VOCALIZATION ACTIVITY AT LEKS OF SIX MANAKIN (PIPRIDAE) SPECIES IN EASTERN ECUADOR

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Resumo. – Atividade de vocalização em leks de seis espécies de piprídeos no leste do Equador. – Na maioria das espécies de piprídeos (Pipridae), machos associam-se em arenas de exibição ('leks') onde participam de rituais de cortejo direcionados às fêmeas. No entanto, a estrutura dos leks e a complexidade dos rituais de cortejo variam bastante entre espécies, e espera-se que diferenças nos níveis de agregação espacial e nas características dos rituais de cortejo influenciem padrões inter-específicos de atividade nos leks. Neste estudo, nós comparamos a atividade de vocalização em leks de seis espécies de piprídeos que co-ocorrem no leste do Equador (*Chiroxiphia pareola*, *Lepidothrix coronata*, *Machaeropterus regulus*, *Pipra erythrocephala*, *P. filicauda*, e *P. pipra*) mas que variam na estrutura dos leks e na complexidade dos rituais de cortejo. Nossos resultados mostram que, primeiro, padrões diários de atividade para cada espécie foram consistentes entre leks e ao longo da estação reprodutiva, permitindo comparações inter-específicas relevantes. Segundo, espécies com leks clássicos ou com rituais de cortejo mais complexos em geral mostraram níveis mais altos de atividade de vocalização; no entanto, componentes específicos de produção vocal (e.g., níveis de vocalização por macho ou por lek, flutuações temporais em níveis de vocalização, etc.) variaram entre espécies. Este estudo contribui para o nosso entendimento de como a estrutura social e a facilitação social entre machos influenciam a atividade em leks.

Abstract. – Most manakins (Pipridae) are lek-breeding species in which males engage in courtship displays directed toward females. Yet, the structure of leks and the complexity of the displays vary widely across species. Differences in male clustering and display attributes are expected to influence inter-specific patterns of lek activity. Here, we investigate how lek structure and display complexity affect vocalization activity at leks of six manakin species that co-occur in eastern Ecuador (*Chiroxiphia pareola*, *Lepidothrix coronata*, *Machaeropterus regulus*, *Pipra erythrocephala*, *P. filicauda*, and *P. pipra*). Our results showed that, first, daily patterns of lek activity within species were consistent spatially (among leks) and temporally (across the breeding season), allowing for meaningful inter-specific comparisons. Second, that both lek structure (male spacing) and display complexity were predictors of vocal activity at leks but specific components of the vocalization output (e.g., output per male or per lek, temporal fluctu-

ations in output levels) varied among species. This study adds to our understanding of how social structure and male-male social facilitation influence activity at leks. *Accepted 10 August 2011*.

INTRODUCTION

Most manakins (Pipridae) are lek breeders with strong sexual dimorphism and, often, elaborate male courtship displays (Snow 2004). For much of the year, male manakins aggregate at traditional lek sites and spend a large part of their day displaying (i.e., calling, singing, dancing), both to defend and advertise their territories and to attract receptive females (Lill 1976, Schwartz & Snow 1978, Foster 1981, Bostwick 2000, Heindl 2002, Castro-Astor *et al.* 2007, DuVal 2007). Display behavior and vocalization activity are both known to have strong consequences for reproductive fitness for manakins (Ryder *et al.* 2008b, 2009; Durães *et al.* 2009) and should be under strong selection. In manakins, some elements of display repertoires tend to be conserved across phylogenetic history and, as a consequence, have been critical for reconstruction of the historical relationships among species (e.g., Prum 1990, 1994; Bostwick 2000). It is unclear, however, whether other attributes of display, such as periodicity and rate, show consistent patterns within species that can give us insights into the dynamics of mate attraction and male-male competition among species with different lek characteristics.

Restricted to Neotropical forests, "true" manakins (*sensu* Ridgely and Tudor 1994) reach their highest diversity in Amazonia. Thus, Amazonian forests provide an ideal setting for comparisons of reproductive behavior of lek-breeding manakins. Here, we describe daily vocal-display activity among leks of six species of manakins that co-occur in eastern Ecuador. Although males of all six species aggregate at lek sites, several compo-

nents of the lek system and display behaviors differ, such as the degree of male clustering at leks (classic vs. exploded), number of males per lek (lek size), presence of cooperative display behaviors and complexity of the display repertoires (Snow 2004, Durães *et al.* 2008, 2009; Ryder *et al.* 2008b, 2009, 2011).

