and 89.3% of variance on Puma (Table 3). In general, manakin leks separated along axes of elevation and slope heterogeneity. *Machaeropterus regulus* and *P. erythrocephala* leks occurred at higher elevations on both plots and overlapped greatly in environmental space but not in geographic space. On Harpia, *P. pipra* leks tended to be in more topographically dissected areas, whereas *C. pareola* leks were at lower elevations on flatter terrain. Similarly, on Puma, *C. pareola* and *P. filicauda* leks were in lower, flatter areas, whereas *P. pipra* and *L. coronata* leks were at intermediate elevations. Most separation among species in Puma occurred along the first discriminant function axis.

On Harpia, 60% of the leks were assigned correctly to species on the basis of their environmental characteristics, whereas 64% were classified correctly on Puma; the expected correct classification by chance alone would be ~17%. When *M. regulus* and *P. erythrocephala* were assigned to the same group, correct classification improved to 70% on Harpia. Similarly, considering *M. regulus* and *P. erythrocephala* as one group, almost all misclassified leks on both plots (a total of 17 of 20 misclassified leks) fell into the environmental space of *L. coronata*; 15 of 16 *L. coronata* leks were classified correctly on Harpia, whereas 14 of 16 were classified correctly on Puma.

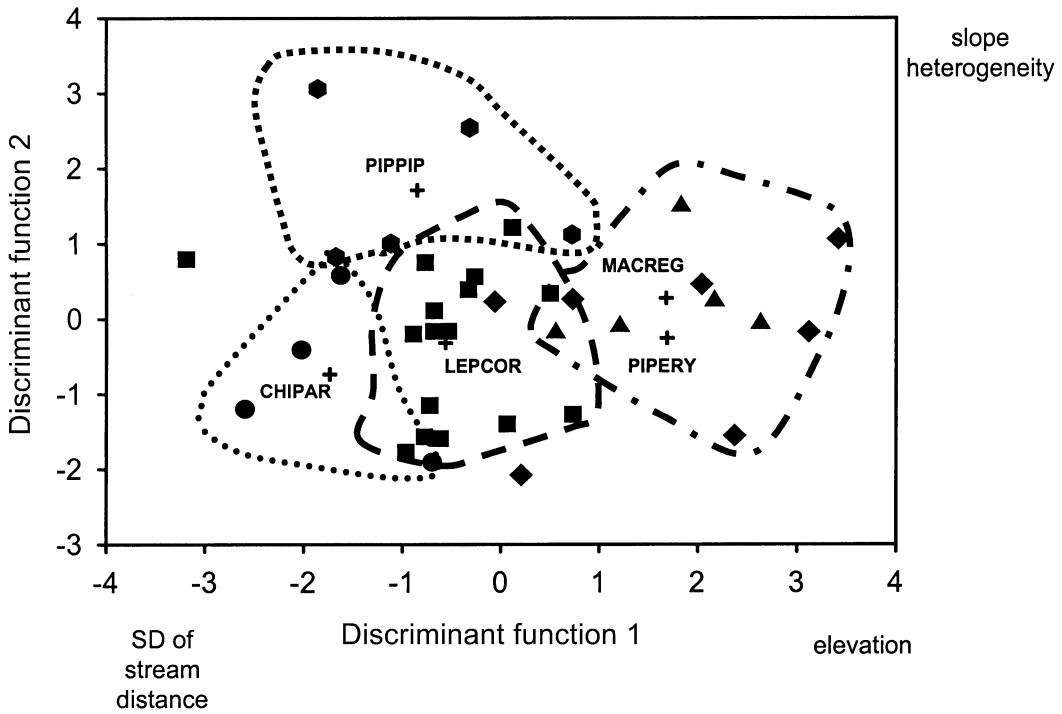


FIG. 2. Location of observed leks ($n = 37$) in environmental space on the Harpia plot based on results of discriminant function analysis. Group boundaries were drawn by hand on the basis of classification results in the graph of observed leks. Squares = *Lepidothrix coronata*, diamonds = *Pipra erythrocephala*, circles = *Chiroxiphia pareola*, upward triangles = *Machaeropterus regulus*, hexagons = *P. pipra*, plus signs = species centroids.

TABLE 2. Number of manakin leks, number of territorial males on leks, and range of lek area (m^2) found on the two 100-ha study plots, Harpia and Puma.

