ORIGINAL ARTICLE

WHITE-CROWNED MANAKIN (*DIXIPHIA PIPRA*) USE OF SPACE IN THE ECUADORIAN AMAZON

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Abstract · Animal patterns of space use have fundamental consequences for ecological processes such as animal-mediated seed dispersal. This study examines the use of space of an understory frugivore: the White-crowned Manakin (*Dixiphia pipra*) during the non-breeding season at Tiputini Biodiversity Station in Ecuador. We radio-tracked seven individuals of different sexes and ages. We found that White-crowned Manakins have relatively small home ranges varying from 1.19 to 5.73 ha. The home ranges of male juveniles (2.25 ± 0.62 SE) were larger than that of the adult males (1.20 ± 0.01 SE), but smaller than those of females (4.27 ± 0.77 SE). Females and second-year males were found to perform more long distance flights outside their core home range than hatch-year or adult males. These movement differences suggest that they disperse seeds longer distances and more evenly across their home range. Adult and hatch-year males appear to perform more short distance seed dispersal events. We argue that these contributions are complementary, and that White-crowned Manakins are key dispersal agents that have a significantly influence in the structure and composition of understory plant communities in the Amazon rainforest.

Resumen · Uso de espacio del Saltarín Coroniblanco (*Dixiphia pipra*) en la Amazonía Ecuatoriana
Los patrones de uso espacial utilizados por animales tienen consecuencias fundamentales en procesos ecológicos, tales como la dispersión de semillas. Este estudio examina el uso espacial de una especie frugívora de sotobosque: el Saltarín Coroniblanco (*Dixiphia pipra*) durante el ciclo no-reproductivo en la Estación de Biodiversidad de Tiputini en Ecuador. Seguimos por radio telemetría a siete individuos de diferentes sexos y edades. Encontramos que el Saltarín Coroniblanco tiene un rango de hogar relativamente pequeño, variando entre 1,19 a 5,73 ha. El rango de hogar de los machos juveniles (2,25 ± 0,62 EE) es más grande que el de los machos adultos (1,20 ± 0,01 EE), pero más pequeño que el de las hembras (4,27 ± 0,77 EE). El estudio encontró que las hembras y los machos de segundo año realizaron vuelos más largos fuera del núcleo de su rango de hogar, comparado con machos juveniles del año o machos adultos. Estas diferencias sugieren que podrían dispersar semillas a mayores distancias y de manera más homogénea a lo largo de su rango de hogar. Los machos adultos y los juveniles del año parecen llevar a cabo eventos de dispersión de semillas a distancias más cortas. Nosotros argumentamos que estas contribuciones son complementarias y que los Saltaríenes Coroniblancos son agentes de dispersión claves, influenciando considerablemente la estructura y la composición de las comunidades de plantas del sotobosque en el bosque tropical lluvioso de la Amazonía Ecuatoriana.

Key words: Ecuador · Home range · Lek · Manakin · Pipridae · Radio telemetry · Seed dispersal · Space use

INTRODUCTION

Having knowledge of animal use of space can help us to better understand key ecological and evolutionary processes (Naef-Denzer 1994), as well as identify habitat requirements for conservation planning and management (Davis et al. 2014). Animal movements can be influenced by many factors such as topography (Westcott 1994), food distribution (Pyke 1984), competition (MacArthur & Levins 1964), predation (Jefferies & Lawton 1984; Suhonen et al. 1994), mate availability (Bradbury & Gibson 1983), among others. These factors may play different roles for individuals of different ages and sexes (Westcott & Graham 2000), and could also vary between

seasons (e.g., reproductive vs non-reproductive seasons, Théry 1992). This is particularly true in species with lek mating systems, where males, females, and juveniles play very different roles in reproduction. In these systems, adult males cluster in space and defend a small territory where they perform courtship displays to prospective females with the purpose of copulation. Females freely visit display territories to choose mates, after which they perform all parental duties without help (e.g., Bradbury & Gibson 1983, Ligon 1999). In some lekking species, juvenile males have delayed plumage maturation (e.g., Foster 1987, McDonald 1993, DuVal 2005, Ryder & Durães 2005, Doucet et al. 2007, Ryder & Wolfe 2009) and it can take them a few years to gain access to reproduction (Tori 2008, Ryder et al. 2008, Duval & Kempenaers 2008, but see Alatalo et al. 1996). Juvenile females typically join the reproductive pool faster (WPT pers. observ.).