Basic studies on natural history of birds (and other organisms) often provide much of the background needed for development of theory-based studies (e.g., on evolution of reproductive behavior). Yet, such information often is hard to obtain and often hard to publish. Here, we contribute to our understanding of the natural history of six species of manakins by describing and comparing patterns of vocal activity within leks (in different periods of the breeding season), between leks of the same species (at the same time of the season), and among species. Further, we discuss some potential relationships between vocal activity and lek structure in these species. We focused on vocal activity because it is rarely studied in manakins despite the fact that acoustic signals carry farther than visual signals and likely serve as the initial or long-distance attractant for females McDonald 1989, 2010). Moreover, vocal activity is likely a good proxy for the more elaborate courtship display characteristic of manakins and is known to be correlated with male attendance rates (e.g., *Pipra pipra*, Tori 2008). Finally, vocal activity can be measured simultaneously for multiple males providing us with a lek-wide index of male sexual advertisement.

METHODS

Research was conducted at Tiputini Biodiversity Station (TBS, 0º38'S, 76º08'W), a 650-ha

biological station located within Yasuní Biosphere Reserve, Orellana Province, eastern Ecuador. Vegetation is lowland, wet, evergreen forest comprised primarily of *terra firme* and *várzea*; for a more detailed site description see Loiselle *et al.* (2007a). We studied vocal activity at leks of six syntopic manakins: Golden-headed Manakins (*Pipra erythrocephala*) form classical leks, whereas Blue-backed (*Chiroxiphia pareola*), Blue-crowned (*Lepidothrix coronata*), Western Striped (*Machaeropterus regulus striolatus*), Wire-tailed (*Pipra filicauda*), and White-crowned (*Pipra pipra*) manakins form exploded leks (*sensu* Prum 1994; see Snow 2004 for descriptions). Males of two species have either obligate (*C. pareola*) or facultative (*P. filicauda*) coordinated displays.

Vocal activity was documented at two leks of each species in late December 2003 and late February/early March 2004 (February thereafter). These periods are within the main breeding season, which extends from November to April, for all six species of manakins in the region. Evidence of breeding activity (nests, females with well-developed brood patches, females traveling with young, etc.) has been found during these months for all six species (Tori *et al.* 2006, Ryder *et al.* 2008a; pers. observ., 2001–present). Lek sizes vary across species but, within species, samples were taken at leks with comparable numbers of territorial males. Leks were located on two 100-ha study plots where manakin leks have been mapped as part of a long-term study of the demographic and reproductive consequences of lek structure and social organization (e.g., Ryder *et al.* 2006, 2008b, 2009, 2011; Loiselle *et al.* 2007a, 2007b; Durães *et al.* 2008, 2009; Tori 2008, Durães 2009).

In December, up to five observers monitored lek activity continuously from 06:00–12:00 h or 12:00–18:00 h on alternate days over six days; in February, six observers monitored lek activity over the same time periods over four days. This resulted in 12-h sampling periods at each lek (two per species) in both December and February. We coordinated activities so that the maximum number of species could be observed simultaneously (four species in December, six in February) to control for possible weather effects on lek activity. All observations occurred during periods with no rain. At each lek, observers scored the number of songs or calls heard over each 30-min time period. With the possible exception of *Pipra filicauda* (one lek) and *Pipra pipra*, all males on a given lek were within hearing distance of the observer. Observers also scored the number of males heard on the lek during the last 5 min of each 30-min block.

