

SONG DESCRIPTION AND INDIVIDUAL VARIATION IN MALES OF THE COMMON PAURAQUE (*NYCTIDROMUS ALBICOLLIS*)

Luis Sandoval¹ & Ignacio Escalante

Laboratorio de Bioacústica, 2060, Escuela de Biología, Universidad de Costa Rica, San José, Costa Rica. *E-mail*: nachoescalante@gmail.com

¹*Current address*: Department of Biological Sciences, University of Windsor, 401 Sunset Avenue, Windsor, Ontario, Canada, N9B3P4.

Resumen. – Descripción del canto y variación individual en los machos del cuyeo (*Nyctidromus albicollis*). – El conocimiento acerca del comportamiento vocal de las especies de Caprimulgidae es escaso y sólo incluye observaciones anecdóticas sobre los despliegues vocales, o breves descripciones usadas en análisis taxonómicos. Hasta ahora, dentro de ninguna especie se ha investigado ni descrito la estructura espectral ni temporal de sus vocalizaciones en una población. Brindamos la primera descripción espectrográfica de las vocalizaciones de los machos, y analizamos la variación individual en una población de cuyeos (*Nyctidromus albicollis*), un habitante de tierras bajas que se distribuye desde el sur de Texas hasta el noreste de Argentina, los cuales se congregan para cantar. Grabamos las vocalizaciones de 17 machos en el bosque seco estacional del Parque Nacional Palo Verde, Costa Rica. Encontramos cuatro individuos cantando solos, cuatro en pares y nueve en tríos. Las vocalizaciones producidas por los machos duraron en promedio 2.39 ± 0.91 s, tuvieron un ámbito de frecuencia de 320.6 Hz la más baja y 3333.0 Hz la más alta. Encontramos variación individual significativa dentro de la población, basada en características del canto, lo que sugiere que el canto refleja la identidad del macho. También, nuestro análisis preliminar mostró que los individuos en grupos fueron más similares en sus vocalizaciones de lo que fueron con los individuos en grupos distantes.

Abstract. – Knowledge of the vocal behavior in the goatsuckers family (Caprimulgidae) is scarce and includes primarily anecdotal observations of vocal displays or brief descriptions used in taxonomic analyses. Until now, neither spectral or temporal structures of within-species vocalizations have been investigated and described at the population level in Caprimulgidae. Here we provide the first spectrographic description of male vocalizations, and analyze individual vocal variation within a population of Common Pauraque (*Nyctidromus albicollis*). This species occurs from southern Texas to northeastern Argentina, and congregates to sing during the night. We recorded vocalizations of 17 males in the seasonal dry forest of Palo Verde National Park, Costa Rica. Of these 17 males, four birds sang solo, four sang in pairs, and nine sang as part of a trio. Songs produced by males lasted on average 2.39 ± 0.91 s, and ranged in frequency from 320.6 Hz, the lowest recorded per individual, to 3333.0 Hz, the highest recorded per individual. We found significant individual variation in song features within the population, suggesting that male song encodes individual identity. Also, our preliminary analyses showed that individuals in groups were more similar in their song than they were to individuals in distant groups. *Accepted 9 March 2011.*

Key words: Common Pauraque, *Nyctidromus albicollis*, Caprimulgidae, Costa Rica, individual vocal variation, male group singing, non-passerine bird vocalizations.

INTRODUCTION

Despite being a common and widespread non-passerine bird family, knowledge of vocal

behavior in the Caprimulgiformes (night-hawks, nightjars, and poorwills) is limited. These nocturnal singing birds are thought to use vocalizations to defend territory and

attract mates (Schwartz 1968, Quesnel 1993). Vocal behavior in this group has been described informally through anecdotal notes and observations (Marshall 1978, Stevenson *et al.* 1983, Mills 1986, Quesnel 1993, Thurber 2003). Caprimulgid vocalizations have also been shown to be useful for taxonomic and phylogenetical purposes (Mees 1977, Fry 1988, Garrido & Reynard 1998, Sangster & Rozendaal 2004, Larsen *et al.* 2007), based on the assumption that the songs of birds in this family are genetically determined, and that song differences are related to species differences.

The Common Pauraque (*Nyctidromus albicollis*) is an abundant lowland species commonly found in open fields, pastures, and gravel roads (Edwards 1983), and ranges from southern Texas to northeastern Argentina (Stiles & Skutch 1989, AOU 1998). Males of this nocturnal species are territorial (Edwards 1983), and their territories can be either isolated or clustered. When territories are clustered together, two or more males may aggregate to engage in a chorus (Stiles & Skutch 1989, Thurber 2003). Due to spatial variation in male distribution as well as the possibility of individual song variation (Thurber 2003), the Common Pauraque is a good species to study the effect of neighbors on the song characteristics of males. Our goals were to (1) provide the first spectrographic description of the Common Pauraque's song, and (2) to provide the first analysis of fine structural variation in male songs within a population of Caprimulgidae. Additionally, we conducted a preliminary test of the hypothesis that the spatial distribution of Common Pauraque males may influence temporal and spectral features of their songs.

METHODS

Study area. We studied a population of Common Pauraque in Palo Verde National Park,

Guanacaste Province, Costa Rica (10°20'N, 85°21'W; 15 m a.s.l.). The study area is tropical seasonal dry forest, but was previously a cattle pasture that was left to regenerate naturally in 1972, when the area became protected (Hartshorn 1983). The area is now dominated by bullhorn shrubs (*Acacia collinsii*) along the roadside and at the forest edges. Common tree species include *Enterolobium cyclocarpum*, *Bombacopsis quinata*, *Guazuma ulmifolia*, *Bursera simaruba*, *Tabebuia guayacan*, and the introduced *Parkinsonia aculeate*, which is found surrounding a seasonal lagoon (Chavarría *et al.* 2001).