Differences in individual space use can have significant effects in ecological processes such as seed dispersal. Seed dispersal is the movement of seeds away from a parental plant. It can be advantageous for many reasons such as escaping high mortality caused by distance/density dependence due to crowding or disease near the parental plant, by allowing the seed to arrive to rare sites with higher probability of survival, or by finding suitable sites that are unpredictable in space and time (e.g., tree fall gaps; Wenney 2001). Typically most seeds are moved relatively short distances (Wilson 1993), however long-distance dispersal events are crucial for population spread, population dynamics, and for the maintenance of genetic connectivity (Trakhtenbrot et al. 2005).

The objective of this study was to describe the use of space and the potential role as seed disperser of a lekking species of the family Pipridae, the White-crowned Manakin (*Dixiphia pipra*). To our knowledge, only one previous study examined movement patterns by this species using radio-marked individuals (Théry 1992), however, data available were collected mostly during the breeding season and at one single location (French Guyana), despite its wide geographic range. Here we examined space use by individuals of different sexes and ages during the non-breeding season at Tiputini Biodiversity Station in the Ecuadorian Amazon rainforest. We predicted that female space use (measured as home ranges size, home range overlap and distance traveled in 30 minutes) would be greater than those of adult males, because adult males are constrained by their need to defend territories which are a requirement for reproduction. Moreover, we predicted that juvenile males would have larger home ranges (hereafter HR) than adult males and females. Juvenile males are expected to visit multiple leks to maximize their social affiliations with other males, and increase their chances to inherit a territory (Ryder et al. 2008) and become established in a lek to gain potential access to reproduction. Ages and sexes with larger HRs were predicted to perform longer distance seed dispersal events.

METHODS

Study site. The research was conducted in a 100 ha plot (Harpia plot) at Tiputini Biodiversity Station (hereafter TBS) located along the Tiputini River in the Orellana province in eastern Ecuador (~0°38'S, 76°08'W). TBS encompasses 650 ha of largely undisturbed rainforest, located within the 1.5 million ha Yasuní Biosphere Reserve. The Harpia plot elevation ranges from 201 to 233 m a.s.l. (Durães et al. 2007). It is gridded (100 x 200 m grid lines), and trails are georeferenced and marked every 50 m (for more information see Loiselle et al. 2007a).

Study species. White-crowned Manakins are small passerines in the family Pipridae. They are sexually dimorphic; adult males are black with white crowns and napes, and females are olive-green with blue-grey heads (del Hoyo et al. 2004). Juvenile males fledge the nest with plumage coloration similar to females, and they usually show some signs of definite male plumage (i.e., white feathers in crown and black feathers in body) after their first year (i.e., end of first breeding season). Males acquire full adult plumage late in their second-year (Ryder & Durães 2005). White-crowned Manakins display on exploded leks, in which males are in auditory but not visual contact (Castro-Astor et al. 2007, Tori 2008).

White-crowned Manakins inhabit the understory. They are mainly frugivorous (Worthington 1982, Tori 2008), but they also consume some insects (Fair et al. 2013, WPT pers. observ.). They eat a wide diversity of soft fleshy fruits and arillate seeds; consuming the pulp or aril and discarding the seed via regurgitation or passage through the gut. Loiselle et al. (2007b), in a short-term study conducted at our study site, reported that White-crowned Manakins consumed 44 different fruit species. Fruits from the families Melastomataceae, Rubiaceae, and Araceae make up a large proportion of Manakin diets (Krijger et al. 1997, Loiselle and Blake 1990).

Home range and spatial movement estimates. We set up mist nets to capture White-crowned Manakin individuals around fruiting trees in previously known manakin capture locations within the Harpia plot during June–July 2009 and 2014, and June 2011 (non-breeding season: when males are not fully active at leks; breeding season: November–April, Durães 2009). Green individuals with unknown sex were molecularly sexed (Griffiths et al. 1998). All individuals were tagged with a radio transmitter that weighted less than 5% of their body mass (models BD-2N/0.51 g and BD-2N/0.39 g, Hollohil Systems Ltd). Radio transmitters were attached using Rappole harnesses (Rappole & Tipton 1991). We employed triangulation telemetry and recorded simultaneously the direction (i.e., bearings) of the bird with respect to three observers in known locations (mean ± SE time interval between recordings 14.99 ± 0.354 minutes) for 5 to 9 days (until all areas known to be used