We estimated the average per capita vocalization rate by dividing the number of vocalizations during each 30-min period by the average number of males heard during that period (number of vocalizations/male/30 min). Within species, patterns of daily activity were compared between leks and between time periods (December vs February) with Kolmogorov-Smirnov tests, contrasting number of vocalizations/male in 30-min intervals throughout the day. Across species, we used Kruskal-Wallis tests to compare number of vocalizing males, total number of vocalizations recorded at the lek (i.e., vocalization output at the lek level), or number of vocalizations/male (i.e., vocalization output at the individual level); all three variables were measured in 30-min intervals. We also compared vocalization activity throughout the day across species based on the coefficients of variation (CV) in lek activity, where CV = standard deviation/mean of relativized vocalization rate across the day; vocalization rate was relativized by dividing the total number of vocalizations in each 30-min period by the total number of vocalizations recorded over the 12-h period.
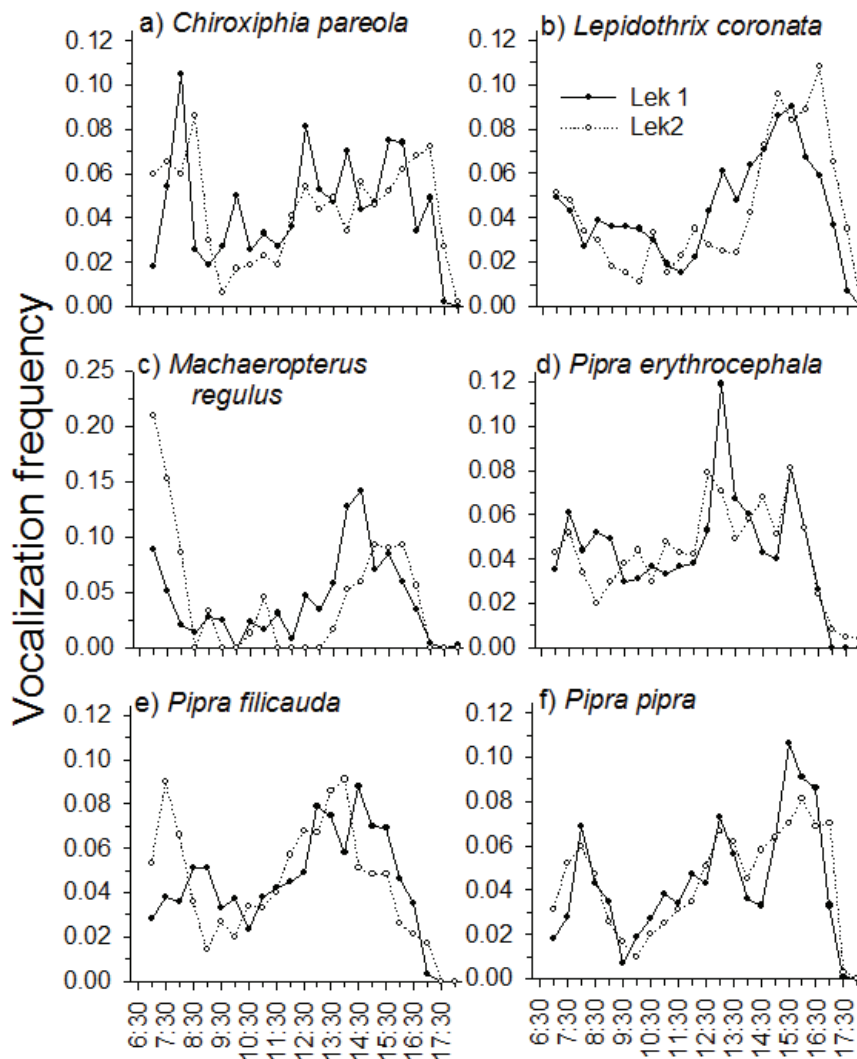
FIG. 1. Relativized vocalization frequency during the day (06:00–18:00 h) for six species of manakins in eastern Ecuador. Vocalization frequency was relativized by dividing the total number of vocalizations in each 30-min period by the total number of vocalizations recorded over the 12-h period. Each graph represents two leks, with values for each lek averaged across two time periods (December and February). Note the difference in scale along the ordinate axis for *Machaeropterus regulus*.

RESULTS

Daily lek activity, as measured by relative vocalization rate, followed a generally bimodal pattern for all species, with a shorter period of high activity in early morning and another, more prolonged, period in the afternoon (Fig. 1). Activity at leks of *C. pareola* and *P. erythrocephala* was more evenly distributed across the day than at leks of other species, as

TABLE 1. Comparisons of daily activity at leks between months (December 2003 vs February 2004) for each of two leks and between leks for each month, for six species of manakins in eastern Ecuador. Numbers represent Z-values from Kolmogorov-Smirnov tests used to compare number of vocalizations/30 min, standardized by average number of vocalizing males, during the day (06:30–18:00 h), with $n = 48$ for each comparison. Coefficient of variation (CV) = standard deviation/mean of relativized vocalization frequency, value averaged over the two leks and for the months; vocalization frequency was relativized by dividing the total number of vocalizations in each 30-min period by the total number of vocalizations recorded over the 12-h period. * - $P < 0.05$; ** - $P < 0.01$; after Bonferroni corrections, * - $P > 0.05$; ** - $P < 0.05$.

