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INDIVIDUAL VARIATION AND LEK-BASED VOCAL DISTINCTIVENESS IN SONGS OF THE SCREAMING PIHA (*LIPAUGUS VOCIFERANS*), A SUBOSCINE SONGBIRD

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Abstract.—One long-standing ornithological paradigm holds that song learning in oscine songbirds has a cultural component, whereas suboscine songbirds inherit songs genetically. Recent studies reveal that suboscine song may be more variable and complex than previously realized. Several suboscine species show marked individual variation in their songs—variation that may play a role in individual recognition and neighbor–stranger discrimination—and a few suboscine species show indications of song learning. We investigated individual variation in the vocalizations of a suboscine passerine, the Screaming Piha (*Lipaugus vociferans*), from recordings of 26 males at four lek sites along the Tambopata River in Peru. Male Screaming Piha songs consist of quiet introductory syllables followed by two explosively loud syllables that sound like an emphatic *pee haw*. We used three complementary methods to examine variation in song characteristics. Spectrogram cross-correlation revealed significant consistency within individual males and variability among males. Analysis of fine structural characteristics revealed that all measured song features were significantly less variable within individuals than among individuals. Canonical discriminant analysis based on these 13 song features correctly classified 93.2% of songs by individual and 76.4% of songs by lek site. Our results indicate that there is sufficient consistency in song features within males and sufficient variation among males for identification of individuals on the basis of songs and, to a lesser extent, that song features vary with the lek site of the singer. We conclude that Screaming Pihas sing songs that are individually distinctive and bear a lek signature. *Received 24 July 2007, accepted 8 April 2008.*

Key words: individual variation, lek, *Lipaugus vociferans*, Screaming Piha, song learning, suboscine songbirds.

Variación Vocal Individual y Distinción de Arenas de Cortejo de acuerdo a los Cantos de *Lipaugus vociferans*, un Paseriforme Suboscino

Resumen.—Un paradigma que ha perdurado por bastante tiempo en la ornitología sostiene que en los paseriformes oscinos el aprendizaje del canto tiene un componente cultural, mientras que en los paseriformes suboscinos los cantos son heredados genéticamente. Estudios recientes han revelado que el canto de los suboscinos puede ser más variable y complejo de lo que se pensaba. Varias especies de suboscinos presentan una marcada variación individual en sus cantos—variación que puede tener un papel en el reconocimiento individual y en la discriminación de vecinos extraños—y unas pocas especies de suboscinos presentan algunas indicaciones de aprendizaje del canto. Investigamos la variación individual de las vocalizaciones de un paseriforme suboscino, *Lipaugus vociferans*, con base en 26 grabaciones de machos pertenecientes a cuatro arenas de cortejo a lo largo del Río Tambopata en Perú. Los cantos de los machos de *L. vociferans* consisten de unas sílabas introductorias silenciosas seguidas por dos sílabas fuertes y explosivas que suenan como un enfático *pi ja*. Utilizamos tres métodos complementarios para examinar la variación en las características del canto. Análisis de correlación cruzada de espectrogramas demostraron que existe consistencia entre los cantos de cada macho y variabilidad significativa entre machos. El análisis de las características estructurales finas reveló que todos los caracteres del canto medidos fueron significativamente menos variables en un mismo individuo que entre individuos. Los análisis de discriminación canónica con base en 13 caracteres del canto clasificaron correctamente el 93.2% de los cantos por individuo y el 76.4% de los cantos por arena de cortejo. Nuestros resultados indican que existe suficiente consistencia en los caracteres del canto de un mismo macho y suficiente variación entre diferentes machos para permitir la identificación de individuos con base en los cantos, y en menor grado, que los caracteres del canto individual varían con la asamblea de cortejo de origen del cantor. Concluimos que los individuos de *L. vociferans* emiten cantos que son distintos a nivel individual, y que presentan una marca propia de la arena de cortejo de origen.

