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Not just a pretty song: an overview of the vocal repertoire of *Indri indri*

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Summary - *The vocal behaviour of wild indris inhabiting the area near Andasibe was studied by means of all occurrence sampling. We provide a quantitative overview of the vocal repertoire of Indri indri, describing qualitative contextual information and quantitative acoustic analysis for all the utterances we recorded from adult individuals. Other than the song, the repertoire of Indri indri comprises 8 vocal types uttered by the adults. Future studies are necessary to explore whether vocalisations uttered in different contexts have different functions and how these functions relate to acoustic structure.*

Keywords - *Strepsirhine primates, Vocal behaviour, Acoustic structure, Ambient noise.*

Introduction

To investigate the relationship between vocal and non-vocal behaviour, it is crucial to analyse vocal signals making up the vocal repertoire of a species, to describe vocal types and, where possible, provide information regarding the variation of acoustic parameters between and within vocal types. The study of vocal repertoires can provide information about the factors that affect signalling and how vocal signals influence the behaviour of receivers, thereby indicating the function of the signals. Information concerning the acoustic structure and the context, or contexts, of vocal production can lay the foundation for further studies on a species, and provide researchers with the basic knowledge necessary for designing detailed studies on the relationship between vocal communication and social behaviour, or to perform cross-specific comparisons (Owings & Morton,1998; Owren & Rendall, 2001).

The indri (*Indri indri*) is a particularly interesting species for the study of vocal communication for at least three reasons. It lives in small family groups in lowland to mid-altitude primary and secondary rainforest of eastern Madagascar (Garbutt, 1999; Pollock, 1979), spending most of its time in the dense canopy. Each group has a relatively stable home range and shows exclusive territoriality. In order to regulate spacing between neighbouring groups in the forest, all group members emit a complex howling call, which can be broadcast over several kilometres.

In the present study, we aimed to provide a comprehensive overview of the vocal repertoire of the indri (*Indri indri*) with special attention to those utterances that do not occur during the indri song. Previous studies of the indri's vocal communication focussed their attention on the song (Pollock, 1975, 1986; Oliver & O'Connor, 1980; Haimoff, 1986; Thalmann *et al.,* 1993; Geissmann & Mutschler, 2006; Sorrentino *et al.*, in press). The indri song is a vocal display in which one or more individuals emit a sequence of notes separated by short pauses (Pollock, 1986). Songs last 40-250 s and are usually introduced by three or four "roars" uttered simultaneously by several members of a group (Pollock, 1986); then, one at a time, or sometimes in pairs, the members of the group produce a long "modulated howl" (Petter & Charles-Dominique, 1979), or "song proper" (Pollock, 1986). Previous investigators agreed that the main functions of indri songs are related to territorial announcement and defence (Petter *et al.*, 1977; Petter & Charles-Dominique, 1979; Pollock, 1986; Geissmann & Mutschler, 2006). We aimed at improving knowledge of the indri repertoire, providing a robust classification of the utterances based on quantitative acoustic descriptions as well as contextual information for each of the vocal types. Our hypothesis is that, as in other non-human primates, certain vocal types occur in several behavioural contexts, while others are strictly associated with particular contexts, or referential.

In the indri, as in most primates, phonation is usually the result of an expiratory airflow, which causes oscillation of the vocal folds to produce sounds. The acoustic correlate of the rate of vocal fold vibration is the fundamental frequency (F0) of the vocal signal. By changing the stiffness and length of the vocal folds, mammals (including humans) can modify the periodicity of vocal fold vibration and vary the F0 characteristics of a vocal sound over time.

Our second goal was to quantify the vocal flexibility of this species, analysing F0 variation quantitatively across the vocal types. We expected that, as for many non-human primates, F0 variation would be marked between different vocal types and limited within vocal type.

Materials and Methods

Study areas

We conducted the study in a mid-altitude montane rain forest near Andasibe, Madagascar. The small village of Andasibe lies between the capital Antananarivo and the east coast, ca. 30 km east of Moramanga. Previously covered with continuous forest, the region now has only fragments of forest (Dolch, 2003). We collected data in three different sites: the 810 ha Analamazaotra Reserve (18° 56' S, 48° 25' E); Mitsinjo Forest Station (18° 56' S, 48° 24' E), a 250 ha area 200 m from the border of the Analamazaotra Reserve; and Mantadia National Park, 10,000 ha situated 20 km from the other two sites (Powzyk & Mowry, 2003). The climate is humid with a mean annual rainfall of 1700 mm, a mean annual temperature of 18°C, and an atmospheric humidity >70%; elevation ranges between 850-1220 metres and mean canopy cover is 87.6 ± 4.3% (Stephenson, 1994; Powzyk & Mowry, 2003; Biebouw, 2009).

Data collection

We recorded the vocalisations of ten groups of indris. Six groups were recorded in Analamazaotra Special Reserve, one group in Mantadia National Park, and three groups in Mitsinjo Forest Station. Of these groups (Tab. 1), three were usually exposed to tourist groups (contributing for 38% of the study sample), and three more were seldom visited by tourists (contributing for 23%). The other four groups were habituated by V. S. before the beginning of the recording sessions (contributing for 39%). The total number of individuals recorded was 28: 14 males, 13 females, and one infant of unknown sex (Tab. 1). We observed and recorded only one group per day, for a total of 160 days. We usually followed the same group for a minimum of four consecutive days, during September-December of four consecutive years (2005-2008). We carried out survey walks daily from 06.00 h to 13.00 h.