Recording methods. We recorded song from 17 individuals at night (20:00 to 23:00 h CST) on 3 and 4 April 2009. Weather conditions (mean \pm SD) varied little during both nights (Organization for Tropical Studies 2010 meteorological data collected at 10°20'38"N, 85°20'18"W): air temperature ($26.33 \pm 1.27^\circ\text{C}$, CV = 5%), relative humidity ($74.85 \pm 10.22\%$, CV = 14%), wind speed ($1.65 \pm 0.97 \text{ m s}^{-1}$, CV = 58.33), and no rain. The moon was at full phase on both nights when we collected recordings.

We recorded seven males during the first night and 10 the second night. Males recorded on the second night were separated by at least 400 m from males recorded on the first night. Recorded birds sang along a 3.3 km-long transect formed by a straight gravel road and roadside pastures. We recorded each bird once, and recorded males sequentially to avoid recording the same individual twice, following Barrantes *et al.* (2008) and Fitzsimmons *et al.* (2008). Because Common Pauraque males are territorial during the time of year we recorded their songs (Schwartz 1968, Edwards 1983), the probability of an individual male singing from the same location on two consecutive nights is high. Therefore, as in the studies mentioned above, we confirmed the presence of the birds recorded previously on both nights by visual and/or

aural observations. We recorded each bird for at least 2 min from a distance of 2 to 10 m, using a Marantz PMD 620 digital recorder and a Sennheiser ME66 directional microphone. We recorded birds for a minimum of 2 min because during a natural song bout males sing an average of 21 songs min^{-1} . Thus, this sampling method provided a large number of songs collected within a short period of time. During recording sessions we positioned the microphone directly in front of the singing focal male in an attempt to reduce interference from neighboring males. In recordings of groups of singing males, this allowed us to confidently identify the focal male because his vocalizations were always the highest in amplitude.

We visually surveyed the study site to check for non-vocal male birds within a 20-m radius around the focal male. We also checked for female paurques, which differ in plumage from males (Stiles & Skutch 1989). This ensured that differences observed in male songs were not influenced by the presence of females, which has been suggested to affect song characteristics (Kroodsma 2009). We used a 20 m radius around males as our measure because birds farther than 20 m were likely not detectable at night.

It has been demonstrated recently that individual variation in vocalizations of some avian species may result from differences among multiple recording sessions, rather than from individual variation itself (Wilson & Mennill 2010). We suggest that the influence of multiple recording sessions may be most pronounced when recording birds that learn their songs, rather than birds with innate songs such as the Common Pauraque (Kroodsma 2004, Catchpole & Salter 2008). However, we interpret our results carefully in light of this possible effect that multisession recordings could cause individual differences, and we discuss the possible effects of multisession differences in our results.

Spatial location. We classified each recorded individual according to its proximity to other birds. We classified singing individuals as in a group (when birds were singing in pairs or trios and were located within a 10 m radius of each other), or as a solo bird (when a bird was singing at least 50 m from other males). The closest distance between two consecutively calling groups of males or two consecutive solo birds was 240 m. To analyze relationships between groups of males and song similarity, we mapped each bird's location within the study site.

Song analyses. We used Raven 1.2.1 (Charif *et al.* 2004) to generate song spectrograms digitized at 44,100 Hz and 16 bits. Our spectrograms were made at a time resolution of 11.6 ms, frequency resolution of 86.1 Hz, and transform length of 512 points. We focused the song description on only the fundamental notes, because our recording equipment may not have picked up low-amplitude harmonics in all cases. We randomly selected 10 songs from the recordings of each individual for analysis (Fig. 1), excluding *a priori* from that selection the first and the last song collected in the recording session. We excluded these two songs because it is impossible to have the time between previous or subsequent songs, measurements included in our study. Also, we did not analyze songs that were overlapped by other songs. For each song, we measured the lowest (LF), highest (HF), and maximum frequencies (MF) (MF is the frequency at which maximum energy occurred in the song); the duration of the song (ΔT); and the average time between previous and subsequent song (TBS; Fig. 1). Because our microphones were not calibrated, we could not standardize distances to focal males; thus, we only included measurements of spectral characteristics in the analyses. We also measured song rate (number of songs per minute). Song recordings are archived at the Laboratório de

