

ARE MALES AND FEMALES OF THE YUNGAS MANAKIN (*CHIROXIPHIA BOLIVIANA*) ECOLOGICALLY REDUNDANT AS SEED DISPERSERS?

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Resumen. – ¿Son los machos y hembras del Saltarín Yunga (*Chiroxiphia boliviana*, Aves: Pipridae) ecológicamente redundantes como diseminadores de semillas?. – Los saltarines Yunga son pequeñas aves de sotobosque con un sistema de reproducción basado en leks y con dimorfismo sexual. Ya que los machos y las hembras difieren en características relacionadas al forrajeo, aquí analizo si también difieren en sus dietas y en su rol como dispersores de semillas. Aunque limitados por el tamaño de muestra, mis resultados sugieren que machos y hembras no son ecológicamente redundantes: sus dietas sí difieren, pero muestran un patrón opuesto al esperado. Los machos dispersan mayor diversidad de semillas, incluyendo especies diseminadas por murciélagos, pero con menor efectividad que las hembras, mientras que éstas parecen ser especialmente importantes para diseminar frutos de melastomatáceas. El dimorfismo en el pico no explica las diferencias en consumo de frutos, pero sí el dimorfismo comportamental.

Abstract. – Yungas Manakins (*Chiroxiphia boliviana*) are small understory frugivorous birds with a lek-based mating system and sexual dimorphism. As sexes differ in feeding-related traits, I examined whether they also differ in their diets and role as seed dispersers. Although restricted by sample sizes, my results suggest that sexes are not redundant as seed dispersers. They do differ in their diets yet following a pattern contrary to expectations. Males disperse more seed species including several bat-dispersed seeds but are less effective dispersers than females, while the latter seem to be especially important for melastome berries' dispersal. Bill dimorphism does not explain fruit consumption differences, but behavioral dimorphism does. Accepted 23 May 2012.

Key words: Yungas Manakin, *Chiroxiphia boliviana*, Bolivia, diet, ecological redundancy, Melastomataceae, Pipridae, seed dispersal, sexual dimorphism.

INTRODUCTION

Manakins (Pipridae) are small Neotropical frugivorous birds that show marked sexual morphological and behavioral dimorphism (Snow 2004). Most of them possess a lek-based mating system on which males typically perform complex, acrobatic courtship displays to attract females (Prum 1994, Snow 2004). Females choose among males at these arenas (McDonald 1993, Shorey 2002, Snow

2004) and are entirely responsible for nesting and parental care (Snow 2004). According to the Intersexual Competition Hypothesis, manakin sexes should differ in traits related to feeding ecology (Selander 1966, Hedrick & Temeles 1989, Shine 1989), and these differences may affect their seed dispersal roles (Loiselle *et al.* 2007).

The Yungas Manakin (*Chiroxiphia boliviana*) is the only abundant Pipridae in the Bolivian Eastern-Andean montane forests. It

is an important seed disperser in early successional areas (Montaño-Centellas 2004, 2007) providing an important service to forest regeneration (Gorchov *et al.* 1993). Yungas Manakin males are larger than females but have significantly smaller bills (Doucet 2006), a dimorphism that could have important consequences on life-history traits of this species. Manakins are 'gulers'; they mostly swallow whole fruits (Snow 2004), and can be considered as gape-size limited frugivores (Wheelwright 1985). As gape size in gulers is positively correlated with the mean and maximum size of fruits eaten but not with the minimum (Wheelwright 1985), larger-billed birds (Yungas Manakin females) are expected to have a wider spectrum of edible fruits (than males). This may translate into non-redundancy of sexes as seed dispersers (Loiselle *et al.* 2007). Ecologically redundant dispersers are those that contribute with the same seed rain, providing a similar ecological service, and usually individuals of a same species are assumed to be ecological equals. Here I examine if Yungas Manakins sexes are redundant as seed dispersers, by comparing male and female droppings obtained from captured birds in an agricultural landscape in an Andean montane forest of Bolivia.