For the purpose of this research we obtained research permits from Direction des Eaux et Forêts in 2005 (N° 197 /MINENV.EF/SG/ DGEF/DPB/SCBLF/RECH), 2006 (N° 172/06 /MINENV.EF/SG/ DGEF/DPB/SCBLF), 2007 (N° 0220/07 /MINENV.EF/SG/ DGEF/DPSAP/ SSE) and 2008 (N° 258/08 /MEFT/SG/ DGEF/ DSAP/SSE).

Tab. 1 - Composition of the study groups (2005-2008).

Group	Fieldsite	Number of recorded individuals	Composition	Number of recording sessions	Number of vocalizations per group
1R§	Analamazaotra SR	4	1AF; 2AM; [1SAF]*	25	512
2R§	Analamazaotra SR	3	2AM; 1JM	7	80
3R#	Analamazaotra SR	4	1AF; 2AM; [1AM]**	7	63
5R	Analamazaotra SR	2	1AM; [1AF]**	2	7
6R	Analamazaotra SR	3	1AF; 1SAF; 1AM	11	596
XR#	Analamazaotra SR	1	1AF	1	1
ASF§	Station Forestière	3	1AF; 1AM; 1JM	8	48
YSF#	Station Forestière	5	2AF; 1SAF; 1AM; 1I	14	313
WSF	Station Forestière	2	1AF; 1AM	5	40
1M	Mantadia NP	1	1SAF	3	10
		TOT. 28		TOT. 82	TOT. 1670

§ usually visited by tourists, # seldom visited by tourists.

Analamazaotra SR: Analamazaotra Special Reserve; Station Forestière: Station Forestière Mitsinjo; Mantadia NP: Mantadia National Park.

* departed since 2008, ** departed since 2007.

M = male, F = female, ? = sex unknown.

Age classes according to Pollock 1986: A = adult (>6 years), SA = subadult (>3 years), J = juvenile (<3 years), I = infant (<1 year).

Recording methods

We recorded calls using Marantz PMD671 solid-state recorders on compact flash memory cards. Recorders were equipped using Sennheiser MKH-60 (with windscreen) and ME66 (with Sennheiser MZW66 windscreen) shotgun microphones. Sounds were digitised at 44.1 kHz sampling rate, 16 bits amplitude resolution. No recording was taken when tourists were near the focal group, nor were vocalisations elicited by means of playbacks. We only recorded spontaneously occurring vocalisations. Recording sessions took place when researchers could directly see the animals and follow them in the forest. The distance between the researcher and the focal indri could range from 3 m to approximately 10 m. A recording session ended when the distance between the animal and the microphone exceeded 10 m or the animal fled away. For each utterance, we noted the identity of the vocaliser and the behavioural context. Behaviours occurring concomitant with vocalisations were recorded and coded into broad categories as follows: rest (remaining still or quietly monitoring the environment), foraging (searching, obtaining and eating food), travel (moving for a distance greater than 10 m), vigilance (looking into vegetation, either quickly moving the head or with the head stationary), aggression (chasing or fighting between group members), agonistic (negative interaction without physical contact), territorial advertisement (sequential singing of the indri song), anti-predatory [in presence of terrestrial or aerial predators or potential predators (e.g. dogs, mongooses), or human observers]. Recording sessions usually lasted 10 to 45 minutes, depending on the animal movements. We analysed a total of 82 recording sessions (Tab. 1).

The software Praat 5.1.15 (Boersma & Weenink, 2009) was used for visual inspection and selection of high quality vocalisations. These utterances were identified on the basis of their intensity, the absence of overlapping vocalisations, and the degree of background noise (e.g. insects, birds, rain). We analysed a total of 1670 vocal signals, 1514 of which were used in the discriminant function analyses.

The recording equipment we used for noise recordings was the same as that used for vocalisations. We considered 455 sound files, the duration of which was a minimum of 2 s, recorded before and after indri vocalisations. All ambient noise recordings were made at heights ranging between 1.5 and 4 m, with the microphone orientated at about 45° above the horizontal towards the canopy, in order to record at the strata mainly used by the indris. Recordings were taken between 06.00 and 13.00 h.

Acoustic analyses

Taking the perspective of the source-filter theory (Fant, 1960), we analysed the vocalisations in the light of their being the combined product of two independent mechanisms: vibration of the vocal folds and filtering of the supra-laryngeal vocal cavities. Several studies have demonstrated how non-human primate acoustic signals are shaped by both these events (Fitch, 1997; Rendall *et al.*, 2005; Gamba & Giacoma, 2006).

We carried out all acoustic analyses using a window length of 0.05 s. The time range of the operating screen window was usually set to 3 s during the acoustic analyses. We set the frequency range to 0-10 kHz and dynamic range to 35 dB.

For each call, independent of the vocal category to which it was assigned, we measured the duration of the whole vocal emission (DUR); three larynx-related features — average fundamental frequency (MeF0), minimum fundamental frequency (MiF0), maximum fundamental frequency (MaF0); and four vocal tract-related acoustic features — average first formant (F1), average second formant (F2) and average third formant (F3, see Fig. 2 in Gamba & Giacoma, 2008 for details).