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Suboscine songbirds (suborder Tyranni) constitute ~20% of the largest avian order, Passeriformes (Sibley and Monroe 1990). However, our knowledge of bird song and its functions is based almost exclusively on studies of oscine songbirds (suborder Passeri). Oscine and suboscine birds are typically distinguished by different systems of song development; learning is critical for normal development of song in oscines, whereas song appears to develop innately, without learning, in suboscines (Kroodsma 1984). Evidence for innate song development comes from the most intensively studied group of suboscines, the New World suboscine flycatchers (Kroodsma 1984). However, recent evidence suggests that vocal learning may have evolved relatively recently among the cotingas (Cotingidae), a family of suboscines that diverged from New World flycatchers ~35 mya and is largely confined to South America (Ohlson et al. 2007). Kroodsma (2005) provided compelling evidence for song learning in two cotinga species: the presence of vocal dialects that shift within a bird's lifetime in Three-wattled Bellbirds (*Procnias tricarunculata*) and the case of a Bare-throated Bellbird (*P. nudicollis*) learning a different species' song when tutored in captivity. These observations reveal that the taxonomic boundaries between learning and nonlearning passerines may be blurred and that cotingas may present a special system for evaluating whether learning is involved in song development in this large but under-studied suborder.

Song characteristics must vary substantially between individuals for vocal recognition or individual discrimination to be possible; among-individual variation must be high in relation to within-individual variation (Falls 1982). Individual variation has been demonstrated in many passerine species (reviewed in Falls 1982). However, evaluation of individual variation has been neglected in the songs of suboscine passerines. Most studies of suboscines lack large sample sizes of songs and quantitative analysis (reviewed in Lovell and Lein [2004b]; but see recent exceptions in Lovell and Lein [2004b] and Wiley [2005]). Recently, studies have begun to test for evidence of neighbor–stranger discrimination in suboscines, with mixed results. For example, there was no evidence of neighbor–stranger discrimination in Spotted Antbirds (*Hylophylax naevioides*; Bard et al. 2002), marginal evidence in Acadian Flycatchers (*Empidonax virescens*; Wiley 2005), and strong evidence in Alder Flycatchers (*E. alnorum*; Lovell and Lein 2004a). Working with suboscine Neotropical manakins, Trainer and McDonald (1995) demonstrated repeatable inter-individual differences in song production in Long-tailed Manakins (*Chiroxiphia linearis*). Taken together, these studies suggest that suboscine song may be more variable and complex than we have realized; individual variation, which may be used for individual recognition or neighbor–stranger discrimination, is likely important for many suboscine passerines.

One interesting group of suboscines is the cotinga genus *Lipaugus* (the pihas), which consists almost entirely of polygynous species that are sexually monomorphic and advertise with elaborate acoustic displays (Ridgely and Tudor 1994, Snow 2004, Ohlson et al. 2007). Like many cotingas, pihas follow a promiscuous, lek-based mating system where males advertise their position with extended periods of song (Snow 2004). The Screaming Piha (*Lipaugus vociferans*) is a gray thrush-sized bird that lives in the midstory and canopy level of rainforests in Amazonia and northeastern Brazil (Ridgely and Tudor 1994) and is regarded as one of the loudest birds on Earth, with an average sound-pressure level of 111.5 dB at a distance of 1 m (Nemeth 2004).

To quantify variation in the songs of Screaming Pihas, we recorded 26 males from four lek sites in the Amazonian lowlands of eastern Peru and conducted detailed spectrographic analyses of their songs. We used three complementary methods of analysis to examine variation in song characteristics: (1) spectrogram cross-correlation, (2) analysis of fine structure (detailed measurements of frequency and temporal characteristics), and (3) discriminant analyses. These analyses allowed us to determine whether variation in Screaming Piha songs may provide cues to individual identity and lek membership.

