The vocal communication of the mongoose lemur (Eulemur mongoz): phonation mechanisms, acoustic features and quantitative analysis

B. Nadhurou[a], M. Gamba[a], N.V. Andriaholinirina[b], A. Ouledi[c] & C. Giacoma[a]

[a] Department of Life Sciences and Systems Biology, University of Turin, Via Accademia Albertina 13, 10123 Torino, Italy

[b] Faculty of Science, University of Mahajanga, Mahajanga, Madagascar

[c] Faculty of Science and Technology, University of Comoros, Moroni, Union of Comoros
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B. Nadhurou [1,4], M. Gamba [1], N.V. Andriaholinirina [2], A. Ouledi [3] and C. Giacoma [1]

[1] *Department of Life Sciences and Systems Biology, University of Turin, Via Accademia Albertina 13, 10123 Torino, Italy*
[2] *Faculty of Science, University of Mahajanga, Mahajanga, Madagascar*
[3] *Faculty of Science and Technology, University of Comoros, Moroni, Union of Comoros*

We recorded vocalisations of wild *Eulemur mongoz* groups in Madagascar and the Comoros Islands, as well as from habituated captive groups housed in European and Madagascan zoos. Each vocalisation was quantitatively described by means of an acoustic analysis procedure implemented in Praat, and vocal types were distinguished both by ear and by the visual screening of spectrograms. Vocal signals were then associated with the context in which they were produced, to explore whether they occur only in specific behavioural contexts or are uttered in a range of situations. We found that mongoose lemurs possess highly context-specific aerial alarm calls and territorial calls, while the 'croui-croui' is usually emitted to communicate between individuals regrouping at sunset. The other calls we recorded, such as those including low-pitched pulse trains sometimes followed by harmonic elements, were not tightly associated with a particular context. Mongoose lemur utterances included calls produced with closed mouths and the involvement of nasal resonance, or with constant degrees of mouth opening or mandible 'articulation' during phonation. We observed 15 vocal types, nine of which were entered into a multivariate model that classified vocal types with a high degree of reliability. The second and third formants played an important role in discriminating among types of calls.

KEY WORDS: vocal repertoire, behavioural contexts, nasal calls, Madagascar, Comoros.

INTRODUCTION

In primate species, the study of vocal repertoires represents an important step in the description of the relationship between communication and social behaviour, including many behavioural aspects useful for implementing management plans and

conservation actions (TERRY et al. 2005; LAIOLO 2010). Diurnal and cathemeral lemurs have vocal repertoires of comparable size (15.40 ± 7.24, MCCOMB & SEMPLE 2005) to those of other primates (16.64 ± 8.59, MCCOMB & SEMPLE 2005), but for most species we can only rely on qualitative descriptions (PAILLETTE & PETTER 1978; PETTER & CHARLES-DOMINIQUE 1979; PEREIRA et al. 1988; MACEDONIA 1993; MACEDONIA & STANGER 1994; STANGER & MACEDONIA 1994; CURTIS & ZARAMODY 1999; GOSSET et al. 2001). The quantitative analysis of vocalisations has shown that variability in lemur calls may provide information on sex (GIACOMA et al. 2010), individual identity (ODA 2002; LELIVELD et al. 2011; GAMBA et al. 2012a) and the emotional state of the emitter (ZIMMERMANN 2009). The ability to recognise age, sex and individuals can be an important tool in management and conservation activities (TERRY et al. 2005). However, identification of these potential cues requires a quantitative and detailed description of the vocal repertoire.

Mongoose lemurs (*Eulemur mongoz* Linnaeus 1766) are mid-sized and arboreal, and change their activity rhythm from diurnal to nocturnal seasonally (MITTERMEIER et al. 2010). The species shows sexual dimorphism, the males having red beards and red cheeks and the females having white beards and darker faces. They eat mostly fruit and live in small groups of up to six individuals (NADHUROU 2014), with a single adult pair. Previous research showed that males and females form strong pair bonds and live in proximity. Pair-bonded lemurs exchange mutual anogenital marking, participate in the care of offspring and are usually territorial. Mongoose lemurs are usually considered socially monogamous primates, where females are dominant over males and show higher levels of intra-sexual aggression (CURTIS & ZARAMODY 1998).

