Chorus Song of the Indri (*Indri indri*: Primates, Lemuridae): Group Differences and Analysis of Within-group Vocal Interactions

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The loud chorus songs of the group-living lemur *Indri indri* are a striking feature of rainforest areas of eastern Madagascar. Despite some research on the conspicuous vocal display of the indri, two hypotheses have not been addressed: do groups differ in the acoustic properties of their songs, and is there evidence of coordinated singing between individuals within groups. We recorded and analyzed the songs of three indri groups to examine these two questions. To answer the first question, we made quantitative spectral measures on songs of the three groups and performed multivariate analyses of the acoustic features of the notes constituting the songs. Our results showed songs of the three groups differed significantly, although there was overlap between groups. To answer the second question, we classified note types and quantified their occurrence as overlapping and abutting pairs. We found non-random associations between sequential note types in all three indri groups. These associations were consistent among groups, suggesting that individuals follow consistent answering rules when contributing to choruses. Whether indris use acoustic group identifiers in management of behavioral strategies and how within-group coordinated note production might function remain unknown. We compare our results to a number of taxonomically diverse species that live in groups and broadcast chorus and duet vocal signals.

A number of mammalian and avian species live in communal social groups and broadcast group vocal choruses (Baker, 2009; McComb, Packer, & Pusey, 1994; Mech, 1970; Seddon, 2002). The indri (*Indri indri*) is a group-living and vocal chorusing lemur species occupying rain forest habitat in eastern Madagascar. Groups range in size from about 2-6 individuals, comprising an adult breeding pair and up to several subadult offspring (Pollock, 1975, 1979). A group occupies a defended area (Pollock, 1986) on the order of 25 ha (Glessner & Britt, 2005), and like group territories in a number of bird and mammal species, the great majority of foraging and social behavior is carried out within the territory (Pollock, 1977). Previous studies have suggested chorus singing is involved in territory defense (Geissmann & Mutschler, 2006; Pollock, 1986).

Singing behavior, occurring principally in the morning (peak 0800-0930 hrs, Geissmann & Mutschler, 2006), consists of a series of notes constituting a group chorus. The song is sung by several, if not always all, of the members of a given group. Songs tend to be about a minute in duration, although some can be up to 2-3 minutes long, during which there is a constant

emanation of sound from the group (Figure 1). In a song of a minute duration there are about 30 notes uttered by the group. The chorus is a loud signal that humans can hear as far as 2-4 km away from the vocalizing group (Maretti, Sorrentino, Finomana, Gamba, & Giacoma, 2010; Pollock, 1986). Songs from one group can be easily heard by neighboring indri groups; often one group's chorus elicits responses from other groups (Giacoma, Sorrentino, Rabarivola, & Gamba, 2010).

When studying group vocal signals in a species, an important early goal is to understand the structure of the signal: the frequency and temporal properties of the constituent acoustic elements and the way they are organized in the chorus delivery. We examine signal structure in two ways (1) variation between groups (potentially raising questions about information content and function), and (2) structural/syntactical regularities within and across groups. Thus, our first hypothesis is that chorus songs contain information that could convey group identity. To date, no indri research investigated whether acoustic properties of indri songs differ between groups. If differences occur between several neighboring groups in an area, it is possible that the song communicates group identity, not simply occupancy of an area (Baker, 2004, 2009).

Our second hypothesis is that there is structure within a song that implies vocal interactions between individuals. Although a previous study has suggested individuals seem not to coordinate their singing (Pollock, 1986), anecdotal evidence from other research identified instances of temporally coordinated vocalization by two members of a group, which the authors called 'duetting' (Haimoff, 1986; Thalmann, Geissmann, Simona, & Mutschler, 1993). No research has yet quantitatively examined within-group song structure to substantiate such coordination. During an indri song, notes of two group members often overlap, or the notes of two animals may occur sequentially with no temporal overlap. To test our second hypothesis, we tested for non-random associations between consecutive note types comprising overlapping and abutting note-pairs (Logue, 2007a; Thalmann et al.,1993).
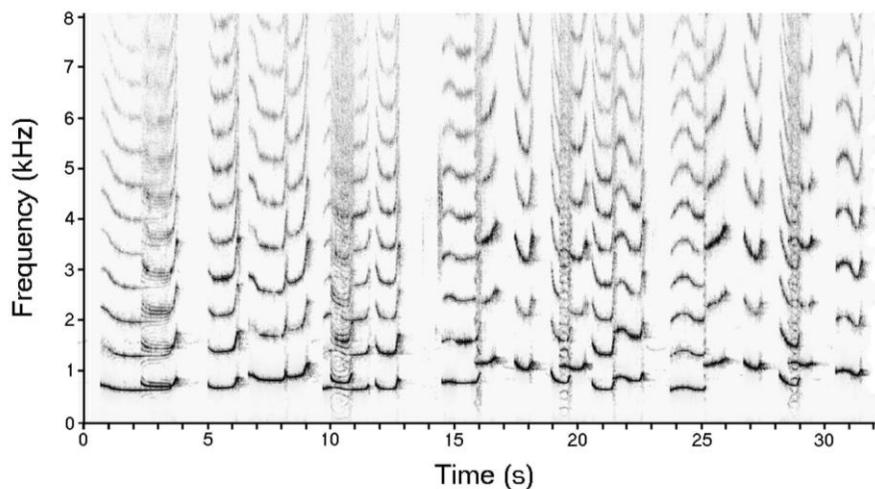
Figure 1. First 32 seconds of an indri song illustrating the approximately 10 harmonics observed in an 8 kHz sound window. Several cases of overlapping and abutting notes are present in this song segment of 21 notes. Introductory "bark" notes not illustrated at the onset of this song.