Methods

General Field Techniques

We recorded Screaming Pihas at the Explorer's Inn Research Station adjacent to the Tambopata National Reserve in western Amazonia, Madre de Dios, Peru (12°50'S, 69°17'W). Recordings were collected between 22 and 26 February 2007, between 0730 and 1300 hours, using directional microphones (Sennheiser ME66, ME67, MKH70) and solid-state digital recorders (Marantz PMD660). Males were clustered in four exploded leks, each separated from neighboring leks by ≥1 km. Males' positions within the leks were stable within the period of our recording sessions, allowing individual identification based on singing location (~40 m between neighboring males). After a recording session, we mapped the positions of males within the lek in relation to habitat features and other males, and we are confident that identification of unbanded individuals by location was reliable. Sampling of each lek usually occurred on the same day, and we moved from one male to the next, further ensuring that no individual was accidentally sampled twice. We recorded 524 songs from 26 males (range: 8–61 songs male^{-1}; mean ± SE = 17.58 ± 3.45 songs male^{-1}; lek A, $n = 4$ males; lek B, $n = 6$ males; lek C, $n = 3$ males; lek D, $n = 13$ males). We recorded 75–100% of resident males at each lek. For our detailed analyses, we included 10 songs from each individual, though two males sang only eight songs during our recording sessions, resulting in 9.85 ± 0.11 songs male^{-1} included in the analyses. If we had >10 songs recorded for a male, we selected the 10 songs with the highest-quality recording (songs with no overlap by neighboring birds and minimal background noise).

Sound Analysis

Spectrogram cross-correlation.—We conducted cross-correlation for the 8 or 10 songs recorded from each of the 26 males (256 songs in total). We filtered the recording of each song to reduce background noise outside the frequency range of Screaming Piha songs (high-pass frequency: 450 Hz; low-pass frequency: 6,000 Hz), and we normalized the amplitude of each song to –1 dB in AUDITION (Adobe, San Jose, California). We performed spectrogram cross-correlation analyses in SASLAB PRO (Avisoft Bioacoustics, Berlin; 450 Hz high-pass cutoff frequency; 50 Hz maximum frequency deviation; 0.3 identification threshold). We correlated one template song for each male against all 255 other songs. In selecting template songs, we chose the best-recorded song for each male that had exactly two introductory syllables and two complete *pee haw*
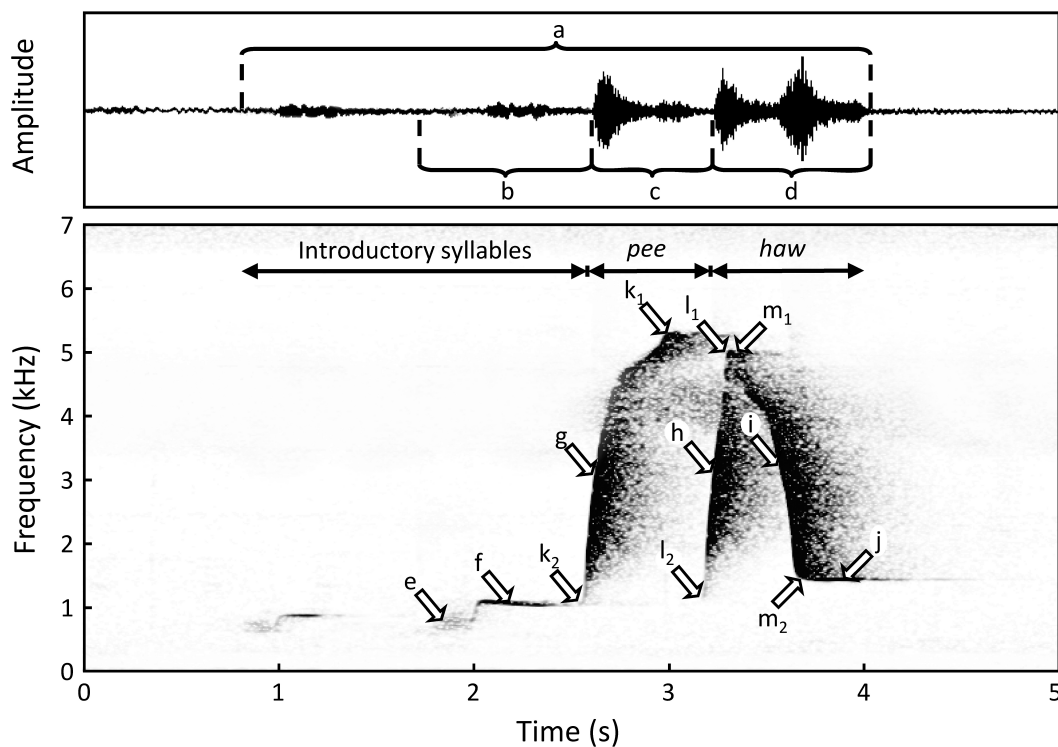
Fig. 1. Waveform and spectrograph depicting a typical Screaming Piha song recorded along the Tambopata River, Peru, highlighting the 13 song features measured in the present study. Letters correspond to time (a–d) and frequency (e–m) features used to evaluate individual- and lek-level variation in songs (see text for measurement descriptions).

syllables; this was the most common song variant and the only variant recorded from every male (see below).