The mongoose lemur is a conspicuously vocal species. The first qualitative description of four *Eulemur mongoz* vocalisations recorded in the wild can be found in TATTERSALL & SUSSMAN (1975). PETTER & CHARLES-DOMINIQUE (1979) recognised eight vocal types (snort, creeeee, sneeze, hon, greeee, creeeeeeeeeee, contact-rejection call, distress calls) and assigned them to five categories (contact calls and contact-seeking calls, distant communication calls, alarm calls, contact-rejection calls, and distress calls). With the sole exception of the hon given by infants, all these vocal types were identified by MACEDONIA & STANGER (1994) in the repertoire of the mongoose lemur colony maintained at Duke University Primate Center (DUPC). CURTIS & ZARAMODY (1999) described nine calls assigned to pulse trains (screech, grunt, sneeze, snort, creak and warble) or to tonal vocalisations (hmm, rap and cak), and added the grunt-sneeze and the snort-hmm to the vocal types described in previous studies.

The conservation status of the mongoose lemur (*Eulemur mongoz*) has become critical in recent times. The species is under unprecedented strong pressure, because its already-fragmented habitat is continuously being reduced (PETTER et al. 1977; TATTERSALL 1982; MITTERMEIER et al. 2010) and because its distribution in certain areas has become restricted to the vicinity of water bodies (RASMUSSEN 1998). In northwestern Madagascar, the species occurs in dry deciduous forests from sea level to 400 m (MITTERMEIER et al. 2010, and references therein), or from sea level to 1128 m in the Comoran humid forests of Mohéli and Anjouan (NADHUROU 2014), where it has been introduced by humans (PASTORINI et al. 2003; MITTERMEIER et al. 2010).

A greater understanding of the vocal repertoire of mongoose lemurs can be used to monitor population processes (LAIOLO 2010), and to contribute to a better understanding of their social behaviour. In this contribution, we describe the acoustic structure of their vocalisations quantitatively and classify the most common vocal types. We analysed the acoustic structure from the perspective of the source-filter theory of sound

production (FANT 1960), and investigated the variability of temporal parameters, fundamental frequency (hereafter, F0) and formants. We also examined the behavioural contexts associated with the emission of each vocalisation type. Our objectives were to estimate repertoire size and to identify sources of variability for the various vocal types, so as to provide researchers with a quantitative basis for further investigations (e.g. variability among individuals, populations and congeneric taxa).

MATERIALS AND METHODS

Study areas and subjects

The field work for this study was conducted between 2008 and 2010 in the western dry forests of Antsilahiza, Bombetoka-Belemboka and Ankatsabe-Analabe in Madagascar, and on the Island of Anjouan in the Union of the Comoros.

Bombetoka-Belemboka is a New Protected Area (NAP) situated in the Boeny region in northwestern Madagascar (15°54′01.8″S 046°13′56.7″E) and covers a total area of 71.943 ha of mangroves and dry deciduous forest (SCHWITZER et al. 2013). In Bombetoka-Belemboka, group size ranged from three to six individuals (see Supplemental Data, SM1, which is available from the article's Taylor & Francis Online page at http://dx.doi.org/10.1080/03949370.2015.1039069).

The Antsilahiza forest is situated in the Mitsinjo district, 80 km from Katsepy (16°04′12.3″S, 045°55′12.12″E; ANDRIAHOLINIRINA et al. 2006). In the Antsilahiza forest, group size ranged from two to three individuals (see Supplemental Data, SM1).

The Ankatsabe-Analabe forest is located in the Mariarano municipality, Mahajanga II district, within the Boeny region (16°04′12.3″S, 045°55′12.12″E; OLIVIERI et al. 2005). In this area, mongoose lemurs are severely hunted for food. In the Ankatsabe-Analabe forest, group size ranged from two to four individuals (see Supplemental Data, SM1).