Species	Between leks		Between leks		CV in lek activity
	Lek 1	Lek 2	Dec	Feb	
Chiroxiphia pareola	0.72	1.73**	1.30	0.87	0.59
Lepidothrix coronata	0.72	1.01	1.44*	1.30	0.63
Machaeropterus regulus	0.58	1.73**	1.59*	0.58	0.63
Pipra erythrocephala	1.59*	1.16	0.58	1.16	0.58
Pipra filicauda	0.72	0.72	0.58	0.87	0.62
Pipra pipra	1.88*	0.72	1.59*	0.72	1.13

shown by the slightly lower coefficients of variation in vocalization rate; *P. filicauda*, *L. coronata* and *P. pipra* had comparable variation in daily activity at leks. Activity at leks of *M. regulus* fluctuated the most throughout the day, with several blocks of time with very few or no vocalizations recorded (Fig. 1, Table 1).

Daily lek activity was, overall, consistent within species, both between leks and time periods (December 2003 vs February 2004, Table 1, Fig. 1). Distribution of call rates differed between time periods at the same lek in only four out of 12 comparisons (i.e., comparing the same lek between December and February; after Bonferroni corrections for multiple tests, only two comparisons would be considered significant; Table 1); rates differed between leks within a given time period in only three out of 12 comparisons (Table 1; none would be considered significant after correction for multiple tests).

The six manakin species differed in number of males vocalizing simultaneously at the leks ($\chi^2 = 189.02$, df = 5, $P < 0.001$; Fig. 2a): leks of *P. erythrocephala* and *P. filicauda* had the

most vocalizing males, followed by *P. pipra*, *L. coronata*, and *C. pareola*; leks of *M. regulus* had the fewest males vocalizing. Manakins also differed in total number of vocalizations at the lek per 30 min ($\chi^2 = 192.65$, df = 5, $P < 0.001$; Fig. 2b), with vocalization rate highest at leks of *C. pareola*, *P. erythrocephala*, and *L. coronata*, intermediate at leks of *P. pipra*, and lowest at leks of *P. filicauda* and *M. regulus*. Finally, the number of vocalizations/male per 30 min differed among manakin species ($\chi^2 = 203.36$, df = 5, $P < 0.001$; Fig. 2c), with vocalization output per male being higher for *C. pareola*, followed by *L. coronata*, then by *P. erythrocephala*, *P. pipra*, and *M. regulus*; males of *P. filicauda* had the lowest output rate among the six species.

DISCUSSION

Lekking species evolve under strong sexual selection, and the strong variance in male reproductive success often observed in these species (DuVal & Kempenaers 2008, Durães et al. 2009, Ryder et al. 2009) has been taken as
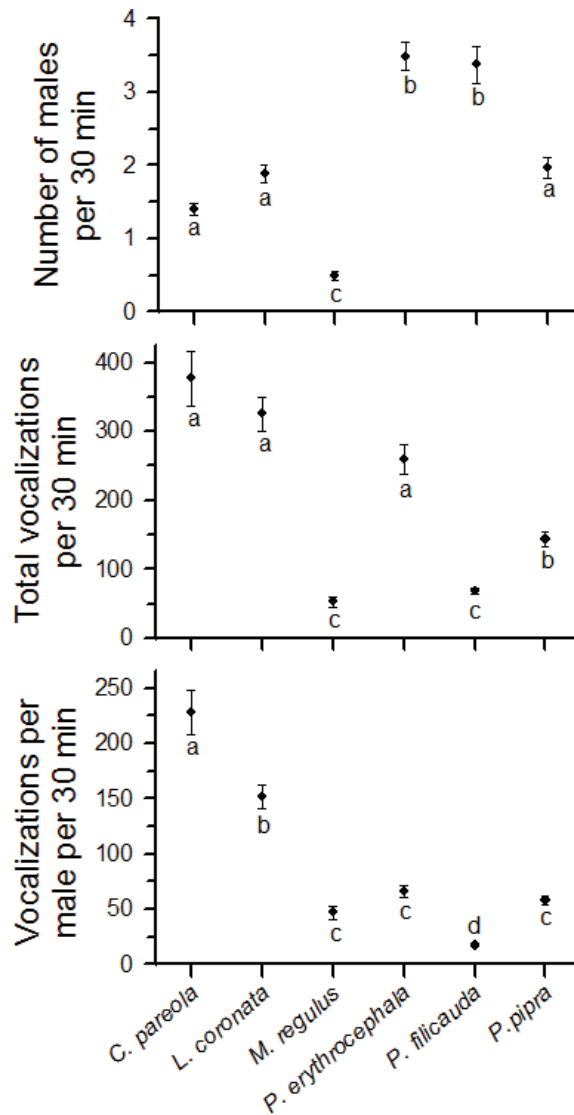
FIG. 2. Number of vocalizing males (a), total number of vocalizations at the lek per 30-min (b), and number of vocalizations/male/30 min (c) at leks of six manakin species. Values are averages (± 1 SE) over two leks per species; each lek was observed for a 12-h period (06:00–18:00 h) once in December 2003 and once in February 2004. Homogeneous groups, as defined by Dunnett T3 multiple-comparison tests for groups with unequal variances, are denoted by similar letters.

