

FORAGING BEHAVIOR OF TWO SPECIES OF MANAKINS (PIPRIDAE) IN MIXED-SPECIES FLOCKS IN YASUNÍ, ECUADOR

Galo Buitrón-Jurado

Museo de Zoología, Escuela de Biología, Pontificia Universidad Católica del Ecuador,
Avenida 12 de Octubre y Roca, Aptdo. 17-01-2184, Quito, Ecuador.
E-mail: galobuitronj@yahoo.es

Resumen. – Comportamiento de forrajeo de dos especies de saltarines (Pipridae) con bandadas mixtas en el Parque Nacional Yasuní, Ecuador. – La participación y comportamiento de forrajeo de los saltarines Coroniazul (*Lepidothrix coronata*) y Coroniblanco (*Dixiphia pipra*) en bandadas de especies mixtas de sotobosque se estudió entre los años 2003–2004 en una parcela de 50 ha de bosque tropical lluvioso, localizada en la ribera sur del río Tiputini (00°40'S, 76°23'W, 273 m s.n.m.), Parque Nacional Yasuní, Ecuador. Se realizaron observaciones para determinar la frecuencia de participación y las diferencias en el comportamiento de alimentación de ambas especies de saltarines en bandadas de especies mixtas de sotobosque. El Saltarín Coroniazul fue encontrado más frecuentemente que el Saltarín Coroniblanco como parte de estas asociaciones. Sin embargo, ambas especies no presentaron diferencias significativas en el tiempo de participación dentro de las bandadas. Ambas especies no difirieron en la altura de forrajeo, método de ataque de presas y uso de sustratos mientras se alimentaron con bandadas mixtas, probablemente debido a su similar morfología y tamaño corporal, y estrategia reproductiva en leks dispersos. En el Saltarín Coroniazul, se encontró diferencias significativas en el tiempo de permanencia en bandadas de los machos adultos comparado a los individuos de plumaje verde (hembras y juveniles). Estos últimos forrajearon con bandadas mixtas por un mayor tiempo que los machos, lo que sugiere que las hembras y los juveniles podrían capturar insectos para obtener un suplemento proteico. La participación de los saltarines en bandadas mixtas podría influir en las actividades reproductivas de esta especie.

Abstract. – I studied the membership and foraging behavior of Blue-crowned (*Lepidothrix coronata*) and White-crowned (*Dixiphia pipra*) manakins while accompanying mixed-species flocks in Yasuní National Park, Ecuadorian Amazonia. Observations were conducted during 2003–2004 in a 50-ha plot of evergreen tropical rainforest located in the south bank of the Tiputini River (00°40'S, 76°23'W, 273 m a.s.l.). Blue-crowned Manakins were found accompanying mixed-species flocks more often than White-crowned Manakins. The time that these species stayed within the mixed-species flocks (membership period) did not differ significantly between them. Also, Blue-crowned and White crowned manakins showed a similar foraging behavior within flocks. Both species performed similar manoeuvres, and did not differ in their foraging heights and substrates. This high resemblance is probably related to their similar morphology, body size and mating strategy in dispersed leks. In Blue-crowned Manakins, adult males and green-plumaged birds (females and juveniles) showed significant differences in the participation time within flocks. Green-plumaged birds foraged for a longer time within flocks than males. This fact suggests that females and juveniles participation with flocks could permit to capture insects, a proteic supplement, that could influence in the reproductive activities of this species. *Accepted 9 February 2008.*

Key words: Ecuador, Amazonia, *Lepidothrix coronata*, *Dixiphia pipra*, manakins, mixed-species flocks, foraging behavior.

INTRODUCTION

Bird foraging ecology has been one of the main issues of community ecological research. Despite the fact that tropical forests possess the highest bird species richness, few studies on bird foraging ecology have been developed in the tropics. However, these studies have provided key insights on the usage of resources, spatial distribution, species density, and influence of diet on mating systems on insectivorous and frugivorous birds (Beehler & Pruett-Jones 1983, Beehler 1987, Rosenberg 1990, Scott Sillett 1994). Also, the specialization on certain resources could explain the high bird species diversity found in the Neotropics (e.g., Powell 1989, Scott Sillett 1994, Marra & Remsen 1997, Naoki 2007). The study of closely related species can reveal important aspects of their coexistence as the understanding of resource use patterns among species within habitats. Then, it is still necessary to obtain more data about the ecology of tropical bird species.

Manakins (Pipridae) are a group of 47 species of small forest-dwelling birds, exclusively Neotropical in their distribution (Remsen *et al.* 2006). The strong sexual dimorphism and the spectacular reproductive displays of lekking species in several genera (e.g., *Pipra*, *Machaeropterus*, *Corapipo*, *Chiroxiphia*) are well-known (Prum 1994, Snow 2004), although information on their foraging behavior is sparse. Previous studies of manakin's ecology have focused on their complex mating displays, patterns of habitat use and forest capture rates (e.g., Robbins 1985, Théry 1990, Blake & Loiselle 2002). These studies showed the influence of food and other resources on mating strategies and spatial distribution of the species within habitats. For example, Heindl & Winkler (2003) found that males of four species of manakins preferred to display at heights in the forest

where the variation in environmental light more effectively promotes their color patterns. In the same way, the density of fruit-bearing plants is the main factor that affects spatial distribution of manakin leks in Ecuador (Ryder *et al.* 2006). Indeed, in Neotropical rainforests, manakins play an important role as seed-dispersers of understory shrubs, especially from the families Melastomataceae and Rubiaceae (Kriger *et al.* 1997, Loiselle & Blake 1998). A great number of manakin species, however, complement their diets with insects and other arthropods (Marini 1992).