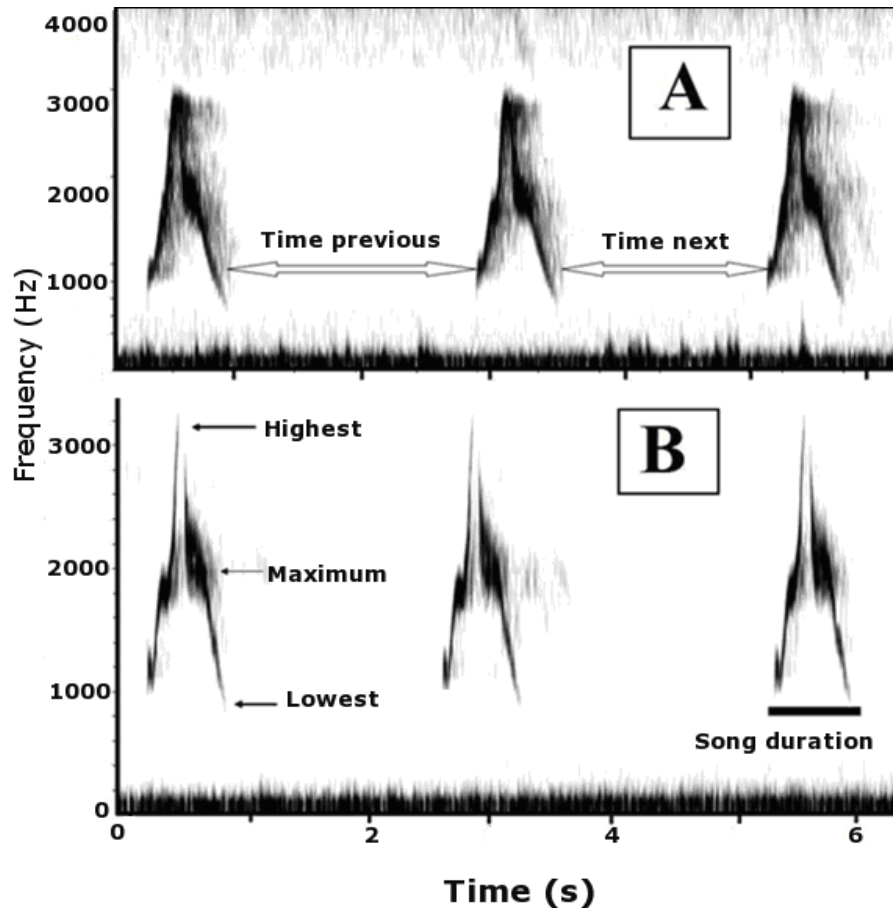


FIG. 1. Spectrogram of songs of three Common Pauraques (*Nyctidromus albicollis*), with the temporal and spectral variables measured. A) Songs representative of those produced by 15 males. B) Variation of the song found in only two males, with a discontinuity at the song's frequency peak (see text). Recordings were obtained at Palo Verde National Park, Costa Rica, 3 and 4 April 2009.

Bioacústica, Escuela de Biología, Universidad de Costa Rica.

Statistical analyses. We used a Multiple Analysis of Variance (MANOVA) to describe differences between individuals' songs according to the five song measures used (ΔT , LF, HF, MF, and TBS). We analyzed relationship between song similarity and spatial location in male groups using a MANOVA. We determined

whether songs of individual males and groups of males could be classified on the basis of our song measurements using a stepwise discriminate function analysis (DFA) for each MANOVA. Cross-validation for each DFA was performed in Systat 11 (Systat 2004) using the Jackknife procedure, which uses the function computed from all the data except the case being tested to calculate the percentage of correct classifications.

We used the coefficients of variation (CV) to assess the pattern of song variability within (CV_w) and among males (CV_a) for each of the five song measurements (Fitzsimmons *et al.* 2008, Gasser *et al.* 2009). We used analyses of variance (ANOVA) to compare whether the observed variability in song measures was different between CV_w and CV_a . We also calculated the ratios of co-efficients of variance within- or among males (CV_a/CV_w) as a measure of relative among-male variability for each song measure. When the ratio is >1.0 for a given measure, this measure is relatively more variable among males than within males and may facilitate individual discrimination (Tobias & Seddon 2009).

We calculated a centroid for each male in a group based on the first three canonical axes that explained 96% of song variance, identified by another DFA including only the males in the groups. We calculated the distance between males according to the male's spatial position. We then calculated pairwise comparisons of all individuals according to the centroid values (absolute differences between centroids) and geographical distance. Both matrices of difference were used to perform a Mantel test correlation using Euclidian distance between the song differences and geographic distance of males in groups. MANOVA and DFA tests were performed using SYSTAT 11 (Systat 2004), and Mantel tests were conducted using Isolation by Distance web service 3.16 (Jensen *et al.* 2005). All results are presented as means \pm SD.

RESULTS

Song description. Out of the 17 Common Pauraques males we recorded, nine were in trios, four were in pairs, and four sang alone. Male songs begin with a brief downward frequency modulation followed by a large upward and

then downward frequency modulation that appeared as an inverted "V" shape in spectrograms (Fig. 1). We observed harmonics in several recordings. The songs ended with an additional frequency modulation. The songs showed a duration of 0.61 ± 0.07 s (range: 0.46–0.81 s), and a inter song interval of 2.39 ± 0.91 s, with a lowest frequency of 761.14 ± 173.90 Hz, a highest frequency of 3072.51 ± 178.78 , and a maximum frequency of 2331.07 ± 423.81 Hz. Two solitary birds showed a discontinuity in the peak section of their songs (Fig. 1b); one individual had discontinuities that averaged 0.056 ± 0.017 s and the other had discontinuities of 0.040 ± 0.011 s. Males sang on average 20.1 ± 5.05 songs per minute (range: 9.4–28.5). All recorded individuals sang from a position on the ground. Most of them sang on the gravel road or at the roadside, in the cattle fields, or at forest edges with dispersed trees.

