# Display behaviour, social organization and vocal repertoire of Blue-backed Manakin *Chiroxiphia pareola napensis* in northwest Amazonia

GHISLAINE CÁRDENAS-POSADA,[1]* 🅳 CARLOS DANIEL CADENA,[1] JOHN G. BLAKE[2] & BETTE A. LOISELLE[2,3]

[1]*Departamento de Ciencias Biológicas, Laboratorio de Biología Evolutiva de Vertebrados, Universidad de los Andes, Apartado 4976, Bogotá, Colombia*

[2]*Department of Wildlife Ecology and Conservation, University of Florida, Gainesville, FL 32611, USA*

[3]*Center for Latin American Studies, University of Florida, Gainesville, FL 32611, USA*

Members of the avian family Pipridae (manakins) have served as a model system for studies aimed at understanding cooperation among individuals, traits involved in sexual selection and the evolution of female preferences. These studies rely on a detailed natural history baseline, yet multiple manakin taxa remain unstudied, precluding comparative analyses and assessment of geographical variation. The Blue-backed Manakin *Chiroxiphia pareola* is a widely distributed species with four recognized subspecies; however, most published information on display behaviour, social organization and vocalizations are derived from an island population of one subspecies, *Chiroxiphia pareola atlantica*. To describe the social organization and patterns of activity of the subspecies *C. p. napensis*, we studied a population in eastern Ecuador and collected data from seven display areas or leks within the Tiputini Biodiversity Station. We used focal observations, camera traps and automatic song recorders to collect information for the field seasons from January to March 2013 and video cameras from February to March 2014. Males were active most of the day with a peak in activity at noon. Display areas were occupied by one to five males, ranging from > 2 to > 18 years old. The vocal repertoire included duet song displays and a variety of calls. We provide sonograms for all six observed vocalizations, including two previously unrecorded vocalizations for the species, and comment on the possible behavioural context of each vocalization. We describe five distinct display elements and the dance display behaviour, and highlight differences relative to other species of the genus. The first part of the dance display involved cooperative dancing, whereas the second part was a solo display, usually performed by alpha males. Our work reveals some differences between *C. p. napensis* and *C. p. atlantica*, such as a possible aggressive interaction between males of different ages and hierarchical status that has not been reported before and the apparent absence of mechanical wing sounds in *C. p. napensis*. The data reported here help advance our knowledge of the evolution of display behaviour among manakins.

**Keywords:** camera traps, Ecuador, manakin, natural history, sexual selection, sonograms.

The display behaviours of birds have long been of interest to many naturalists and researchers because of the existence of often elaborate elements, the physical and physiological challenges inherent in displaying, and the implications for

sexual selection, especially in non-resource-based mating systems (Darwin 1871, Fiske *et al.* 1998). Displays produced by manakins (Pipridae) have been the subject of many studies over the past 50 years. Most manakins have marked sexual dimorphism in which males aggregate in display areas or leks and produce elaborate courtship displays to attract and mate with females (Emlen &

*Corresponding author.
Email: xicaykero@gmail.com

Oring 1977, Foster 1977, 1981, 1987, Davis 1982, Prum 1990, DuVal 2007, Durães *et al.* 2009, McDonald 2010). Females visit male leks only to copulate, and then build nests and rear offspring without any assistance from males (Emlen & Oring 1977, Hidalgo *et al.* 2008). Because males provide no direct benefits to females, male traits and courtship behaviour are probably the only cues females may use to assess male quality prior to mating. All these characteristics provide ample opportunities for intense sexual selection (Skutch 1949, Foster 1976, 1983, Emlen & Oring 1977, Snow 2004).

Manakins in the genus *Chiroxiphia* exhibit some of the most impressive courtship displays of any of the Pipridae because of their elaborate cooperative behaviours, where pairs or groups of males dance and sing in coordinated fashion at display perches (Snow 1956, 1963, 1971, Gilliard 1959, Foster 1977, 1981). In most *Chiroxiphia* species, male hierarchies exist within leks, with alpha males at the top of the hierarchy, followed by beta males as the main cooperative partners, and gamma or floating males at the bottom of the hierarchy (Snow 1963, Foster 1977, 1981). Reproductive success of alpha males depends on cooperation with beta males (McDonald 1989a,b, Trainer & McDonald 1995, DuVal & Kempenaers 2008, DuVal 2012); this cooperative behaviour seems paradoxical given the intense sexual selection reported for the genus and the lack of relatedness between the males that compose the leks (Reynolds & Gross 1990, Kirkpatrick & Ryan 1991, Loiselle *et al.* 2006).

Male Blue-backed Manakins *Chiroxiphia pareola*, as in other species in the genus, perform cooperative dancing and singing displays. The species comprises four subspecies that inhabit wet lowland forests (500–1700 m elevation) of Trinidad and Tobago (*Chiroxiphia pareola atlantica*); the Guyanas, Venezuela and parts of Amazonian Brazil (*Chiroxiphia pareola pareola*); eastern Venezuela, Ecuador, Colombia and Perú (*Chiroxiphia pareola napensis*); and Perú and Amazonian Brazil (*Chiroxiphia pareola regina*; Ridgely & Tudor 1994, Clements *et al.* 2013). However, all the information on display behaviour available for *C. pareola* is derived from two populations of the subspecies *C. p. atlantica* studied in Trinidad and Tobago (Snow 1956, 1963, Gilliard 1959); little is known about the displays of the other subspecies. Using information gathered with novel automated sampling equipment, we describe the display areas,

seasonal and daily patterns of activity at display areas, social organization, vocalization repertoire and display behaviour of a colour-ringed population of the previously unstudied subspecies *C. p. napensis* in the Ecuadorian Amazon. The information presented here provides a baseline for subsequent phylogenetic, ecological and behavioural studies and helps advance knowledge of the evolution of display behaviour in manakins.
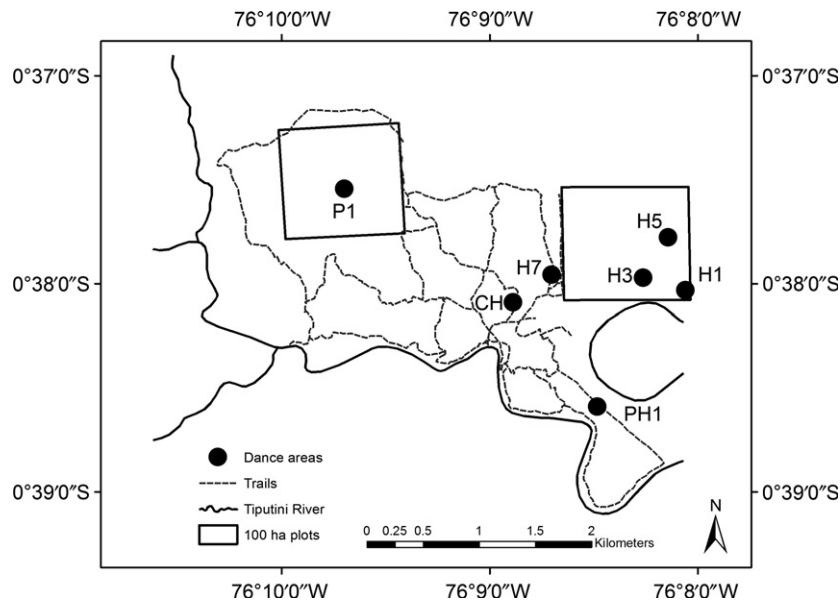
## METHODS

### Study site

We studied Blue-backed Manakins at Tiputini Biodiversity Station (TBS), a 650-ha area of lowland wet forest located in Orellana Province, Amazonian Ecuador (~0°38′S, 76°08′W). TBS is embedded within the Yasuní Biosphere Reserve, which encompasses ~1.7 million ha of lowland wet forest, including a national park and two indigenous reserves. TBS has approximately 30 km of trails and two 100-ha plots (named Harpia and Puma), where studies on the ecology and behaviour of manakins have been conducted since 2001 (Loiselle *et al.* 2006, 2007, Blake & Loiselle 2008, Hidalgo *et al.* 2008, Durães *et al.* 2009, 2011, Ryder *et al.* 2009a,b). Fieldwork for this study was conducted from January to March 2013, when most of the data were collected. Another field season was conducted from February to March 2014, to record videos and to obtain additional data for the description of the dance displays. There were no major differences in the composition of male hierarchies between the 2 years of data collection with the alpha males remaining the same, as did display activity. Both field seasons were within the timeframe of the peak of the breeding season reported previously for TBS (Durães *et al.* 2011).