by the bird were well sampled). In one case (adult male 2) the battery of the transmitter died after 3 days and we were able to collect only two full days of telemetry data. In order to avoid triangulation errors due to the movement of the bird, the three observers took highly synchronized measurements (Schmutz & White 1990) using two-way radios. We ensured that all birds had telemetry recordings across the day from dawn to dusk. We entered our data (observer locations and bearings) into the program LOAS™ 4.0.3.8 (Ecological Software solutions LLC) and used the maximum likelihood estimator (accuracy 0.000001, 60 iterations) to calculate bird locations (x, y coordinates) for each telemetry recording. We discarded all measurement sets that did not form triangles or had an error ellipse area greater than 5000 m² (for details see LOAS™ 4.0.3.8, Ecological Software solutions LLC). We then used R (version 2.12), Geospatial Model Environment (GME) and ArcGIS (version 10.1, minimum bounding geometry - convex hull) to estimate the HR of all individuals. We calculated HRs using two methods (1) 100% Minimum Convex Polygon (MCP), a widely used method that draws a boundary polygon around all the known bird locations (provides information about extent of an individual's HR and allows comparisons across studies); and (2) Kernel-density Estimators (50% and 90%), which provide a HR estimate (probability density function) based on a probabilistic measure of animal space use (provides information about utilization of space within the HR). For the Kernel-density Estimator we used the least-squares cross-validation smoothing parameters (LSCV, Worton 1995). To examine if we had appropriate sampling effort to estimate accurate HRs using MCP, we created HR area accumulation curves for each radio-tracked individual. To do this, we randomly drew 5 locations at the time (until all locations were included) and built accumulation curves using HR area as the predictor variable. We fitted a polynomial (second order) equation and assumed appropriate sampling if the curve reached a stable asymptote.

To compare HR overlap (100% MCP) between individuals we used ArcGIS (version 10.1). We created raster layers for individual HRs (cell size 1 m²), and reclassified each layer giving a value of 1 to any cell within the HR and a value of 0 to cells outside the HR. Next we added each pair of layers using raster calculator and calculated the HR area overlap by adding the total area of cells with a value of two.

To get a better sense of the mobility of this species and their potential for seed dispersal within their HR, we calculated the straight-line Euclidean distance each individual traveled in 30-minute intervals. Time intervals were selected to mimic the maximum gut-transit time found for 14 species of labeled fruit (families: Araceae, Malpighiaceae, Cyclanthaceae, Dilleniaceae, Annonaceae, Salicaceae, and Rubiaceae) in two closely related species (Red-capped Manakin *Ceratopipra mentalis*, Golden-collared Manakin *Manacus vitellinus*; for details see Worthington 1989).

Using these data, we ran a One-way ANOVA comparing the average movement among individuals, and we conducted Tukey HSD post hoc comparisons. Data were transformed to fulfill parametric assumptions. Statistical analyses were conducted in SPSS (version 23).

RESULTS

We estimated the HR of seven individuals: two males in adult definitive plumage (A males), one second-year male (SY male), one hatch-year male (HY male), and three females. The number of telemetry locations used to calculate HR estimates ranged from 73 to 205 with a mean of 121.42 (± 18.81 SE). For all individuals we used larger samples sizes than the minimum number of locations recommended by some authors in the literature (> 30 locations; Seaman et al. 1999). Moreover, our HR area accumulation curves suggest that our MCPs are good representations of the HR during the non-breeding season, since all individuals reached a relatively stable asymptote with the sample sizes used (Figure 1, Table 1).

The mean (± SE) 100% MCP HR size was largest for females (4.27 ± 0.77 ha), followed by juvenile males (2.25 ± 0.62 ha) and adult males (1.20 ± 0.01 ha). The second-year male showed a larger MCP HR (2.87 ha) than the hatch-year male (1.64 ha). An equivalent pattern but with smaller HR areas were found using 50% and 90% Kernel-density Estimators (Table 1, Figure 2 A-G). In all cases, individuals' use of space was very heterogeneous, spending 50% of their time in an area as small as 9–26% of their HR.

MCP HRs of White-crowned Manakins of all ages and sexes largely overlap with each other (Table 2, Figure 2H). Female HRs overlap with male HRs even outside the breeding season. Male HRs overlap more with other individuals. Female HRs were not found to overlap with each other, however we believe this lack of overlap is influenced by chance due to small sample sizes (population was not comprehensively sampled).

The straight-line Euclidean distance traveled by individuals during 30 minutes ranged from 3.53 to 178.34 m for females (n = 104), from 2.02 to 242.36 m (n = 75) for juvenile males, and from 4.44 to 79.23 m (n = 52) for adult males. We found a significant difference in the distance traveled in 30 minutes among individuals of different sexes and ages ($F_{6, 224} = 7.86$, $P < 0.001$, Figure 3). Females and the second-year male tended to travel longer distances than adult and hatch-year males. Statistical results for pairwise post hoc comparisons are shown in Figure 3. Similar result were found for 15- and 45-minute intervals (data not shown).