Method

Location and Subjects

Baker-Médard collected behavioral observations and audio recordings of 3 indri groups (Groups 1-3) at the Analamazoatra Reserve from 1-28 November 2003. Established in 1970, the reserve (also called Perinet) is located approximately 100 km east of Antananarivo and includes 810 ha of primary and secondary rainforest. The field work comprised 75 hrs of contact with the subjects including behavioral observations and tape recording. Two guides who knew the sex-age composition and territory ranges of the three groups aided in observations and data collection. Individuals within each group were identified by pelage color and patterns as well as body shape and size. This short-term study provides a 'snapshot' of chorus singing in the three indri groups. There was no opportunity to cover possible seasonal changes in the indri communication system.

The three groups were contiguous in an approximately linear configuration. Each group comprised five individuals ranging in age. Group 1 consisted of one adult female, one adult male, two juvenile females, and one ~18 month old male. Group 2 consisted of one adult female, one adult male, one juvenile female, one juvenile male, and one ~8 month old male. Group 3 consisted of one adult female, one adult male, one juvenile female, one juvenile male, and one ~6 month old female. We did not observe individuals under one year of age contribute to a group chorus. Observation conditions were generally good, but a subject could at any time be partly hidden in foliage.

Recording and Data Extraction

Individuals ranged in distance from 2.5 m to 15 m to the recording device and generally did not move while vocalizing. Even though an individual uttering a song note might be out of direct viewing, its location in the foliage was easy to pinpoint for recording. We made no sound level measurements, but these long-distance signals are so loud we are confident that we recorded all notes of each song. Moreover, two groups occupying neighboring territories did not come together at their border area to sing. Groups were far enough apart, a minimum of 300 m, that it was easy to assign all recorded notes to the focal group. We made recordings with a Sony TCM-210DV cassette recorder and Sony condenser microphone (Sony Corp., New York, NY, USA) onto Maxell type I tape and later transferred to a PC using Real Time Spectrogram (Kay Elemetrics, now Kay Pentax, Montvale, NJ, USA) to create wave files. We filtered these files to remove low frequency noise (high pass cutoff 500 Hz) and carried out quantification using Sound Analysis Pro (v. 1.04, Tchernichovski & Mitra, 2004) for measurement of acoustic features. Adobe Audition (v. 1.5, Adobe Systems Inc., San Jose, CA, USA) provided spectral displays for the detailed visualization and classification of note types.

We extracted values of the acoustic features of indri notes from spectral derivatives of the sounds (Baker & Logue, 2003; Tchernichovski & Mitra, 2004; Tchernichovski, Nottebohm, Pesaran, & Mitra, 2000). The features we used were: (1) note duration, (2) harmonic pitch (a cepstrum estimate of the fundamental frequency), (3) FM (frequency modulation is the change in frequency with time), (4) AM (amplitude modulation is the change in the amplitude envelope with time and does not reflect amplitude associated with distance to the microphone), (5) mean frequency (average power across frequencies of the note), (6) goodness of pitch (how much of the sound energy is concentrated in the pitch), and (7) Wiener entropy (measure of the breadth and evenness of the spectrum of a sound: pure tones have low entropy, broadband 'noisy' sounds have high entropy). The structure of the features is not affected by the amplitude of the recording.

This analysis software (and the features measured) is designed to derive information from harmonically organized sounds like those of the indri song, and ideal for examination of possible differences between groups. Attention directed only to isolated fundamental frequencies of notes and ignoring harmonic structure would sacrifice considerable information in terms of how a song sounds to a neighboring group. Values of the features were extracted automatically across a note from a succession of narrow and overlapping time windows (data window 9.27 ms, advance window 1.36 ms) and saved to an Excel (2007, Microsoft Corp., Redmond, WA, USA) spreadsheet. Mathematical formulations of these acoustic features and details of their derivations are described in Tchernichovski and Mitra (2004) and Tchernichovski (2012).

Between-group Analysis

To test our hypothesis that indri songs differed between groups, we examined the songs of the three groups to determine if their overall acoustic structures differed. For this we used the measured features of constituent notes of each group's songs and performed multivariate analyses on the values. Our sample comprised 9 songs (392 notes) for group 1, 10 songs (374 notes) for group 2, and 5 songs (385 notes) for group 3.

In our recordings, any given indri song contained some notes in temporal isolation from other notes, but many notes occurred as "note-pairs" (842 cases overall) that overlapped or abutted each other. Overlapping pairs

included two notes that partially co-occurred temporally. Abutting pairs included two notes that temporally abutted at different frequencies, and pairs in which the two notes were contiguous. Abutting pairs were so close together (< 30 ms), we could not reliably measure a time lag between them with the software cursors. More rarely notes occurred in a complex of three notes (45 of 842 cases across the three groups), usually a longer note overlapped by two other notes.

We made measurements with Sound Analysis Pro of temporally isolated notes as well as two and three note complexes. These notes were the experimental units for the group discrimination analyses. Some individual notes and note complexes were partly masked by ambient noise and thus were not used for measurement of acoustic features, but were still used in classification of types of notes used in analysis of within-group song structure. The two- and three-note complexes formed a large proportion of an indri song (mean 73% of notes) and thus were also included in song characterization. Overlapping vocal phrases in some duetting bird species also constitute a large proportion of the collaborative song and may be an important part of group identity (Mann, Dingess, Barker, Graves, & Slater, 2009).

We used linear discriminant analysis (LDA) to quantify group differences in relation to the seven acoustic features. A given indri song comprises a population of notes represented in multivariate space, and we ask if the three indri groups (i.e., 'subjects' in the LDA) are discriminable when compared this way. We obtained assignment probabilities from LDA from jack-knifed cross-validation by the method of one-at-a-time omission. We examined suitability of the correlation matrices of the variables with the Kaiser-Meyer-Olkin test and the 'condition' by Bartlett's Sphericity Test. In all cases these tests indicated the matrices were not identity matrices and were suitable for multivariate testing.