### General field methods

We focused sampling efforts on seven display areas or leks; four were located in or immediately adjacent to the Harpia plot, one in the Puma plot, one near the Chorongo trail and one adjacent to the Parahuaco trail (Fig. 1). Display areas or leks are defined as the area where alpha males spend most of the daytime to vocalize, display and interact with other males and to attract, display and copulate with females. Each display area usually included one to several dance perches, defined as

**Figure 1.** Map of Tiputini Biodiversity Station in eastern Ecuador, where field-work was conducted. Dots indicate the location of each of the seven display areas studied (see Table 1). Trails were mapped by Andrew Jarvis and Mark Mulligan; 100-ha plots were established and mapped by J. G. Blake and B. A. Loiselle.

the physical spot (i.e. tree branch, stick, liana, etc.) where males perform a dance display. Many of these display areas had previously been identified, mapped and characterized and most of the males had been ringed with a unique combination of colour rings and a numbered aluminium leg ring. Efforts to categorize the age and social status of each ringed male (alpha, beta, floater) at each display area have occurred annually since 2002 (Loiselle *et al.* 2006, 2007).

We visited each display area at least four times per week for 2-h periods of continuous monitoring between 06:30 and 18:00 h and made focal observations. Observers sat quietly 8–12 m from a focal display perch and recorded male ring colours, number and identity of males present at the display area, type of activity (singing, dancing), male–male interactions, female visits and any other behaviours. We calculated minimum age for ringed males from their capture histories (B.A. Loiselle & J.G. Blake unpubl. data). Blue-backed Manakins, like Lance-tailed Manakins *Chiroxiphia lanceolata* (DuVal 2005), experience a 4-year plumage maturation process; ages were calculated according to the plumage of the bird during the first year of capture. In their hatch-year, males are olive green, during the second year they grow a red cap and some black feathers appear on the

face, during the third year a blue patch on the back and some black feathers in the body appear, and in the fourth year they reach full adult plumage (DuVal 2005, B.A. Loiselle unpubl. data). Thus, if a bird was in adult plumage in the first year of capture, an age of 4+ years was assigned and minimum age in the observation year was estimated based on the date of first capture.

During the 2013 field season, unringed males were captured using mist-nets and ringed at the end of the field season. In an effort to record most of the displays and behaviours, we identified at least two primary dance perches for each year for each display area, and GPS points (Garmin, Oregon 450) were taken for every display area and every dance perch. Dance perches were located by following the vocalizations made by males during cooperative dance displays.

Every time a dance perch was identified, we marked a nearby shrub with flagging tape indicating the orientation, distance from the observer, height of the perch, ring colour combination (when possible), date and age class, and behaviour (e.g. singing or not) of the bird. For the 2013 field season, we placed camouflaged camera-traps (PC800 HyperFire Professional Semi-Covert IR; Reconyx, Inc., Holmen, WI, USA) 1–2 m from the dance perch at each display area to record

**Table 1.** Sampling effort with camera traps and acoustic monitors to characterize the activity of Blue-backed Manakins *Chiroxiphia pareola napensis* in 2013 at Tiputini Biodiversity Station.

| Display area | Sampling dates | Days sampled for vocal activity | Acoustic monitors, h analysed | Days sampled for perch activity | Days sampled with photos with records | Camera, h | Number of photos with records |
|---|---|---|---|---|---|---|---|
| Chorongo | 21 Jan–18 March | 9 | 90 | 55 | 30 | 820.8 | 2154 |
| Harpia 7 | 21 Jan–17 March | 12 | 91 | 53 | 23 | 738.0 | 615 |
| Harpia 3 | 21 Jan–18 March | 11 | 101 | 54 | 18 | 813.0 | 881 |
| Harpia 1 | 04 Feb–18 March | 11 | 120 | 38 | 20 | 488.0 | 2303 |
| Harpia 5 | 30 Jan–18 March | 10 | 99 | 46 | 26 | 1083.0 | 2947 |
| Parahuaco | 01 Feb–18 March | 10 | 93 | 46 | 34 | 968.5 | 1906 |
| Puma | 28 Jan–18 March | 12 | 120 | 39 | 20 | 418.5 | 1030 |

The number of days sampled for vocal and perch activity, the number hours of acoustic data analysed, the number of days sampled where birds were recorded on the dance perch and the total time cameras were deployed are provided. In addition, the total number of photos with records of manakins on the dance perch are provided for each display area.

continuously male visits, dance displays, and female visits and copulations. Cameras were set to take photos every 5 s from 06:30 to 16:30 h to sample the time manakins were potentially active on the dance perch. In total, we sampled for 5330 camera hours, obtaining a total of 11 836 photos of manakins (Table 1). Most photographs were monochromatic due to low light conditions.

To record vocal repertoire and characterize vocal activity at each display area, we sampled male Blue-backed Manakins at their display areas over 9–12 days during the 2013 field season (Table 1) using automatic acoustic recorders (Songmeter SM2+; Wildlife Acoustics, Inc., Maynard, MA, USA) with two omni-directional microphones (SMX-II Weatherproof Acoustic Microphone). Each microphone was attached to the recording box using a 10-m cable and was placed near one of the two primary dance perches. Acoustic recorders were programmed to record stereo at a sampling rate of 16 kHz in *.wav format. We programmed the recorder to operate during a time frame of 10 h/day, from 06:30 to 16:30 h, and to save data in separate files of 1 h of recording time. Recorders collected song data for periods of seven consecutive days, between the last week of January and the third week of February 2013, before the beginning of the rainy season. A total of 1865 h of audio recordings were obtained but only 714 h were analysed for this study, mainly because of audio quality (Table 1).

In both field seasons, display dances were also recorded using video cameras (Panasonic HX-WA2 HD Camcorder (Panasonic Corp., Secaucus, NJ, USA) and Canon Vixia HF G30 Full HD Camcorder (Cannon USA Inc., Melville, NY, USA)). Cameras were mounted on a stake/tripod within 2–4 m of the dance perch and programmed to record for periods of 1 or 3 h at a time depending on the camera used. In 2013, a total of 133 h were recorded, obtaining 36 min of male visits and displays in total. In 2014, a total of 43 h were video-recorded, obtaining 24 min of male visits and displays. The low duration of display activity captured on video reflects the relative rarity of these behaviours.

## Activity patterns at display areas

To describe daily activity on display areas, we set camera traps to record the date and time when photos were taken. To characterize attendance at display areas, we determined the total number and duration of male visits per day. We defined a male visit as an instance when an adult male (alpha or beta) was sitting on the dance perch, calling from the perch or cleaning it. The durations of visits and dance displays were calculated as the time elapsed between the first photo in which the bird appeared or a display behaviour was observed, until the time of the last photo in which the bird was on the perch or displaying. A visit was considered to have ended when males were absent from the dance perch for more than 60 s. We combined data from different dance perches within a display area for each date and all variables were standardized by the number of hours sampled per date for analyses. Information on sex, age and colour-ring combination of the individuals visiting the perches was collected from the photos when possible.