In the archipelago of the Comoros, vocalisations were collected at three sites on the isle of Anjouan (Bambao Mtsanga, Dziani and Dzitso). Dziani (12°12′10.7″S, 044°28′44.2″E) and Dzitso (12°12′31.7″S, 044°28′09.8″E) are located near the village of Tsembéhou. The site of Bambao Mtsanga is located along the national road to Domoni (12°11′32.1″S, 044°30′23.4″E). All three localities occur in agricultural areas. In Anjouan, group size ranged from two to three individuals (see Supplemental Data, SM1).

Between the years 2000 and 2011, we also collected vocalisations from captive mongoose lemurs. The following zoos were visited for this investigation: Mulhouse Zoo (France), Parc Botanique et Zoologique de Tsimbazaza (hereafter PBZT; Antananarivo, Madagascar), Banham Zoo (UK), Linton Zoo (UK), Colchester Zoo (UK) and Parco Natura Viva (hereafter PNV; Bussolengo, Italy). All six captive groups received daily diets mainly consisting of fruit and vegetables, and water ad libitum. All subjects were maintained on a natural light/dark daily cycle and were treated in accordance with the 'Guidelines for the treatment of animals in behavioural research and teaching' (ASAB 2012), and the '*Eulemur* (*Eulemur* spp.) care manual' (AZA 2013). In captivity, group size ranged from two to five individuals (see Supplemental Data, SM1).

In all study sites, we were granted formal approval for our access to the animals by the appropriate authorities.

Vocal behaviour

Recorded individuals and group and site information are shown in SM1.

To understand the situations in which calls were uttered, we collected contextual, qualitative information during the emission of vocalisations, based on vocal categories described in previous studies (PETTER & CHARLES-DOMINIQUE 1979; MACEDONIA & STANGER 1994). We used contextual information as an indicator of the broad motivational frame in which each vocalisation was

emitted, and of its possible functional role. In accordance with previous studies on mongoose lemurs and on other primate species (MACEDONIA & STANGER 1994; STANGER & MACEDONIA 1994; HAUSER 1996; CURTIS 1997; CURTIS & ZARAMODY 1999), we considered the following behavioural contexts: aggression (attack or receive aggression from a conspecific, threatening of an individual, competing for food or space), fight (physical aggression with injuries), aerial or terrestrial anti-predator behaviour (alarm in the presence of potential predators), group cohesion (when individuals regroup, or maintain contact during rest periods, feeding or travelling), affiliative behaviours (e.g. mother–infant or amicable interactions), alertness (when animals reacted to an external disturbance, e.g. sounds), territorial advertisement (signal territorial occupancy), territoriality (territorial defence), or during veterinary manipulation.

We used the term 'long range' for those calls that can be heard (by the human ear) from a distance of 20–30 m, and thus probably serve an inter-group signalling function (e.g. to advertise territorial occupation). We used the term 'short range' for those vocalisations that can be directed at individuals within close proximity to the signaller, or within its social group (McGREGOR & DABELSTEEN 1996). We used the term 'vocal type' to describe a group of vocalisations with a common basic acoustic structure (GAMBA & GIACOMA 2007), and the term 'unit' to indicate a basic sound element of a vocalisation (LEMASSON & HAUSBERGER 2011). We called 'pulse' a single portion of the repeating pattern appearing in the spectrograms and oscillograms. The duration of a pulse is the duration of a single glottal cycle. We used the term 'multi-unit' for vocalisations in which we recognised portions with different acoustic structures, but not necessarily separated by a silent gap. The term 'repeated unit' was used to identify multi-unit calls composed of several structurally similar units, separated by a silent gap shorter than the unit duration (LEMASSON & HAUSBERGER 2011). We did not identify units separated by a silent gap that was longer than unit duration as constituting a series. We indicated as 'harsh' sounds (see FISCHER & HAMMERSCHMIDT 2002; BAKER 2004) those vocal types showing a remarkable amount of broadband noise (FITCH et al. 2002).

Recordings and acoustic analysis

We recorded spontaneously emitted vocalisations, avoiding the use of visual stimuli and/or acoustic playbacks. Recordings in the wild were collected making every effort to minimise inter-actions with the subjects. Recordings on captive animals were taken following the European Association of Zoos and Acquaria (EAZA) guidelines, as well as measures required by each specific institution. Recording distance usually ranged between 2 and 7 m. We did our best to orientate the microphone towards the mouth of the caller, but we cannot exclude that vocalisations recorded at different orientations entered the analysis.

