

NEST SITE SELECTION BY BLUE-CROWNED (*LEPIDOTHRIX CORONATA*) AND WIRE-TAILED (*PIPRA FILICAUDA*) MANAKINS IN LOWLAND ECUADOR

José R. Hidalgo¹, John G. Blake², Bette A. Loiselle², Thomas B. Ryder³, Renata Durães⁴, & Wendy P. Tori⁵

¹5967 Arlington Blvd., Richmond, California, 94805, USA.

²Department of Wildlife Ecology and Conservation, PO Box 110430, University of Florida, Gainesville, Florida, 32611, USA. *E-mail*: john.blake@ufl.edu

³Smithsonian Conservation Biology Institute, National Zoological Park, Migratory Bird Center, P.O. Box 37012-MRC 5503, Washington, D.C., 20013, USA.

⁴Department of Ecology and Evolutionary Biology, 400 Lindy Boggs Center, Tulane University, New Orleans, Louisiana, 70118, USA.

⁵Earlham College, 801 National Road West, Richmond, Indiana, 47374, USA.

Resumen. – Selección de sitios de anidamiento por dos especies de saltarines, *Lepidothrix coronata* y *Pipra filicauda*, en tierras bajas de Ecuador. – Este estudio examina la selección de sitios de anidamiento por dos especies de saltarines, Saltarín Coroniazul *Lepidothrix coronata* y Saltarín Cola de Alambre *Pipra filicauda* (Aves, Pipridae) que co-ocurren en bosques húmedos tropicales de tierras bajas en el este de Ecuador. Ambas especies construyen nidos simples de tipo taza y ambas sufren altas tasas de depredación de nidos. Se midió la vegetación circundante para 25 y 27 nidos de *L. coronata* y *P. filicauda*, respectivamente. También se realizaron medidas correspondientes de la vegetación en sitios aleatorios pareados con los sitios de anidamiento. Las dos especies de aves utilizaron algunas especies de plantas huésped en común para la construcción de nidos, sin embargo con frecuencias diferentes. A pesar de algún solapamiento en las características de vegetación circundante a los nidos, las dos especies difirieron en la ubicación de los sitios de anidamiento. La similitud en sitios de anidamiento fue mayor entre nidos de la misma especie que entre especies. La vegetación circundante a los sitios de anidamiento fue diferente a la encontrada en sitios aleatorios, sugiriendo que los saltarines seleccionan aspectos específicos del ambiente cuando construyen nidos.

Abstract. – This study examines nest-site selection by two manakin species, Blue-crowned *Lepidothrix coronata* and Wire-tailed *Pipra filicauda* (Aves, Pipridae), that co-occur in lowland wet forest of eastern Ecuador. Both species build simple open-cup nests and both experience high rates of nest predation. Surrounding vegetation was measured for 25 and 27 nests of *L. coronata* and *P. filicauda*, respectively. Corresponding measurements were made of vegetation at random locations near nest sites. The two species used several host-plant species in common for nest building but with different frequencies. Despite some overlap in characteristics of vegetation that surrounds nests, the two species differed in nest-site locations. Similarity in nest sites was greater among nests of a given species than between species. Vegetation surrounding nest sites differed from that at random locations, suggesting that manakins select specific aspects of the environment when building nests. *Accepted 28 February 2012.*

Key words: Blue-crowned Manakin, Wire-tailed Manakin, habitat, life history, nest-site selection, Pipridae.

INTRODUCTION

Identification of factors that affect patterns of habitat selection, species coexistence and life-history traits is central to evolutionary ecology (Partridge & Harvey 1988, Konishi *et al.* 1989). During breeding seasons, birds must select nest sites that provide a balance between acquiring necessary resources for reproduction and minimizing the risk of predation (Steele 1993). Response to nest-predation pressures may be particularly important for understanding avian life-history variation in environments where predation rates are high, such as lowland, tropical wet forests (Ricklefs 1969, Skutch 1985, Martin 1993a, Ryder *et al.* 2008). Consequently, natural selection should favor birds that select habitats and exhibit traits that reduce the negative effects of nest predation, given the importance of reproductive success to fitness (Martin 1993b).