Because the forest canopy was dense and the cameras only took colour photos when enough sunlight hit them, information on the colour of rings or the plumage colour of birds on the photo could only be collected infrequently. Therefore, we used focal observations to confirm the identity and the attendance of the males present at each lek. We considered a male part of a lek when attendance at the lek was more than 80% of the sampling time.

To characterize the vocal activity of Blue-backed Manakins, we examined spectrograms of all the recording files obtained for all display areas to assess the recording quality and to filter out problematic files (e.g. those in which microphones did not function properly or where rain did not allow adequate recording). We then manually analysed the 714 h of good recordings using the software Adobe AUDITION 1.5 (Adobe Systems Incorporated, 2004, San Jose, CA, USA). Using the software SONGSCOPE version 4.0 (Wildlife Acoustics Inc., 2007–2011, Agranat 2009, Buxton and Jones 2012), we built an automatic song-recognition model (Recognizer) to search for and automatically identify the most common vocalization for the Blue-backed Manakin (a '*pchrrr*', see below) across all files for the 714 h. To build the automatic recognition model, we supplied the software with 10 good-quality reference '*pchrrr*' calls from each display area obtained at different hours and on different days as training data to capture the extent of the natural vocal variation. Following an initial model construction, we adjusted software parameters to achieve a balance between a high recognition rate (sensitivity) and a low false-positive rate (specificity; Table S1).

Using the recognition model, we calculated the number of vocalizations per hour for each display area and then averaged data for all display areas to describe the daily pattern of activity for the population. We also examined the seasonal pattern of activity per display area by averaging the number of vocalizations per day and then examined the population-level pattern by averaging data across display areas. Data were standardized by the number of hours sampled per day and per display area.

To describe the vocal repertoire of the Blue-backed Manakin, we first identified the calls or songs by listening to recordings and examining spectrograms in AUDITION 1.5 and then calculated the duration, frequency, rate and number of phrases per call. Spectrograms for graphic display were obtained using SYRINX 2.6 (Burt 2006). To understand and infer the context of usage of each vocalization type (e.g. beta male or female present), as well as to assign a new vocalization type to the subspecies, we only used audio data that were synchronized with focal observations, photos or videos.

Focal observations, sequences of photos and videos from both seasons were used to describe the elements of the dance display behaviour of Blue-backed Manakin. The elements of the dance display were described following the terminology of Snow (1963) to allow for comparisons with existing studies on congeneric species.

## RESULTS

### Display areas and social organization

Display areas consisted of one to five males consistently seen within a 100-m$^2$ area (Table 2). These areas included one alpha or dominant male, one beta or cooperative male and some gamma or floater males, which usually were younger males that move between display areas. In these areas, we found floater individuals in green and adult plumages of all ages and also males in adult plumages that were part of the lek, ranging in age from 4+ years to 18+ years (Table 2). Within each display area, male Blue-backed Manakins had four to six dance perches. Display perches were live horizontal branches, lianas or vines usually within 50 cm to 1 m off the ground. Very often, when alpha or beta males were sitting on the display perches to practise display manoeuvres, they pecked at the

**Table 2.** Characteristics of the number of dance perches and males found on the seven *C. p. napensis* display areas in 2013.

| Display area | No. of dance perches found | No. of males at the area | No. of alpha, beta and gamma males | Alpha male, min age (years) |
|---|---|---|---|---|
| Chorongo | 2 | 3 | 1,1,1 | 9+ |
| Harpia 1 | 2 | 2 | 1,1,0 | 5+ |
| Harpia 3 | 3 | 2 | 1,1,0 | 16+ |
| Harpia 5 | 6 | 5 | 1,1,3 | 13+ |
| Harpia 7 | 2 | 2 | 1,1,0 | 9+ |
| Parahuaco | 4 | 4 | 1,1,2 | 6+ |
| Puma | 2 | 1 | 1,0,0 | 18+ |

wood to remove leaves, twigs, seedlings or moss; this made the perch look whiter than other nearby vines or lianas and very clean, without bark or dirt. Males concentrated most activity on only a few of the four to six dance perches, with one perch serving as the main dance-display arena, which was used primarily by alpha males to practise dance-display manoeuvres with beta males and to display when females were present. We refer to practice displays as manoeuvres performed by males on a dance-display perch in the absence of a female. The secondary dance-display perch was usually the preferred dance-display perch of beta males and it was primarily used to practise elements of the dance display by solitary males or alpha or beta males in conjunction with subordinate males.

A total of 21 dance perches were found in 2013 (two to six per area; Table 2) and an additional four in 2014. In some areas (Harpia 3), dance perches were found early in the field season (in the first week), but in others (Harpia 7) the main dance perch was only found late in the season (in the seventh week), probably due to variation in activity levels among display areas. When females were visiting, males would move between the two most important dance perches. These movements were probably attempts to bring or attract the female to the main dance perch, as well as to position the female in relation to the perch, probably to give her better visibility. Dance perches for some display areas varied from one year to another (e.g. display area Chorongo moved about 150 m from 2013 to 2014), mainly because old dance perches were no longer available (lianas broke, habitat changed or was no longer suitable).

## Vocalizations

Male Blue-backed Manakins had a repertoire consisting of at least six distinct vocalizations. These included invitation calls uttered by solitary individuals (non-synchronized), duet vocalizations (only synchronized) and display vocalizations uttered by two or more males (synchronized and non-synchronized, Fig. 2). Examples of each vocalization have been uploaded onto Xenocanto (catalogue numbers: XC177783, XC177788, XC177790, XC177794, XC177795).
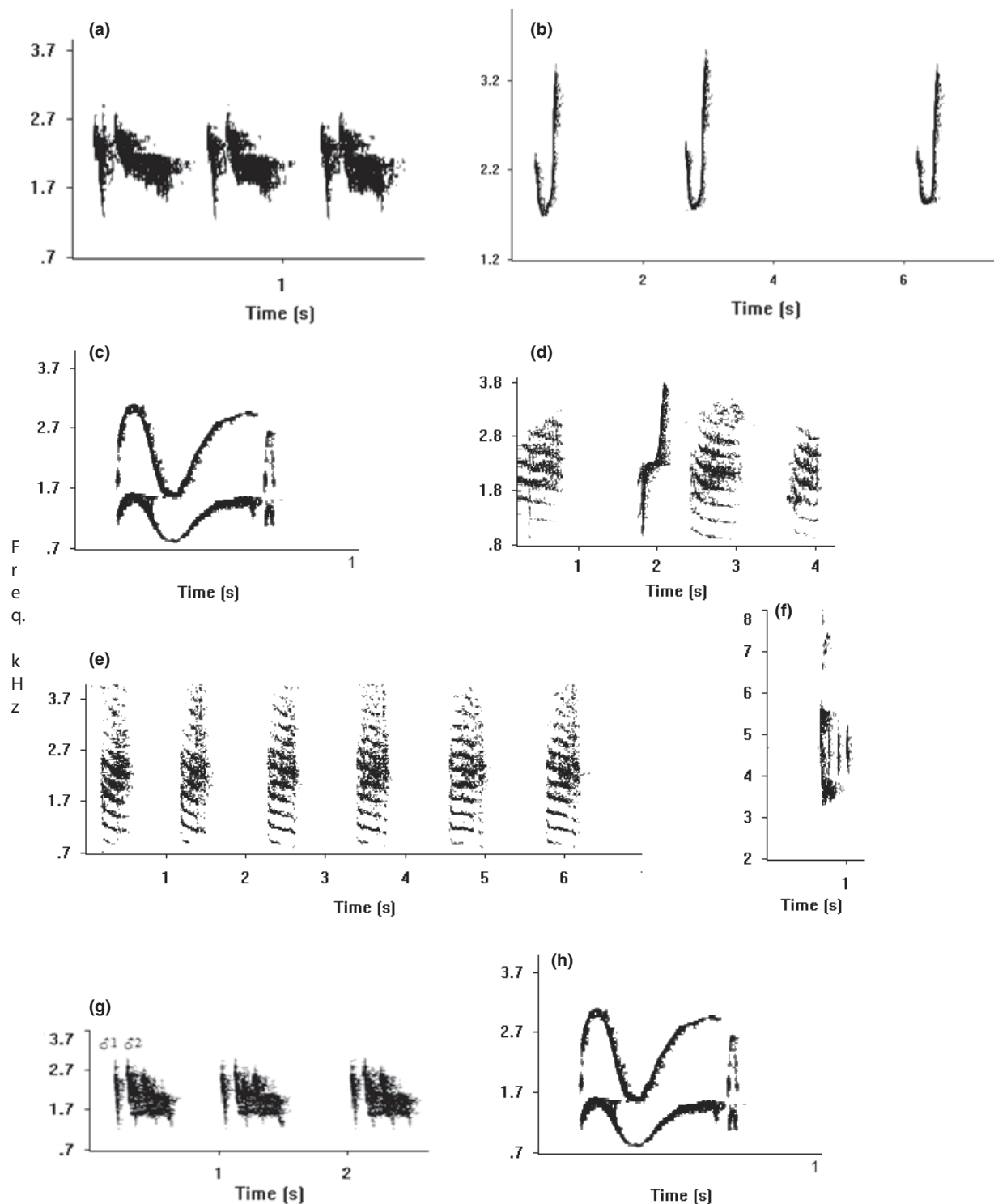
The most common vocalization was a 'pchrrr' call with duration of 0.32–0.43 s and a frequency range of 1.3–2.7 kHz (XC177795, Fig. 2a). This call was uttered by solitary males (primarily alpha males) perched anywhere from about 1.5 up to about 20 m high in their display area, in phrases of one to seven calls at a mean ± sd rate of 14.4 ± 6.9 calls/min. The 'pchrrr' vocalization was loud enough to be heard from c. 100 m and may function as a signal of attendance at the display area and to attract other males to sing along and, primarily, to attract females. Sometimes one or two males would later join in with 'pchrrr' songs. Once a duet-bout began, the 'pchrrr' calls of the multiple males start to match up, such that their vocalizations eventually are given almost simultaneously in a highly synchronized fashion.