Several species of manakins have been reported foraging with mixed-species flocks of insectivorous birds. These include Club-winged (*Machaeropterus deliciosus*) and Golden-winged (*Masius chrysopterus*) manakins in the Andean cloud forests, and the Helmeted Manakin (*Antilophia galeata*) in the Brazilian Atlantic rainforest (Willis 1966, Prum & Johnson 1987, Marini 1992). Additionally, manakin association with mixed-species flocks occurs in the humid tropical rainforest, where Blue-crowned (*Lepidothrix coronata*), Green (*Chloropipo homochlora*) and White-crowned (*Dixiphia pipra*) manakins have been anecdotally reported as participants (Hilty & Brown 1986, Ridgely & Tudor 1989, Hilty 2003).

Blue-crowned and White-crowned manakins are sympatric in eastern Ecuador (Snow 2004). Many classifications have considered White-crowned and Blue-crowned manakins close relatives inside the genus *Pipra* (Ridgely & Tudor 1989, Remsen *et al.* 2006). Nevertheless, recent evidence in syringeal anatomy and behavior indicate that the genus *Lepidothrix* is much closer to other manakin genera than to *Pipra* while the phylogenetic relationship of the White-crowned Manakin seems closer to *Pipra* than to *Lepidothrix*, although it has not been completely solved (Prum 1994, Bostwick 2000, Snow 2004, Prum pers. com.).

In spite of this, Blue-crowned and White-crowned manakins share a similar size, morphology and mating strategy. Males of both species display solitarily at dispersed leks (male territories of 10–40 m in diameter with 2–7 adjacent territories) inside the forest executing rapid flight manoeuvres in low branches (Prum 1994, Heindl & Winkler 2003). Skutch (1969) described the Blue-crowned Manakin display as a series of back-and-forth darts tracing erratic courses between twigs below 1.5 m above the ground to guide females to the nuptial perch, while the male produces a little, harsh sound beating the wings. The White-crowned Manakin display is described as short stereotyped flights in the periphery of tree crowns located at the edges of canopy gaps (Heindl & Winkler 2003, Snow 2004). However, White-crowned Manakin leks show a sparser distribution than Blue-crowned Manakin leks (Heindl & Winkler 2003).

Anecdotal observations of Blue-crowned and White-crowned manakins suggest differences in flock participation among them. Blue-crowned manakins have been more frequently observed accompanying understory mixed-species flocks (Ridgely & Tudor 1989, Snow 2004). This provides the opportunity to determine their interspecific competition role on foraging behavior since Amazonian understory mixed-species flocks are prominent because of their long-term permanency, highly complex structure, and the inclusion of an important part of bird community, including frugivorous birds as manakins and cotingas that participate at least as facultative followers (Stotz 1993, Jullien & Thiollay 1998). The main goal of this paper is to provide detailed information on the foraging behavior of Blue-crowned and White-crowned manakins and the quantification of each species association while accompanying understory mixed-species flocks in Yasuní National Park (PNY), Ecuador.

STUDY AREA AND METHODS

I observed understory mixed-species flocks in a 50-ha forest plot established in Yasuní National Park, eastern Ecuador. The plot is located 1.5 km east from the Yasuní Research Station (Yasuní National Park) (00°40'S, 76°23'W, 273 m a.s.l.). The canopy in the plot is 25–30 m tall, with some small clearings as a result of natural tree falls. Most of the plot is *terra firme* forest, except in the north-eastern section where there is a patch of swamp forest with abundant palms. The 50-ha plot is divided by a grid of parallels trails every 100 m, which facilitate the location of the flocks in the forest.

The Yasuní National Park has 982,000 ha and is classified as lowland evergreen moist tropical rainforest (Valencia *et al.* 2004). Average annual rainfall in the study area is around 3000 mm with an average temperature of 25°C (monthly means vary from 18 to 35°C) (Valencia *et al.* 2004). Detailed descriptions of the vegetation in the Yasuni area are provided in Romero-Saltos *et al.* (2001) and Valencia *et al.* (2004). There are few indigenous Waorani settlements north of the Yasuní National Park, which have resulted in an increase in hunting activities. Despite this impact, sensitive mega fauna (jaguar, deer, peccary) are still present (Valencia *et al.* 2004).