Individual variation. We did not find any non-singing individuals or females within a 20 m radius around the singing males or on the trail between solo males or two consecutive groups of males. We found high individual variation in the time (ΔT and TBS) and frequency (LF, HF, and MF) characteristics of song among male pauraques (MANOVA: $F_{5,80} = 31.7$, $P < 0.001$). Significant differences were also found among males when song variables were analyzed separately with post hoc tests ($F_{16,153} > 9.0$, $P < 0.001$; for all comparisons, see Table 1). The DFA cross validation correctly classified 75% of each song according to the male who sang it, using the LF, HF, MF, and DT measures (Wilks' lambda = 0.001, $F_{64,589} = 43.4$, $P < 0.001$). The five song measurements varied more among males (CV_a) than within males (CV_w) (ANOVA: $F > 7.5$, $P = 0.01$; for all comparisons, see Table 2). The ratio of CV was greater than 1 for each of the five song measurements (Table 2), suggesting

TABLE 1. Frequency (Hz) and time (s) characteristics (means \pm SD) for the songs of 17 male Common Pauraques (*Nyctidromus albicollis*) recorded at Palo Verde National Park, Costa Rica, 3 and 4 April 2009.

Males	Song duration (s)	Time between songs (s)	Frequency (Hz)			
			Lowest	Highest	Maximum	Range
1	0.52 \pm 0.01	2.19 \pm 0.65	689.91 \pm 37.77	3215.28 \pm 45.88	2362.50 \pm 123.44	2525.37 \pm 44.45
2	0.64 \pm 0.02	3.74 \pm 0.83	661.77 \pm 40.73	3184.33 \pm 91.18	2793.76 \pm 39.51	2522.56 \pm 95.41
3	0.68 \pm 0.01	2.93 \pm 0.89	753.50 \pm 39.32	3143.48 \pm 64.42	2484.36 \pm 141.50	2389.98 \pm 77.63
4	0.63 \pm 0.03	2.24 \pm 1.39	774.20 \pm 51.87	3146.78 \pm 82.00	1968.80 \pm 0.00	2372.58 \pm 81.43
5	0.58 \pm 0.02	1.80 \pm 0.52	398.18 \pm 67.55	2595.84 \pm 97.40	2053.15 \pm 128.45	2197.66 \pm 96.92
6	0.61 \pm 0.02	1.63 \pm 0.19	662.98 \pm 34.07	3185.23 \pm 58.24	2662.51 \pm 79.08	2522.25 \pm 58.37
7	0.58 \pm 0.01	1.50 \pm 0.50	462.44 \pm 24.71	3170.07 \pm 39.44	1621.89 \pm 289.97	2707.63 \pm 51.60
8	0.55 \pm 0.03	2.13 \pm 0.61	815.78 \pm 51.51	2937.55 \pm 29.63	2371.88 \pm 303.18	2121.77 \pm 58.36
9	0.65 \pm 0.03	2.89 \pm 1.17	946.83 \pm 48.80	3078.09 \pm 24.32	2259.39 \pm 378.75	2131.26 \pm 42.96
10	0.51 \pm 0.01	2.30 \pm 0.34	733.55 \pm 44.57	3023.25 \pm 20.26	2587.50 \pm 79.06	2289.70 \pm 39.84
11	0.57 \pm 0.05	2.47 \pm 0.53	961.57 \pm 68.93	3056.79 \pm 24.46	2559.39 \pm 345.32	2095.22 \pm 76.16
12	0.69 \pm 0.07	2.66 \pm 0.72	826.48 \pm 40.80	2897.08 \pm 45.16	2587.52 \pm 221.85	2070.60 \pm 45.39
13	0.68 \pm 0.08	2.00 \pm 0.25	965.45 \pm 73.24	2989.60 \pm 13.56	1940.64 \pm 125.40	2024.15 \pm 78.22
14	0.68 \pm 0.08	2.20 \pm 0.56	1056.47 \pm 78.37	3123.51 \pm 79.54	1884.37 \pm 419.91	2067.04 \pm 114.01
15	0.63 \pm 0.05	3.83 \pm 3.10	802.13 \pm 68.75	3165.81 \pm 131.37	2643.72 \pm 314.98	2363.68 \pm 147.20
16	0.59 \pm 0.04	2.31 \pm 0.65	773.09 \pm 37.96	3226.36 \pm 40.66	2878.09 \pm 45.26	2453.27 \pm 71.02
17	0.55 \pm 0.02	1.83 \pm 0.43	655.20 \pm 20.56	2757.07 \pm 44.86	1968.76 \pm 407.45	2101.87 \pm 37.25

TABLE 2. Frequency (Hz) and time characteristics of the songs of 17 males of the Common Pauraque (*Nyctidromus albicollis*), revealing that songs are significantly more variable among than within-males according to the coefficient of variation (CV). LF = lowest frequency, HF = highest frequency, MF = maximum frequency, DT = song duration, TBS = time between songs. We used $\alpha = 0.01$ to reject the statistical hypothesis of similarity between CV_a and CV_w due to multiple comparisons using the same data. Degrees of freedom are 1, 25 for all comparisons. Palo Verde National Park, Costa Rica, 3 and 4 April 2009.

Variable	Mean \pm SD	CV_a	CV_w	Ratio CV_a/CV_w	F	P
LF	761.15 \pm 13.34	0.23	0.07	3.53	250.07	< 0.001
HF	3052.71 \pm 13.71	0.06	0.02	3.32	132.82	< 0.001
MF	2331.07 \pm 32.50	0.18	0.09	2.01	16.66	< 0.001
DT	0.61 \pm 0.005	0.11	0.05	2.07	23.22	< 0.001
TBS	2.39 \pm 0.070	0.35	0.21	1.67	7.52	0.01

that all measures could encode information about individual identity.