METHODS

From April to October 2002 and February to March 2003 I captured birds in the agricultural landscape nearby the former Tunquini Biological Station (hereafter TBS, 67°52'W and 16°11'S, 1450 m a.s.l.), a research station in the Andean montane forests of Bolivia. TBS' landscape is dominated by secondary old-growth forest with small agricultural and young-growth patches (resulting both from abandoned plantations and from natural slides and gaps; Paniagua-Zambrana *et al.* 2003). I chose four mist-net sites each of which was a small (0.5–1 ha) coffee-and-

citrus shade-plantation surrounded by an old-growth secondary forest matrix. Beside the planted native species (i.e., *Inga* sp.), several non-planted early-growth species were present in the sites (Tordoya 2006).

Between seven and ten mist-nets were placed at each site for four days monthly and opened from sunrise until 17:00 h, comprising a total effort of 3728 net hours (cf. Ralph *et al.* 1996). Captured Yungas Manakins' sex and age were determined by external characterization (Ralph *et al.* 1996): birds with at least rudimentary distinguishable red crown and black dorsal plumage were registered as males; birds with green plumage without the former characteristics were registered as females only if external aspect suggested maturity (old or new incubation patches and molting). Green birds lacking these characteristics were not included in the analysis. Additionally, three repeated measures (to the nearest 0.02 mm) of each bird's tarsus length and bill length, width, and depth (at the nares) were taken and compared with Doucet's (2006) measurements to confirm bird sex. Birds were kept for approximately one hour in cloth bags, with a plastic dish at the bottom, to collect droppings. Rectrix tips were cut following numerical codes for each individual, to recognize recaptures. The relationship between males' and females' monthly captures (excluding recaptures) was analyzed with a Spearman correlation test.

Collected fecal samples were transferred to filter paper and tagged with a bird capture code. Seeds in each sample were separated, identified to species level and compared with a reference collection at the Bolivian National Herbarium (LPB). Following Gorchov *et al.* (1995) I registered only the presence of any given seed species in each fecal sample. For each seed species, frequency of occurrence was calculated for males, females and for all birds summed. I used sample-based species accumulation curves to assess the complete-

ness of food items in Yungas Manakins' diet. To eliminate the order in which fecal samples were added, sample order was randomized 1000 times and smoothed accumulation curves obtained for each sex's diet. Observed accumulation curves were fitted with the linear dependence model $S = a/b(1 - e^{-bx})$, where S is the species richness, x is the added sample number and (a/b) is the expected species richness when the asymptote is reached (Moreno & Halffter 2000). I described male and female diets with species richness (S), proportional composition, and standardized Levin's niche breadth index (B , Colwell & Futuyma 1971). S was compared between sexes with species expected rarefaction curves constructed by randomizing (1000 times) seeds found in each dropping (Gotelli & Colwell 2001). Finally, Pianka's overlap index (O , Pianka 1973) was used to calculate diet overlap between sexes and compared with a null randomized niche overlap model created by 1000 iterations with an algorithm (RA3) that retains niche breadth but randomizes the frequency of each seed in diet (Albrecht & Gotelli 2001). Univariate statistical tests were performed with SPSS v. 11.5 and randomizations with EcoSim v. 7 (2001).

RESULTS

I captured a total of 52 Yungas Manakins, two of which were recaptures and excluded from the analysis. Of the remaining, 31 were categorized as males, 15 as adult females, and 4 could not be sexed and were therefore not included in the analyses. Although more males than females were captured along the year, capture patters were similar for both sexes ($r_s = 0.73$, $P = 0.026$).