I defined a mixed-species flock as a group of two or more species of birds, usually within 25 m of one another, that move in concert and behave cohesively during foraging (Powell 1985, Greenberg 1990). Flocks were followed for a total of 410 h for 7 months: March, August and December in 2003 and February, March, July, and August in 2004. Observations were recorded in the morning from 06:00 to 12:00 h, and in the afternoon from 14:30 to 18:30 h. A concomitant study (Buitrón-Jurado 2005) allowed me to determine the number of flocks and their location in the study plot. The understory mixed-spe-

cies flocks generally consisted of five core species including the Cinereus (*Thamnomanes caesius*) and Dusky-throated (*T. ardesiacus*) antshrikes, and a combination of three species of antbirds including the White-flanked (*Myrmotherula axillaris*), Yasuni (*M. fjeldsaai*), Long-winged (*M. longipennis*), Gray (*M. menetriesii*), and Rufous-tailed (*M. erythrura*) antwrens (Buitrón-Jurado 2005). The Blue-crowned and the White-crowned manakins were regularly found accompanying the flocks in the understory. I included these species as part of a mixed-species flock when I encountered them following the movement of other species for more than 5 min (Stotz 1993) or, according to Chien & Hsiegh (1998), when individuals participated in social interactions that made evident their membership (e.g., calling or responding to potential threats). The nomenclature of the species listed above follows Ridgely & Greenfield (2001).

The participation time of individual manakins within a flock was calculated from their first detection until the individual could no longer be seen interacting with the flock. Participation frequency was calculated as a rate of the number of times that each species was found within a flock divided by the total number of flocks. Because I could follow the movement of a flock for a long period of time (more than 30 min), it was possible to record repetitive, but not consecutive, observations of the same focal individual with the rotation of my attention between the different flock members (*sensu* Rosenberg 1990). I considered my records to be independent because each observation was separated by an interval of at least 5 min. As juveniles and females are both green-plumaged, I could not distinguish them and thus they are included together in the data analysis.

For each observation of an individual manakin, I recorded variables about foraging behavior (foraging manoeuvre, substrate, foliage density and foraging height) with an audio

cassette recorder. These variables are assumed to properly describe foraging behavior (Remsen & Robinson 1990). Foraging height above the ground and foliage density were obtained by means of visual estimates. Foliage density was estimated using a qualitative scale from 0 to 5 according to the amount of incident light on the bird in a imaginary sphere of 1 m where "0" represents absence of vegetation around the bird, and "5" extremely dense vegetation (0–5% of light passes the sphere). Four foraging manoeuvres were recognized: glean is picking food items from a nearby substrate that can be reached without full extension of legs or neck; sally-strike is attacking in a fluid movement without gliding, hovering, or landing, and then returning to a perch; sally-hover is flying from a perch to attack a food item except that the bird hovers at the target substrate at the end of the sally (Remsen & Robinson 1990). A fourth category was conspicuous in the foraging behavior of manakins and it is defined as sally-glean, i.e., the bird snaps stationary prey off an exposed surface during a direct, horizontal or downward approach (Fitzpatrick 1980). Values showed are mean \pm SD.

A Student t-test or its non-parametric equivalent, the Mann-Whitney test, were used to determine differences in foraging height and flock participation time between the two species and within-species plumage classes as described in Sokal & Rohlf (1999). The likelihood-ratio test (G-test) was used to determine significant differences between both species in the use of substrate or foraging manoeuvres. The software SPSS was used for data analysis (SPSS Inc. 2000).

RESULTS AND DISCUSSION

In 112 encounters with understory flocks, usually, only a single individual of Blue-crowned or White-crowned manakins was found each time. On rare occasions, two indi-

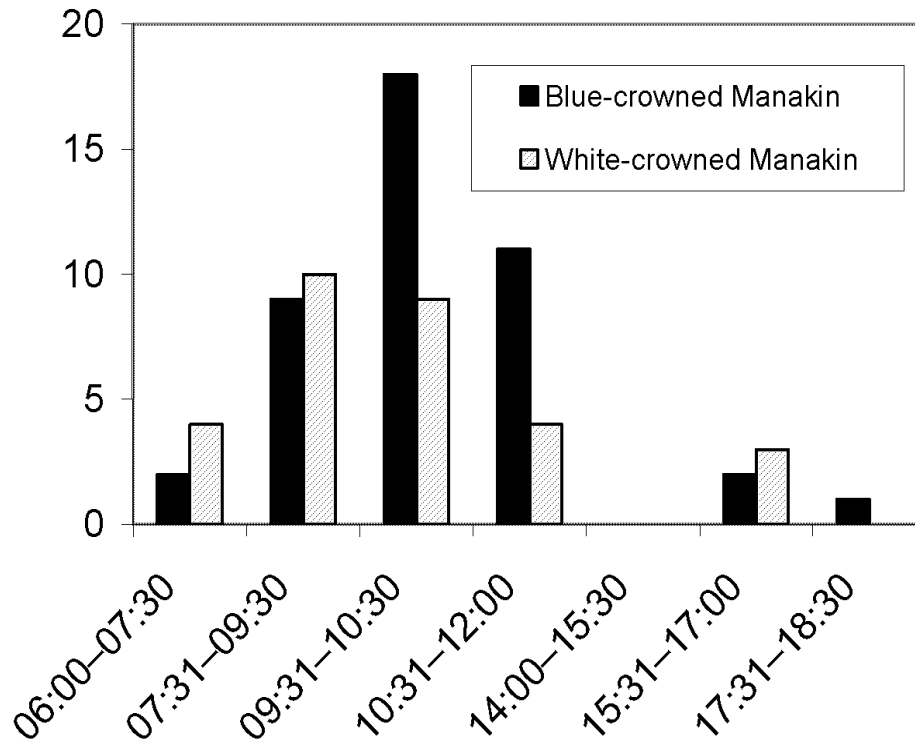


FIG 1. Daily patterns of participation in mixed-species flocks for Blue-crowned and White-crowned manakins in Yasuní National Park.