Song similarity based on location. We found five groups of males: three groups were comprised of three males, and two were pairs. On average, the groups were separated by 517.5 \pm 159.3 m. Males inside each group were separated by less than 10 m. We found high variation among male groups in the time (DT and TBS) and frequency (LF, HF, and MF) of song characteristics (MANOVA: $F_{5,20} = 18.4$, $P < 0.001$). Post hoc tests showed significant differences among groups when song variables were analyzed separately ($F_{4,125} > 5.0$, $P < 0.001$; for all comparisons, see Table 3). The DFA cross validation correctly classified 68% of the songs according to the appropriate group of males using the LF, HF, DT, and TBS measures (Wilks' lambda = 0.12, $F_{16,373} = 22.8$, $P < 0.001$). The first canonical variable segregated the groups according to HF and DT, whereas the second canonical variable included LF and TBS (Fig. 2). We found that males in each group produced songs more similar to the other members within their group than to males in other groups (Mantel test: $Z = 184.9$, $r = 0.43$, $P = 0.008$, Fig. 3).

DISCUSSION

We found that the songs of male Common Pauraques showed high individual variation in frequency and time characteristics, and low variation in song arrangement (only two individuals showed a discontinuity in their songs). The variation in the five song characteristics measured demonstrated that songs are significantly more variable among than within individuals. This suggests that male songs may encode sufficient information to facilitate discrimination between individual males. In contrast to previous studies on species that do not learn songs in which 7 to 18 measures were reported to describe song variation (Lovell & Lein 2004, Wiley 2005, Barrantes *et al.* 2008, Fitzsimmons *et al.* 2008, Sandoval 2008, Araya-Ajoy *et al.* 2009), we found significant individual variation in songs between Common Pauraque males using only four or five song measurements.

We did not record the same individuals on different days because our population of Common Pauraques was unbanded. Thus, certainty of individual identification across multiple sample periods was not possible. This approach has several implications for interpretation of our results. Recent studies have suggested that individual song variation

TABLE 3. Frequency (Hz) and time (s) characteristics (means \pm SD) for the five groups of males of Common Pauraque (*Nyctidromus albicollis*) recorded at Palo Verde National Park, Costa Rica, 3 and 4 April 2009.

Group	No. of males	Song duration (s)	Time between songs (s)	Frequency (Hz)		
				Lowest	Highest	Maximum
1	3	0.61 \pm 0.07	2.95 \pm 0.86	701.73 \pm 54.40	3181.03 \pm 73.59	2546.87 \pm 213.34
2	3	0.59 \pm 0.01	1.64 \pm 0.35	507.87 \pm 122.97	2983.71 \pm 286.94	2112.50 \pm 470.83
3	2	0.58 \pm 0.07	2.60 \pm 0.56	840.19 \pm 118.49	3050.67 \pm 35.57	2423.44 \pm 315.03
4	3	0.65 \pm 0.08	2.38 \pm 0.45	917.83 \pm 89.30	2981.16 \pm 72.87	2362.52 \pm 386.47
5	2	0.65 \pm 0.07	3.02 \pm 1.67	929.30 \pm 148.90	3144.66 \pm 107.90	2264.04 \pm 527.94

may be due to differences in recording sessions caused by ambient differences (e.g., temperature, precipitation, wind speed, and humidity), or individual motivation (e.g., female or predator presence), rather than to individual variation (Ellis 2008, Wilson & Mennill 2010). Variation between recording sessions has yet to be studied in a non-song-learning bird species.

How might multiple recording sessions influence our results? Song characteristics may vary within individuals over time because of a trade-off between time spent singing and time spent foraging. Alternatively, hormone levels may change and affect singing behavior and song characteristics (e.g., rate, amplitude, and duration) (Gil & Gahr 2002, Ellis 2008). For this reason, if we could record all the individuals in the population at the same time, or with short time periods of difference, we could possibly reduce this potential bias. We recorded all the pauraques on two consecutive nights at the beginning of the reproductive season, when it was more probable that all males had similar levels of energy and hormones (Ettinger & King 1980). Differences in weather conditions between recording sessions could affect song transmission by reducing signal propagation or signal quality (Forrest 1994, Bradley & Mennill 2009). Thus, comparing songs recorded in different weather conditions may result in added varia-

tion, especially with respect to song features relating to power and frequency (Forrest 1994, Slabbekoorn *et al.* 2002). Consequently, we did not analyze these characteristics in this study. We had similar weather conditions during both recording sessions (see Methods section). This gives us confidences that weather variables did not greatly affect our results. An individual may vary many song features according to the motivational context (Collins 2004, Catchpole & Slater 2008). We attempted to control for motivation related to mate attraction by surveying 20 m around each male for the presence of a female. Females were absent during the sample period, but this does not mean that before our arrival females were not present. The effect of female presence on male song characteristics and the latency of this effect on singing behavior are unknown. We acknowledge that female presence might have influenced our results, although individual variation in all song variables had a similar range.