Within-group Analysis

A large proportion of song elements occurred as note-pairs. Because the recording circumstances precluded identifying consistently and with certainty the subject uttering each note within the target group, we focused on two-note dyads (Figure 2) so we could be confident that two different animals were involved. A single animal's note production during a group song includes obvious pauses between its individual notes. An individual's inter-note intervals are clear and distinct (not abutting), ranging on the order of 0.75-1.5 s (Giacoma et al., 2010).
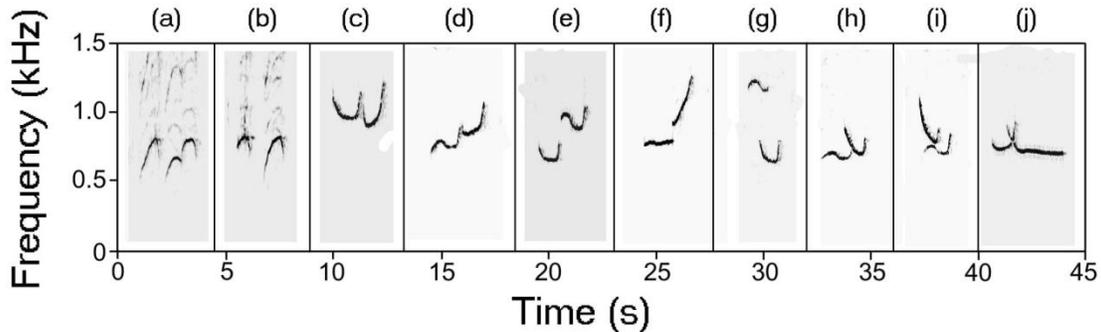

Figure 2. Examples of introductory 'barks' (a, b) that usually occur at the onset of an indri group song chorus but were not considered in our analyses. Abutting (c and d are contiguously abutting; e and f are temporally abutting) and overlapping (g-j) note pair examples used in our analyses of duet structure.

We defined seven classes of notes based upon patterns of frequency modulation (FM) observable on sound spectrograms, an approach used by a previous indri song study (Giacoma et al., 2010) and employed in numerous studies of bird songs (Catchpole & Slater, 2008; Marler & Slabbekoorn, 2004). Seven classes of notes were independently established by two researchers on separate occasions, thus affirming the validity of our note categorization. This visual classification of indri notes is a common and reliable analytical approach to describing vocal variation in indris (Giacoma et al., 2010; Haimoff, 1986; Thalmann et al., 1993). All FM-note types occurred across several frequencies, thus constituting a library of note classes with gradations within each class (Figures 3-5). The pattern of graded note classes (e.g.,, Figures 3-5) is found in many other primate vocalizations (Marler, 1976) as well as in some birds (Miller, 1979). Such a system of note "types" within which graded series occur was suggested earlier for indris (Thalmann et al., 1993).
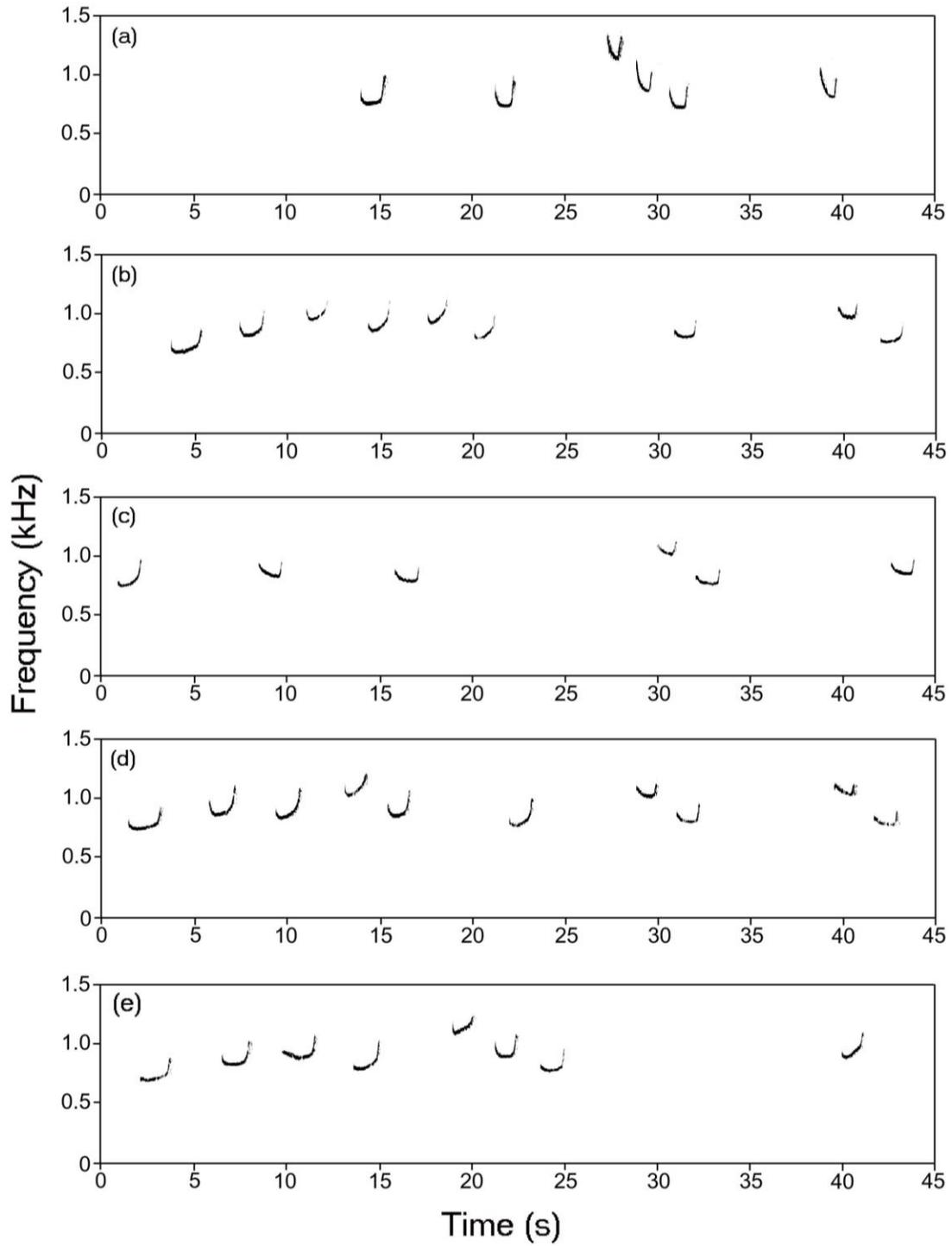
Figure 3. Examples of A-notes in five different indri songs (a-e). In these 45-s sound windows the A-notes are in the positions in which they occurred, but other note-types were deleted, as have harmonics, for the purpose of illustration this note type. The variation in this class of notes is apparent as is the characteristic grading we also found in other note types.