viduals of the same species participated in the same flock ($n = 3$), although in these cases each individual joined and foraged independently one of another. Individuals of both species were occasionally found in the same flock ($n = 5$), but they did not forage at the same time or in the same area.

I registered different participation frequencies for each species. The Blue-crowned Manakin was observed more often within flocks than the White-crowned Manakin (33% vs 19%, out of 112 flocks observed). Both species were observed within the flocks most commonly between 08:00 and 10:00 h (Fig. 1). At this time, usually flocks are actively foraging in the forest (pers. observ.). Both male and green-plumaged individuals of the

two species participated within the flocks. While foraging within the association, both species generally stayed just behind the flock advancing front, perching on exposed branches of understory bushes with a foliage density of 2.4 ± 0.9 (mean \pm SD, $n = 40$) for Blue-crowned, and 2.7 ± 1 (mean \pm SD, $n = 19$) for White-crowned manakins, respectively. While in foraging flocks, manakins remained silent though, on other occasions, adult male Blue-crowned Manakins vocalized from exhibition perches, even until very late in the morning (10:30 h) when they were observed away from these associations.

The time of flock participation was 10.9 ± 9.6 min ($n = 44$) for Blue-crowned and 7.76 ± 5.9 min ($n = 28$) for White-crowned indi-

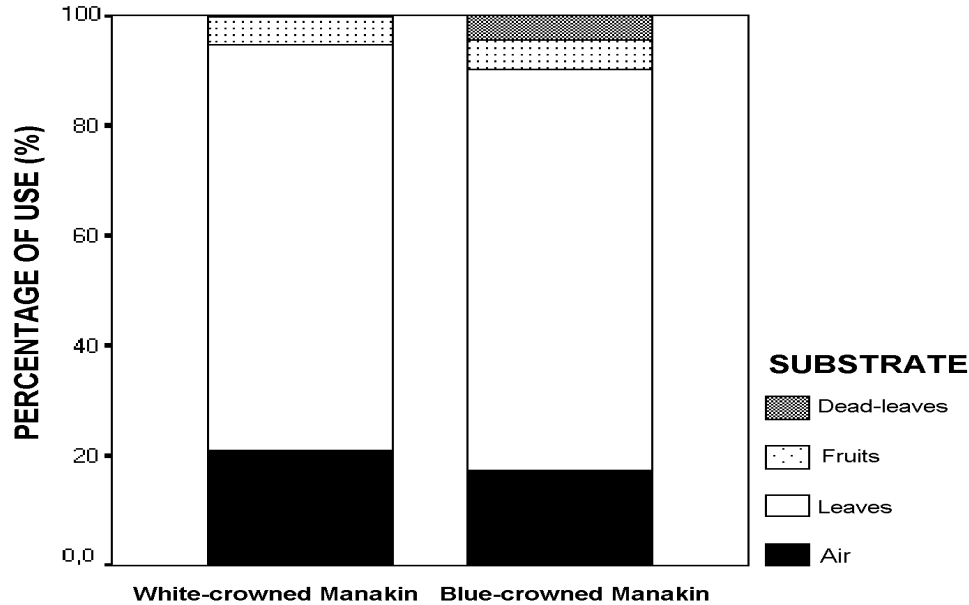


FIG 2. Use of foraging substrates by Blue-crowned ($n = 40$) and White-crowned manakins while accompanying understory mixed-species flocks, in Yasuní National Park, Ecuador. Statistical differences between them were not found ($G = 1.64$, $df = 3$, $P = 0.65$).

viduals. I did not find significant differences in the time of flock-participation between the two species (Mann Whitney test $U = 514.5$, $Z = 1.397$, $P = 0.162$, 2-tailed). Male and green-plumaged White-crowned Manakins foraged with flocks for similar times, with values of 10.3 ± 8.4 min ($n = 9$) for males, and 6.6 ± 4.2 min ($n = 20$) for green birds (Mann Whitney test $U = 73.5$; $Z = -7.84$, $P = 0.433$, 2-tailed). However, female Blue-crowned Manakins foraged within flocks for a longer time than males (Mann Whitney test $U = 130.5$, $Z = -2.616$, $P = 0.009$, 2-tailed). Green-plumaged birds remained with the flocks for 14.83 ± 11.4 min ($n = 23$) compared to males which remained for 6.52 ± 4.1 min ($n = 21$). Despite the similar size of these two manakins species, agonistic interactions between them were not observed during the study (I also never observed both species together in any mixed-flock), nor did I

observe agonistic interactions with other members of the association. Both species joined to flocks along ridges that had a tall forest with canopy over 20 m, though White-crowned Manakins were more frequently observed in swampy forest (31% out of $n = 29$) than the Blue-crowned Manakins (9% out of $n = 44$).