Species	Harpia			Puma		
	Leks (n)	Males (n)	Lek area	Leks (n)	Males (n)	Lek area
<i>Chiroxiphia pareola</i>	4	2–4	920–2,342	4	2–6	3,049–7,697
<i>Lepidothrix coronata</i>	16	1–7	92–7,654	16	1–8	614–7,965
<i>Machaeropterus regulus</i>	5	1–3	184–2,508	2	1	211–1,021
<i>Pipra erythrocephala</i>	8	1–8	244–1,664	5	1–2	64–287
<i>P. filicauda</i>	0	0	0	3	2–12	3,045–16,497
<i>P. pipra</i>	5	4–7	3,803–8,849	4	1–4	642–2,985

The classification of randomly distributed “leks” on the two plots revealed potential limitation in environmental space for some species, especially on Puma. Of the 33 random leks on Puma, 28 (84.8%) were classified as *L. coronata*, whereas 2 leks (6.1%) each were classified as *M. regulus* or *P. filicauda*, and only 1 lek (3.0%) fell into the environmental space characterized by *P. pipra*. On the basis of observed leks, the

expected values given no limitation in environmental space would be 9.1%, 48.5%, 6.1%, 15.2%, 9.1%, and 12.1% for *C. pareola*, *L. coronata*, *M. regulus*, *P. erythrocephala*, *P. filicauda*, and *P. pipra*, respectively. On Harpia, the 37 random leks were distributed more equally, with 10 (27%) leks in *C. pareola* environmental space, 7 (18.9%) in *M. regulus*–*P. erythrocephala*, 6 (16.2%) in *P. pipra*, and the remaining 14 (37.8%) in *L.*

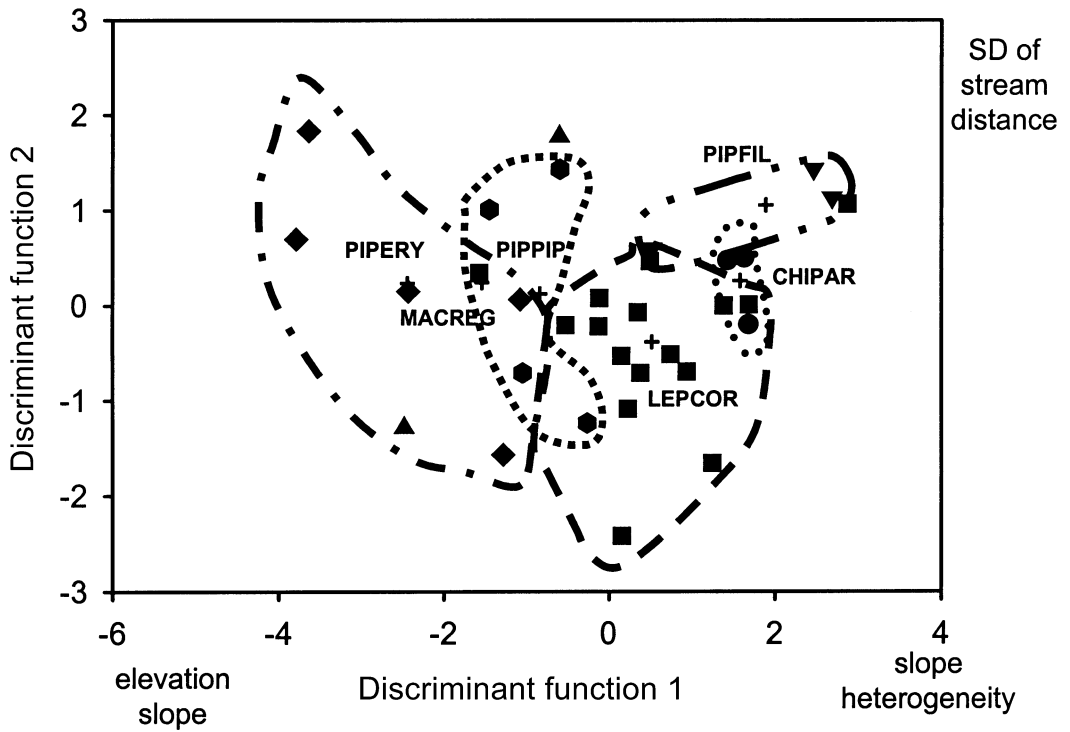


FIG. 3. Location of observed leks ($n = 33$) in environmental space on the Puma plot based on results of discriminant function analysis. Group boundaries were drawn by hand on the basis of classification results in the case of observed leks. Squares = *Lepidothrix coronata*, diamonds = *Pipra erythrocephala*, circles = *Chiroxiphia pareola*, upward triangles = *Machaeropterus regulus*, hexagons = *P. pipra*, downward triangles = *P. filicauda*, plus signs = species centroids.

coronata environmental space. With no limitation in environmental space, the expected values on Harpia would be 10.8%, 43.2%, 32.4%, and 13.5% for *C. pareola*, *L. coronata*, *M. regulus*–*P. erythrocephala*, and *P. pipra*, respectively.