Figure 4. Examples of C-notes in 10 different indri songs (a-j). To illustrate a large number of this note type and the variation observed we isolated segments from 10 different songs, presented here in 5 sets to conserve space. Here too, non-C-notes and harmonics were deleted.
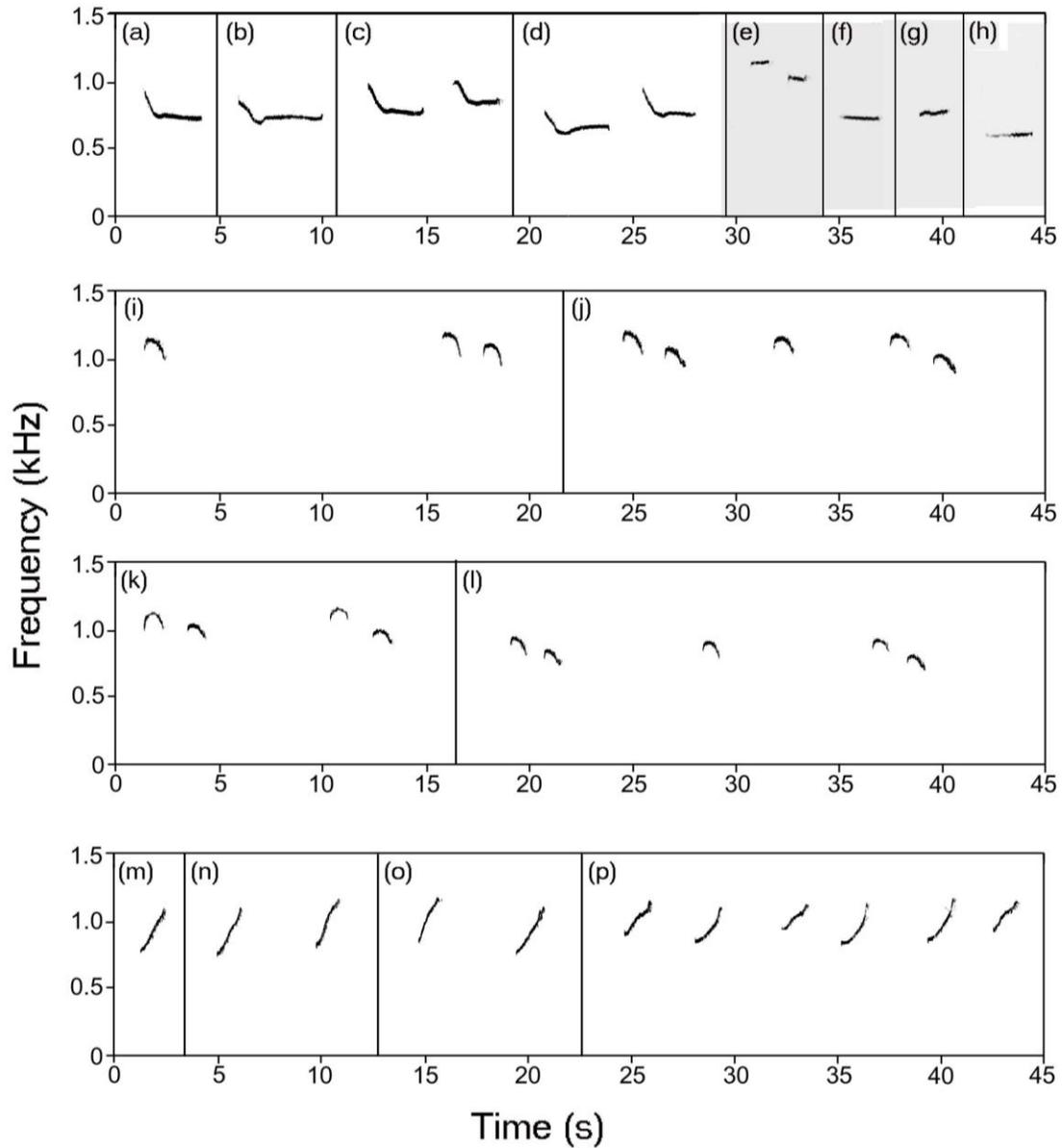
Figure 5. Examples of note types B (a-d), D (e-h) E (i-l) and F (m-p) in several indri songs. B-, D-, E-, and F-notes are not as commo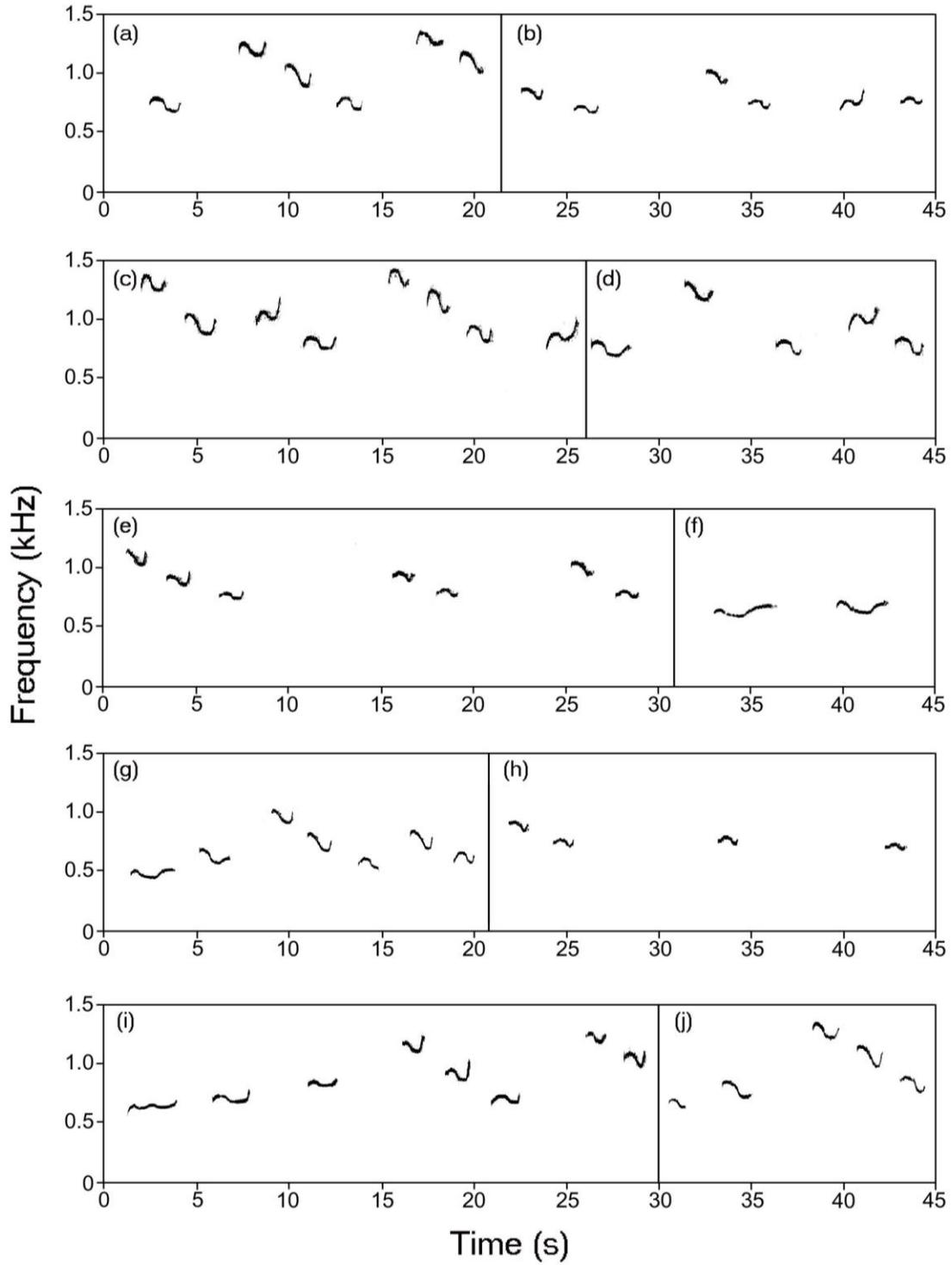n as are A- and C-notes. Thus the segments of sound within each of these 4 sets show either single notes of a given type or, in some cases we found several of a given type temporally close enough to each other to include more than one example of that type in its normal temporal pattern. A- and C-notes were deleted from these note-type examples as were the harmonics.