Within flocks, Blue-crowned Manakins foraged at a height of 4.5 ± 2.5 m ($n = 40$) in the understory, and plumages classes showed no significant differences ($t = 1.09$, $df = 38$, $P = 0.280$). Similarly, White-crowned Manakins foraged at an average height of 4.66 ± 2.4 m ($n = 19$) and showed no significant differences between the two plumage classes ($t = -1.19$, $df = 17$, $P = 0.25$). Almost all prey capture manoeuvres of both species consisted of sallies or gleans (Fig. 2). Blue-crowned Manakins had a major percentage of sally-hovers (10%) compared to White-crowned

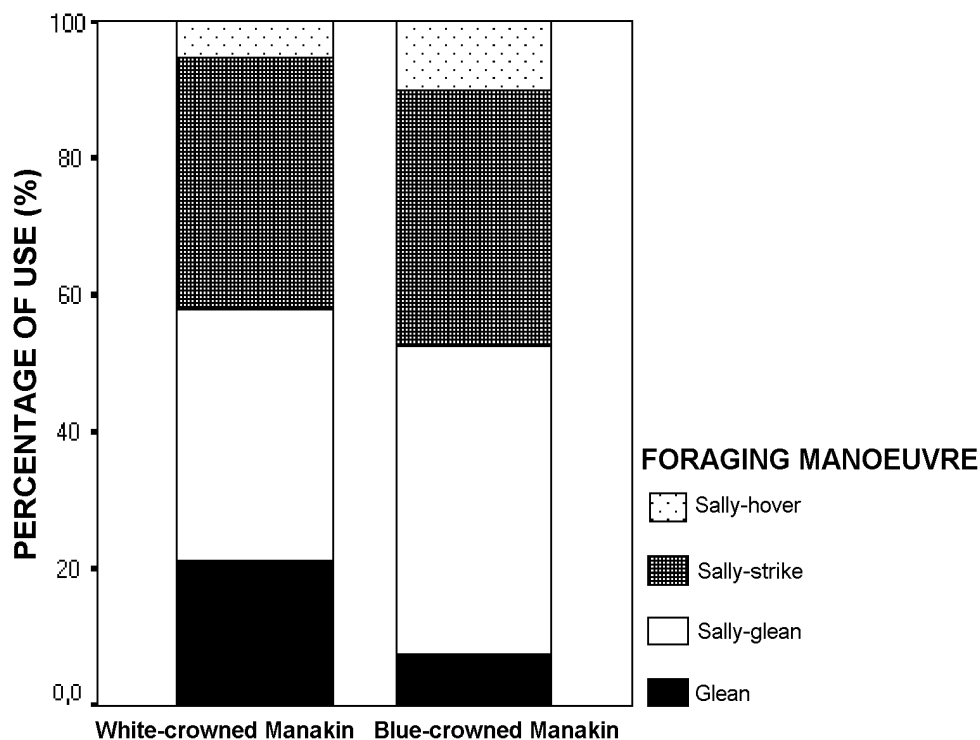


FIG 3. Use of foraging manoeuvres by Blue-crowned ($n = 40$) and White-crowned manakins ($n = 19$) while accompanying understory mixed-species flocks, in Yasuni National Park, Ecuador. Significant statistics between the species were not found ($G = 2.42$, $df = 3$, $P = 0.49$).

Manakins (5.3%) which use more glean manoeuvres (21.1% vs 7.5%) (Fig. 2). Preferred substrate was live foliage for Blue-crowned (62.5%) and for White-crowned (68.4%) manakins (Fig. 3). But, the use of foraging substrates ($G = 1.64$, $df = 3$, $P = 0.65$) and foraging manoeuvres showed no significant differences between the two species ($G = 2.42$, $df = 3$, $P = 0.49$).

In addition to the two focal species, three other manakin species were found in the mixed-species flocks of the study area. These include Blue-backed (*Chiroxiphia pareola*) ($n = 1$), Striped (*Machaeropterus regulus*) ($n = 3$), and Golden-headed (*Pipra erythrocephala*) ($n = 2$) manakins. In Yasuni, it was impossible to distinguish if these species actively joined the

flock (because they usually did not forage with other flocks partners) or were simply in the trajectory of the flock and followed it for a while. In the case of the Golden-headed Manakin, males were only observed in biggest flocks formed by the association of canopy and understory species near to a lek site.

The role of species in mixed-flocks has been defined by their participation's frequency or their behavior in the associations. In this way, the species that promote the cohesion and remain for long time within the flocks are denominated "core", and those that follow the movement of the core species and contribute little to the cohesion of the association are "attendants" (Powell 1985, Greenberg 1990). For manakins, I agree that they are

casual participants in flocks (Stotz 1993), as species that are regularly found outside of flocks and only rarely (and for brief periods) found in association with flocks. The participation frequency observed at Yasuni for the Blue-crowned Manakin, however, suggests that the species participation in mixed-species flocks may be an important part of their ecology. This is further supported by prior observations of this species joining mixed flocks in Central America, Colombia, and Venezuela (Skutch 1969, Hilty & Brown 1986, Hilty 2003) that corresponds to the subspecies of black plumage (Type I *sensu* Ridgely & Tudor 1989). The behavior seems also to happen as well in the rest of its distribution area South of the Amazon River in the SE of Peru and Bolivia (Tello pers. comm.).