A second invitation call, 'cheewee', was also given by males of all status. The 'cheewee' invitation call had a mean duration of 0.34 ± 0.4 s and a frequency range of 1.7–3.4 kHz (XC177783, Fig. 2b). This vocalization was typically given by males sitting on low perches, including the main dance perches, and multiple males may call back and forth. When more males joined the vocalization of the 'cheewee' call, they vocalized in a highly synchronized manner so that their calls sounded like only one male calling and practice dance-display manoeuvres were very likely to occur.

When a duet-singing cycle started, males often perched side by side on a perch high above the ground and sang synchronized 'pchrrr' (Fig. 2g) at a rate of 40–60 repeats/min. The duration of a 'pchrrr' synchronized duetting varied considerably; depending on the activity of the males involved, it could last for as short as 5 min or as long as over an hour. Once a duetting bout had been going on for several minutes, a less common 'wohoo' call may be uttered by either of the males. This call was commonly used when a female arrived and may serve as an invitation to move to the display perch because when one male called, the other approached and then they moved together to the perch. The 'wohoo' call had a mean duration of 0.44 ± 0.2 s with a frequency range of 0.8–1.6 kHz (XC177794, Fig. 2c and 2h).

After both males had come down to the dance perch, a 'whee-ee' was uttered; this usually, but not always, preceded the beginning of the cooperative dance display. The call had a mean duration of 0.40 ± 0.5 s with a frequency range between 0.8 and 3.8 kHz (Fig. 2d). During the cooperative dance display, a series of 'wrang' calls were uttered constantly by both males while performing coordinated hops or cartwheels. The call had a mean duration of 0.70 ± 0.10 s and the frequency range

**Figure 2.** Sonograms of the six vocalizations given by Blue-backed Manakin *Chiroxiphia pareola napensis*: (a) '*pchrr*' call given usually by the alpha male and uttered in the duet call bouts, (b) '*cheewee*' invitation call given to start a duet call bout, (c) '*wohoo*' invitation call given to move to a dance perch, (d) '*whee-ee*' call given at the beginning of a two-male dance bout, (e) '*wrang*' call given during the cartwheel element of the dance display, (f) '*eeek*' call uttered usually by the alpha male at the end of a two-male dance bout indicating to the beta male to leave. (g) Duet singing. (h) Calls that occasionally accompany the '*wohoo*' call.

was 0.7–3.7 kHz (XC177790, Fig. 2e). This call always accompanied the coordinated jumps and cartwheels even if there was no female present. Occasionally, a solitary 'wrang' call may be given by a male perched in the mid-storey away from the display branch. Just prior to initiating the *solo* display (see below), alpha males gave a high-pitched '*eeek*' call that signals the beta male to leave the main dance perch; the '*eeek*' call had a mean duration of $0.20 \pm 0.2$ s and frequency range of 3.1–8.0 kHz (XC177788, Fig. 2f).

We did not detect any mechanical sounds produced by the male's wing when visualizing the sonograms, listening to the song recordings or in any of the focal observations. In the 2014 season, we recorded a video of an apparently aggressive interaction between a first-year male being chased by an alpha male off one of the main dance perches (Video S1).

## Dance displays

Dance displays included single-male dances and two-male dance displays. In 2013, a total of 33 two-male dance displays and 123 single-male displays (of 5330 camera hours) were registered using camera traps; in 2014, four two-male dance displays were registered using video cameras and no single-male displays were recorded (of 43 camera hours). Additionally, from focal observations, we recorded seven two-male dance displays and three single-male dance displays. The duration of the observed two-male dance display bouts was 25–227 s when no females were present (mean: $118.6 \pm 94$ s) and 54–330 s when females were visiting (mean: 164 s $\pm$ 103 s). The *solo* dance displays for females (see below) lasted 31–134 s (mean: $70 \pm 36$ s). All mean values have an error range of $\pm 5$ s given the setting of the frequency interval between successive photos from the camera traps. On other occasions, males have been known to dance for females for up to 21 min, but these long-intensity dance bouts are probably quite rare (B. Loiselle and J. Blake unpubl. data). Males in definitive adult plumages (alpha and beta males) were the only ones involved in dance displays for females. Gamma males usually displayed on secondary dance perches when no females were present. We did not observe more than two males in a coordinated dance display, although the presence of up to four adult males on a main dance perch has been seen with arrival of females to the display area and very short bouts (few seconds) of more than two males displaying have been observed. Synchronized singing, however, did occur more regularly among more than two males, up to the number of adult males associated with the display area.

The dance display consisted mainly of six elements: up-down long jumps, up-down short hops, hovering flights, cartwheels or leapfrog dance, back-and-forth short hops and bouncing, as described previously by Snow (1963) and DuVal (2007; Table 3). In the first part of the two-male dance display, males performed a mix of alternating elements including up-down long jumps, up-down short hops and hovering flights. Males tended to keep to their side of the perch, but sometimes they exchanged sides flying over the male/female and facing him/her when they landed. When performing practice dance displays, males usually repeated and/or skipped some elements of the display. Males also sometimes flew to a higher perch to vocalize briefly and then returned quickly to the dance perch (Video S2).