In our preliminary spatial location analysis, we found that differences in song structure were greater between groups than they were within groups. This could be interpreted as males forming groups according to their own song characteristics, as has been seen in previous studies that showed that individuals that gather to sing are not randomly

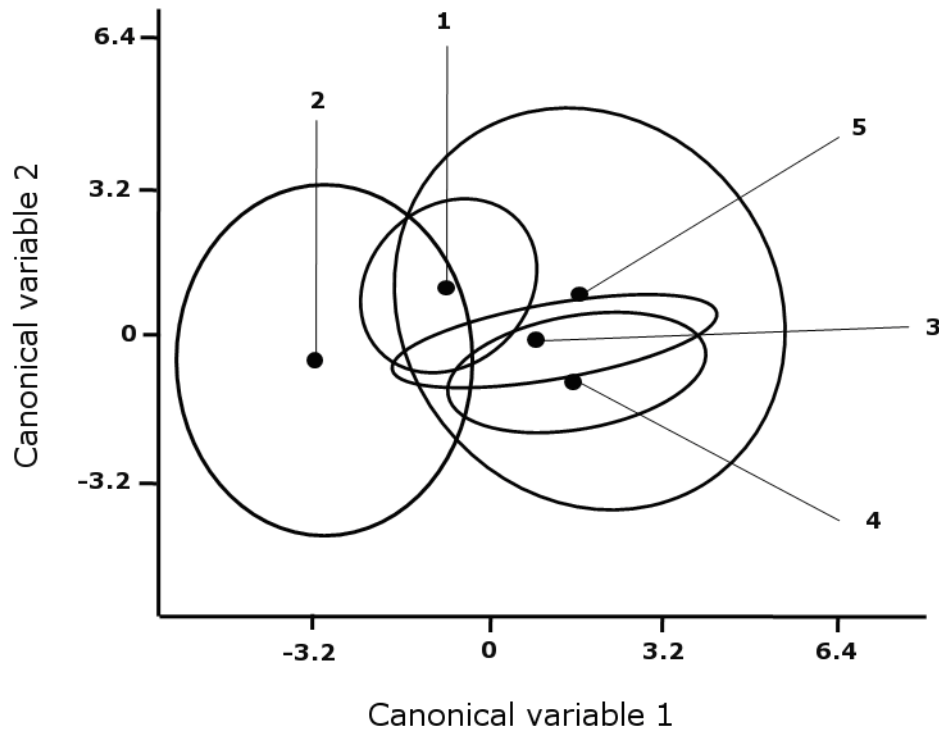


FIG. 2. Discriminant function analysis of five Common Pauraque (*Nyctidromus albicollis*) male groups, according to the song characteristics. The central points are the means of the centroid location and the circles are the 95% confidence interval for each group. Palo Verde National Park, Costa Rica, 3 and 4 April 2009.

distributed (Beecher *et al.* 1994, Beecher & Campbell 2005, Fitzsimmons *et al.* 2008). For example, in two species of *Colibri* hummingbirds, neighbors share song types, whereas distant neighbors do not (Gaunt *et al.* 1994). Similarly, in the Screaming Piha (*Lipaugus vociferans*) male song features vary according to a male's location in the lek (Fitzsimmons *et al.* 2008).

Alternatively, song structure could converge once groups are formed, which has been shown experimentally in Black-capped Chickadees (*Poecile atricapillus*) (Wilson & Menzies 2010), but this needs more study to be proven in Common Paurauques. The lack of data about female mate choice or male-male competition within this species makes our

results difficult to explain. More research is needed to determine if males benefit from singing in groups where males have similar songs, and why solitary singing males exist in the same population. A possible advantage is that singing in groups may increase song loudness, which would permit songs to propagate over greater distances (Wiley 2006). Alternatively, singing in a group could convey an advantage if males singing in groups are preferred by females. Another advantage is that this behavior apparently allows greater overall song production as a group per unit time (43.2 ± 15.6 group song min^{-1}), than solo males in this species (23.4 ± 2.4 male song min^{-1}), because males in groups alternated their song during the pauses of his neighbors.

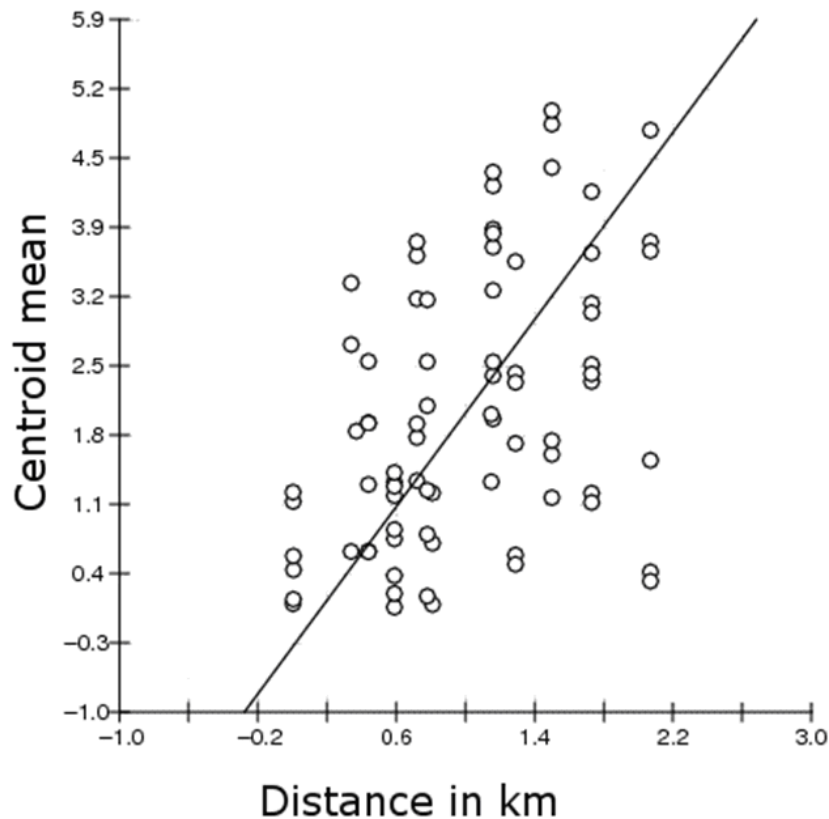


FIG. 3. Relationship between all pairwise comparisons between males in groups according to distance and song characteristics based on the centroid mean obtained from the first three canonical axes in a discriminant function analysis in males of the Common Pauraque (*Nyctidromus albicollis*) recorded at Palo Verde National Park, Costa Rica, 3 and 4 April 2009.