To detect source features (MeF0, MiF0, MaF0), Fast Fourier transforms were generated for all calls (frequency range: 0-12000 Hz; maximum: 50 dB/Hz; dynamic range: 30 dB; pre-emphasis: 6.0 dB/Oct; dynamic compression: 0.0). The actual variation of the fundamental frequency was measured by using the autocorrelation method ["Sound: To pitch (ac)…"], after adjusting the analysis parameters according to the range of variation in each of the vocalisations (Gamba & Giacoma, 2005).

Formants (F1, F2, F3) were studied using linear predictive coding (LPC, Markel & Gray, 1976). Because the vocal signals usually vary with time, this process was done all along the signal frames and then average formants were calculated. Depending on the acoustic characteristics of the vocalisation, we used a window length of 0.03-0.05. Because the number of formants varies with vocal tract length, we measured 3-6 formants depending on the vocal type. Two methods were used in order to check the formants predicted by LPC. First, formant analyses were superimposed over the signal spectrogram. Second, autocorrelation-based LPC spectra were overlaid on independently-derived FFT spectra of the same frames to validate the LPC analysis. The typical setting for the dynamic range was 25 Hz. The formant pattern fitting was inferred during a step-by-step monitored process, where the operator could interrupt the analysis and modify the analysis parameters. The final output file was assembled within PRAAT and exported to a SPSS spreadsheet. We only included variables that could be measured from all vocal types.

We generated a series of frequency spectra to compare frequency distributions of the vocalisations emitted by the indris with those of the forest noise. We then visually inspected all the noise files by means of the spectrograms. Visual inspection and the grouping techniques available in Praat (dynamic time warping) allowed us to select the typical frequency patterns, taking into account the most prominent bands and the background noise (flies, birds, insects…). We then generated spectra from the vocalisation sound files for comparison.

Statistical analysis

We conducted stepwise cross-validation discriminant function analysis using SPSS 17.0 (SPSS Inc., USA) to classify vocalisations based on the vocal type and to verify which parameters were most important in the classification. To reduce the possible effect of pseudo-replication (as in some cases inter-dependence of the data could not be excluded, e.g. because of indris fleeing when they emitted terrestrial alarm calls), we used two different resampling methods: Jackknife cross-validation and a permutation resampling strategy. The Jackknife was performed using the SPSS function in the discriminant analysis. The permutation was performed by resampling the most numerous vocal types, which were then subjected to both original and cross-validated discriminant analyses. This method reduced both the potential influence of pseudo-replication and the influence of the different sample sizes across the vocal types. We randomly generated 70 data sets (total N ranging between 511 and 591) in which the most numerous vocal types, hums and grunts, were down-sampled to 10% of the original sets.

Results

Description of the vocal repertoire

Besides the proper song notes, adult indris possess eight different vocal types, all of which are distinguishable by visual inspection of the spectrograms (Fig. 1) and by ear: roar (Fig. 1a), honk (Fig. 1b), hum (Fig. 1c), short tonal call (Fig. 1d), long tonal call (Fig. 1e), kiss (Fig. 1f), wheeze (Fig. 1g), grunt (Fig. 1h). To complete the description of the vocal repertoire, we provide a spectrogram of infant calls (Fig. 1i) and of the song (Fig. 1j).

A schematic overview of call usage is provided in Table 2, including information concerning the nomenclature used for the same vocal types in previous studies, the general context in which the sound is usually uttered, a short description of the overall acoustic structure, and a description of the phonation mechanisms.