A total of 34 fecal samples were collected: 11 contained only fruit pulp and no seeds, 1 was composed only by arthropod remains, and 22 included seeds. Ten species of seeds (from seven families) were registered in the diet of Yungas Manakins (Fig. 1). Females'

fecal samples contained only three species, one of them was not found in any male sample (*Bocconia frutescens*, Papaveraceae). The other two were *Miconia* (Melastomataceae) species (*M. amabilis* and *M. calvescens*). Males' feces contained nine species from six plant families (Fig. 1). Despite the small sample sizes, smoothed accumulation curves reached asymptotes and observed curves fitted the linear dependence model ($R^2 = 0.95$, $P < 0.00001$ for males and $R^2 = 0.89$, $P < 0.001$ for females; Fig 2). Overall, I sampled 81% and 95% of males' and females' diet, respectively. Although rarefaction curves did not reach a clear asymptote they suggest that males' diet is richer than females' (Fig. 2C); even if we add more fecal samples the slopes of these curves will not converge at any point. Diet overlap between sexes was 67% ($O = 0.67$), and even though it was higher than expected, the difference was not significant ($O_{exp} = 0.41 \pm 0.17$ SD, $P = 0.07$, Fig. 1).

DISCUSSION

I found that Yungas Manakin sexes might not be ecologically redundant as seed dispersers. Although limited by sample size, my results show that males and females do exploit feeding resources differently, and differ in their role of seed dispersers (Selander 1966, Hedrick & Temeles 1989, Shine 1989) but fail in explaining whether these differences are due to bill dimorphism (Doucet 2006). Contrary to expectations, smaller-billed males consumed a broader range of fruits at TBS, while diet of females was not only less rich than the diet of males, but was dominated by two species of the same genus (*Miconia*). Moreover, I found no evidence of gape-size restrictions in the diet: *Miconia* berries range between 4 to 5 mm, while some of male consumed fruits such as *Hebanthe occidentales* (Amaranthaceae) and *Tapirira guianensis* (Anacardiaceae) can exceed 6 mm on their smaller

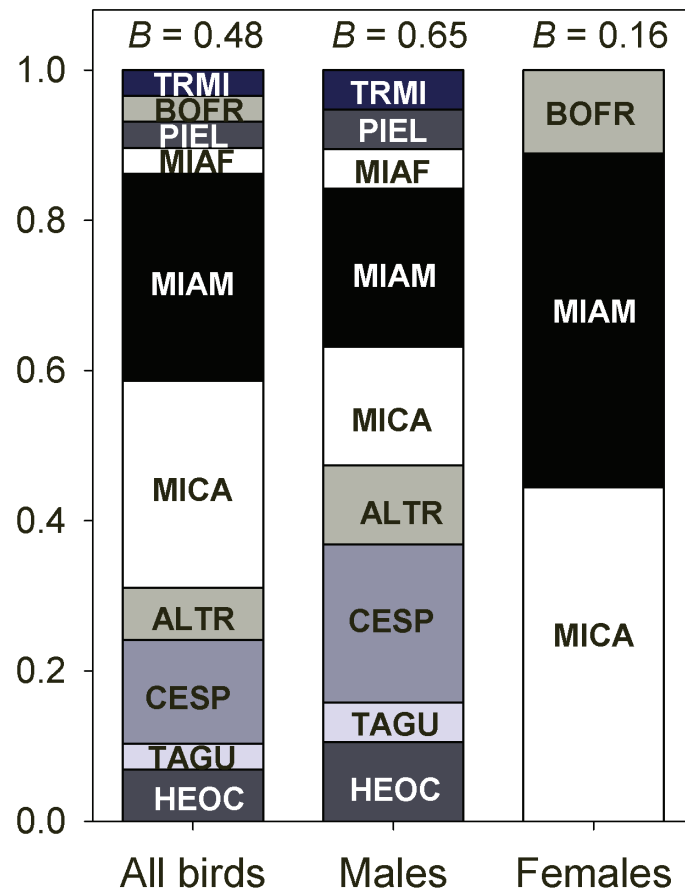


FIG 1. Proportional composition of Yungas Manakin's (*Chiroxiphia boliviana*) diet in an agricultural landscape in a Bolivian montane forest. Values above each column correspond to standardized Levin's index niche breadth (B), whose values range between 0 and 1. Seed species in diets are: HEOC: *Hebanthe occidentalis*, TAGU: *Tapirira guianensis*, CESP: *Cecropia* spp., ALTR: *Alchornea triplinervia*, MICA: *Miconia calvescens*, MIAM: *Miconia amabilis*, MIAF: *Miconia affinis*, PIEL: *Piper elongatum*, BOFR: *Bocconia frutescens*, TRMI: *Trema micrantha*.