DISCUSSION

On our two 100-ha study plots in lowland wet forests of Amazonia Ecuador, six species of lek-breeding manakins are relatively common and regularly observed on our two plots. These six species of manakins are similar in body size and shape (e.g., most average between 9.9 and 13.3 g; *C. pareola* averages 18.8 g, and *P. filicauda* 15.2 g). Diet data are available for four of these manakin species (*L. coronata*, *P. erythrocephala*, *P. filicauda*, *P. pipra*), and these data demonstrate considerable overlap in plant species consumed (niche overlap from 0.79 to 0.98); common food items include fruits of Melastomataceae,

Moraceae, Bromeliaceae, and Araceae (B. Loiselle et al. unpubl. data). The hotspot hypothesis for lek evolution suggests that males aggregate in areas where females commonly occur to maximize possibilities for female visits. Westcott (1994) extended the hotspot hypothesis and predicted that, in ecologically similar species, female movements may be channeled in similar ways by topographic features and, thus, that heterospecific leks should be clustered in space. A second prediction was that the degree of clustering should reflect similarity in diet. We found that leks were not clustered on either plot and, thus, our results do not support the predictions of the hotspot hypothesis as applied to ecologically similar species that co-occur at a site. Failure to support these predictions of the hotspot hypothesis does not necessarily refute its importance in the evolution of lekking behavior in manakins. Rather, our assumption that females that overlap strongly in diet are

TABLE 3. Results of discriminant function analysis for manakin leks on the Harpia and Puma study plots. Leks were *a priori* assigned to groups according to species. Dependent variables included mean and SD values for elevation, slope, and distance-to-stream at leks. The discriminant function model with four functions was significant on the Harpia plot ($\chi^2 = 53.8$, $df = 24$, $P < 0.001$) and was nearly significant on the Puma plot ($\chi^2 = 43.0$, $df = 30$, $P = 0.058$).

Discriminant function	Eigenvalue	Variance	Cumulative percentage	Canonical correlation
Harpia				
1	1.713	64.9	64.9	0.795
2	0.601	22.8	87.7	0.613
3	0.232	8.8	96.5	0.434
4	0.091	3.5	100.0	0.289
Puma				
1	2.217	80.8	80.8	0.830
2	0.235	8.6	89.3	0.436
3	0.166	6.1	95.4	0.378
4	0.108	3.9	99.3	0.312
5	0.019	0.7	100.0	0.136

similar in movements and spatial dispersion may be invalid, or other factors may constrain lek placement. Indeed, Ryder et al. (2006) found that leks of three of these manakin species at our study site (*P. pipra*, *P. erythrocephala*, *P. filicauda*) occurred in areas significantly richer in fruit resources when compared to paired random sites—a result consistent with the predictions of the hotspot hypothesis. These same results also revealed that plant composition around leks of these three species differed, as might be expected if leks were placed in different environmental conditions.

Here, we found that manakin species largely selected different forest environments as lek sites. Forest environments selected by the different species as lek sites likely reflect past selection pressures to maximize reproductive success, phylogenetic constraints, and current ecological constraints and compromises. For example, fine-scale selection of display sites by manakins has been correlated with ambient light conditions (Endler and Théry 1996, Heindl and Winkler 2003). Light environments are influenced by forest canopy cover and vertical stratification of vegetation and, thus, selection for certain environments revealed here, albeit at this macroscale, may reflect selection for fine-scale environmental conditions, such as light environments. We found that few manakin leks overlapped geographically, though leks of *M. regulus* and *P. erythrocephala* occurred in similar forest environments (i.e., generally ridge tops

or hilltops). On Harpia, these hilltop environments were apparently not limiting, as indicated by analyses of random-lek conditions and by the fact that no geographic overlap occurred between the two species. By contrast, we found fewer and smaller leks of *M. regulus* and *P. erythrocephala* on Puma, which suggests a more limited environmental space. Indeed, only 1 of 33 random-lek sites on Puma was matched to *M. regulus* or *P. erythrocephala* lek environments. Further evidence for limited lek space on Puma was the use of the same hilltop as a lek site by both species, though display sites were adjacent rather than completely overlapping (Fig. 2).