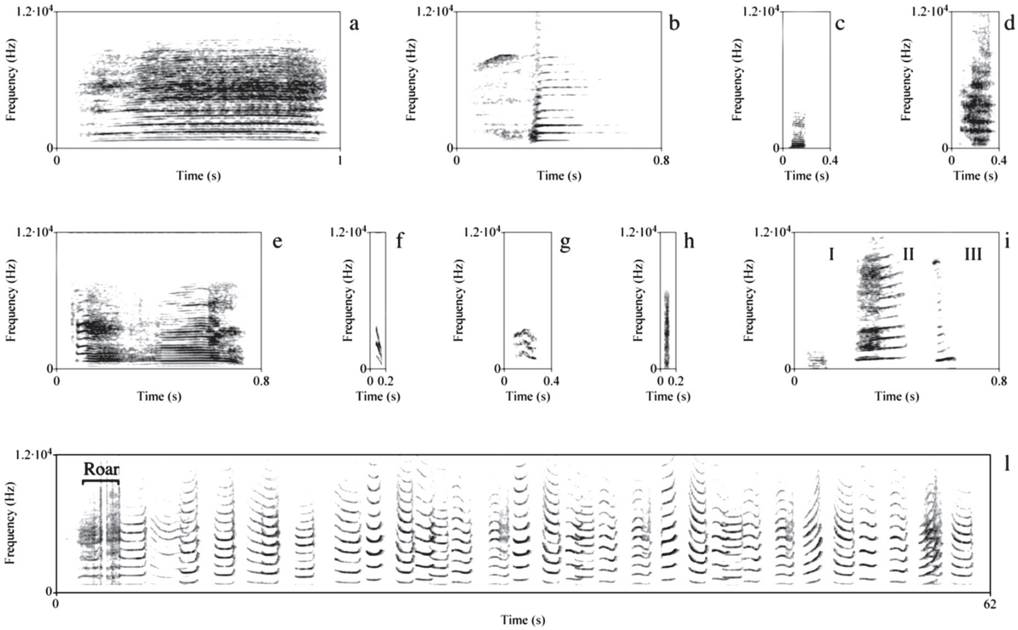

Fig. 1 - Sound spectrograms of* Indri indri *vocal types: Roar (a), honk (b, anticipated by voiced inhalation), hum (c), short tonal call (d), long tonal call (e), kiss (f), wheeze (g), grunt (h), infant calls (hum, iI; contact-seeking call, iII; grunt, iIII) and the indri song (j, showing introductory roars). All spectrograms were generated in Praat 5.1.15 (www.praat.org) with the following parameters: window length: 0.02 sec, time range as shown (max. 0-62 sec); frequency range: 0-12000 Hz; maximum: 100 dB/Hz; dynamic range: 30-55 dB; dynamic compression: 0.0.

Tab. 2 - Definition of the vocal types including synonyms used in previous works, context of emission, description of the call usage and phonation mechanics. References as follows: Petter, 1962 (1); Pollock, 1975 (2); Petter & Charles-Dominique, 1979 (3); Pollock, 1986 (4); Thalmann* et al.*, 1991 (5); Macedonia & Stanger, 1994 (6); Sorrentino* et al.*, (in press) (7); Giacoma* et al.*, (in press) (8).

Call Type	Synonyms	Context	Description	Phonation
Roar	Roar (4, 6), bark (3), waa note (5), aboiement (1)	Anti-predatory	Loud and harsh vocalization used as a standalone vocal signal in the presence of aerial predators.	Mouth open
Honk	Honk (3, 6), klaxon (1), exhaled hoot (2), honk note (5)	Anti-predatory	Alone, or together with other group individuals, indris produce rhythmic, rapid alerting calls given in series of short loud notes. These calls are given when terrestrial predators (e.g. fossa) or potential predators (e.g. mongoose, dog) are present. Non-habituated indris emitted this also in presence of human observers. Inhalation before the uttering of honks is sometimes visible from the spectrograms.	Mouth open
Hum	Hum (2), weak grunt (3)	Foraging, rest and travel	Low-pitched and low-intensity vocalization frequently uttered back to back by one or more individuals to maintain close contact with the group during resting activities or group displacement.	Mouth barely closed
Short tonal call	Previously undescribed	Aggression	Short harsh tonal vocalization usually associated with physical aggression. It is often given in between long tonal calls.	Mouth partially open
Long tonal call	Previously undescribed	Aggression	Long tonal vocalization usually associated with physical aggression. It is emitted in sequence during agonistic interactions.	Mouth barely closed
Kiss	Kiss (2), kiss-like sound (3)	Vigilance, agonistic	In response to disturbance indris reacted with calls of medium intensity. In stress-related contexts these vocalizations are often produced during a grunt bout or before a song. Kiss is often the first unit of the so-called ‘cri d’amour’, followed by wheeze.	Snapped pursed lips
Wheeze	Wheeze (2, 3), wheezing grunt (6)	Vigilance, agonistic	Typically closely associated with a kiss, the wheeze is a rapid air expulsion blown through open lips. It is often emitted in competitive intra-group situations or in response to potentially dangerous or noxious stimuli and intruders.	Mouth fully open
Grunt	Grunt (2, 3, 6)	Vigilance, agonistic	Short, low-pitched pulse trains often given in series rather than alone. Animals uttered these sounds in agonistic contexts, during conflict intra-group interactions or as a warning signal.	Mouth closed or barely open
Infant calls	Previously undescribed	Various	Three different vocal types were recognized: a contact hum, intercalated with those given by the mother, an harmonic contact-seeking call and a vocalization similar to the grunts produced when the infants were agitated or anxious.	Variable degree of mouth opening
Song	Song (6, 7, 8), song proper (4), modulated howl (3)	Territorial advertisement	Males and females of the group participate in a chorusing song, mainly consisting of harmonic frequency modulated notes, usually introduced by three or four “roars”. Plays a role in intergroup communication, proclaiming the occupation of a territory and transmitting cues for inter-group avoidance.	Variable lip protrusion and mouth opening

Roar (Fig. 1a)

Roars are loud tonal vocalisations showing harmonic structure merged with a prominent chaotic pattern. Individuals always emitted roars in series of 2 or more units rather than singly. We have observed that roars are usually given in short series in the presence of aerial predators (aboiements, Petter, 1962; barks, Petter & Charles-Dominique, 1979; roar, Pollock, 1986; Macedonia & Stanger,1994; waa notes, Thalmann *et al.*, 1993), but they can also occur at the beginning of the song (Fig. 1l) and, more interestingly, can occur during the honk series emitted by certain individuals. More than one group member generally gave roars on the same occasion. Indris tended to grasp the vocal sac after producing songs or uttering roars.

Honk (Fig. 1b)

Previous studies also reported the utterance of an alarm call used in the presence of terrestrial predators (klaxon, Petter, 1962; exhaled hoot, Pollock, 1975; honk, Petter & Charles-Dominique, 1979; Macedonia & Stanger, 1994; honk notes, Thalmann *et al.*, 1993). Honks are loud tonal vocalisations where great energy is concentrated over the harmonics. They are usually given in bouts of six or more elements and, in some cases, these bouts can have roars in between the honk elements. It is not clear whether honks and roars are uttered in the same series in particular contexts or if they both play a role as deterrents of terrestrial predators or humans. Inhalation of air between the honks in a series may be voiced (as can be seen in Fig. 1b). They were often emitted by single individuals, both males and females, when they fled and disappeared in the vegetation. We observed up to three individuals simultaneously uttering the honk series in the same situation, but only seldom. Indris usually produce a series of honks with the head raised (Pollock, 1975; Petter & Charles-Dominique, 1979).