Manakins are well known for their lek-breeding systems, where males cluster together in display arenas (leks) to attract females; females visit leks to select a mate and subsequently carry out all activities related to nesting (Wiley 1991, Snow 2004). Environmental characteristics of lek sites vary among manakin species in eastern Ecuador (Loiselle *et al.* 2007a). Females, on the other hand, often have territories and nests away from leks (Durães *et al.* 2007), so characteristics of nest sites may differ from those associated with leks. Specific characteristics of those nest sites, and whether such characteristics differ among and within species, are not well described.

Predators may develop search images for nests, so species that co-occur may reduce probabilities of nest predation by selecting nest sites that differ from those of similar species, thereby reducing the apparent density of nests (Martin 1988). Thus, we might expect manakins, who share many behavioral and

ecological features, build similar-looking, small, open-cup nests, and co-occur in the same general habitat, to have different nest-site preferences. Here, we investigate this possibility by comparing nest-site selection in Blue-crowned (*Lepidothrix coronata*) and Wire-tailed (*Pipra filicauda*) manakins (Pipridae), two species that co-occur in the understory of lowland wet forest in eastern Ecuador (Loiselle *et al.* 2007a). We ask the following specific questions relating to selection of nest sites: 1) Do the two species select non-random sites, in terms of habitat (e.g., vegetation characteristics, amount of overhead cover), for nest placement? and 2) Do nest-site characteristics differ between species?

METHODS

We conducted this study from November 2004 to March 2005 and from December 2005 to March 2006 at Tiputini Biodiversity Station (TBS) (00°38'S, 76°08'W; ~190–270 m a.s.l.), Orellana Province, eastern Ecuador. TBS is a 650-ha biological station located on the north bank of the Tiputini River, adjacent to Yasuní National Park and within Yasuní Biosphere Reserve. TBS has more than 30 km of trails and two 100-ha plots, where research on breeding biology of manakins has been focused (Loiselle *et al.* 2007b, Durães 2009, Durães *et al.* 2008, 2009, Ryder *et al.* 2006, 2008, 2009). Most nests of the two species were located by systematically searching within the two 100-ha study plots, as well as around leks found outside the study plots. Additional nests were located by following radio-tagged females to their nests (see Tori *et al.* 2006). Vegetation surrounding nests was sampled after nesting activity ceased (young fledged or nest lost to predation) to minimize impacts on nesting success.

We used a modified BBIRD-Protocol (Martin *et al.* 1997) to characterize habitat structure at each nest location. We measured

vegetation within a 5-m radius circular plot surrounding each nest. We also measured vegetation at a random site (5-m radius circle) selected by following a random compass bearing to a distance of 100 m from the focal nest. We used 12 variables to characterize nest sites and random locations. All trees (i.e., all stems ≥ 1.3 m tall) in each 5-m plot were categorized by diameter at breast height (DBH) as small (< 2.5 cm DBH), medium (2.5–8 cm), medium-large (8–23 cm), or large (> 23 cm). Plants (other than trees) were categorized as monocots [either small (< 2.5 cm diameter at 5 cm of height) or large (≥ 2.5 cm)], lianas (small, large), *Heliconia* spp. (small), or other stems (small). Total percentage of overhead cover was estimated using a spherical densitometer; four readings, one in each of the cardinal directions, were taken over each nest and results averaged for the total. Lastly, because predators employ different techniques to reach nests, we attempted to estimate nest-site connectivity by counting number of contacts between the host plant and surrounding vegetation. We also collected a sample of the host plant for later identification.