evidence of such selection pressures. At the height of the breeding season, male manakins spend most of the day displaying at leks, which females visit to assess possible mates and to copulate. High and sustained vocalization output might improve the reproductive

success of a given male both when competing with males from other leks (i.e., long-distance attraction of females towards the lek) and with males within the lek (i.e., short-distance attraction of visiting females towards a specific court). Once a female has been attracted to a given male's court, display quality, including visual signals, is expected to influence the female's decision to copulate or not.

The six species examined in this study differ in various aspects of their display repertoires and such differences may influence vocalization rates. *Chiroxiphia pareola* has a complex courtship repertoire that includes obligate coordinated display between males (Snow 1963). This species had the highest vocalization output, both at the lek and individual levels. In comparison to most of the other five species, *C. pareola* also had more sustained vocal activity at the lek, with vocalization output relatively even and high throughout the course of the day, except for a sharp decrease in activity in late morning. High vocalization output throughout the day also characterized *C. linearis* (McDonald 2010), although in this case there was a distinct unimodal pattern, with a broad peak from about noon to 15:00 h. *Pipra erythrocephala*, the only classical-lek species in this study, also has complex display movements and songs (Lill 1976). Vocalization output per male was relatively low, but because of the high number of males vocalizing simultaneously, vocalization output at the lek level was high. In addition, as in *C. pareola*, vocalization levels were relatively sustained during the course of the day, increasing somewhat in the afternoon. Finally, *P. filicauda* has a complex display repertoire that includes facultative, coordinated movements between males (Schwartz & Snow 1978, Heindl 2002). In this species, many males vocalize simultaneously, but the vocalization output per male (and, consequently, at the lek level) was low. Further, fluctuations in lek activity during the day

for *P. filicauda* were similar to that of other species with simpler display repertoires (*L. coronata*, *P. pipra*). In summary, we can describe the lek activity of these three species as few males that vocalize a lot for most of the day (*C. pareola*), many males that have relatively low but sustained vocalization output over the course of the day (*P. erythrocephala*), or many males that vocalize little, with higher fluctuation in output during the course of the day (*P. filicauda*).

The other three manakin species have exploded leks and generally less complex songs (*L. coronata*, *P. pipra*, *M. regulus*; Sick 1967, Prum 1990, Snow 2004, Castro-Astor *et al.* 2007). These species generally had (a) fewer males vocalizing simultaneously, although numbers of *L. coronata* and *P. pipra* were similar to those of *C. pareola*; (b) lower levels of vocalization output per male than in *C. pareola*, but similar or higher output compared to *P. erythrocephala* and *P. filicauda*; (c) lower (*P. pipra*, *M. regulus*) or similar (*L. coronata*) vocalization rates at the lek level when compared to *C. pareola* and *P. erythrocephala*, but higher or similar rates to *P. filicauda*; and (d) greater fluctuations in vocalization output during the course of the day.

All species followed a general bimodal pattern in activity during the day, with a shorter peak in early morning, a drop in late morning, and a second, longer peak in activity in the afternoon. Periods of low activity likely represent times of the day when males leave the lek to forage or engage in non-courtship activities (e.g., bathing, resting). Yet, we found that, except for *M. regulus*, some males are always present at the leks, such that vocalization activity only rarely is completely interrupted before late afternoon (17:30–18:00 h).

In conclusion, our study shows, first, that many manakin species follow a similar bimodal trend in lek activity during the day, but specific patterns of lek activity are more consistent within species (with low variation

across leks or time periods) than among species, which allows for meaningful inter-specific comparisons. Second, our study suggests that manakin species with stronger male-male competition (i.e., species with classical leks) and species with more elaborate displays (with or without coordinated displays) generally show greater levels of activity at leks, although the importance of specific components of vocalization output (e.g., vocalization output per male or per lek, temporal fluctuations in output levels) varies among species. These differences are not, however, clear-cut when compared to activity levels at leks of manakin species with exploded leks and generally simpler display repertoires. Some of these latter species have much lower activity levels (e.g., *M. regulus*), whereas others are comparable for several of the above-mentioned components (e.g., *L. coronata*).

ACKNOWLEDGMENTS

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