DISCUSSION

Our results only partially support our predictions about HR size among sex and age groups in White-
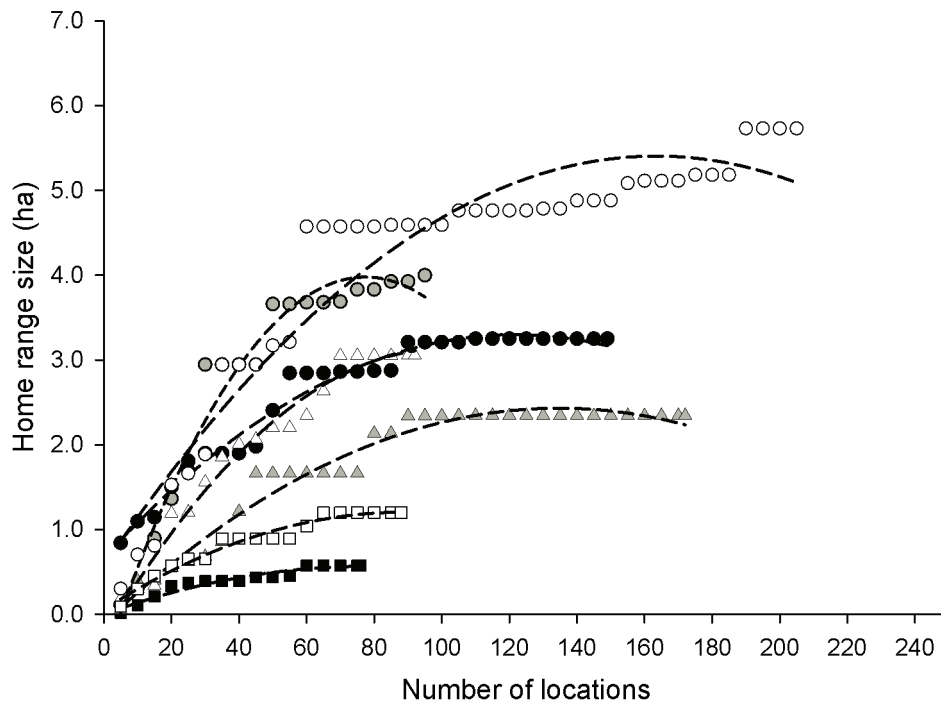
Figure 1. Home range area accumulation curves (using 100% Minimum Convex Polygons) and polynomial second order functions for three White-crowned Manakin (*Dixiphia pipra*) females (grey, black and white circles respectively), two adult males (white and black squares) and 2 juvenile males (hatch-year male: grey triangles and second-year male: white triangles) at Tiputini Biodiversity Station, eastern Ecuador.

crowned Manakins. We found that female HRs are about 3.5 times larger than those of adult males, but juvenile males have intermediate HR sizes (1.9 times smaller than females). In lek-mating systems, males are expected to have high territory attendance to maximize reproductive success (e.g., Fiske et al. 1998, Karubian et al. 2012). We found that males are more sedentary maintaining a close watch of their territories even outside the breeding season. Females are usually solitary (WPT pers. observ.) and their movements are not constrained by territorial defense, so they are able to move more freely among resources (e.g., food, bathing sites, mates, etc.) and have larger HRs. Second-year males were found to have larger HRs and longer trip distances than hatch-year males. As a consequence females and second-year males move more widely and are expected to perform more long distance seed dispersal events. Our results suggests that differences in age and sex have a strong effect on individual movement patterns that can be translated into important consequences in seed-dispersal patterns.

Home ranges and space use. We found that White-crowned Manakins have a relatively small HR (1.19–5.73 ha) compared with many other tropical understory frugivores such as Ochre-bellied Flycatcher (Tyrannidae: *Mionectes oleaginous*, 28.4 ± 3.7 ha; Wescott & Graham 2000), Swallow-tailed Manakin (Pipridae: *Chiroxiphia caudata*, 1.6–15.6 ha; Hansbauer et al. 2008), Golden-headed Manakin