Recordings of wild-ranging animals were obtained using an M-Audio Microtrack 24/96 equipped with a Sennheiser K3U microphone and a Sennheiser ME88 capsule, and using focal animal sampling methods (ALTMANN 1974). Recording in zoos was carried out with a Sony TCD-D100 digital tape recorder (DAT) using Sennheiser K3U/ME88 and Sony EMS-907 microphones.

DAT recordings were digitised at a sample rate of 44.1 kHz (16-bit resolution, mono format) using an analog-digital (AD) converter and edited using SoundForge 7 software (Madison Media Software Inc., Sony Corporation of America, USA); Microtrack files (44.1 kHz, 16-bit resolution, mono format) were transferred to hard disk using a USB cable.

After a preliminary qualitative analysis of all the recordings, we selected vocalisations of sufficient quality to allow acoustic analysis, and saved them in separate files. We excluded from the analysis those vocalisations that overlapped with others (e.g. other lemur species or birds), or had a very low amplitude difference from the background noise (e.g. the fundamental frequency was not recognisable from the frequency spectrum). The total sample of selected vocalisations comprised 3114 calls, emitted by 67 mongoose lemurs (38 males, 28 females and one juvenile), belonging to 23 groups. We considered only groups for which we recorded at least one session of 1 hr, and based our analysis on 60 hr of useful recording. We grouped the recorded signals into distinct categories by comparing spectrograms on the basis of the number of units (pulses and overall duration) and spectral features (e.g. harmonic vs noisy), modulation and intensity. We used an identification key

to summarise the procedure employed in the a priori classification of vocalisation types (see Supplemental Data, SM2).

The classification procedure we adopted allowed labelling calls and assigning them to a specific vocal type by integrating aural perception, visual inspection of spectrograms and previously available descriptions (MARETTI et al. 2010). While paying special attention to frequency and duration characteristics, BN, MG and CG performed a visual inspection of the printed spectrograms of each call in the sample. A careful analysis of previously published information led to the recognition of all the vocal types described in the literature for *Eulemur mongoz*. We followed the spectrograms of PETTER & CHARLES-DOMINIQUE (1979) in identifying calls, with later additions by MACEDONIA & STANGER (1994) and GAMBA & GIACOMA (2007, for *E. coronatus*).

We analysed calls from a source-filter theory perspective (FANT 1960), according to which the spectral structure of the vocal signal is the result of the combination of two independent mechanisms: vibration of the vocal folds and filtering of the supra-laryngeal vocal cavities (TAYLOR & REBY 2010; GAMBA et al. 2012b). Previous studies of primate acoustic signals have shown that both vocal fold vibration and supra-laryngeal filtering shape auditory communication in primates (FITCH 1997; RENDALL et al. 2005; GAMBA & GIACOMA 2006; GAMBA et al. 2012a) and other mammals (REBY & MCCOMB 2003). For each call, regardless of the vocal category to which it was assigned, we measured 11 acoustic properties using Praat (BOERSMA & WEENINK 2006, Institute of Phonetic Sciences, University of Amsterdam). Praat software is usually applied to human speech, but can be modified to study animal utterances because of its flexibility and programmability (RENDALL et al. 2004; HARRIS et al. 2006). We measured five larynx-related features, i.e. average fundamental frequency (F0mean), minimum fundamental frequency (F0 min), maximum fundamental frequency (F0max), and fundamental frequency at the beginning (F0start) and at the end (F0end) of the utterance. To detect these source-related features, Fast Fourier transforms were generated for all calls (frequency range: 0–15,000 Hz; dynamic range: 30 dB). The actual variation of the fundamental frequency (F0) was measured using the autocorrelation method ('Sound: To pitch (ac)...') after adjusting the analysis parameters according to the range of variation for each vocalisation (GAMBA & GIACOMA 2005, 2007, 2008). To verify the F0 estimation, we investigated the waveform indicating the time between occurrences of a particular feature and calculated the period of the signal. We then measured three vocal tract-related acoustic features, i.e. average first formant (F1), average second formant (F2) and average third formant (F3) (Fig. 1). Formants were studied using linear predictive coding (LPC, MARKEL & GRAY 1976), which is based on the assumption that the vocal signal is produced by a wideband pulse train generated at the glottis. In nonhuman primates, the signal then passes through the vocal tract (throat, mouth or nose) representing a tube characterised by its resonances, which produces the formants. LPC estimates the frequency values corresponding to each formant. Because the vocal signals usually vary over time, this process was carried out along all the signal frames and average formants were calculated. Depending on the acoustic characteristics of the vocalisation, we used a window length of 0.04–0.06 sec. Since the position and number of formants vary with vocal tract length, we detected 5–7 formants depending on the vocal type. Two methods were used to check the formants predicted by LPC: formant analyses were superimposed on the signal spectrogram (following RENDALL et al. 2005), and autocorrelation-based LPC spectra were overlaid on independently derived FFT spectra of the same frames, to verify the accuracy of the LPC analysis. Typical settings were 15,000 Hz for the maximum formant and 22.0 dB for the dynamic range. The formant pattern fitting was determined using a step-by-step monitored process, where the operator could interrupt the analysis and modify its parameters. We then recorded the duration of the whole vocal emission (DUR), the percentage of time required to reach the F0 min (Pt2 min), and the percentage of time required to reach the F0max (Pt2max). A Praat script was used to automate file opening, editing and saving of the measurements (GAMBA et al. 2012a).