diameter. At TBS, both sexes supplemented their diet with occasional lipid-rich arilate seeds (Skutch 1980); males consumed *Alchornea triplinervia* (Euphorbiaceae) while females consumed *Bocconia frutescens* (Papaveraceae). Females feeding on *B. frutescens* is particularly important as during my study year no other bird species fed on it (of ~ 400 feces containing seeds; Montaña-Centellas 2007).

Given that melastome berries are not especially nutritious, the predominant feeding of Yungas Manakin females - and not males - on *Miconia* was initially surprising, yet it could be explained by two non-exclusive phenomena: 1) in the Neotropics melastome berries contain on average more sucrose than bird-consumed Piperaceae and Moraceae fruits (Baker *et al.* 1998), the other two most

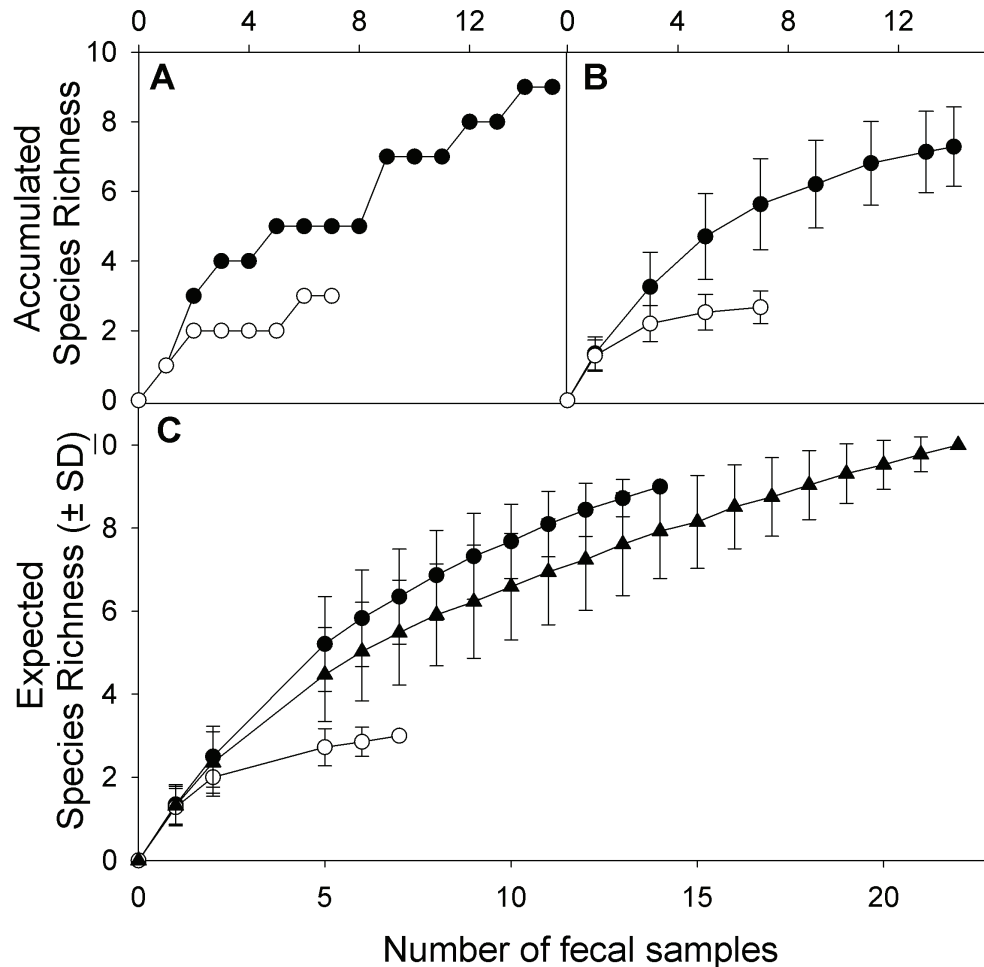


FIG 2. Yungas Manakin (*Chiroxiphia boliviana*) males (black circles), females (open circles), and all birds summed (black triangles), observed (A) and randomized (B) sample-based accumulation curves showing seed species accumulation as a function of sample effort, and rarefaction curves (C) showing expected plant species richness S in bird diets for different sample sizes. Accumulated species richness in (B) is presented as $S \pm$ SD.

abundant families found in males' droppings, and 2) because of their phenotypic plasticity, *Miconia* berries in open areas, such as plantations, may have significantly more sugar contents than the same species in old-growth forests (Lumping & Boyle 2009). Even when guplers can not select fruits based on sugar contents (Levey 1987), *Chiroxiphia* manakins can learn the exact position of feeding

resources (Foster 1977). If so, female Yungas Manakins may remember specifically sugary *Miconia* shrubs and consume them preferentially.

Besides nutrient content, different foraging patterns and traveling time of males and females (Sick 1967) might result in differences in fruit selection. Smaller home-ranges and feeding times in males (Graves *et al.* 1983)

may imply that selection of resources responds directly to local availability. Yungas Manakin males' diet includes both bird-dispersed fruits and those preferred by non-avian frugivores. Most of the latter are locally super-abundant and were also registered in bat droppings at TBS (Tordoya 2006). Interestingly, Gorchov *et al.