During their association with flocks, both species of manakins captured principally arthropods. The preys of both manakins consisted of small insects like flies (Diptera), and one time a male White-crowned Manakin ate a blue homopterous, probably a leafhopper (Cicadellidae). Only on three occasions they were seen foraging for fruits while moving with the other species. A green-plumaged White-crowned Manakin took a red fruit from an unidentified Rubiaceae at 0.5 m of height and, on two occasions, a male and a green-plumaged Blue-crowned Manakin ate the white fruits of a Melastomataceae. Outside the flocks, fruits could be important in the diet of these species in the study area (pers. observ.) and for the White-crowned Manakin fruit availability seems important in the spatial distribution of leks in Ecuador (Ryder *et al.* 2006).

Interestingly, Blue-crowned and White-crowned manakins at Yasuní did not show significant differences in the participation time within flocks or in the use of substrates or attack manoeuvres. These results probably are related to the reliance on fruit as a principal element in the diet of the two species

(Snow 2004), although quantitative data about their diet are not available. In general, manakins have small home ranges and feed in short sessions at resource-rich localities near their leks (Ryder *et al.* 2006). It is interesting because both manakin species share a similar morphology and lek system (dispersed leks), although, at Yasuní, others species of manakins occur with the White-crowned and Blue-crowned manakins. These other species, the Golden-headed and Blue-backed manakins, are highly frugivorous and have a concentrated or cooperative lek system (Ridgely & Tudor 1989, Prum 1994). As noted by Beehler (1987), the diet and the foraging ecology are important factors influencing avian mating strategies of passerine lekking species. In birds of paradise, species with dispersed leks are partially insectivorous, in contrast to species using concentrated lek that have a more frugivorous diet (Beehler & Pruett-Jones 1983). As in the Blue-crowned and White-crowned manakins at Yasuní, in New Guinea, the King Bird of Paradise (*Cicinnurus regius*) that uses dispersed leks forages within mixed-species flocks (Beehler & Pruett-Jones 1983). Previous observations of manakins accompanying understory mixed-species flocks indicated that Blue-crowned are more frequently found than White-crowned manakins (Hilty 2003, Snow 2004), and the same happened in Yasuní, although both species of manakins were attendant species within flocks. The major occurrence of Blue-crowned Manakins in understory flocks is possible because of the use of the lowest forest levels for courtship, whereas White-crowned Manakins choose the highest display sites (Heindl & Winkler 2003), or because of a higher abundance in the forest of the Blue-crowned than the White-crowned manakins (Loiselle *et al.* 2007). The similarity in the foraging behavior of Blue-crowned and White-crowned manakins is not surprising because both species share a similar morphology,

body size and mating strategy (Snow 2004, Prum 1994). However, Blue-crowned Manakins used a major proportion of wing-powered manoeuvres (sally-glean and sally-hover) than White-crowned Manakins. The different participation frequencies within flocks could provide a mechanism for decreasing interspecific competition between these two similar species, as well as for differences in lek placement (Loiselle *et al.* 2007).

Some benefits provided for mixed-species flocks include a decrease in predation or a facilitation in the capture of dispersed preys like insects, and these benefits are not mutually exclusive (King & Rappole 2001). My observations of the two species of manakins with mixed flocks suggest a possible benefit in insect foraging where both species could obtain a protein supplement in their diet by mean of the beater effect of other individuals in the flock. In the case of White-crowned Manakins, males remained for a longer time with flocks compared to females, but differences were not significant. It is possible that fruits could be more important in the diet of White-crowned Manakins than insects and, for this reason, differences between plumages classes in the flock participation time were not found. The opposite situation occurred with Blue-crowned Manakins where green-plumaged birds remained for almost twice more time than males. Insects seem to be especially important for Blue-crowned Manakins because females and juveniles follow ant-swarms (Willis & Oniki 1992). This behavior was also noted in Yasuní. On one occasion, a female Blue-crowned Manakin was observed foraging at an ant swarm (*Eciton* sp.) where it remained for a short time (5 min) in the company of several obligate ant-following species like the Sooty (*Myrmeciza fortis*), Bicolor (*Gymnopithys leucaspis*), Lunulated (*G. lunulata*) and White-plumed (*Pithys albifrons*) antbirds.