We used Discriminant Function Analysis based on 12 vegetation variables to determine if characteristics of vegetation differed among groups, with groups defined by real and associated random nest-site locations. We ran one DFA for all four groups combined, followed by separate DFAs for pairwise comparisons; pairwise analyses were run because a DFA of four groups provides an overall test of significance among groups but does not indicate differences between pairs. Vegetation data were log-transformed ($\ln + 1$) prior to analyses to fit assumptions of normality and homogeneity of variances. We report eigenvalues, percentage of variance explained by each canonical discriminant function, and overall significance of the full model. We ran one-way ANOVAs for each discriminant function of the overall DFA, followed by multiple-com-

parison (Least Significant Difference, LSD) tests to examine level of pair-wise differences in mean values for each function among the four groups. We compared variation of scores along the discriminant axes using *F*-ratio tests, to examine the relative degree of variability in nest environments.

RESULTS

We measured vegetation around 25 nests of *L. coronata* and 27 nests of *P. filicauda*. In addition, we measured vegetation at 17 random sites near nests of *L. coronata* and 23 sites near nests of *P. filicauda*. Time limitations precluded measuring random sites near each real nest.

Lepidobrix coronata tended to select small shrubs or treelets for nest sites (i.e., < 1 m), whereas *P. filicauda* tended to nest in small or medium trees (i.e., > 2 m). Although the two species used some of the same plant species for nest sites, they differed in the frequency with which different species were selected (Fig. 1). Two species (*Rinorea viridifolia* and *R. lindeniana*, Violaceae) served as hosts for 20% and 60% of *L. coronata* and *P. filicauda* nests, respectively; $> 40\%$ of *L. coronata* nests were found in the same species of *Rudgea* (Rubiaceae) (Fig. 1).

The DFA based on all four groups indicated a significant overall separation among groups ($\chi^2 = 98$, $df = 36$, $P < 0.001$); the first two functions explained 86% of variation in characteristics of vegetation around nest sites and random locations (Table 1). The first axis largely reflected a gradient from areas with small stems and large trees to areas with greater amounts of overhead cover; the second axis indicated a gradient from areas with small stems and large trees to areas with greater numbers of lianas (Figs 2, 3). When all four groups were considered together, 76% of *L. coronata* nests were classified correctly (i.e., as belonging to *L. coronata* group) and 59% of *P. filicauda* nests were