Of the seven classes of notes, we utilized six in our analysis, excluding the "barks" (termed "roar" or "waa" in some studies) that usually initiates a song. This note type was confined to the onset of a song and not involved in pairs of notes otherwise. Each note class is distinct from other classes (Figures 3-5). We arbitrarily assigned letters (A-F) to the six classes of notes included in our analysis. When viewed on a spectrogram A-notes are concave upward with a single inflection point, B-notes are L-shaped and of longer duration than most other note types, C-notes are wave-like

with two inflection points, D-notes are of constant frequency, E-notes are concave downward with a single inflection point, and F-notes are linear, or nearly so, increasing in frequency with time. Some F-notes tend to grade into the A-note class, with more of an exponential increasing frequency rather than a strictly linear increase. However, quantitatively, F-notes of both forms are comparatively rare, so we did not attempt to evaluate this possible distinction further.

To examine note-type associations, we tested whether indris combine note-types non-randomly when singing note-pairs. For each group, we generated a 6 x 6 matrix describing the observed frequency of all possible pairs of first notes and second notes. Pearson correlation analysis of partial Chi-square values revealed strong positive associations between the overlapping and abutting matrices for all three groups (for all three groups: $r > 0.55$, $df = 36$, $p < 0.001$). Thus, the patterns of note-type association in the overlapping note pairs were very similar to those in the abutting note pairs. We therefore pooled the overlapping and abutting data. We derived the Chi-square value associated with each matrix, which we called the "observed chi-square" (X^2_{obs}) value. Rather than relying on the assumptions of the classical chi-square hypothesis test, which can be biased when data are sparse, we used a Monte Carlo approach to generate a custom null distribution for each group. The Monte Carlo model simulates a group that utters the observed number of each type of first note and second note, but combines first and second notes randomly to form note-pairs. We used the randomly generated note-pairs to populate a 6 x 6 matrix, from which we derived a "simulated chi-square" (X^2_{sim}) value. This simulation was repeated 10,000 times to generate a null distribution of chi-square values. The proportion of the null distribution that was greater than or equal to the observed chi-square value defined the realized p-value. This procedure tests the null hypothesis that second notes are randomly assorted with respect to first notes. Because we were not able to identify the individual emitting each note, we designed this analysis to allow us to make inferences about note order (controlling for group identity), rather than individuals' decisions.