The second part of the cooperative dance display involved a cartwheel element, in which males jumped one over another resembling the movement of a wheel, and with every repetition they crouched, lifting their tail and showing the blue-back patch and red head to the female, slid backwards and then leaped over the other male. During these cartwheels, the two males faced the female while performing the manoeuvre and as the dance display advanced, the cartwheels

**Table 3.** Elements and sequences of the two-male and solo-male (pre-copulatory) dance displays of *Chiroxiphia pareola napensis*.

| Display | Elements |
| --- | --- |
| Two-male dance display | Up-down long jumps |
| | Up-down short hops |
| | Hovering flights |
| | Flights to higher perches |
| | Cartwheels |
| | 'eek' call |
| Solo (pre-copulatory) dance display | Back-and-forth short hops |
| | Bouncing |
| | Hovering flights |
| | Copulation |

A complete courtship display is a combination of several elements and includes repetition of elements in a consistent way. When practising, males could skip or repeat some of the dance display elements.
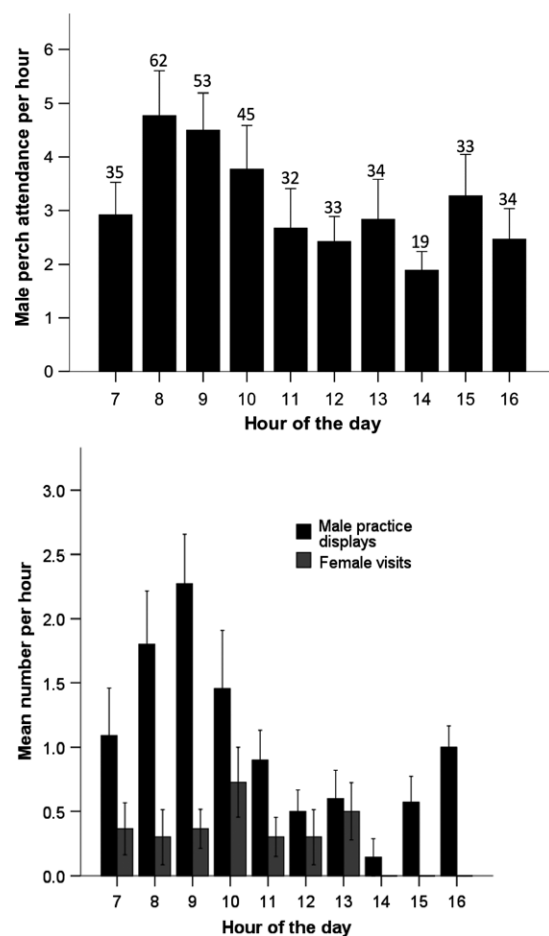
became faster and more synchronized. During the cartwheel display, males sang the '*wrang*' vocalization continuously; females might slide forward on the perch or retreat, but most of the time they remained relatively still (Video S3). When a female moved away from the dance perch, males usually followed and continued with the cartwheel dancing on any branch near the female, seemingly trying to invite her to come back to the dance perch. In the final jump of the cartwheel element, the alpha male uttered the '*eeek*' call; this call indicated to the beta male to depart from the dance perch and afterwards the alpha male continued dancing a *solo* display. On some occasions, after a short delay, the beta male might return and the two-male dance display would resume. This two-male back-and-forth dance display and *solo* display by the alpha may be repeated multiple times during one female visit.

During the *solo* dance display by the alpha male, beta males usually stayed near the dance perch and sometimes uttered '*cheewee*' or '*pchrrr*' calls. The *solo* dance display by the alpha male consisted of back-and-forth short hops and hovering flights followed by bouncing manoeuvres executed in the presence of the female; the alpha males did not vocalize during this *solo* dance (Video S4). Females may also hop and jump during the *solo* dance when receptive and, after that, copulation may or may not occur, with the male landing on top of the female (Video S5). In some cases when copulation did not occur during the *solo* dance display, the two-male dance display resumes and the *solo* dance display is repeated by the alpha for the same female. Following copulation, the males leave and the female may remain on the perch and preen prior to departing. Practice dance displays were also performed in the absence of females by pairs of males and by solitary males, including young males in pre-definitive plumage.
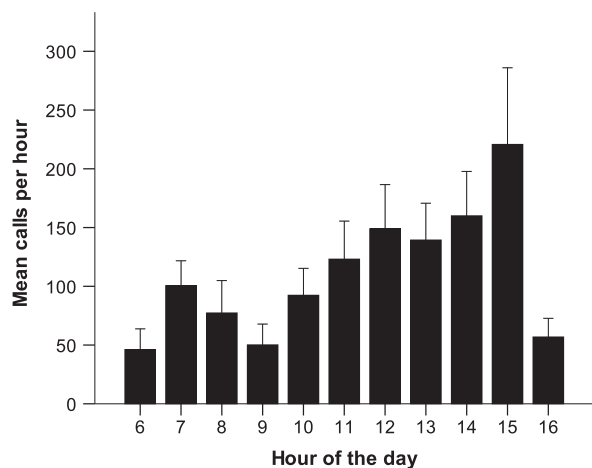
## Daily and seasonal activity

A total of 377 male visits in 2013 (0.073 mean visits/h sampled, sd = 0.031) and 16 male visits in 2014 (0.37 mean visits/h sampled) from 19 individuals across all display areas were recorded during part of the breeding seasons. Male Blue-backed Manakins were active at dance perches for most of the day; perch attendance and practice displays had a peak of activity between 08:00 and 11:00 h, followed by a slowdown at



**Figure 3.** Male and female Blue-backed Manakin daily activity from 07:00 to 16:00 h based on data from camera traps for the 2013 field season; note peaks in activity at mid-morning and at the end of the sampling period. (Upper panel) Mean numbers of male perch visits per hour; (lower panel) female visits and male practice displays summed across all days and then averaged across display areas. Bars represent one standard error, and sampling effort was 5330 camera-hours (~530 h per hour of the day). Data consist of 380 male perch visits, 32 female visits and 123 male practice displays. Numbers on top of the error bars in the upper panel represent the total number of visits registered per hour. Note that female visits occurred in a time frame between early in the morning until noon with higher number of visits between 10:00 and 13:00 h; surprisingly this pattern is more similar to the copulation data described by McDonald (2010) for Long-tailed Manakin than to the data on female visits found for the same species.
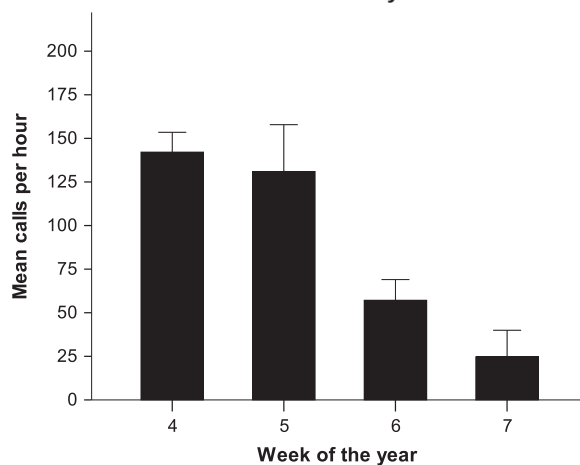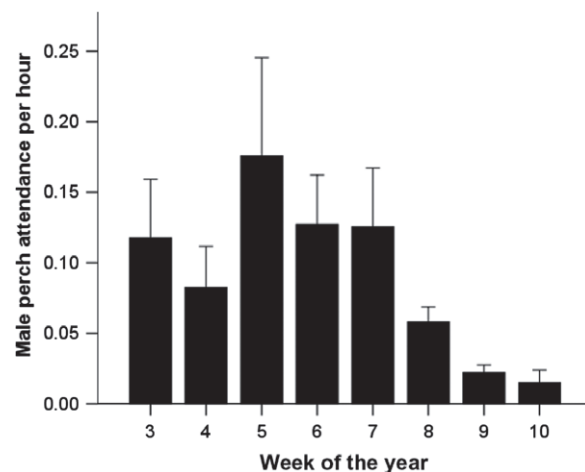
noon and a second increase in activity in the afternoon between 15:00 and 16:00 h (Fig. 3a and 3b). Female visits were only registered in the morning up to 13:00 h; no visits were recorded by camera traps in the afternoon (Fig. 3b). Males were seen taking baths in streams near their

**Figure 4.** Male Blue-backed Manakin daily vocal activity based on data from automatic audio recording devices for the 2013 field season (72 h were recorded per each time interval of the day). Data were averaged over all display areas and represent the mean number of *'pchrrr'* calls emitted per hour. Note the bimodal pattern of vocal activity, with a more pro-longed peak in the afternoon, a result very similar to what has been reported previously for Long-tailed Manakins (McDonald 2010). Bars represent one standard error.

display areas, usually at noon and at the end of the day when a slowdown in perch attendance activity occurred.