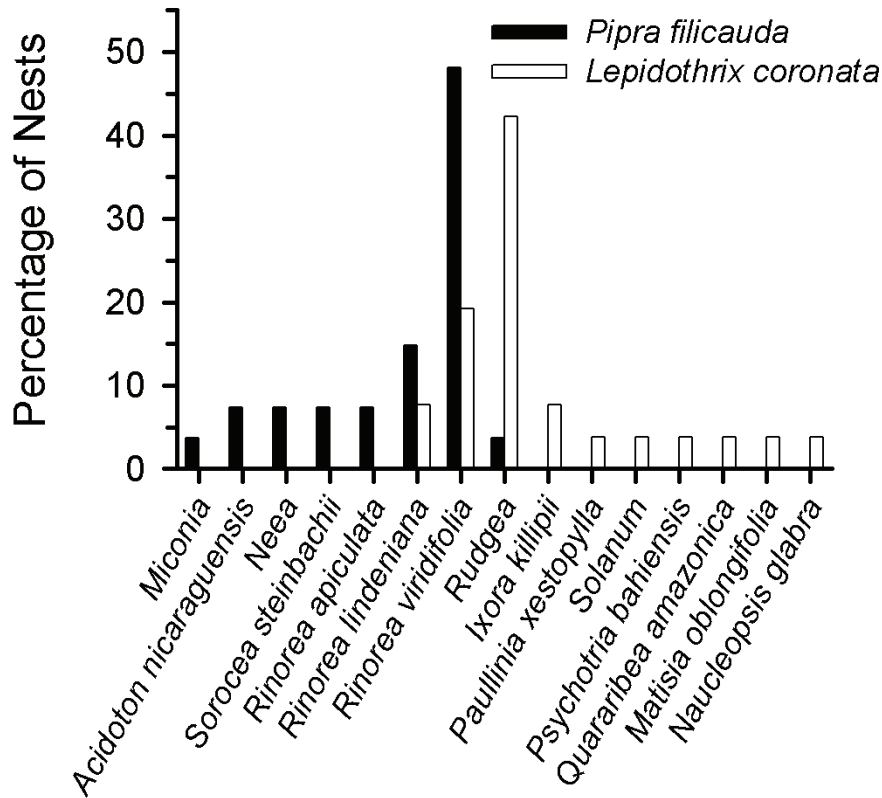


FIG 1. Plant species used by *Pipra filicauda* and *Lepidothrix coronata* for nest sites.

classified correctly, suggesting somewhat greater variability or less specificity in nest sites of the latter species.

Separate DFAs indicated significant separation between *L. coronata* nest sites and random locations ($\chi^2 = 32.1$, $df = 12$, $P < 0.001$), between *P. filicauda* nests and associated random sites ($\chi^2 = 24.0$, $df = 12$, $P = 0.02$), and between *L. coronata* and *P. filicauda* nest sites ($\chi^2 = 22.5$, $df = 12$, $P < 0.05$). In the pairwise analysis, 84% of *L. coronata* nests and 82% of *P. filicauda* nests, respectively, were classified correctly. The two groups of random nest locations did not differ ($\chi^2 = 16.6$ $df = 12$, $P = 0.165$).

Despite overlap among samples (Figs 2, 3), ANOVA (followed by a multiple comparison test) indicated that mean scores for real nest sites differed between the two species along the first axis of the DFA and that real nest sites differed from means of corresponding random locations; random locations associated with the two species did not differ for the first axis (Table 2). In contrast, means for real nest sites did not differ along the second axis but mean values for random locations did differ from each other and from real nest sites (Table 2). Variances did not differ between species for real or random locations along either axis (based on F -ratio tests,

TABLE 1. Results of discriminant function analysis of vegetation surrounding nest sites of *Lepidothrix coronata*, *Pipra filicauda*, and corresponding random locations (see text) at Tiputini Biodiversity Station, Ecuador.

Discriminant function	Eigenvalue	Variance	Cumulative percentage	Canonical correlation
1	1.019	65.1	65.1	0.710
2	0.332	21.2	86.3	0.499
3	0.214	13.7	100.0	0.420

TABLE 2. Means (\pm SD) of the three discriminant functions for real and random nest-site locations of *Lepidothrix coronata* and *Pipra filicauda* at Tiputini Biodiversity Station, Ecuador. Overall significance of ANOVA is shown for each function; means not sharing the same letter are significantly different based on post-hoc multiple comparison test (LSD).

Discriminant function	<i>Lepidothrix</i> real nest	<i>Lepidothrix</i> random	<i>Pipra</i> real nest	<i>Pipra</i> random	F	P
1	-1.36 \pm 1.13 ^A	0.99 \pm 1.0 ^B	-0.25 \pm 1.01 ^C	1.04 \pm 0.83 ^B	29.9	< 0.001
2	-0.04 \pm 0.87 ^A	0.99 \pm 1.10 ^B	0.04 \pm 0.86 ^A	-0.74 \pm 1.19 ^C	9.7	< 0.001
3	0.40 \pm 0.85 ^A	0.26 \pm 1.05 ^A	-0.69 \pm 0.96 ^B	0.19 \pm 1.15 ^A	6.3	< 0.001

$P > 0.05$, all comparisons) but *L. coronata* nest sites were characterized by a wider range of values along the first and third DFAs (Fig. 3; third axis not shown).