Ecological limitations of lek placement may have population implications. We suggest that the relatively lower abundance of *P. erythrocephala* and *M. regulus* on Puma reflects limited environmental space for leks. Limited lek environmental space may also be an explanation for lower abundance of *P. pipra* on the Puma plot and of *P. filicauda* on the Harpia plot. Leks of the former species were generally found near streams on relatively steep slopes. Streams are common on Puma but the terrain is mostly flat. By contrast, *P. filicauda* leks are often found in relatively open forest environments in flat terrain, often in areas that are seasonally inundated. On Puma, these forest environments exist; but on Harpia, only the southeast section of the plot is regularly inundated and, indeed, this is the area where *P. filicauda* is most often observed or captured. In 2005, a *P. filicauda* lek

was found ~50 m off the southeast corner of the Harpia plot by T.B. Ryder.

Despite separation along discriminant function axes, overlap in environmental space occurs, resulting in misclassifications of leks. Such misclassifications may reflect true environmental overlap in lek placement (e.g., *P. erythrocephala* and *M. regulus*), as discussed above; they may reflect errors in our maps of lek locations or errors in the GIS databases for elevation, slope, and streams; or such misclassifications may indicate that these rather coarse-grained features are not adequate to identify the characteristics needed for a particular species. However, it is also likely that "misclassification errors" reflect establishment of leks in less-than-optimal sites. For example, if there is habitat limitation, either because of environmental constraints (e.g., few hilltop environments on the Puma plot, or inundated forest on the Harpia plot) or because of habitat saturation by conspecifics, leks may be placed in suboptimal locations. We have no evidence, however, that misclassified leks are consistently smaller in size (i.e., number of males) than correctly classified leks, or that such leks are occupied by younger males that may later recruit into other leks, though many had fewer males.

What factors promote establishment of leks in suboptimal environments? Faced with little or no chance of reproductive success at established leks, leks in suboptimal environments may represent the best alternative strategy for some males. Currently, we are studying the reproductive success of male manakins using paternity analysis and lek observations, and we expect to find significant variance in male mating success both within and among leks, as reported elsewhere for manakins (e.g., Snow 1962a, McDonald 1989). In particular, we hypothesize that leks placed in apparently suboptimal environments are less successful but still may represent a potentially successful strategy for males when compared with alternatives (i.e., being a floater or a low-ranking male in a peripheral position of an "optimally located" but large lek; Kokko 1997). The key to success of a lek is largely determined by its efficiency in intercepting females (e.g., Kokko 1997, Fiske et al. 1998, Kokko et al. 1998). If suboptimal leks still occur in environments where females are likely to be encountered, the relative benefits of establishing leks in suboptimal environments may exceed the costs, especially if males can

attract others to join, thus increasing lek size and the potential encounter rate of females.

In summary, we found no evidence that leks of these ecologically similar manakin species were clustered, as would be predicted by the hotspot hypothesis. Instead, we found a strong environmental signal for lek placement, which suggests that males aggregate at sites that contain distinct environmental features. These features may be tied to fine-scale features of the environment, such as ambient light conditions or availability of suitable display perches or they may be located near areas where intraspecific female densities are higher. In either case, it seems that these selected forest environments may be limiting, thus placing restrictions on lek placement and size. The ecological limitations observed here may also explain the observed local (i.e., 100-ha study plots) variation in population abundance of manakins.

ACKNOWLEDGMENTS

We are very grateful to the following individuals who helped establish the 100-ha study plots or assisted in collecting field data: J. Narvaez, F. Narvaez, A. Garcia, J. C. Rodriguez, J. Andy, K. Holbrook, T. Sommers, U. Valdez, J. Hidalgo, and J. Fair. We also thank the staff of the Tiptuni Biodiversity Station, especially J. Guerra, K. Swing, D. Romo, C. de Romo, R. Bustamante, O. Godoy, and J. Fabara, who have made our visits to the site so rewarding. We thank T. Erwin and T. Kunz, who initially encouraged our investigations in this megadiverse region. Finally, we are indebted to the National Science Foundation (IBN 0235141 and DEB 0304909), National Geographic Society (7113-01), Fulbright U.S. Scholars Program, Brazil CAPES Fellowship Program, and the University of Missouri-St. Louis, including the International Center for Tropical Ecology and the Office of Research, for providing funds. This manuscript benefited greatly from comments by D. Westcott, J. H. Vega Rivera, and an anonymous reviewer.

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Associate Editor: J. H. Vega Rivera