Males were vocally active throughout the day, but we noticed they usually remained silent when groups of parrots or monkeys were crossing their display areas. Males showed a small peak in vocal activity early in the morning, followed by a slow-down and then a steady increase in activity with a daily peak in mid-afternoon (Fig. 4). Patterns of daily vocal activity were opposite to those of male perch attendance, practice dance displays and female visits; for example, the peak for perch atten-dance was higher in the early morning, whereas the vocal activity peak was higher in the afternoon (Figs 3a and 4). In terms of the seasonal pattern of activity for the population, we found that for the 2013 field season, male activity at perches across display areas was higher between the third week of January and the third week of February (the first 5 weeks of monitoring) and dropped significantly thereafter (Fig. 5a). Similarly, male vocal activity was higher during the first 2 weeks of February and dropped significantly thereafter (Fig. 5b). The third week of February was very rainy in 2013, which may have caused the reproductive season to end early relative to past years when manakins have been studied at TBS.



**Figure 5.** (Upper panel) Temporal variation in male Blue-backed Manakin perch activity based on 380 male visits to perches over the 2013 field season, revealing higher perch activity between the third and seventh weeks of the year. (Lower panel) Temporal variation in male Blue-backed Mana-kin vocal activity for the 2013 field season based on 720 h sampled, showing higher vocal activity between the fourth and fifth weeks of the year. Week 3 is the last week of January and week 10 the third week of March. Data were averaged over all the display areas and represent mean values of the number of perch visits/hour recorded with camera traps (upper panel) and the number of calls per hour recorded with auto-matic audio recording devices (lower panel). Bars indicate one standard error. Only 4 weeks were sampled, given the avail-ability of the recording equipment.

## DISCUSSION

Using automated data-recording devices such as camera traps and acoustic recorders for a field study on avian behaviour has several advantages. First, one can complete an intense sampling effort in a relatively short period of time. Secondly, the use of this technology alleviates observer bias and

may cause less disturbance to the birds than direct observation. Thirdly, the data are captured in digital form, which allows one to re-examine behavioural data and confirm results, which could be more reliable than notes taken by an observer. Lastly, multiple locations can be sampled at the same time, reducing the potential impact of day to day variation in weather etc. These advantages allowed us to conduct a comprehensive characterization of the display behaviour, social organization and vocal repertoire of a heretofore unstudied population of the Blue-backed Manakin.

Display areas of the Blue-backed Manakin in Amazonian Ecuador can be defined as areas containing a group of dance perches dominated by an alpha male which are also often occupied by one beta male and several gamma males (see also Gilliard 1959, Snow 1971). At each display area, generally two males performed dance displays for females, but the *solo* dance display was performed only by the alpha male. At the Puma display area, only one male was observed displaying in both seasons and no beta male was identified, a result similar to that described by DuVal (2007) for *C. lanceolata*. Displaying alpha males at our sites were between 5+ and 18+ years of age. Our finding of a male being still reproductively active up to at least 18 years of age is remarkable and probably one of the oldest reported for the genus *Chiroxiphia*. The oldest males of Lance-tailed Manakin and Long-tailed Manakin *Chiroxiphia linearis* were 13 and 15 years old, respectively (McDonald 1993, DuVal 2012). The 18+ year-old alpha male was the same male at the Puma display area for which we could not find a beta partner, which may reflect a reduction in the connectivity of the social network as males senesce.

Male Blue-backed Manakins were active most of the day but had a bimodal pattern of perch and vocal activity, with peaks early in the morning and in the afternoon. The peak of perch activity was longer in the morning, which may be related to pairs of males or solitary males practising dance displays, and shorter in the afternoon, whereas vocal activity had a shorter peak early in the morning and a more prolonged one in the afternoon. A similar bimodal pattern of vocal activity, with slight differences, was documented in an earlier study conducted at the same site based on focal observations (Durães *et al.* 2011), but the results are not directly comparable because the previous work reported vocal activity per lek in

periods of 30 min averaged by number of males, whereas we report mean number of '*pchrrr*' calls per hour across the seven leks. The daily activity pattern of male Blue-backed Manakin documented in this study differed from the pattern reported for the Lance-tailed Manakin, which has a more homogeneous pattern of activity during the day (DuVal 2007). The daily pattern we observed seems very similar to what has been reported for Long-tailed Manakins, which have a bimodal pattern of vocal activity with a slight early-morning peak and high effort into the late afternoon (McDonald 2010), matching the pattern seen in our study (Fig. 4).

Female visits occurred throughout the morning but were more common at noon, probably in association with the peak in male perch activity. Moreover, the pattern of female visits in Blue-backed Manakin shown here is more similar to the pattern of copulation activity than to the pattern of female visits found for Long-tailed Manakin by McDonald (2010), where most copulations occurred at midday.