When our tests for non-random note-type associations produced statistically significant results, we then analyzed which specific note-type associations were more or less common than would be expected if indris combined notes at random. We identified these associations by running the same kind of simulations as described above, but focusing on the partial chi-square value in each cell of the matrix. The observed partial chi-square values were compared to null distributions of corresponding partial chi-square values generated by randomly combining notes over 10,000 randomizations. Finally, p-values were calculated based upon the region of the null distribution that was greater than or equal to the observed value. This procedure generated 108 p-values (6 rows x 6 columns x 3 groups), raising concerns about multiple testing. We therefore quantified the false discovery rate (FDR; Storey, 2002) associated with each hypothesis test. The false discovery rate, Q, is the expected proportion of false positives for which we consider a given p-value and all lower p-values to be statistically significant. We interpreted as significant those tests in which both p and Q were < 0.05. Estimates of Q were generated by the program 'QVALUE' (Dabney & Storey, 2004), using all default settings. Monte Carlo simulations were conducted with the PopTools (Hood, 2010) add-in for Microsoft Excel 2007 (Microsoft Corp., Redmond, WA).

Results

Group Differences in Chorus Songs

We conducted four analyses to examine acoustic differences between the three indri groups. In the first analysis we randomly selected one song from each group to form a set and then formed four additional sets randomly chosen (without replacement) from the remaining songs, thus controlling for song-within-group variation. We used LDA on each of the five sets. All five analyses showed the three groups to be significantly differentiated (Wilks' $\lambda = 0.225$, 0.197, 0.536, 0.388, 0.239; all p-values < 0.0001). Jack-knifed classifications were (proportion correctly classified in each set): 0.80, 0.83, 0.61, 0.61, 0.73; mean 0.72; expected values of 0.33 if assignments are random.

Second, to present visually the overall degree to which songs of the three groups clustered within groups and overlapped between groups we ran LDA on the combined song notes of the five songs from each of the three groups. This resulted in Wilks' $\lambda = 0.580$, $p < 0.0001$, jack-knifed proportion of notes correctly classified = 0.61, Figure 6). All three pairwise Hotelling's tests were significant as well: group 1 vs. 2, $p = 0.004$; group 1 vs. 3, $p = 0.002$; group 2 vs. 3, $p = 0.010$). The point plot (Figure 6) indicates that group 3 is somewhat more

differentiated from the other two than groups 1 and 2 are from each other. It is clear, however, that song notes do not occur in separate group-specific clusters in multivariate space. Instead there is considerable scatter of notes within groups and overlap between groups.

Third, to take advantage of all the data available and illustrate the total variation among the three groups, we ran LDA on all notes from all songs recorded for each group (group 1: 9 songs, 275 notes; group 2: 10 songs, 223 notes; group 3: 5 songs, 220 notes). This analysis also revealed significant differentiation of the three groups (Wilks' $\lambda = 0.613$, $p < 0.0001$; proportion correctly classified = 0.60). We inspected the weightings of each acoustic feature on the discriminant functions as well: Wiener entropy (0.89), goodness of pitch (0.78), frequency (0.68), amplitude modulation (0.52), pitch (0.34), syllable duration (0.24), and frequency modulation (0.18).

Fourth, to provide a comparison for the between-group results, we ran LDA on acoustic features of song notes within each group. Our reasoning was that if groups are to be discriminable by the notes of their songs then the accuracy of assignment of notes to songs within a group should be less than the accuracy of note-assignment to songs between groups. This is equivalent to saying that the within group variance in song structure is small relative to the between-group variance. We found the accuracy of assignment of notes to songs within groups was considerably less than that found for assignments between groups: within Group 1, 0.378; within Group 2, 0.296; within Group 3, 0.327.
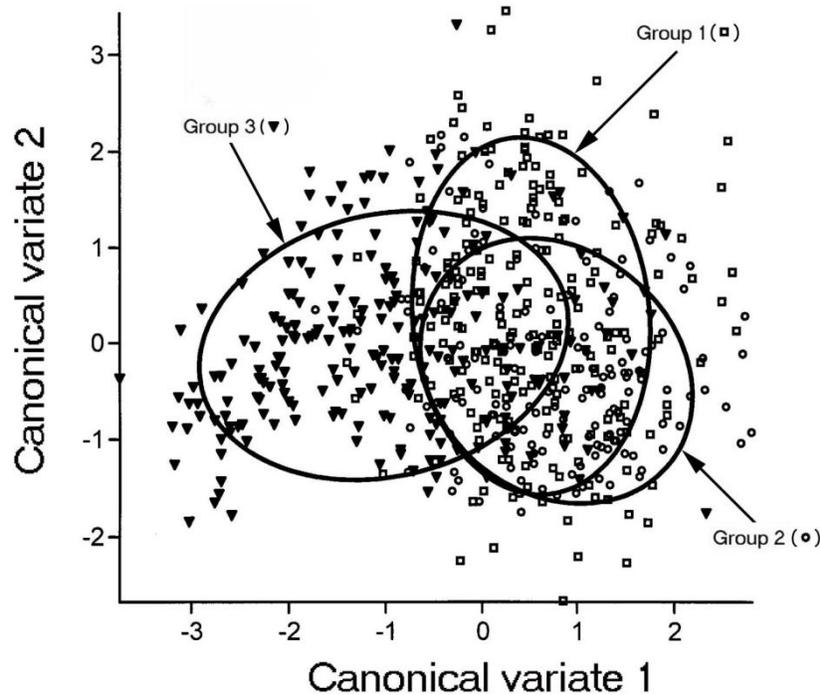

Figure 6. Scatterplot of locations of indri notes from songs of three groups along two canonical variates derived from multivariate linear discriminant analysis. Each group contributed 5 songs to this analysis. Solid ovals are 75% frequency ellipses for the notes of each of the groups.