As proposed for other lekking species, the greatest predictor of mating success in polygynous birds is the lek-residency time (Ryder *et al.* 2006) thus, in the case of both manakins species, males may forage very near to their leks, minimizing travel time and maximizing lek residency time (Ryder *et al.* 2006). This fact is possibly the main cause of the significant differences in participation times between male and green-plumaged Blue-crowned Manakins. The proteic contribution of this foraging type, however, could be important for the demands of reproductive or growing activities in female and juvenile Blue-crowned Manakins that foraged for more time with the flocks than males. Théry (1997) found important differences in the wing shapes of five sympatric manakins in Guyana, including White-crowned and White-fronted (*Lepidothrix serena*) manakins; wings of females appear to be adapted for higher mobility in large home ranges. Also, it is known, that passerine females change their foraging behavior as a result of the demands for the reproductive activities. Dobbs & Martin (1998) found that the females with nestlings of the Red faced Warbler (*Cardellina rubrifrons*) increased their prey attack rate and shifted to hover sallying compared to egg-laying and incubating females. In Blue-crowned Manakins, females were in charge of the incubation and nestling periods by themselves and it is suggested that their longer participation within flocks could allow them to catch more insects and obtain a protein supplement. By means of a longer participation within flocks, females could reduce the intraspecific competition with males, but more data are needed to demonstrate this hypothesis.

ACKNOWLEDGMENTS

I am very grateful to the staff of the Yasuni Research Station, especially to the Station Manager Dr. Friedemann Köster who pro-

vided the logistic support for the study of the understory mixed bird flocks. Invaluable corrections that improve the manuscript were done by Dr. Tjitte de Vries and Juan Fernando Freile. Thanks to José Tello for sharing his observations in Peru and kindly reviewing earlier versions of this manuscript. I am also indebted to H. Romero-Saltos & Gaby Lopéz for comments on the English translation. References and bibliographic material were kindly provided by M. Metz, E. Willis and J. Rappole. My study in Yasuní was financially supported by Repsol-YPF and the Pontificia Universidad Católica del Ecuador through the project “Estructura, composición y densidad de aves de bandadas mixtas en la ECY”.

REFERENCES

- Bechler, B. M. 1987. Birds of paradise and mating system theory – Predictions and observations. *Emu* 87: 78–89.
- Bechler, B., & S. G. Pruett-Jones. 1983. Display dispersion and diet of birds of paradise: a comparison of nine species. *Behav. Ecol. Sociobiol.* 13: 229–238.
- Blake, J. G., & B. Loiselle. 2002. Manakins (Pipridae) in second-growth and old-growth forest: patterns of habitat use, movement and survival. *Auk* 119: 132–148.
- Bostwick, K. S. 2000. Displays behaviors, mechanical sounds, and evolutionary relationships of the Club-winged Manakin (*Machaeropterus deliciosus*). *Auk* 117: 465–478.
- Buitrón-Jurado, G. 2005. Competencia interespecífica en aves de bandadas mixtas de sotobosque en el Parque Nacional Yasuní. Tesis de Licenciatura, Pontificia Universidad Católica, Quito, Ecuador.
- Chen, C., & F. Hsieh. 2002. Composition and foraging behaviour of mixed-species flocks led by the Grey-checked Fulvetta in Fushan Experimental Forest, Taiwan. *Ibis* 144: 317–330.
- Doobs, R. C., & T. E. Martin. 1998. Variation in foraging behavior among nesting stages of female Red-faced Warblers. *Condor* 100: 741–745.
- Fitzpatrick, J. W. 1980. Foraging behavior of Neotropical tyrant flycatchers. *Condor* 82: 43–57.
- Greenberg, R. 1990. Birds of many feathers: the formation and structure of mixed-species flocks of forest birds. Pp. 521–568 *in* Boinski, S., & P. A. Garber (eds). *On the move: How and why animals travel in groups*. Princeton Univ. Press, Princeton, New Jersey.
- Heindl, M., & H. Winkler. 2003. Vertical lek placement of forest-dwelling manakin species (Aves, Pipridae) is associated with vertical gradients of ambient light. *Biol. J. Linn. Soc.* 80: 647–658.
- Hilty, S. L. 2003. *Birds of Venezuela*. Princeton Univ. Press, Princeton, New Jersey.
- Hilty, S. L., & W. Brown. 1986. *A field guide to the birds of Colombia*. Princeton Univ. Press, Princeton, New Jersey.
- Jullien, M., & J. M. Thiollay. 1998. Multi-species territoriality and dynamic of Neotropical forest understory bird flocks. *J. Anim. Ecol.* 67: 227–252.
- King, D., & J. H. Rappole. 2001. Mixed-species bird flocks in dipterocarp forest of North-Central Burma (Myanmar). *Ibis* 143: 380–390.
- Krijger C. L., M. Opdam, M. Théry, & F. Bongers. 1997. Courtship behaviour of manakins and seed bank composition in a French Guianan rain forest. *J. Trop. Ecol.* 13: 631–636.
- Loiselle, B. A., & J. G. Blake. 1998. Diets of understory fruit-eating birds in Costa Rica: Seasonality and resource abundance. *Stud. Avian Biol.* 13: 91–103.
- Loiselle, B. A., J. G. Blake, R. Duraes, T. B. Ryder, & W. Tori. 2007. Environmental and spatial segregation of leks among six co-occurring species of manakins (Pipridae) in Eastern Ecuador. *Auk* 124: 420–431.
- Marini, M. A. 1992. Foraging behavior and diet of the Helmeted Manakin. *Condor* 94: 151–158.
- Marra, P. P., & J. V. Remsen Jr. 1997. Insights into the maintenance of high species diversity in the Neotropics: Habitat selection and foraging behavior in understory birds of tropical and temperate forests. *Ornithol. Monogr.* 48: 445–483.
- Naoki, K. 2007. Arthropod resource partitioning among omnivorous tangers (*Tangara* spp.) in