Some of the differences found between subspecies of *C. pareola* are related to geographical differences in the timing of the main peak of the reproductive season. Previous studies have reported that the breeding season for most bird species, including *C. p. napensis* in the Ecuadorian Amazon, extends between November and April, with the moulting season starting in mid- to late March (Durães *et al.* 2011). Our study shows that *C. p. napensis* had high breeding activity between January and February, which differs from the March to June reproductive season reported for *C. p. atlantica* in Trinidad and Tobago (Snow 1963, 1971), although more sampling across the rest of the year would be necessary to establish the peak of the reproductive season for *C. p. napensis*. Differences in breeding seasons probably reflect differences in rainfall patterns; the dry season in Trinidad and Tobago is between January and May, whereas in western Amazonia the rainiest months are from April to June, January and August are relatively dry, and December and January are often very dry (Blake *et al.* 2011).
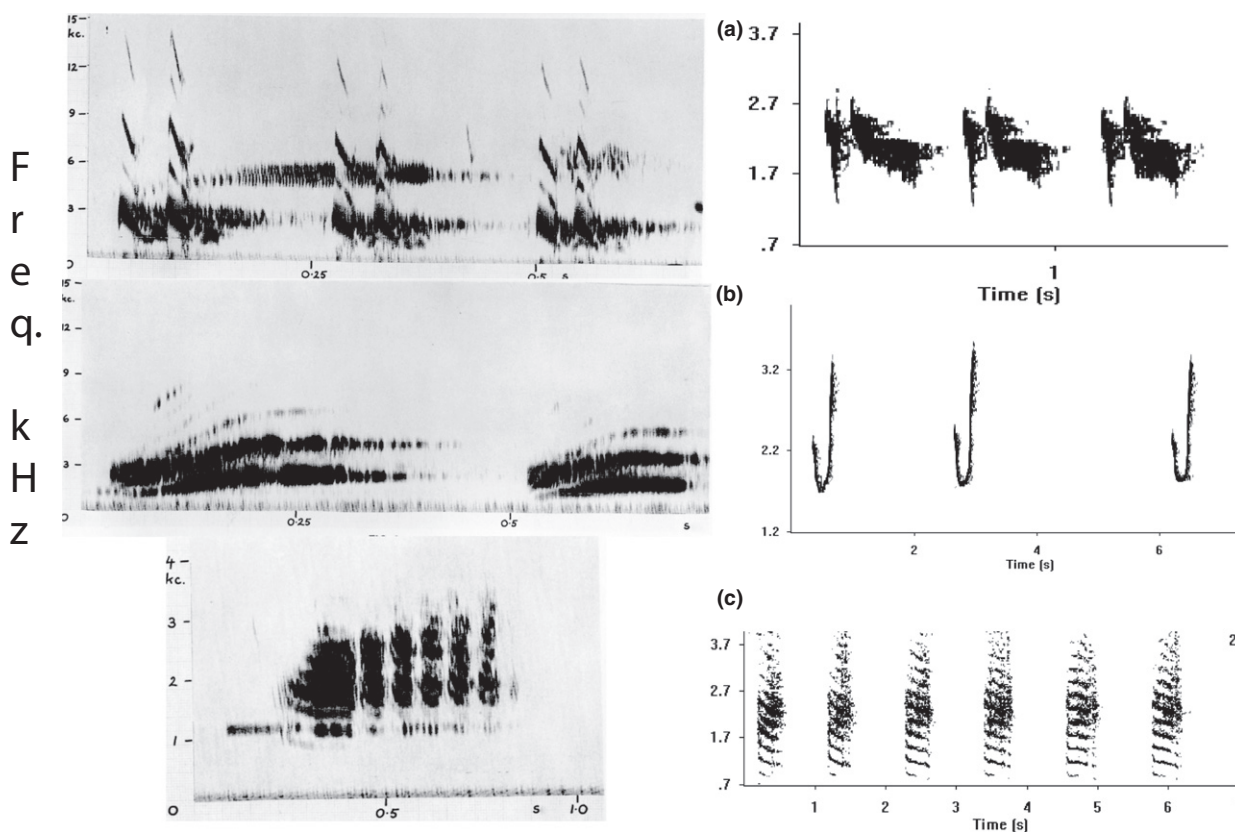
We documented a repertoire of six different vocalizations for the Blue-backed Manakin, adding two vocalization types to the previously reported repertoire for the subspecies *C. p. atlantica* (Snow 1963): the '*wohoo*' and the '*whee-ee*'. The two most common vocalizations were the '*pchrrr*' and the

'chee-wee' calls. The vocalization repertoire appears to be more limited than that of the Long-tailed and Lance-tailed Manakins, but several elements are shared with these species (e.g. calls for duet singing, two-male dance display and end of two-male dance display). The 'pchrrr' call of C. p. napensis was similar to the 'toledos' reported in the Long-tailed Manakin (McDonald 1989a) and to the 'quericos' of the Lance-tailed Manakin (DuVal 2007). The 'cheewee' calls were similar to the 'wit' of Long-tailed Manakin (Trainer & McDonald 1993), whereas the 'wrang' call was similar to the 'nraawnraawnraaw' call of Lance-tailed Manakin (DuVal 2007) and the 'nyanyownh' of Long-tailed Manakin (Trainer & McDonald 1993). The 'eek' call has been reported in Lance-tailed Manakin, also as 'eek' (DuVal 2007) and in Long-tailed Manakin, as a 'weent' (Slud 1957, Turner & McDonald 1993, Lukianchuk & Doucet 2014).

The vocal repertoire of C. p. napensis exhibits substantial differences from C. p. atlantica in the two main vocalizations. The structures of the 'pchrrr' call and the 'cheewee' calls are very different in length and frequency (Fig. 6a and 6b). In contrast, the 'wrang' call performed during the cartwheels seems much conserved between the two subspecies (Fig. 6c).

We reported an average vocalization rate of 120 calls/h in Blue-backed Manakin, which is lower than previous reports (Durães et al. 2011). This difference could be attributed to the sampling method used to estimate vocalization rate. Durães et al. (2011) used focal observations and calculated vocal activity per hour using all the calls and sounds previously reported for the species. In contrast, we used automatic vocalization recorders and only used the 'pchrrr' vocalization to estimate vocal activity per hour to facilitate automatic analysis of the data. We did not detect any mechanical sounds in this population, which differs from what was described by Snow (1963) for C. p. atlantica. However, more detailed observations may be needed to rule out completely the occurrence of this type of sound in C. p. napensis.



**Figure 6.** Comparison of sonograms of the calls described for *Chiroxiphia pareola atlantica* (left) with the calls described for *Chiroxiphia pareola napensis* in this study (right). (a) Sonograms of the 'pchrrr' call (plate I, fig. 1 in Snow 1963), (b) sonograms of the 'cheewee' call (plate I, fig. 3 in Snow 1963), (c) sonograms of the 'wrang' call (plate II, fig. 4 in Snow 1963).

The display behaviour of *C. p. napensis* was very similar to what has been reported previously for other populations of this species (Snow 1956, 1963, Gilliard 1959), but differs from that of other *Chiroxiphia* species. For example, no '*pip*' flights were observed, in contrast to the Lance-tailed Manakin (DuVal 2007). Similarly, butterfly flights are not part of the *solo* dance display of the Blue-backed Manakin, which instead incorporates bouncing elements that differ from those of the Long-tailed Manakin (McDonald 1989b). Additionally, from comparisons among the videos taken in this study (e.g. Video S2) and videos published for the other species (Long-tailed Manakin http://www.uwyo.edu/dbmcd/lab/ltmvideo.htm; Lance-tail Manakin http://www.youtube.com/watch?v=cAwevkUaB2Q), it seems that the dance display of the Blue-backed Manakin and the Lance-tailed Manakin are more similar with respect to the speed with which the cartwheel or leapfrog dances are executed, relative to the slower Long-tailed Manakin dance. This difference in the speed of the performance of these elements may be related to the length of the tail, which may limit speed in the Long-tailed Manakin.

In conclusion, our work has provided new information on the social organization, display and vocal repertoire of a population of *C. p. napensis*, revealing similarities to and differences from other conspecific populations and closely related species. Such similarities and differences can contribute to our understanding of the evolution of lekking behaviour, sexual selection and the evolution of cooperative systems among manakin species. The baseline information reported here is also key for future analyses testing hypotheses about male reproductive success, female mate choice and social interactions.

## REFERENCES

**Agranat, I.** 2009. *Automatically Identifying Animal Species From Their Vocalizations*. Maynard, MA: Wildlife Acoustics Inc.

**Blake, J.G. & Loiselle, B.A.** 2008. Estimates of apparent survival rates for forest birds in eastern Ecuador. *Biotropica* **40**: 485–493.

**Blake, J.G., Mosquera, D., Guerra, J., Loiselle, B.A., Romo, D. & Swing, K.** 2011. Mineral licks as diversity hotspots in lowland forest of eastern Ecuador. *Diversity* **3**: 217–234.

**Burt, J.** 2006. *Syrinx software 2.6 h*. Downloaded from http://www.syrinxpc.com/ (accessed 4 October 2013).

**Buxton, R.T. & Jones, I.L.** 2012. Measuring nocturnal seabird activity and status using acoustic recording devices: applications for island restoration. *J. Field Orn.* **83**: 47–60.

**Clements, J.F., Schulenberg, T.S., Iliff, M.J., Sullivan, B.L., Wood, C.L. & Roberson, D.** 2013. *The eBird/Clements checklist of birds of the world: Version 6.8*. Downloaded from http://www.birds.cornell.edu/clementschecklist/download/ (accessed 6 August 2013).