Fine structural measurements.—Sounds were measured in SASLAB PRO using a frequency resolution of 22 Hz and a temporal resolution of 2.9 ms (FFT: 1,024 points; 75% frame size). We measured the fine structure of 13 song features (letters refer to labels in Fig. 1): (a) length of the entire song; (b) length of the last introductory syllable; (c) length of the *pee* syllable; (d) length of the *haw* syllable; (e) frequency of maximum amplitude (FMA) of the lower-amplitude, lower-frequency first half of the last introductory syllable; (f) FMA of the higher-amplitude, higher-frequency second half of the last introductory syllable; (g) FMA of the *pee* syllable; (h) FMA of the ascending portion of the *haw* syllable; (i) FMA of the descending portion of the *haw* syllable; (j) FMA of the tonal, terminal portion of the *haw* syllable; (k) bandwidth of the *pee* syllable (frequency at the highest-frequency portion of the *pee* syllable minus the frequency at the beginning of the *pee* syllable); (l) bandwidth of the ascending portion of the *haw* syllable (frequency at the highest-frequency point of the *haw* syllable minus the frequency at the beginning); and (m) bandwidth of the descending portion of the *haw* syllable (frequency at the highest-frequency point of the *haw* syllable minus the frequency at the point where the *haw* syllable levels out). The start and end time of song elements were determined using SASLAB PRO's automatic parameter measurements (settings: –22 dB relative to maximum amplitude, hold time 500 ms).

Coefficients of variation.—We calculated the mean ± SE for all 13 fine structural characters across the 8 or 10 songs measured for each male. We used coefficients of variation (CV) to quantify the magnitude of variability for each song characteristic. We calculated among-male coefficients of variation (CV_a) and within-male coefficients of variation (CV_w) and conducted analyses of variance (ANOVAs) on each of the 13 characteristics to compare among- and within-male variability. The ratios of among- to within-male coefficients of variation (CV_a/CV_w) were used as a measure of relative among-male variability for each song feature. A CV_a/CV_w ratio >1.0 indicates that a particular song feature is more variable among than within individuals and could potentially be used as a cue of individual identity.

Discriminant analyses.—We used canonical discriminant function analysis on the 13 song measurements to determine whether songs of individual males and lek sites could be classified on the basis of fine structural measurements. All statistical analyses were conducted in JMP, version 5.1 (SAS, Cary, North Carolina); all tests were two-tailed. Significance threshold for comparisons of 13 fine structural characteristics was adjusted to 0.0038 to correct for multiple comparisons. All values are presented as means ± SE.

Results

The songs of Screaming Pihas typically began with low-amplitude introductory syllables that consecutively rose in pitch, escalating to an explosive two-syllable *pee haw* phrase (Fig. 1). The namesake terminal phrase contains a rapidly ascending,

frequency-modulated *pee* syllable and a complex *haw* syllable that features three components: an ascending frequency-modulated portion, a descending frequency-modulated portion, and an unmodulated terminal portion. On average, males sang 2.04 ± 0.40 min^{-1}, and song rate showed a significant negative relationship with time of day ($R^2 = 0.16$, $n = 26$, $P = 0.046$). Songs featured variable numbers of low-amplitude introductory syllables, ranging from one to four, though two introductory syllables was most common (Fig. 2). All individuals varied the number of introductory syllables within a song bout, such that the number of introductory syllables was not obviously individually distinctive. Occasionally, males omitted portions of the song by dropping entirely the introductory syllables, the *haw* syllable, or the entire *pee haw* phrase. Males frequently sang isolated introductory syllables that did not escalate into the full song, at an average rate of 4.14 ± 0.81 isolated introductory syllables min^{-1}. Example songs of 12 males from three different leks are shown in Figure 3.