Hum (Fig. 1c)

Hums were heard when animals were about to move, and accompany leaping locomotion (hum, Pollock, 1975; Macedonia & Stanger, 1994; weak grunts, Petter & Charles-Dominique, 1979). The hums are low-frequency and low intensity guttural calls emitted both singly and in bouts. They can be given by adults and youngsters and usually occur during foraging, individual and group movements and rest. They apparently serve as group-cohesion calls.

Short tonal call (Fig. 1d)

Short tonal calls were usually given during intra-group conflicts, when the indris interacted aggressively with physical contact. They were uttered infrequently, sometimes intercalated between long tonal calls, and showed a clear formant structure. Indris produced these calls with the mouth partially open.

Long tonal call (Fig. 1e)

Long tonal calls were used in the same context as the short tonal calls, but were of longer duration and lower F0. They were uttered infrequently compared to the other calls in the repertoire. They were usually given in bouts and showed a clear harmonic structure with evident formants. During phonation, the mouth is partially open.

Kiss (Fig. 1f)

A first type of contact-rejection call is the so-called kiss, which is usually emitted when individuals are frightened or anxious (Macedonia & Stanger, 1994; Pollock, 1975) or in cases of disturbance (Petter & Charles-Dominique, 1979). During vigilance, indris rapidly produce a kiss and then a wheeze (Pollock, 1975; Petter & Charles-Dominique, 1979). Because of the human smack-like sound at the start of this utterance, Malagasy people named this sound ‘cri d’amour’. Eighty-five percent of the kisses we recorded were associated with wheezes in the cri d’amour. Neither the kiss nor the cri d’amour is usually given in bouts. During the kiss, indris showed lip movements that resembled human lip smacking. They are also emitted during agonistic interactions between group members, which usually did not end with physical aggression.

Wheeze (Fig. 1g)

The wheezes are low intensity calls given during exhalation. They had a F0 of 814 + 317 Hz and average duration of 0.37 + 0.13 s. They are often given as the second and closing element of the cri d'amour, but can also occur as single calls, and did so in 15% of the cases we recorded. They do not occur in bouts.

Grunt (Fig. 1h)

Grunts could be uttered when the indris were frightened or anxious (Pollock, 1975; Macedonia & Stanger, 1994) or during aggressive behaviours (Petter & Charles-Dominique, 1979). They showed a clearer, low-pitched, pulsed structure when compared to hums. In contrast to hums (also called weak grunts), grunts were uttered in vigilance and agonistic contexts. During phonation, the mouth can be closed or barely open.

Infant calls (Fig. 1i)

Although mother-infant vocal communication is doubtless present in *Indri indri*, previous studies have not described these calls (Petter & Charles-Dominique, 1979). We recognised three different vocal types given by three infants (< 8 months), during the phase when they were still periodically carried on their mothers' backs. The first type was similar to hums given by the adults (Fig. 1iI). The infant could utter hums intercalated with those given by the mother. The second was a harmonic contact-seeking call (Fig. 1iII), which usually occurred when the mother went off to feed or moved away from the offspring. A third call type was similar to grunts (Fig. 1iIII), and was usually produced when the infants were vigilant or rapidly moved. This often happened when they were performing their first solitary explorations or were attempting to leap among tree branches near their mothers.

Song (Fig. 1j)

The song of the indri is a special case in which males and females of a group participate in a chorusing song. Songs usually last 40-250 s and are introduced by three or four "roars" uttered by several members of a group at the same time (Pollock, 1986). The main functions hypothesised for the song are related to proclamation of an occupied territory and transmitting cues for inter-group avoidance (Petter & Charles-Dominique, 1979; Petter *et al.*, 1977; Pollock, 1986; Geissmann & Mütschler, 2006; Sorrentino *et al.*, in press; Giacoma *et al.*, in press). A role in inter-group communication is supported by the fact that the song notes are very conspicuous and loud. To enhance song transmission through the forest, the indris move to the tops of the trees before calling, which enables the call to be heard up to 3-4 km away (authors' pers. obs.). Moreover, the activity of one group seemingly stimulates other groups in a chain-reaction that can spread all over the forest. Geissmann & Mütschler (2006) verified that more than 37% of all songs occurred from 8.00 am to 9.30 a.m. According to these authors, this clear-cut morning peak in vocalising activity supports the territorial announcement hypothesis because calling in the early morning may be sufficient to inform neighbours of the continued presence of the territory holders. However, it is also possible that songs play a role in inter-group spacing, facilitating avoidance of group encounters at territorial boundaries, because songs are sometimes repeated during the day (from 04.45 until 11.00 hours, occasionally from 14.30-16.30) and exceptionally at night (Petter, 1962; Petter & Charles-Dominique, 1979; Petter *et al.*, 1977; Powzyk, 1997; Garbutt, 1999; authors pers. obs.). Within a song, excluding the roar, up to 8 different harmonic frequency-modulated note types can be produced, with males giving six note types (Sorrentino *et al.*, in press) and females emitting seven different note types (5 of which are shared with males, Giacoma *et al.*, in press). All note types are sexually dimorphic and may possibly provide listeners with information about the sex of the emitter and group composition. Other possible functions of the songs are currently being investigated (Giacoma *et al.,* in press).