(Pipridae: *Ceratopipra erythrocephala*, 3.0–22.7 ha), White-fronted Manakin (Pipridae: *Lepidothrix serena*, 2.8–24.1 ha), White-bearded Manakin (Pipridae: *Manacus manacus*, 2.1–20.3 ha), White-throated Manakin (Pipridae: *Corapipo gutturalis*, 2.0–10.0 ha), and Brown-winged Schiffornis (Tityridae: *Schiffornis turdina*, 14.3–20.1 ha) (Théry 1992, but see Durães et al. 2007). Our HR estimates are relatively consistent with the only other study that estimated HRs in White-crowned Manakins in French Guiana (Théry 1992, see Table 1). However, Théry found that immature males had the largest HRs (Table 1), and the HR estimates (100% MCP) resulting from his study were substantially larger than ours, exceeding our mean HR estimates for all sexes and ages by more than 45% (female: 4.27 vs. 9.0 ha, male: 1.20 vs. 2.2 ha, and second-year male: 2.25 vs. 19.8 ha). These differences could be the result of many reasons. First, both studies used telemetry methods that could have resulted in different levels of accuracy when estimating bird locations. In Théry's study, bird locations (i.e., fixes) were recorded by a single observer from stations placed every 20 m in the field. This methodology does not account for triangulation errors due to fast movements by the radio-tracked bird (see Schmutz & White 1990). In our study, we recorded bird locations by three observers simultaneously. Durães et al. (2007), using a similar synchronized telemetry technique in a closely related manakin species (Blue-crowned Manakin, *Lepidothrix coronata*), found similar female HR areas than ours (100% MCP:

Table 1. Number of days followed, number of locations used for home range (HR) calculations, polynomial model information, and HR sizes in hectares (100% Minimum Convex Polygon and Kernel-density-Estimators) of seven White-crowned Manakin (*Dixiphia pipra*) individuals monitored during the non-breeding season at Tiputini Biodiversity Station, Ecuador. Females showed larger HRs than males. Young males (HY = hatch-year, SY = second-year) showed larger HRs than adult males (A = adult). For the sake of comparison, we list previously published HR sizes for White-crowned Manakins measured during the breeding (BS) and non-breeding seasons (NBS, Théry 1992). [*] Telemetry was conducted only for 2 full days because of transmitter battery failure.