Note-pairs in Indri Songs: Non-random Association of Note Types

Our tests for non-random note type associations were statistically significant in all three groups (Group 1: $N = 125$ note-pairs, $X^2_{obs} = 78.6$. Avg $X^2_{sim} = 25.34$, $p = 0.0007$; Group 2: $N = 154$. $X^2_{obs} = 74.9$, Avg $X^2_{sim} = 25.1$, $p = 0.0025$; Group 3: $N = 142$, $X^2_{obs} = 87.97$, Avg $X^2_{sim} = 25.17$, $p = 0.0133$). In all three groups, combinations A-C and C-A occurred more than expected by chance, and combinations A-A and C-C occurred less than expected by chance (Figure 7a-c). In Group 2, A-F occurred less than expected by chance. The patterns were very similar in all three groups, so we pooled the data and ran another analysis. A separate FDR control was applied to this analysis. The pooled analysis indicated the presence of eight non-random associations comprising four pairs of reciprocal associations (as an example of a reciprocal association, both A-F and F-A occurred at lower rate than would be expected from random associations; Figures 7d, 8). The note types that were non-randomly associated in the pooled data (A, C, and F) were also the most numerous notes in our sample.
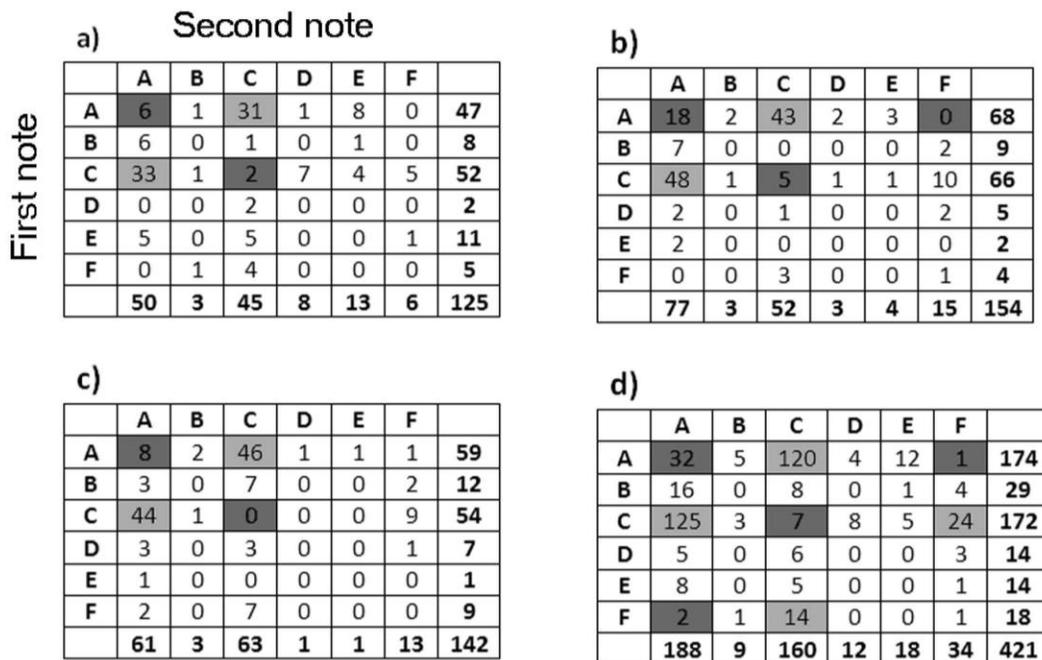
a) Second note / First note

	A	B	C	D	E	F	
A	6	1	31	1	8	0	47
B	6	0	1	0	1	0	8
C	33	1	2	7	4	5	52
D	0	0	2	0	0	0	2
E	5	0	5	0	0	1	11
F	0	1	4	0	0	0	5
	50	3	45	8	13	6	125

b)

	A	B	C	D	E	F	
A	18	2	43	2	3	0	68
B	7	0	0	0	0	2	9
C	48	1	5	1	1	10	66
D	2	0	1	0	0	2	5
E	2	0	0	0	0	0	2
F	0	0	3	0	0	1	4
	77	3	52	3	4	15	154

c)

	A	B	C	D	E	F	
A	8	2	46	1	1	1	59
B	3	0	7	0	0	2	12
C	44	1	0	0	0	9	54
D	3	0	3	0	0	1	7
E	1	0	0	0	0	0	1
F	2	0	7	0	0	0	9
	61	3	63	1	1	13	142

d)

	A	B	C	D	E	F	
A	32	5	120	4	12	1	174
B	16	0	8	0	1	4	29
C	125	3	7	8	5	24	172
D	5	0	6	0	0	3	14
E	8	0	5	0	0	1	14
F	2	1	14	0	0	1	18
	188	9	160	12	18	34	421

Figure 7. Pairwise associations of two note complexes in indri songs of three groups a) group 1, b) group 2, c) group 3), and d) pooled over all three groups. Row labels represent the first note of a note pair, column headings represent the second note of the pair, the numbers in each cell represent the observed frequency of that note combination, and the bold numbers on the border represent row and column totals. Dark grey shaded cells indicate pairs occurring less frequently than expected, light grey marks pairs that occurred more frequently than expected.
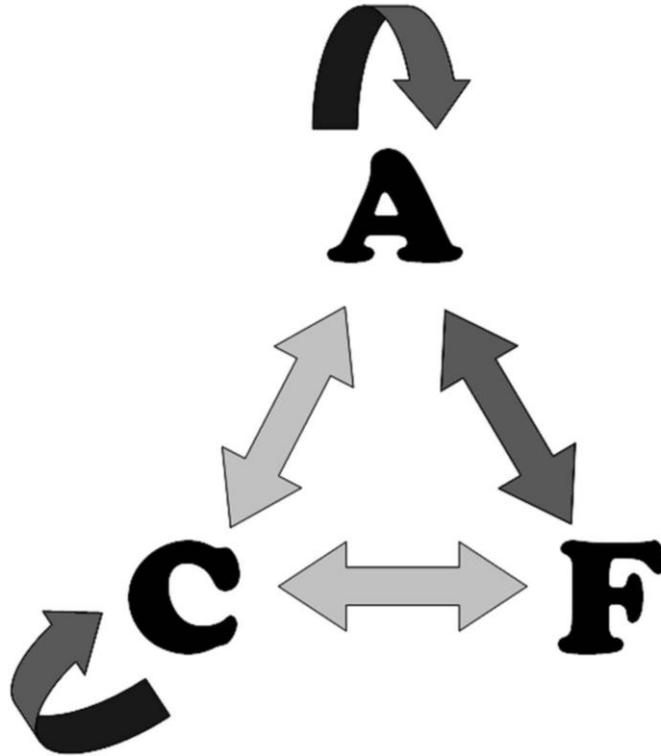
Figure 8. Flow diagram of associations between three indri note types occurring in pairs, based upon summation of all three indri groups. Eight non-random associations of notes are depicted. Double-sided arrows indicate reciprocal transitions between two different notes, and curved arrows represent a note's transition to itself. Light grey shaded arrows indicate note type pairs with significantly positive association, dark grey arrows with significantly negative associations.