DISCUSSION

Similar species that occur in the same general habitat often differ in their use of specific aspects of that habitat or resources found therein. Leks of male manakins in eastern Ecuador generally differ in several environmental characteristics, meaning that most leks do not overlap in space (Loiselle *et al.* 2007a). In contrast to the marked differences in lek locations, nests of the two species tend to show less pronounced, but still significant, differences. Both species build relatively inconspicuous open-cup nests comprised of fungal rhizomorphs, leaf material and spider webs; nests are suspended in a horizontal fork within a few meters of the ground (Snow 2004, Hidalgo *et al.* 2008). *Pipra filicauda* nests tend to be larger, reflecting the size difference

between females of the two species (*L. coronata*, 10.7 \pm 1.02 g, N = 189; *P. filicauda*, 15.9 \pm 1.43 g, N = 101; JGB and BAL, unpubl. data), farther from the central stem of the host plant, and higher off the ground than nests of *L. coronata* (Hidalgo *et al.* 2008). Nest height likely reflects differences in heights of the plants the two species typically select for their nests.

Nests of both species tended to be found in areas of open forest with varying amounts of understory vegetation (Hidalgo *et al.* 2008). Although there was some overlap in characteristics of vegetation surrounding nests, *L. coronata* and *P. filicauda* nonetheless differed in some fine-scale characteristics of nest sites and differed in selection of host plants used for nesting. *Lepidothrix coronata* preferred to nest in small shrubs of the genus *Rudgea*, found in areas characterized by smaller stems and large trees. In contrast, *P. filicauda* nested more often in small trees of the genus *Rimorea*, in areas with smaller trees and higher overall cover. Given that vegetation structure differed

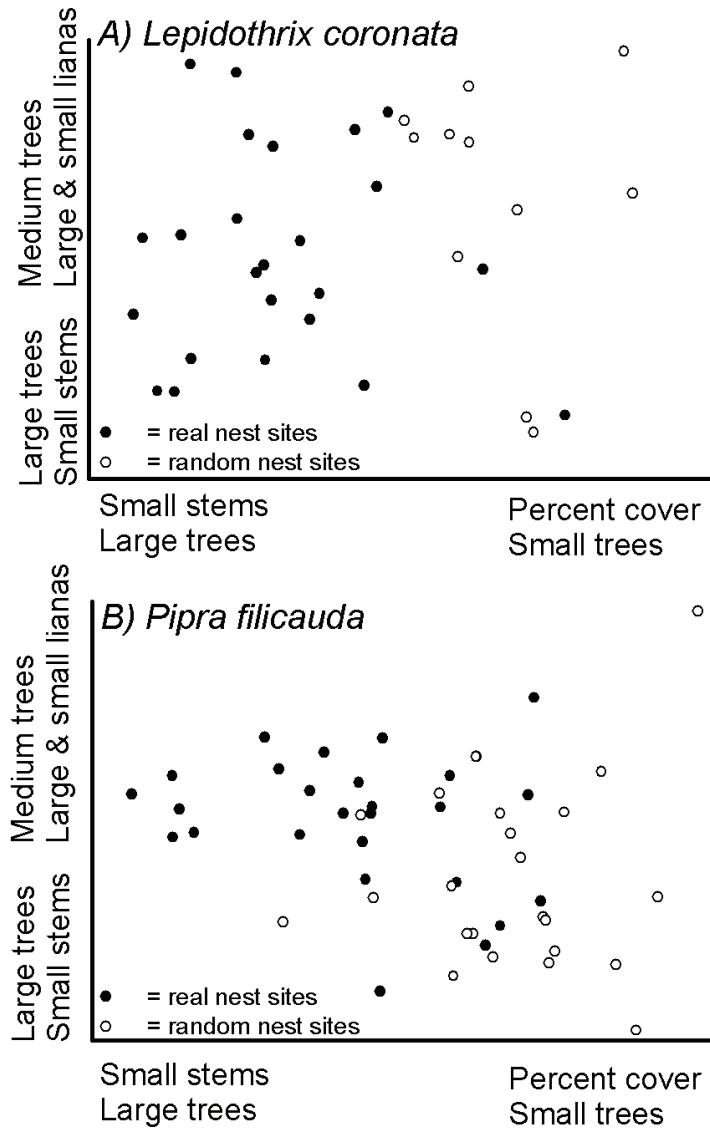


FIG 2. Ordination (DFA) of real and random nest-site locations for A) *Lepidothrix coronata* and B) *Pipra filicauda*. DFA was based on all four groups. The two variables most positively and negatively associated (based on standardized discriminant function coefficients) with each axis are shown.