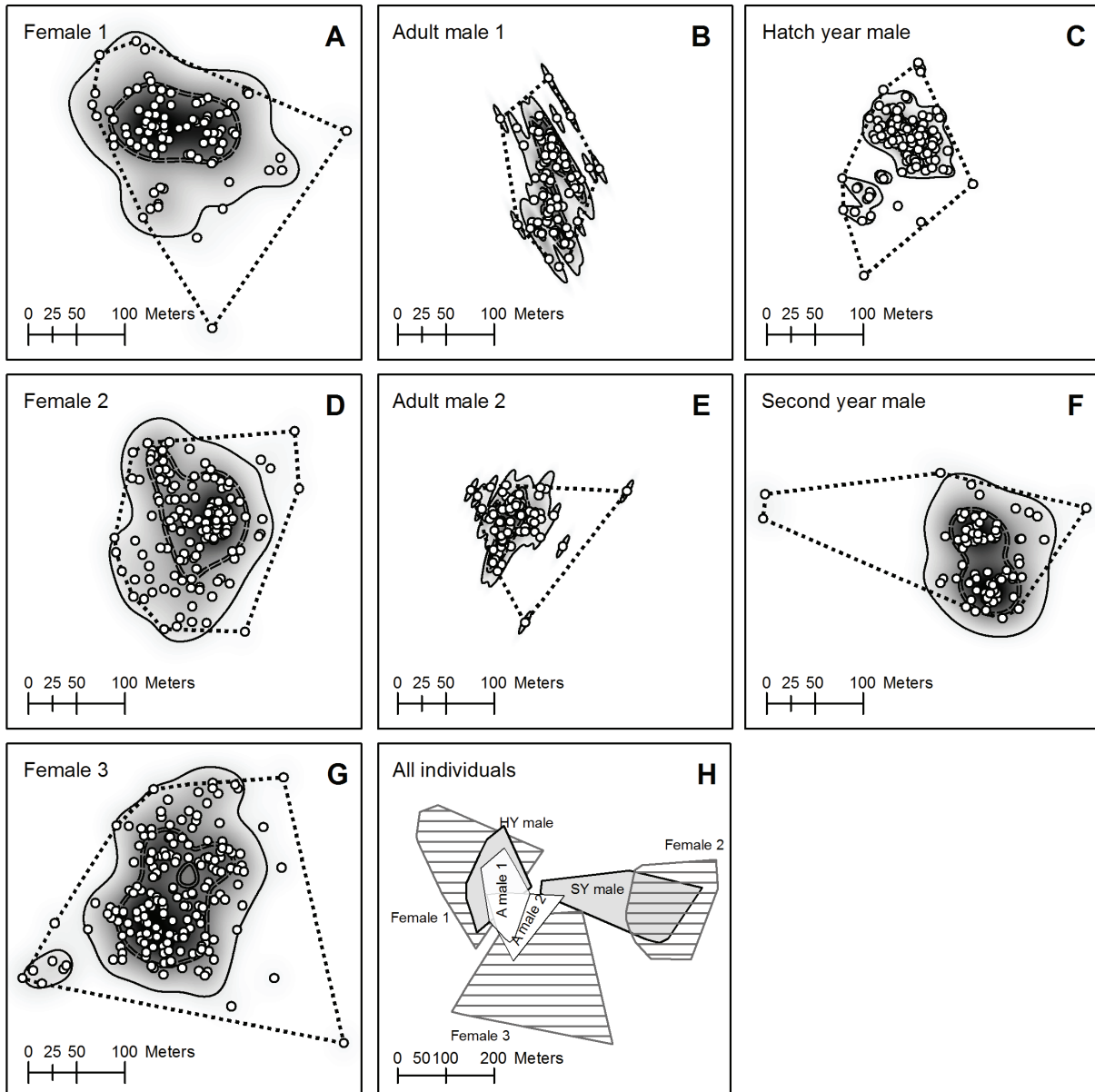| Sex/age	# of days followed	# locations	Polynomial model					MCP (ha)	Kernel (ha)		HR sizes (ha) reported by Théry 1992
			Equation	R^2	F	df	P		50%	90%	
Female 1	8	93	$y = -5478.89 + 1170.04x - 7.56 x^2$	0.97	228.40	2,16	<0.001	4.00	0.82	3.08	
Female 2	7	141	$y = -6676.54 + 432.57x - 1.78x^2$	0.97	505.14	2,27	<0.001	3.09	0.81	2.70	8.8, 9.2 (BS)
Female 3	9	205	$y = 5682.176 + 592.14x - 1.81x^2$	0.91	453.49	2,38	<0.001	5.73	1.01	3.20	
A male 1	5	87	$y = 547.48 + 258.05x - 1.45x^2$	0.96	202.78	2,15	<0.001	1.20	0.26	0.92	
A male 2 [*]	3	73	$y = 8.54 + 145.04x - 0.93x^2$	093	91.96	2,13	<0.001	1.19	0.17	0.63	2.1, 2.3 (BS), 30 (NBS)
HY male	9	165	$y = -1073.83 + 377.35x - 1.40x^2$	0.97	491.23	2,32	<0.001	1.64	0.16	0.75	Na
SY male	5	86	$y = -2537 + 670.870x - 3.32x^2$	0.98	311.98	2,16	<0.001	2.87	0.52	1.8	18.7, 20.9 (BS)

Figure 2. White-crowned Manakin (*Dixiphia pipra*) home ranges (HRs) during the non-breeding season at Tiputini Biodiversity Station, eastern Ecuador. Panels A-G show individual HRs using a 100% Minimum Convex Polygons (dotted line) and Kernel-density Estimators (50%: double hatched line; and 90%: solid line). White circles depict bird locations. Panels are drawn to the same scale for comparisons. Panel H shows HR overlaps for 100% Minimum Convex Polygons for females (female 1–3), adult (A male 1–2), hatch-year (HY male) and second-year (SY male) males. Note the change in scale for panel H.

4 ha, 95% confidence intervals 2–6 ha). Second, HR estimates can be influenced by small sample sizes and the statistical properties of the HR estimator used. Minimum Convex Polygon estimates have the limitation that the size of the HR tends to increase as sample size increases (Boulanger & White 1990). This is an unlikely explanation for the differences found, since our cumulative HR area results suggest that our HR estimates reached a relatively stable asymptote and therefore should be good estimates of HR sizes. Third, the HR estimations reported by Théry were done mostly during the breeding season, while our estimates were done in the non-breeding season. It is likely that bird movements significantly change across seasons, because individuals need to fulfil different life-history needs throughout the year. For example, female 3 HR did not overlap with any lek (WPT pers. observ.), thus she will need to extend her HR during the breeding season to get access to mates, and could also potentially alter her movement patterns due to parental activities (e.g., feeding chicks, traveling with fledglings). In this sense, our female HR estimates are probably conservative, since females might travel large distances outside their normal ranges to fulfill reproductive needs. Lastly, the differences found between studies might be explained by differences in bird movements due to variations in habitat characteristics or bird behaviors

Table 2. Pair-wise comparison matrix of the percent of area of overlap between 100% Minimum Convex Polygon home ranges (HRs) of White-crowned Manakin (*Dixiphia pipra*) females , adult (A), hatch-year (HY) and second-year (SY) males in eastern Ecuador. Cells below the diagonal report the presence or absence of HR overlaps between pairs of individuals. Cells above the diagonal report the percent HR overlap (% area of the HR) of individuals in the row, followed by the percent of HR overlap of the individuals in the column.