Discussion

From our analyses we draw two conclusions. First, the quantitative approaches we used to evaluate acoustic differences between indri groups suggest the three groups were discriminable to a significant degree by the acoustic features of constituent notes of the songs. Although there was considerable scatter of note characteristics within groups, and overlap among the groups, the accuracy with which notes were classified to the correct song between groups was consistently greater than the accuracy with which notes were classified to the correct song within groups. This indicates songs within a group are similar, but differ from songs of other groups. Second, from our examination of the categorical classification of types of notes uttered in note-pairs, we found across all three indri groups a pattern of consistent and strong non-random associations between note types.

Group Differences

A number of group-living bird and mammal species produce vocal choruses (e.g., Baker, 2004, 2009; Bradley & Mennill, 2009; Harrington, 1989; Lehner, 1978; McComb et al., 1994; Mech, 1970; Pereira, Seeligson, & Macedonia, 1988; Seddon, 2002; Tenaza, 1976; Wiley &

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Wiley, 1977). In such species, more than two individuals are usually involved in producing a chorus, during which there may be some temporally distinct vocal units, and some overlapping vocal units. Although the structure of the vocal chorus itself exhibits considerable variation across species, a first-order question is whether choruses of the groups differ.

We found significant differences in chorus songs between the three sampled indri groups. As in the majority of studies of group chorus behavior, we do not know if the animals involved make similar discriminations. Nor do we know if the chorus reveals useful information on, for example, group size, age or sex of individuals in a group, although that is a frequent speculation. However, even in the few species in which sex-specific or group size information was demonstrated in the chorus, it is seldom determined if such information is used by an audience of other groups.

Two notable exceptions investigating information content of group chorus vocalizations showed numerical assessment of group size with playback field tests on female African lion prides (*Panthera leo*, McComb et al., 1994), and the subdesert mesite, a bird endemic to Madagascar (*Monias benschi*, Seddon & Tobias, 2003). In these cases, conspecific audience groups responded differently to playback of choruses of larger groups compared to choruses of smaller groups. In the lion case, Grinnell and McComb (1996) suggested an adaptive advantage to group chorusing because maternal lions in larger groups are better able to defend their cubs from infanticidal males than are smaller groups or single maternal lions. Such results encourage hypothesis testing on what kinds of information are encoded in group choruses of various species, but there are significant challenges inherent to this kind of research.

Given the emerging knowledge of group differences in indri choruses, together with possible sex-specific information contained therein (Giacoma et al., 2010), playback experiments on free living groups could bring useful advances, such as testing whether choruses function as keep-out signals or convey other kinds of information. Major impediments to conducting such experiments on indris are the potential risk to the animals and the ethical and logistical problems attendant to removal of a group, or certain individuals, and substituting their natural chorus with recordings (normal or altered) broadcast from a loudspeaker (Krebs, Ashcroft, & Webber, 1978). This latter paradigm of testing would be important given that playback with the natural group in place would likely produce misleading results (Pollock, 1986).

Within-group Singing Patterns

The second question we asked about indri choruses was whether there were organizational (syntactical) rules of note production within a chorus. Our results on non-random associations of note types demonstrated a strong pattern of two-note associations. The relevant note-pairs in these associations were the same in all three groups. We interpret this result to be analogous to the non-random phrase-type association characterizing duets in many bird species (Hall, 2009; Logue, 2005) as well as sex specific note type associations described in titi monkeys (Müller & Anzenberger, 2002).

Duet patterns in several primate species show that duetting tends to co-occur with social monogamy and territoriality (e.g., in several gibbons, *Hylobates* sp.; a langur, *Presbytis potenziani*; a tarsier, *Tarsius spectrum*; titi monkeys, *Callicebus*; and the indri) (Haimoff, 1986; Robinson, 1981). These cases, as well as recent work on duetting bird species, raise the hypothesis that the coordinated nature of the vocal duet by pair-mates represents cooperative defense of the territory, among other functions (Hall, 2004, 2009; Logue 2005, 2007a). If this hypothesis is true, then it may be possible to determine if the quality of duet performances signals

to conspecific audiences the group's resource holding potential or their willingness to escalate territorial defense (Hall & Magrath, 2007). At least one bird species appears to encode individual identity in the duet structure (Logue, 2006) and use duets to locate the pair-mate (Logue, 2007b), providing for even more refined cooperation between the pair.

As a general conclusion we see the production of a vocal signal (chorus) by a social group as presenting important research opportunities, with an ultimate goal of discovering functional significance. To that end our approach was to explore baseline questions, such as whether there are discernible song differences between groups. Our finding of non-random associations of note-types during chorus song also leads to enquiry on function. Does coordination in note production represent cooperation or conflict, and is it salient to inter- or intra-group dynamics? We hope our indri analyses will be useful in approaching such questions and will encourage similar work on other species that produce vocal choruses.

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