Spectrogram cross-correlation.—Spectrogram cross-correlation scores were significantly higher within males than among males (within-male score: 0.71 ± 0.01; among-male score: 0.56 ± 0.01; Wilcoxon matched-pairs signed-ranks test: $W = -175.5$, $n = 26$, $P < 0.0001$). There was no relationship between a male's spectrogram cross-correlation score for his own songs and his spectrogram cross-correlation score for the songs of other males ($R^2 = 0.0012$, $n = 26$, $P = 0.86$). The spectrogram cross-correlation scores for a male compared with other males within his lek site (0.57 ± 0.01) were not significantly different from those for a male compared with males in other leks (0.56 ± 0.01; Wilcoxon matched-pairs signed-ranks test: $W = -41.5$, $n = 26$, $P = 0.30$).

Coefficients of variation.—The ratio of the CV among males (CV_a) to the CV within males (CV_w) revealed that all 13 song features were more variable among males than within males (sign test: $P = 0.0002$). The variability was significantly greater among males for each of the 13 song features individually (ANOVA: all
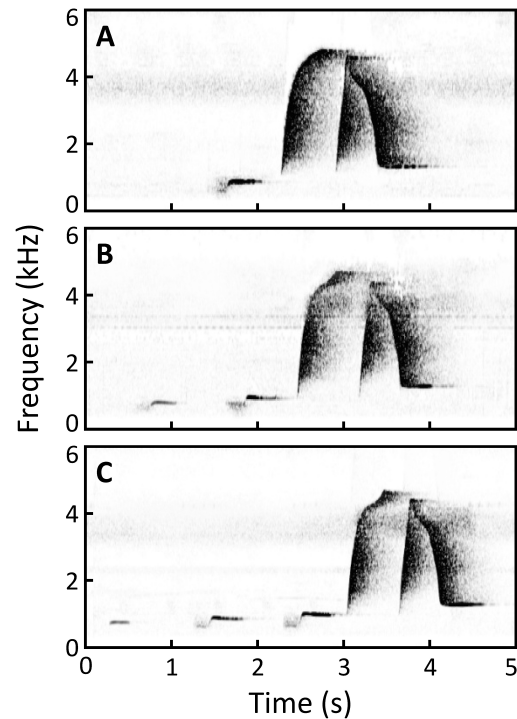

FIG. 2. Three examples of typical Screaming Piha vocalizations recorded from one individual male along the Tampbopata River, Peru, demonstrating variation in the number of low-amplitude introductory syllables given before the *pee haw* syllables.

$F > 3.13$, all $P < 0.003$; see Table 1), which demonstrates that all measured song features could potentially encode information about individual identity.

TABLE 1. Fine structural characteristics of Screaming Piha songs are significantly more variable among males than within males, as revealed by analysis of coefficients of variation (CV) for 13 variables measured for 8–10 songs each for 26 Screaming Pihas.

Variable	Mean ± SE	Mean CV_a (%)	Mean CV_w (%)	Ratio CV_a/CV_w	F ratio[a]
Length of entire song (a)	3.19 ± 0.030	15.14	12.36	1.22	3.27
Length of last introductory syllable (b)	0.74 ± 0.006	13.97	9.05	1.54	5.67[b]
Length of *pee* syllable (c)	0.59 ± 0.002	5.10	1.37	3.72	87.40
Length of *haw* syllable (d)	0.92 ± 0.005	8.12	6.22	1.30	6.53
FMA start of introductory syllable (e)	789.36 ± 3.260	6.55	5.13	1.28	4.69[c]
FMA end of introductory syllable (f)	1,158.50 ± 5.303	7.28	4.55	1.60	10.02[d]
FMA of *pee* (g)	2,961.80 ± 40.205	21.72	15.76	1.38	3.62
FMA upsweep of *haw* (h)	2,843.79 ± 17.649	9.93	8.69	1.14	3.13
FMA downsweep of *haw* (i)	2,908.88 ± 14.000	7.70	6.47	1.19	3.59
FMA tail of *haw* (j)	1,452.34 ± 1.577	1.74	0.56	3.10	62.49
Bandwidth of *pee* syllable ($k_1 - k_2$)	4,264.10 ± 12.793	4.78	1.35	3.54	91.92
Bandwidth of *haw* upsweep ($l_1 - l_2$)	3,955.04 ± 10.265	4.15	1.55	2.68	51.51
Bandwidth of *haw* downsweep ($m_1 - m_2$)	3,760.94 ± 8.326	4.94	1.05	4.70	91.56