Sex/age	Female 1	Female 2	Female 3	A male 1	A male 2	HY male	SY male
Female 1	-	0	0	0	0	0	47.8,51.3
Female 2	No	-	0	18.8, 62.6	4.1, 13.8	37.9, 92.8	0
Female 3	No	No	-	1.8, 8.8	8.1, 39.0	0	0
A male 1	No	Overlap	Overlap	-	46.8, 47.2	68.1, 50.0	0
A male 2	No	Overlap	Overlap	Overlap	-	16.6, 12.1	49.7, 20.6
HY male	No	Overlap	Overlap	Overlap	Overlap	-	0
SY male	Overlap	No	No	Overlap	Overlap	No	-

between study sites. Regardless of these differences, both studies are consistent with the hypothesis that adult males are more stationary than females because they need to defend territories and display for females in order to have access to reproduction (territoriality appears to be a pre-requisite for reproduction in this species, Tori 2008). Interestingly, our results differ significantly from Théry's HR sizes for males during the non-breeding season. Théry argued that male HRs during the non-breeding season are unstable, and can cover up to 30 ha in 5 days. To the contrary, our results suggest that male White-crowned Manakins stay close to their established territories year round, probably defending their display sites from potential contesters even outside the breeding season.

Our HR results also show that males visit other neighboring territories within their lek, but they do not perform long-distance flights to visit other leks during the non-breeding season. We also found that female, male, and juvenile HRs overlap in space. Although our data provides no information on the social interactions between individuals, it demonstrates space-use sharing among individuals of different ages and sexes. This information is consistent with previous reports that suggest that manakins can feed at fruiting trees (Leck 1969, Lill 1976) and interact at bathing sites (Théry 1992) with little to no aggression among conspecifics. Tolerance of other individuals across the HR is not expected to be the same for individuals of all sexes. Adult males for instance have antagonistic interactions with other adult males within their territories (about 4.7% of their HR area) at leks during the breeding season (Tori 2008), and they have been found to respond to playback and bird dummies within their territories during the non-breeding season (WPT pers. observ.). As far as we know, there is no evidence that females or hatch-year males would engage in antagonistic interactions with conspecifics within their HRs.