Statistical analysis

To ascertain that qualitatively identified acoustic types corresponded to objectively discrete phonetic categories, we used multivariate statistical tests. To avoid pseudoreplication,
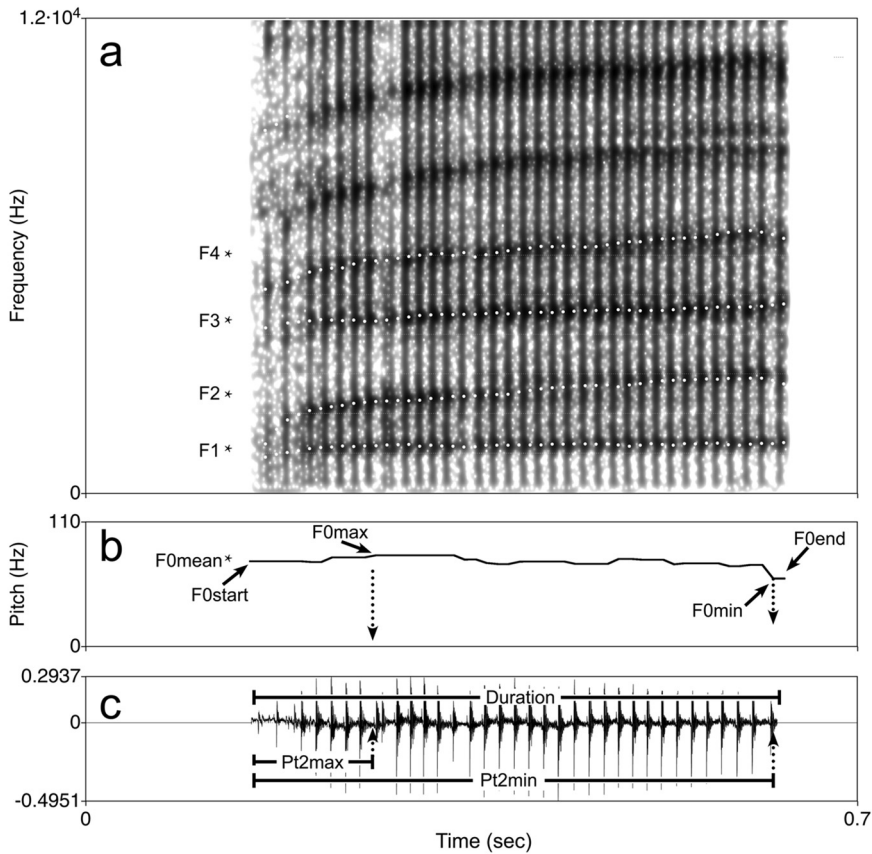
Fig. 1. — (a) Spectrogram of an alarm long grunt with formant analysis (overlaid). We tracked formants punctually, and then the mean values were used in the analysis (F1 = first formant, F2 = second formant, F3 = third formant, F4 = fourth formant). (b) The respective pitch contour analysis. Along with the average fundamental frequency (F0mean), the arrows indicate the other parameters we measured: maximum fundamental frequency (F0max), minimum fundamental frequency (F0min), start fundamental frequency (F0start), final fundamental frequency (F0end). (c) The waveform of the same vocalisation where duration (DUR), percentage of time required to reach F0 min (Pt2 min), percentage of time required to reach F0max (Pt2max) are indicated.