[a] F values for ANOVAs comparing among- and within-male variation for each variable; all F ratios are significant at $\alpha = 0.05$ when Bonferroni corrected to $P \leq 0.0038$ across 13 comparisons. Degrees of freedom are 25 and 230 for all variables except the three measurements of introductory syllable characteristics because some songs were given without introductory syllables.
[b] df = 25 and 224.
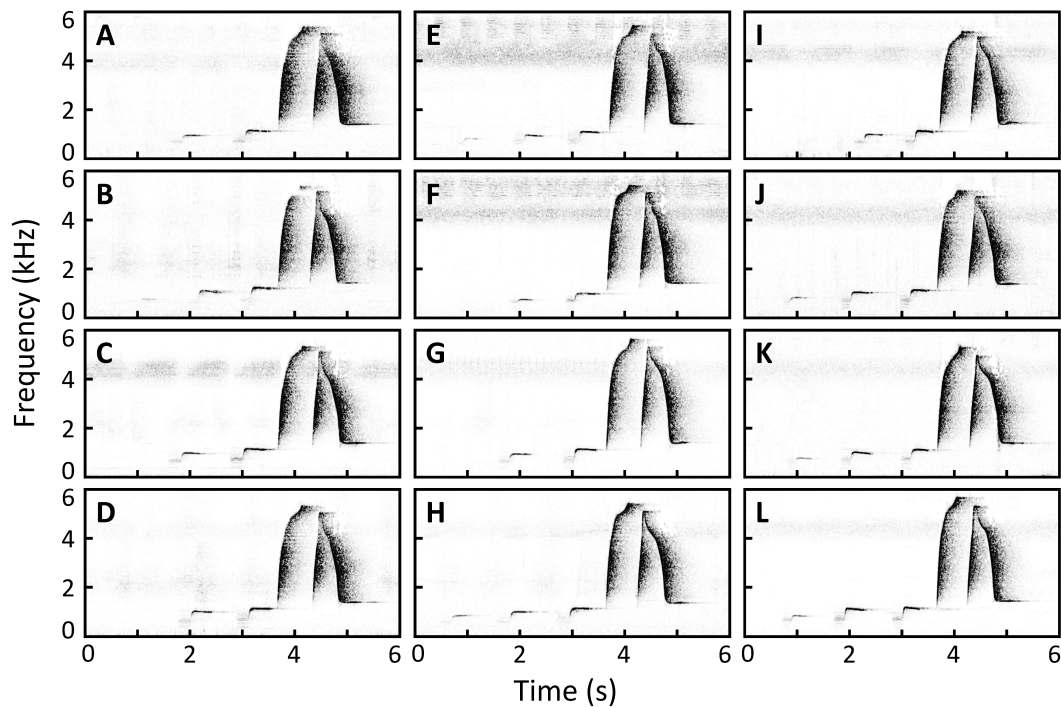[c] df = 25 and 226.
[d] df = 25 and 227.

FIG. 3. Sound spectrograms of songs of 12 male Screaming Pihas. Males depicted in spectrograms A–D are from a common lek, males E–H are from a second lek, and males I–L are from a third lek.

Discriminant analyses.—Canonical discriminant function analysis based on 13 fine structural features assigned 93.2% of songs to the correct male, well above the level of chance correct assignment of 3.8%. Variables with strong loadings on the first and second canonical axes for this individual-level discriminant analysis were length of the *pee* syllable and bandwidth of the descending portion of the *haw* syllable. A second canonical discriminant analysis assigned 76.4% of songs to the correct lek, well above the 25% level of correct assignment expected by chance. Variables with strong loadings on the first and second canonical axes for this lek-level analysis were length of the *pee* syllable, bandwidth of the *pee* syllable and both of the frequency-modulated portions of the *haw* syllable, and frequency of the terminal portion of the *haw* syllable.