Seed dispersal potential. Manakins have been reported as important seed dispersers for some prevalent plant families in the Neotropics (e.g., Wheelwright et al. 1984, Loiselle & Blake 1999, Loiselle & Blake 2002). As lek breeding birds, White-crowned Manakins of different sexes (Karubian et al. 2012) and ages are expected to have different reproductive strategies that can lead to different effectiveness as seed dispersers (Cestari & Pizo 2013). Males have been suggested to be more constrained than females and juveniles in the potential for seed movement (long-distance dispersal) because they are required to spend considerable time at aggregated display sites to get access to reproduction (Loiselle et al. 2007b). Our findings are consistent with these arguments. We found that females and second-year males had larger HRs, performed more long-distance flights outside their core HR, and traveled farther distances during 30-minute intervals (representative gut-passage time). The mean seed dispersal distance for females (55.47 ± 7.10 m) and the second-year male (57.40 m) in 30 minutes is about 1.8 times larger than the one found for resident males (29.77 ± 2.55 m). Our study suggests that the majority of seeds ingested by males are deposited in the lek neighborhood (HR core area). Surprisingly, the only hatch-year male we followed showed similar seed-dispersal potential as adult males (31.74 m). Females and second-year males generate a more extensive and even distribution of seeds, and are more likely to be responsible for long distance dispersal events. Adult and hatch-year males appear to provide complementary dispersal services, dispersing seed at smaller distances and in a more clumped distribution. Radio-tracking revealed that adult males spent large amounts of their time in very small core areas around leks. It is possible that leks could act as ecological seed traps, where clumped seeds within territories (e.g., area under favorite display perches) might have lower survival probabilities due to crowding (Cestari & Pizo 2013). However, Ryder et al. (2006) reported a higher incidence of fruiting trees and fruit biomass within White-crowned Manakin leks at TBS. Other authors have also reported higher density of seeds with no apparent effect on seedling survival in leks of
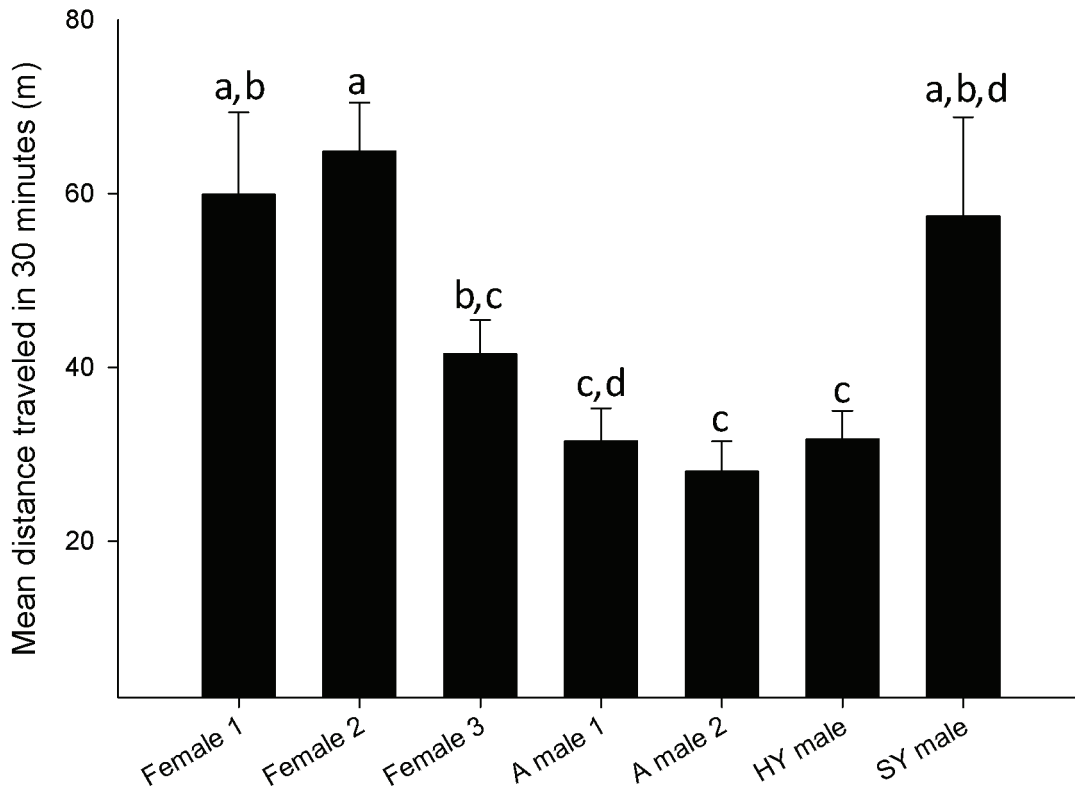
Figure 3. Mean distance traveled (± SE) by White-crowned Manakin (*Dixiphia pipra*) individuals during 30-minute intervals. Bars with similar letters are not significantly different from each other (Tukey's HSD, $P > 0.05$). Females and second-year males (SY male) tended to travel farther distances than males. Surprisingly the hatch-year male (HY male) moved similar distances as the adult males (A male).

the Long-wattled Umbrellabird (*Cephalopterus penduliger*) in Ecuador (Karubian et al. 2012). This suggests that even sedentary displaying males could play an important role in seed dispersal, and have a large influence in the structure and composition of plant communities.

To the best of our knowledge, this is the first study that provides significant insight into how differences in life history strategies of White-crowned Manakins can drive important consequences for seed dispersal even outside the breeding season. Our results suggest that individuals of different sexes and ages are not equivalent in their ecological role as seed dispersers. Females and second-year males make longer movements, thus distributing relatively few seeds at lek sites. In contrast, hatch-year and adult males act mainly as short-distance seed dispersers within their HR core area. We argue that these contributions are complementary and that White-crowned Manakins are key dispersal agents for many understory plants in the Amazon rainforest. We acknowledge that our small sample sizes limit the level of our inference, and we understand that this study is not capturing all the variability in space use for different sexes and ages. Further studies are required to provide insight on individual movement patterns during the breeding season, as well as to examine whether individuals of different ages and sexes bring seeds to sites with different environmental characteristics that affect the probability of plant recruitment.

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