**Darwin, C.** 1871. *The Descent of Man and Selection in Relation to Sex*. London, UK: John Murray.

**Davis, T.** 1982. A flight-song display of White-throated Manakin. *Wilson Bull.* **94**: 595–598.

**Durães, R., Loiselle, B.A., Parker, P.G. & Blake, J.G.** 2009. Female mate choice across spatial scales: influence of lek and male attributes on mating success of Blue-crowned Manakins. *Proc. R. Soc. B* **276**: 1875–1881.

**Durães, R., Blake, J.G., Loiselle, B.A., Ryder, T.B., Tori, W.P. & Hidalgo, J.R.** 2011. Vocalization activity at leks of six manakin (Pipridae) species in eastern Ecuador. *Ornitol. Neotrop.* **22**: 437–445.

**DuVal, E.H.** 2005. Age-based plumage changes in the Lance-tailed Manakin: a two-year delay in plumage maturation. *Condor* **107**: 917–922.

**DuVal, E.H.** 2007. Cooperative display and lekking behavior of the Lance-tailed Manakin (*Chiroxiphia lanceolata*). *Auk* **124**: 1168–1185.

**DuVal, E.H.** 2012. Variation in annual and lifetime reproductive success of Lance-tailed Manakins: alpha experience mitigates effects of senescence on siring success. *Proc. R. Soc. B* **279**: 1551–1559.

**DuVal, E.H. & Kempenaers, B.** 2008. Sexual selection in a lekking bird: the relative opportunity for selection by female choice and male competition. *Proc. R. Soc. B* **275**: 1995–2003.

**Emlen, S.T. & Oring, L.W.** 1977. Ecology, sexual selection, and the evolution of mating systems. *Science* **197**: 215–223.

**Fiske, P., Rintamäki, P. & Karvonen, E.** 1998. Mating success in lekking males: a meta-analysis. *Behav. Ecol.* **9**: 328–338.

**Foster, M.S.** 1976. The nesting biology of the Long-tailed Manakin. *Wilson Bull.* **88**: 400–420.

**Foster, M.S.** 1977. Odd couples in manakins: a study of social organization and cooperative breeding in *Chiroxiphia linearis*. *Am. Nat.* **111**: 845–853.

**Foster, M.S.** 1981. Cooperative behavior and social organization of the Swallow-Tailed Manakin (*Chiroxiphia caudata*). *Behav. Ecol. Sociobiol.* **9**: 167–177.

**Foster, M.S.** 1983. Disruption, dispersion and dominance in lek-breeding birds. *Am. Nat.* **122**: 53–72.

**Foster, M.S.** 1987. Delayed maturation, neoteny and social system differences in two manakins of the genus *Chiroxiphia*. *Evolution* **41**: 547–558.

**Gilliard, E.T.** 1959. Notes of the courtship behavior of the Blue-backed Manakin (*Chiroxiphia pareola*). *Am. Mus. Novit.* **1942**: 1–19.

**Hidalgo, J.R., Ryder, T.B., Tori, W.P., Durães, R., Blake, J.G. & Loiselle, B.A.** 2008. Nest architecture and placement of three manakin species in lowland Ecuador. *Cotinga* **29**: 57–61.

**Kirkpatrick, M. & Ryan, M.J.** 1991. The evolution of mating preferences and the paradox of the lek. *Nature* **350**: 33–38.

**Loiselle, B.A., Ryder, T.B., Durães, R., Tori, W.P., Blake, J.G. & Parker, P.G.** 2006. Kin selection does not explain male aggregation at leks of four manakin species. *Behav. Ecol.* **18**: 287–291.

**Loiselle, B.A., Blake, J.G., Duraes, R., Ryder, T.B. & Tori, W.** 2007. Environmental and spatial segregation of leks among six co-occurring species of manakins (Pipridae) in eastern Ecuador. *Auk* **4**: 420–431.

**Lukianchuk, K.C. & Doucet, S.M.** 2014. Cooperative courtship display in Long-tailed Manakins: predictors of courtship success revealed through full characterization of display. *J. Ornithol.* **155**: 729–743.

**McDonald, D.B.** 1989a. Cooperation under sexual selection: Age-graded changes in a lekking bird. *Am. Nat.* **134**: 709–730.

**McDonald, D.B.** 1989b. Correlates of male mating success in a lekking bird with male-male cooperation. *Anim. Behav.* **37**: 1007–1022.

**McDonald, D.B.** 1993. Demographic consequences of sexual selection in the Long-tailed Manakin. *Behav. Ecol.* **4**: 297–309.

**McDonald, D.** 2010. A spatial dance to the music of time in the leks of Long-Tailed Manakins. *Adv. Study Behav.* **42**: 55–81.

**Prum, R.O.** 1990. Phylogenetic analysis of the evolution of display behavior in the Neotropical manakins (Aves: Pipridae). *Ethology* **84**: 202–231.

**Reynolds, J.D. & Gross, M.R.** 1990. Cost and benefits of female mate choice: is there a lek paradox? *Am. Nat.* **136**: 230–243.

**Ridgely, R.S. & Tudor, G.** 1994. *The Birds of South America. Vol. 2. The Suboscine Passerines*. Austin: University of Texas Press.

**Ryder, T.B., Parker, P.G., Blake, J.G. & Loiselle, B.A.** 2009a. It takes two to tango: reproductive skew and social correlates of male mating success in a lek-breeding bird. *Proc. R. Soc. B* **276**: 2377–2384.

**Ryder, T.B., Tori, W.P., Blake, J.G., Loiselle, B.A. & Parker, P.G.** 2009b. Mate choice for genetic quality: a test of the heterozygosity and compatibility hypotheses in a lek-breeding bird. *Behav. Ecol.* **21**: 203–210.

**Skutch, A.F.** 1949. Life history of the Yellow-Thighed Manakin. *Auk* **66**: 1–24.

**Slud, P.** 1957. The song and dance of the Long-tailed Manakin, *Chiroxiphia linearis*. *Auk* **74**: 333–339.

**Snow, D.W.** 1956. Courtship ritual: the dance of the manakins. *Anim. Kingdom* **59**: 86–91.

**Snow, D.W.** 1963. The display of the Blue-backed Manakin, *Chiroxiphia pareola*, in Tobago, W.I. *Zoologica* **48**: 167–176.

**Snow, D.W.** 1971. Social organization of the Blue-backed Manakin. *Wilson Bull.* **83**: 35–38.

**Snow, D.W.** 2004. Family Pipridae (Manakins). In del Hoyo, J., Elliot, A. & Christie, D.A. (eds) *Handbook of the Birds of the World. Vol. 9. Cotingas of Pipits and Wagtails*: 110–169. Barcelona: Lynx Edicions.

**Trainer, J.M. & McDonald, D.B.** 1993. Vocal repertoire of the Long-tailed Manakin and its relation to male-male cooperation. *Condor* **95**: 769–781.

**Trainer, J.M. & McDonald, D.B.** 1995. Singing performance, frequency matching and courtship success of Long-Tailed Manakins (*Chiroxiphia linearis*). *Behav. Ecol. Sociobiol.* **37**: 249–254.

**Wildlife Acoustics, Inc.** 2007–2011. *Song Scope Bioacoustics Software 4.0 Documentation*. Concord, MA: Wildlife Acoustics, Inc.

## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Table S1.** Parameters used in the SongScope version 4.0 software to create the recognizer pattern.

**Video S1.** An adult male Blue-backed Manakin chasing a young male.

**Video S2.** Practice dance display involving two male Blue-backed Manakins.

**Video S3.** Dance display for a female by two male Blue-backed Manakins.

**Video S4.** One male Blue-backed Manakin practising the solo dance display.

**Video S5.** Pre-copulatory dance and copulation in a pair of Blue-backed Manakins.