Quantitative assessment of the vocal types

We excluded from the quantitative analysis all utterances emitted by infants and the song, as it has already been targeted by previous studies (Sorrentino *et al.*, in press).

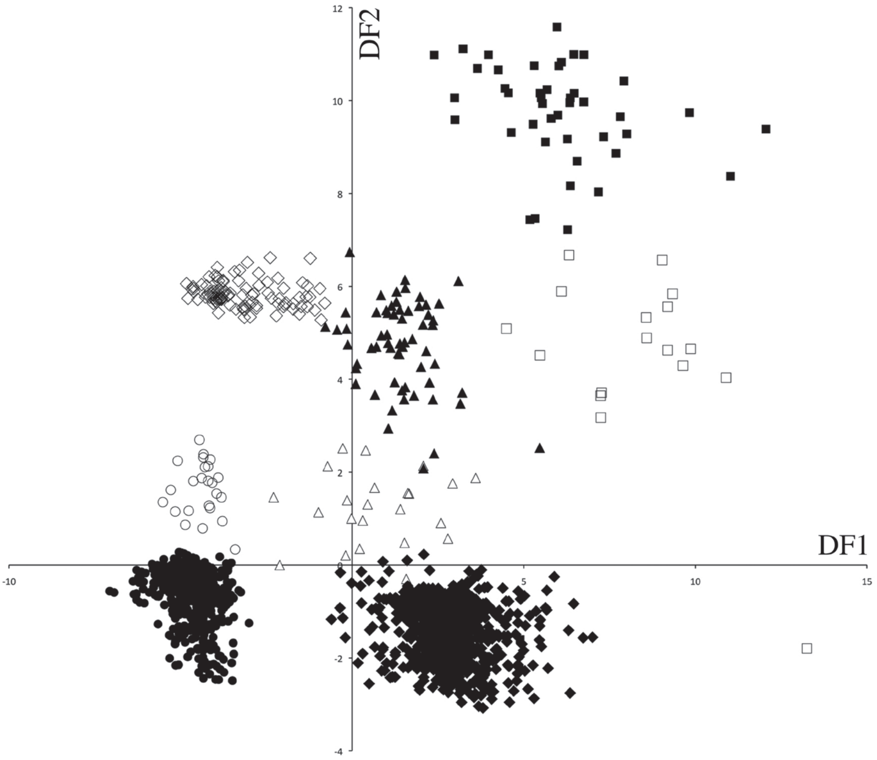

Fig. 2 - Scatter plot of vocal types representing the results of discriminant function 1 and discriminant function 2 of the discriminant analysis (○ = Roar, ◇ = Honk, ● = Hum, Δ = Long tonal call, □ = Short tonal call, ▲ = Kiss, ■ = Wheeze, ♦ = Grunt). All vocal types separate well in these two functions (see Table 4 for loadings).

Descriptive statistics are shown in Table 3. Discriminant function analyses supported the qualitative classifications of vocalisation types. A stepwise discriminant function analysis using the acoustic parameters we measured generated a function that significantly differentiated the vocal types (Wilks' Lambda = 0.005, $F_{7, 1506}$ = 2040.306, $p < 0.001$). The resulting discriminant function correctly classified 96.4% of the vocalisations by vocal type (Fig. 2). The cross-validated function correctly classified 96.0% of these calls. Table 4 shows the canonical loadings of the discriminant function. F3me showed the largest absolute correlation with the first discriminant function (corr.= 0.802), whereas F0 measurements [MaxF0 (0.973), MeanF0 (0.940) and MinF0 (0.880)] are the variables most highly correlated with the second function. These two discriminant functions accounted for 97.3% of the cumulative variance of the model (DF1, χ^2 = 7855.049 df = 49, $p < 0.001$; DF2, χ^2 = 3798.233 df = 36, $p < 0.001$). An inspection of the cross-validation results indicated that honks, hums, short tonal calls, kisses and grunts were correctly assigned more frequently (94%-100%) than wheezes (82%), roars (75%) and long tonal calls (65%).

Stepwise discriminant function analyses were then performed on all 70 resampled datasets and yielded 93.40 + 0.54 % correct classification in the original model and 92.02 + 0.61 % in the cross-validated model. The most important parameters for the classification of the vocalisations according to vocal type were F3me, MaxF0, Duration, MeanF0, F1me, F2me and MinF0.

Tab. 3 - Mean and standard deviation of the acoustic parameters per vocal type. Number of calls we have analysed is reported after the vocal type (N). Parameters we measured were: duration (DUR), average fundamental frequency (MeF0), maximum fundamental frequency (MaF0), minimum fundamental frequency (MiF0), average first formant (F1), second formant (F2) and third formant (F3).