Singing at a high rate could increase the chance for females to approach the group, because high song rates are preferred by females in many bird species (Røedersater *et al.* 1987, Alatalo *et al.* 1990, Eens *et al.* 1991, Wasserman & Cigliano 1991). Females may also be attracted to male groups because they permit the simultaneous evaluation of several males at close range. However, singing in a group may be disadvantageous to males because the probability of pairing with a female that arrives decreases as a function of the number of males in the group.

We provide the first description of song variation inside a population for any Caprimulgidae species, and with a small number of song measurements we demonstrated a significant difference in song features among individual Common Pauraque males. Although we tried to control all the possible external causes of variation in song characteristics during the sample design and recording sessions, our conclusions are not definitive because we did not compare the song of the same individual between multiple recording sessions, as is proposed in the new approach

to demonstrate individual distinctiveness. The male variation we found could be used as a signal to allow recognition of individual males by females or by other males. We found that males in groups tended to sing songs with more similar characteristics than with distance groups. Further studies with banded males are necessary to determine whether females prefer particular male song characteristics, and whether female preferences might account for structural differences and song patterns of males of this species. Also, it is important to determinate the role of song in male-male interactions, how males form groups, and if these groups are stable through time.

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REFERENCES

- Alatalo, R., C. Glynn, & A. Lundberg. 1990. Singing rate and female attraction in the Pied Flycatcher: an experiment. *Anim. Behav.* 39: 601–603.
- American Ornithologists' Union (AOU). 1998. Check-list of North American birds. 7th ed. American Ornithologists' Union, Washington, D.C., USA.
- Araya-Ajoy, Y.-M., J. Chaves-Campos, E. K. V. Kalko, & J. A. DeWoody [online]. 2009. High-pitched notes during vocal contests signal genetic diversity in Ocellated Antbird. *PLoS One* 4(12): e8147.doi:10.1371/journal.pone.0008137.
- Barrantes, G., C. Sánchez, B. Hilje, & R. Jaffé. 2008. Male song variation of Green Violet-ear (*Colibri thalassinus*) in the Talamanca mountain range, Costa Rica. *Wilson J. Ornithol.* 20: 519–524.
- Beecher, M. D., S. E. Campbell, & P. K. Stoddard. 1994. Correlation of song learning and territory establishment strategies in the Song Sparrow. *Proc. Nat. Acad. Sci.* 91: 1450–1454.
- Beecher, M. D., & S. E. Campbell. 2005. The role of unshared songs in singing interactions between neighboring Song Sparrows. *Anim. Behav.* 70: 1297–1304.
- Bradley, D. W., & D. J. Mennill. 2009. Solos, duets and choruses: vocal behavior of the Rufous-naped Wren (*Campylorhynchus rufinucha*), a cooperatively breeding Neotropical songbird. *J. Ornithol.* 150: 745–753.
- Catchpole, C. K., & P. J. B. Slater. 2008. Bird song: biological themes and variations. Cambridge Univ. Press, Cambridge, Massachusetts, USA.
- Charif, R., C. Clark, & K. Frisrup. 2004. Raven 1.2 User's Manual. Cornell Laboratory of Ornithology, Ithaca, New York, USA.
- Chavarría, U., J. González, & N. Zamora. 2001. Árboles comunes del Parque Nacional Palo Verde. Editorial INBio, Heredia, Costa Rica.
- Collins, S. 2004. Vocal fighting and flirting: the functions of birdsongs. Pp. 39–79 in Marler, P., & H. Slabbekoorn (eds). *Nature's music, the science of bird song*. Elsevier Academic Press, San Diego, California, USA.
- Edwards, E. 1983. *Nyctidromus albicollis*. Pp. 590–592 in Janzen, D. H. (ed.). *Costa Rican Natural History*. Univ. of Chicago Press, Chicago, Illinois, USA.
- Eens, M., R. Pinxten, & R. F. Verheyen. 1991. Male song as a cue for mate choice in the European Starling. *Behaviour* 116: 210–238.
- Ellis, J. M. 2008. Decay of apparent individual distinctiveness in the begging callas of adult female White-throated Magpie-Jay. *Condor*