between nest sites and randomly selected locations, our results suggest that both manakin species select nest sites based on specific environmental characteristics.

Differences in use of plant species as nest sites and differences in characteristics of surrounding vegetation may reflect general characteristics of the habitats where nests are

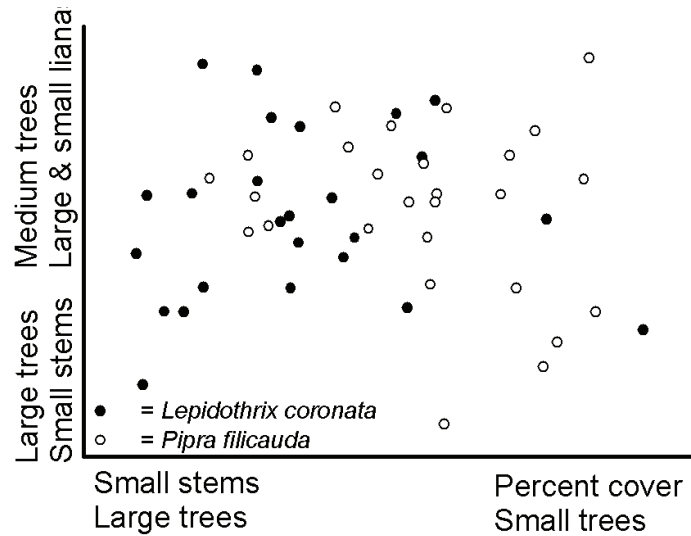


FIG 3. Ordination of nest sites of *Lepidothrix coronata* and *Pipra filicauda*. DFA was based on all four groups. The two variables most positively and negatively associated (based on standardized discriminant function coefficients) with each axis are shown.

found or may be related to predation pressures as both species suffer high rates of nest predation (Ryder *et al.* 2008). On the other hand, nest sites may be selected because they may provide a more favorable micro-climate, better access to resources, or fewer competitors; key factors not only for survival but for offspring success. That females of the two species select non-random sites for nests suggests some benefit to the selection of a given site. For example, real nest sites of *L. coronata* tended to have fewer contacts with surrounding vegetation and fewer small lianas in the vicinity than did associated random locations. Contacts with surrounding vegetation might provide greater access to nests for predators, suggesting that females may select sites that might be slightly less susceptible to predation.

Many descriptions of nests of tropical species, including manakins, are based on relatively few nests, often the first to be found and documented (Foster 1976, Tostain 1988, Marini & Cavalcanti 1992, Snow 2004, Dou-

cet & Mennill 2005). As with most other ecological and behavioral aspects of life histories, there is likely to be variation in nest location, both among geographical regions and among nests within a particular site, as demonstrated by this study. A full understanding of life histories, and the factors that influence them, thus may benefit from additional information on variation in nests and nest locations. Impacts of predation, for example, may vary spatially with consequent impacts on selective pressures. Evaluation of such impacts would, however, require experimental manipulation (e.g., Fontaine & Martin 2006) and is beyond the scope of this study.

It is clear from our study that *L. coronata* and *P. filicauda* are selective in their nest-site placement, yet the strength of selectivity and the degree to which nest characteristics are influenced by predation or other factors remains to be tested. In particular, more tropical studies focusing on predation effects on these two processes are necessary for a better

understanding of the life-history evolution of birds.

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