DISCUSSION

Three complementary methods of acoustic comparison demonstrate that Screaming Pihas sing individually distinctive songs. Spectrogram cross-correlation reveals that within-individual cross-correlation scores are significantly higher than among-individual cross-correlation scores, fine structural analysis demonstrates that all measured song characteristics are significantly more variable among males than within males, and discriminant analyses confirm that song structure is sufficiently distinctive to permit discrimination of individuals and their leks of origin. These results indicate that there is sufficient consistency of song features within males, and sufficient variation among males, for reliable differentiation among songs of individuals and, to a lesser degree, their lek.

In many passerine species, songs facilitate individual recognition by conspecifics via distinctive structural features (reviewed in Stoddard 1996). In Screaming Pihas, we found that length of the *pee* syllable and bandwidth of the *haw* syllable were important features in discriminating singer identity, though all 13 features that we measured showed high potential for contributing to individualization. Given that distinctiveness establishes the limit on recognition, individual recognition seems plausible in the songs of Screaming Pihas, and variation among males seems sufficient to permit individual recognition of neighboring birds. Playback studies, possibly using the classic neighbor–stranger discrimination paradigm (Stoddard 1996), may confirm that birds use this variation to help distinguish between individuals. Given that male Screaming Pihas broadcast songs from positions within exploded leks, we feel that neighbor–stranger discrimination may benefit males by allowing them to monitor the activities of neighboring males. During our recording sessions, males moved around small areas within their exploded leks, routinely revisiting the same song perches. Although their songs likely play an important role in female attraction, their songs may also play an important role in regulating the spacing between males and defending the small display areas within leks.

Individual differences in song features cannot necessarily be interpreted as evidence of vocal learning; differences in song characteristics could arise from individual differences in physical or developmental constraints or from genetic differences among individuals (Gil and Gahr 2002). However, song learning may have recently evolved in polygynous, lekking cotingas, such as bellbirds and pihas, because of strong competition between males for copulations and strong female preference for

male song features (Aoki 1989, Kroodsma 2005). Alternatively, contextual learning, the association of a pre-existing signal with a new context as a result of experience (Janik and Slater 2000), allows individual discrimination based on vocal cues; it seems likely that Screaming Pihas and other suboscines are capable of contextual learning from social interactions. Recent evidence (Kroodsma 2005, present study) reveals that the study of cotinga song is a promising avenue for the study of individual variation, individual recognition, and, perhaps, the evolution of song learning in suboscine passerines.

All three of our analytical methods paint a complementary picture with respect to vocal variation at the level of the individual. However, spectrogram cross-correlation and discriminant analysis yielded different results for variation at the level of the lek. Spectrogram cross-correlation scores within leks were not significantly different from spectrogram cross-correlation scores between leks, whereas discriminant analysis capably differentiated songs from the four different leks. Discriminant analysis based on detailed fine structural measurements is likely the more sensitive of these two approaches; in discriminant analysis, subtle differences can assist in differentiation, whereas these subtleties may be lost in the gestalt approach of spectrogram cross-correlation. We therefore interpret our results as suggesting that variation between males at different leks is small, but present. How within-lek vocal similarities arise in the songs of pihas is an interesting question for future research. This phenomenon could arise if males join the leks of related males, as is seen in some lekking birds (e.g., Höglund et al. 1999, Petrie et al. 1999) though not in others (e.g., DuVal 2007, Loiselle et al. 2007). Alternatively, it may arise because individuals modify or learn their songs on the basis of features of established males in the leks where they ultimately settle.

Our results demonstrate significant differences in song features between individual male Screaming Pihas. The present study is one of the first to document individual variation in songs of a suboscine passerine using quantitative methods. Although recent evidence is compelling, raising young birds in a laboratory environment in isolation of tutors, following the classic protocol of Kroodsma (1984), is an important area for further evaluation of whether songs are learned or innate in cotingas. Future studies should record individuals over multiple years and at different geographic sites and conduct playback experiments to determine whether Screaming Pihas discriminate between individuals using vocal cues. Perhaps because suboscine song is believed to develop normally without learning, most descriptions of suboscine song variation have not been as thorough as those of oscine song. Much more research is needed on this suborder before we can begin to fully understand the evolution and origins of vocal learning. Our finding that Screaming Pihas sing individually distinctive songs adds to growing evidence that there may be a learned component to song in some suboscines and demonstrates that replicated and detectable individual variability exists in this suborder.

ACKNOWLEDGMENTS

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