- Western Ecuador. *Auk* 124: 197–209.
- Powell, G. V. 1985. Sociobiology and adaptive significance of interspecific foraging flocks in the Neotropics. *Ornithol. Monogr.* 36: 713–732.
- Prum, R. O. 1994. Phylogenetic analysis of the evolution of alternative social behaviour in the manakins (Aves: Pipridae). *Evolution* 48: 1657–1675.
- Prum, R. O., & A. E. Johnson. 1987. Display behavior, foraging ecology, and systematics of the Golden-winged Manakin (*Masius chrysoterus*). *Wilson Bull.* 99: 521–539.
- Remsen, J. V., Jr., & S. K. Robinson. 1990. A classification scheme for foraging behavior of birds in terrestrial habitats. *Stud. Avian Biol.* 13: 144–160.
- Remsen, J. V., Jr., A. Jaramillo, M. Nores, J. F. Pacheco, M. B. Robbins, T. S. Schulenberg, F. G. Stiles, J. M. C. da Silva, D. F. Stotz, & K. J. Zimmer. 2006. A classification of the bird species of South America. *American Ornithologist Union*. On line. http://www.museum.lsu.edu/~Remsen/SACC_Baseline.html.
- Ridgely, R., & P. Greenfield. 2001. The birds of Ecuador. Volume 1. Status, distribution and taxonomy. Cornell Univ. Press, Ithaca, New York.
- Ridgely, R., & G. Tudor. 1989. The birds of South America. Volume II. The Suboscine Passerines. Univ of Texas Press, Austin, Texas.
- Robbins, M. B. 1985. Social organization of the Band-tailed Manakin (*Pipra fasciicauda*). *Condor* 87: 449–456.
- Romero-Saltos H., R. Valencia, & J. M. Macía. 2001. Patrones de diversidad, distribución y rareza de plantas leñosas en el Parque Nacional Yasuní y la Reserva Étnica Huaorani, Amazonía ecuatoriana. Pp. 131–162 in Duivenvoorden, J. F., H. Balslev, J. Cavelier, C. Grández, H. Tuomisto, & R. Valencia (eds). *Evaluación de recursos vegetales no maderables en la Amazonía noroccidental*. IBED, Universiteit van Amsterdam, Amsterdam, Netherlands.
- Rosenberg, K. V. 1990. Dead-leaf foraging specialization in tropical forest birds: Measuring resource availability and use. *Stud. Avian Biol.* 13: 360–368.
- Ryder, T. B., J. G. Blake, & B. A. Loiselle. 2006. A test of the environmental hotspot hypothesis for lek placement in three species of manakins (Pipridae) in Ecuador. *Auk* 123: 247–258.
- Scott Sillett, T. Foraging ecology of epiphyte-searching insectivorous birds in Costa Rica. *Condor* 96: 863–877.
- Skutch, A. F. 1969. Life histories of Central American Birds. Volume 3. Pacific Coast Avifauna No. 35, Cooper Ornithological Society, Berkeley, California.
- Snow, D. W. 2004. Family Pipridae (Manakins). Pp. 110–169 in del Hoyo, J., A. Elliot, & D. Christie (eds). *Handbook to the birds of the world Volume 8: Cotingas to pipits and wagtails*. Lynx Edicions, Barcelona, Spain.
- Sokal, R., & F. J. Rohlf. 2003. *Biometry. The principles and practice of statistics in biological research*. W. H. Freeman Company, New York, New York.
- SPSS Inc. 2000. *SPSS. Statistical package for the social sciences*. SPSS Inc., Chicago, Illinois.
- Stotz, D. F. 1993. Geographic variation in species composition of mixed-species flocks in lowland humid forests in Brazil. *Pap. Avulsos Zool.* 38: 61–75.
- Théry, M. 1990. Display repertoire and social organization of the White-fronted and White-throated manakins. *Wilson Bull.* 102: 123–130.
- Théry, M. 1997. Wing-shape variation in relation to ecology and sexual selection in five sympatric lekking manakins (Passeriformes: Pipridae). *Ecotropica* 3: 9–19.
- Valencia, R., R. Foster, G. Villa, J. Svenning, C. Hernández, K. Romoleroux, E. Losos, E. Magard, & H. Balslev. 2004. Tree species distributions and local habitat variation in the Amazon: large forest plot in eastern Ecuador. *J. Ecol.* 92: 214–229.
- Willis, E. O. 1966. Notes on a display and nest of the Club-winged Manakin. *Auk*: 475–476.
- Willis, E. O., & Y. Oniki. 1992. As Aves e as formigas de correicao. *Bol. Mus. Para. Emílio Goeldi, Ser. Zool.* 8: 123–150.