- 110: 648–657.
- Ettinger, A. O., & J. R. King. 1980. Time and energy budgets of the Willow Flycatcher (*Empidonax traillii*) during the breeding season. *Auk* 97: 533–546.
- Fitzsimmons, L. P., N. K. Barker, & D. J. Mennill. 2008. Individual variation and lek-based vocal distinctiveness in songs of the Screaming Piha (*Lipaugus vociferans*), a suboscine songbird. *Auk* 125: 908–914.
- Forrest, T. G. 1994. From sender to receiver: propagation and environmental effects on acoustic signals. *Am. Zool.* 34: 644–654.
- Fry, C. H. 1988. Skulls, songs and systematics of African nightjars. *Proc. Pan-African Ornithol. Congr.* 6: 105–131.
- Garrido, O., & G. B. Reynard. 1998. Is the Greater Antillean Nightjar, *Caprimulgus cubanensis* (Aves: Caprimulgidae), a composite Species? *Ornithol. Neotrop.* 9: 1–12.
- Gasser, H., A. Amézquita, & W. Höld. 2009. Who is calling? Intraspecific call variation in the arboreal frog *Allobates femoralis*. *Ethology* 115: 596–607.
- Gaunt, S. L. L., L. F. Baptista, J. E. Sánchez, & D. Hernández. 1994. Song learning as evidenced from song sharing in two hummingbird species (*Colibri coruscans* and *C. thalassinus*). *Auk* 111: 87–103.
- Gil, D., & M. Gahr. 2002. The honesty of bird song: multiple constraints for multiple traits. *Trends Ecol. Evol.* 17: 133–141.
- Hartshorn, G. S. 1983. Plants. Pp. 118–157 in Janzen, D. H. (ed.). *Costa Rican Natural History*. Univ. of Chicago Press, Chicago, Illinois, USA.
- Jensen, J. L., A. J. Bohonak, & S. T. Kelley. 2005. Isolation by distance, web service. *BMC Genetics* 6: 13. v.3.16 <http://ibdws.sdsu.edu/>
- Kroodsma, D. E. 2004. The diversity and plasticity of bird song. Pp. 108–131 in Marler, P., & H. Slabbekoorn (eds). *Nature's music: the science of birdsong*. Elsevier Academic Press, San Diego, California, USA.
- Kroodsma, D. E. 2009. *Birdsong by the seasons: a year of listening to birds*. Houghton Mifflin Harcourt. Boston, Massachusetts, USA.
- Larsen, C., M. Speed, N. Harvey, & H. A. Noyes. 2007. A molecular phylogeny of the nightjars (Aves: Caprimulgidae) suggests extensive conservation of primitive morphological traits across multiples lineages. *Mol. Phylogenet. Evol.* 42: 789–796.
- Lovell, S. F., & M. R. Lein. 2004. Song variation in a population of Alder Flycatchers. *J. Field Ornithol.* 75: 146–151.
- Marshall, J. T. 1978. Systematic of smaller Asian night birds based on voice. *Ornithol. Monogr.* 25: 1–53.
- Mees, G. F. 1977. Geographical variation of *Caprimulgus macrurus* (Aves : Caprimulgidae). *Zool. Verhandl.* 155: 1–47.
- Mills, A.M. 1986. The influence of moonlight on the behavior of Goatsuckers (Caprimulgidae). *Auk* 103: 370–378.
- Organization for Tropical Studies (OTS) [Online]. 2010. Meteorological data, GPS data and Hydrological data. Available at <http://www.ots.ac.cr/meteoro/default.php?pesta-cion=1> (15 March 2010).
- Quesnel, V.C. 1993. Patterns in the calling activity of the Pauraque Nightjar, *Nyctidromus albicollis*. *Living World, J. Trinidad Tobago Field Nat. Cl.* 1993–1994: 42–47.
- Rædesater, T., S. Jakobsson, N. Andbjer, A. Bylin, & K. Nystrom. 1987. Song rate and pair formation in the Willow Warbler, *Phylloscopus trochilus*. *Anim. Behav.* 35: 1645–1651.
- Sandoval, L. 2008. Función del canto y el territorio en machos de la codorniz de monte *Colinus leucopogon* (Odontophoridae: Aves) durante el periodo reproductivo. M. S. thesis, Univ. de Costa Rica, San José, Costa Rica.
- Sangster, G., & F. G. Rozendaal. 2004. Systematic notes on Asian birds 41. Territorial songs and species-level taxonomy of nightjars of the *Caprimulgus macrurus* complex, with the description of a new species. *Zool. Verhandl.* 350: 7–45.
- Schwartz, P. 1968. Notes on two Neotropical nightjars, *Caprimulgus anthonyi* and *C. parvulus*. *Condor* 70: 223–227.
- Slabbekoorn, H., J. Eilers, & T. B. Smith. 2002. Birdsong and sound transmission: the benefits of reverberations. *Condor* 104: 564–573.
- Stevenson, H.M., E. Einsenmann, C. Winegarner, & A. Karlin. 1983. Notes on Common and Antillean Nighthawks of the Florida Keys. *Auk* 100: 983–988.

- Stiles, F. G., & A. F. Skutch. 1989. A guide to the birds of Costa Rica. Cornell Univ. Press. Ithaca, New York, USA.
- Systat. 2004. SYSTAT 11. Systat Software, Chicago, Illinois, USA.
- Thurber, W. A. 2003. Behavioral notes on the Common Pauraque (*Nyctidromus albicollis*). Ornitol. Neotrop. 14: 99–105.
- Tobias, J.A., & N. Seddon. 2009. Signal jamming mediates sexual conflict in a duetting bird. Curr. Biol. 19: 577–582.
- Wasserman, F. E., & J. A. Cigliano. 1991. Song output and stimulation of the female in white-throated sparrows. Behav. Ecol. Sociobiol. 29: 55–59.
- Wiley, R. H. 2005. Individuality in songs of Acadian flycatchers and recognition of neighbours. Anim. Behav. 70: 237–247.
- Wiley, R. H. 2006. Signal detection and animal communication. Adv. Stud. Behav. 36: 217–247.
- Wilson, D. R., & D. J. Mennill. 2010. Black-capped chickadees, *Poecile atricapillus*, can use individually distinctive songs to discriminate among conspecifics. Anim. Behav. 79: 1267–1275.