Vocalization	DUR (s)	MeF0 (Hz)	MaF0 (Hz)	MiF0 (Hz)	F1 (Hz)	F2 (Hz)	F3 (Hz)
Roar (24)	0.86±0.37	269±39	322±42	243±39	733±106	1512±121	2879±250
Honk (94)	0.26±0.09	637±28	654±23	614±46	1060±142	1918±136	3357±443
Hum (632)	0.49±0.37	133±50	159±48	106±54	568±332	1585±398	2254±159
Long Tonal Call (23)	0.36±0.30	276±67	318±61	249±77	798±278	2442±487	4218±400
Short Tonal Call (17)	0.17±0.08	533±131	584±120	488±155	1918±575	4459±608	7080±539
Kiss (61)	0.09±0.04	584±77	600±73	567±88	1202±221	2982±382	4547±281
Wheeze (51)	0.37±0.13	814±317	858±327	764±305	1838±646	4099±778	6399±898
Grunt (768)	0.06±0.05	137±51	140±50	133±52	923±635	3038±545	4409±412

Tab. 4 - Standardised canonical coefficients of the six discriminant functions explaining 100% of the model's variance.

	Function					
	1	2	3	4	5	6
duration	-0.216	-0.044	0.514	0.045	0.523	0.760
MeF0	0.469	-0.381	-4.215	-4.734	-5.486	4.151
MaF0	-0.51	1.158	3.538	0.783	2.284	-4.045
MiF0	-0.009	0.038	0.754	2.653	4.696	-1.144
F0end	-0.115	0.162	-0.281	1.278	-1.178	0.979
F1	-0.953	0.376	-0.079	0.684	-0.684	0.457
F2	0.773	-0.341	-0.170	-1.127	0.844	-0.073
F3	0.904	0.067	0.362	0.495	-0.339	0.095
% of Variance	65.7	31.5	2.1	0.5	0.2	0.1

Acoustic characteristics of the forest environment

The ambient noise spectra, when averaged across the time range in which we recorded indris, were very similar to each other. The overall mean similarity index was 0.69. Seasonal differences were not evaluated in the present study, nor were recordings taken on days with heavy rain, when indris spent most of the time resting. Noise levels were highest below 600 Hz (Fig. 3), although the sound sources for these low-frequency peaks could differ. They were mainly due to wind and flies. Noise generated from the flies could reach 6000 Hz, while bird calls were usually more prominent between 2800 and 7500 Hz or between 5700 and 8000 Hz, depending on the species singing. Songs from other indri groups usually occupied selected bands between 600 and 2000 Hz (not shown in figure). Insect noise was important between 6000 and 8000 Hz. Recordings from both Analamazaotra Special Reserve and Station Forestière showed a decrease in noise levels around 1800 Hz and a second decline around 8 kHz (Fig. 3).

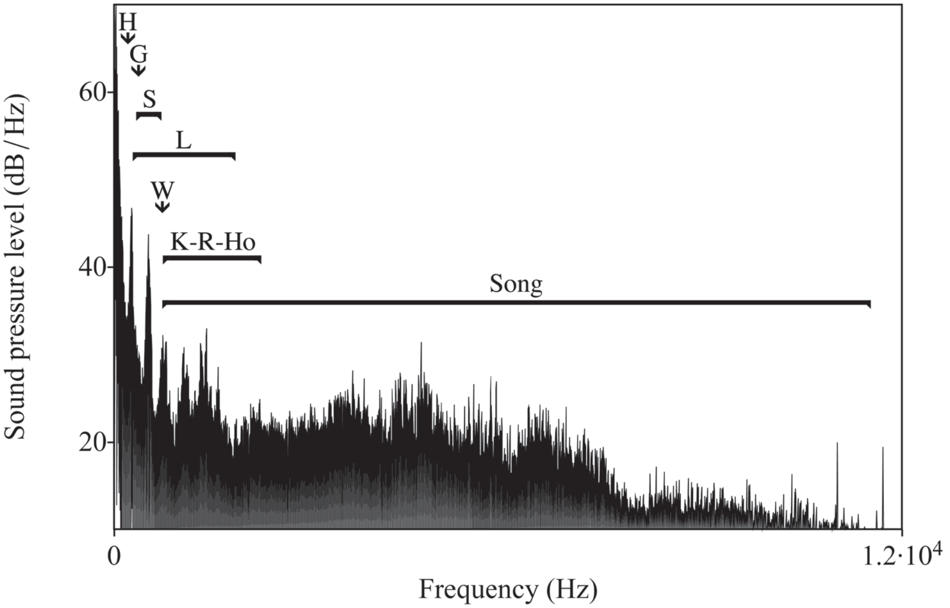

Fig. 3 - Typical frequency spectrum of the ambient noise in Analamazaotra Reserve. Over the spectrum, we highlighted the frequency ranges covered by the most prominent frequency bands of the vocalisations. Arrows indicate hums (H), grunts (G) and wheezes (W). The ranges of the most prominent frequency bands of short tonal calls (S), long tonal calls (L), kisses (K), roars (R), honks (Ho) and the song (Song) are shown.

The song's most prominent components were between 500 and 11000 Hz, while those of the roar, honk and kiss were between 700 and 2200 Hz (Fig. 3). Energy bands for short-range vocalisations were mainly concentrated at low frequencies, typically 200 Hz for hums and 350 Hz for grunts (Fig. 3). Wheezes showed peaks around 1500 Hz (Fig. 3). Short tonal calls showed prominent bands between 320 and 680 Hz, while long tonal calls had a wider range, 250-1800 Hz.

Discussion

We recorded 8 different vocal types within the vocal repertoires of adult wild indris in addition to the song, and found quantitative differences among them. The indri vocal repertoire we recorded is similar to that described briefly and qualitatively in previous studies (Pollock, 1975; Petter & Charles-Dominique, 1979).