* (1995) found that in early succession areas, melastome berries were one of the few resources bats do not feed on and consequently do not disperse. Females seem to disperse fewer plant species but having larger home ranges might imply a higher chance of depositing seeds away from parental plants. On the contrary, males disperse more seeds but as they spend more time in lek areas, they probably deposit more seeds in them. As melastome seedlings have less survival rates in manakin leks (Krijger & Opda 1995) and *Miconia* might be more successful to recruit in *Miconia*-only droppings than in mixed-species droppings (Loiselle 1990), males seem to provide a less effective seed dispersal (Schupp *et al.* 2010), at least for Melastomataceae.

Sample size restrictions of this study rise when comparing Yungas Manakins' diet found here with those described for other manakin genera (Wheelwright *et al.* 1984, Loiselle *et al.* 2007) and *Chiroxiphia* species (Della Flora 2010). However, to increase sample sizes, these studies usually include droppings collected below male displaying perches, and can be strongly biased to sample male diet, masking intersexual differences. Even though this study only partially describes Yungas Manakins' diet, statistical analyses suggest that sampling was sufficient to show sex differences. Larger sample sizes might add seed species to diet, but these new records would be rare and probably unlikely to change the general patterns shown here (Loiselle *et al.* 2007). Moreover, manakins are known to regurgitate the seeds of several fruits, and then dietary analysis based on fecal

samples will not only underestimate niche breadths but will bias analysis to small-seeded species (Loiselle *et al.* 2007). My finding of 11 droppings (32%) including only pulp remains suggest that data herein might be biased in this manner; however, seeds discarded at (or close to) feeding places (parental plants) have less chance to survive (Howe & Smallwood 1982), and therefore will not change my conclusions regarding seed dispersal roles. Considering sexes of dimorphic species as ecological equals might be masking important ecological traits. Just within the *Chiroxiphia* genus, Douchet (2006) described similar dimorphisms for four other species. Although not corresponding directly to bill size, differences among sexes in seed dispersal described here may be likely to occur in other *Chiroxiphia* manakins.

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