Petter & Charles-Dominique (1979) described hums (or weak grunt calls) from indris and sifakas, given when the animals were moving in the forest, and presumably serving as group-cohesion calls. This low intensity vocalisation is frequently uttered to maintain contact within the group during resting activities or shortly before movement. As for the other short range calls, the hums showed a limited number of frequency bands, located in the area where low frequency noise is most evident. Because the sound is difficult to hear and to record, and because it is given during locomotion, future studies should investigate whether the calls produced during feeding are distinguishable from those uttered during locomotion. Grunts were given in tense contexts, in agreement with previous observations (Petter & Charles-Dominique, 1979). The prominent frequency bands in grunt vocalisations were located at the low end of the spectrum; because of their low intensity of emission and competing forest noise, they certainly cannot reach receivers over long distances. Kisses and wheezes were uttered in vigilance and agonistic contexts. They were often associated in the cri d'amour, and cover a similar frequency range. The wheeze shows only one peak around 1500 Hz, while the kiss starts from that frequency and reaches values around 2200 Hz. The indri's alarm system is characterised by two different call types. As in other lemurs (e.g. Varecia spp.), roars serve as alarm calls for aerial predators, probably representing a warning or deterrent to the Malagasy birds of prey (Pollock, 1975; Petter & Charles-Dominique, 1979). Although it was clear that the presence of horseflies sometimes affected the behaviour of indris, we did not find direct evidence that their bites actually stimulated the production of specific vocalisations (contra Petter & Charles-Dominique, 1979). However, we noticed that indris tended to grasp the vocal sac after uttering roars or honks (or producing songs). In the presence of terrestrial predators or human observers approaching the group, indris usually produced series of honks with the head raised (Pollock, 1975; Petter & Charles-Dominique, 1979). Both alarm calls showed relatively wide ranges of prominent frequency bands, and include one of the areas in the spectrum in which the ambient noise level is lowest, facilitating their transmission over long distances. Previous studies have shown that almost all primate species use alarm calls as an anti-predator behaviour, in some species with different alarm calls for different types of predators (Cheney & Wrangham, 1987). The observation that, in lemurs, the terrestrial alarm call serves a less specific function (Fichtel, 2008) is confirmed in this study. Honks are given in the presence of human observers by non-habituated groups and honk series can also show roar units. Roars and honks are loud vocalisations and are the only vocal types, other than the song, which may serve inter-group communication. We observed two types of tonal calls not described in previous studies, which we refer to as long tonal calls and short tonal calls because they differ considerably in duration (Figs. 1d,1e). They are among the vocalisations that carry specific contextual information. In fact, they were recorded only in the context of physical conflict involving two group members. It is not clear at present whether these tonal calls are used in a similar way to the chatter in Varecia spp. and Eulemur spp. (Pereira *et al.*, 1988; Gamba & Giacoma, 2005, 2007). Both these vocal types had prominent bands corresponding to relatively high amplitude in the noise spectra.

Some of the vocal types we have described are usually given in series or associated with other vocalisations, and show a variable degree of association with specific behavioural contexts. However, if we compare the indri's vocal repertoire with those of other species (*Eulemur coronatus*, Gamba & Giacoma, 2007; *Cebus capucinus*, Gros-Louis *et al.*, 2008), it is fairly limited in size. It is known that indris live in small family groups, usually comprising an adult pair and its offspring (Pollock, 1975, 1977, 1979; Powzyk, 1997; Glessner & Britt, 2005). If we take into consideration the theory suggesting that vocal repertoire size and group size are positively correlated in primates (McComb & Semple, 2005), we should expect indris to show a vocal repertoire not exceeding ten vocal types. The indri thus fits predictions that vocal repertoire size is a strong predictor of group size and of grooming time among non-human primates. Indris have an average group size of 4.3 individuals and a very low percentage of the daytime activity period is spent grooming (around 1%, Pollock, 1977; Lehmann *et al.*, 2007). Moreover, indris have a hierarchical social organisation where status is determined by age and sex. This may, as a result, be less demanding in terms of investment in social bond regulation, as is suggested by the fact that only hums serve as group cohesion calls. This is also not surprising if we consider that indri groups are strictly territorial and that group members usually stay in close proximity to one another, never being dispersed in the forest. A third possible explanation for the paucity of cohesion signals is that the song plays a role in maintaining group cohesion. This is a subject for future studies to address, investigating whether individual song contributions provide clues to conspecifics regarding dominance status and individual characteristics. Group members could provide group mates or other conspecifics with this information by modulating the temporal pattern of their singing, the coordination and the timing of their contribution.

The use of long-distance vocalisations adapted to by-pass background noise has been hypothesised for several other species (Brown & Waser, 1984; Zimmermann, 1995), including nocturnal strepsirhines. The indri song shows a large frequency span of prominent bands, including high-frequency regions with low amplitudes in the noise spectra. This suggests that the design of the indri song is optimised to avoid masking by ambient noise.

In terms of function and usage, we have yet to determine whether a specific vocal type may provide recipients with contextual information. This could potentially increase the functional repertoire of the indri and provide new data for the models discussed above. Future studies should also investigate how age, sex and identity of the individuals can affect the structure of these vocalisations and possibly influence the production of call types in the repertoire.

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