statistical analyses were carried out on the individual mean values of each acoustic property per vocal type. To be included in the statistical analysis, an individual must have been sampled at least 3 times for a specific vocal type, and at least three individuals must have been sampled for each type.

We obtained a dataset consisting of 2985 vocalisations belonging to nine vocal types, as follows: grunts (n_{calls} = 2310; n_{ind} = 58); alarm long grunts (n_{calls} = 105; n_{ind} = 24); territorial calls (n_{calls} = 76; n_{ind} = 7); clicks (n_{calls} = 270; n_{ind} = 15); hoots (n_{calls} = 80; n_{ind} = 16); tonal calls (n_{calls} = 29; n_{ind} = 11); snorts (n_{calls} = 52; n_{ind} = 11); croui-croui (n_{calls} = 29; n_{ind} = 8); long grunts (n_{calls} = 34; n_{ind} = 13). Other vocal types did not fit the criteria and were not entered into the quantitative analysis: alarm long grunt clear calls (n_{calls} = 15; n_{ind} = 7); grunt clear calls (n_{calls} = 26;

n_{ind} = 14); grunt hoots (n_{calls} = 41; n_{ind} = 8); chatters (n_{calls} = 21; n_{ind} = 6); screams (n_{calls} = 21; n_{ind} = 1); aerial alarm calls (n_{calls} = 5; n_{ind} = 3).

We used discriminant function analysis (DFA) to identify linear combinations of predictor variables that maximise differences among vocal types. DFA was run using a stepwise procedure, and F-value thresholds for acceptance or rejection of independent variables were set at F = 3.84 and F = 2.71 in all analyses. DFA was run on the call samples following the criteria explained above, but not all vocal types were recorded from all individuals. In DFA, the probability of group membership was selected as equal regardless of differences in group size. This allowed us to check for large differences in group sizes between vocal types. The standardised coefficients (SC) for the most important variables for each of the first four discriminant functions are listed in the Supplemental Data (SM4). The statistical analysis was performed using SPSS version 21 (IBM Corp. Released 2013. IBM SPSS Statistics for Mac OS, Version 21.0. Armonk, NY: IBM Corp, USA).

RESULTS

Identification of vocal categories

Our classification procedure identified 15 distinct vocal types: long grunt, grunt clear call, alarm long grunt, alarm long grunt clear call, grunt, grunt hoot, click, snort, territorial call, croui-croui, hoot, aerial alarm, tonal call, chatter, scream. A spectrogram for each vocal type is shown in Figs 2–3. To increase readability, the time scale of the spectrograms is different in the two figures.

Information on the utterances making up the vocal repertoire of *Eulemur mongoz* is summarised in Table 1. Descriptions of the 15 vocalisations identified according to their spectral and temporal properties are reported in the Supplemental Data (SM3). We reported the mean and standard deviation of the acoustic parameters in Tables 2 and 3.

We noted differences in the frequency of occurrence of some context-specific vocalisations between wild and captive populations, such as the territorial and aerial alarm calls, which were emitted in response to the presence of predators, or the croui-croui, given when the individuals regrouped.

Quantitative discrimination of the vocal types

We included nine vocal types in the discriminant function analysis. Results are shown in Fig. 4 as a scatter plot of the first two discriminant scores (DS). The first four linear DS cumulatively explained 99.3% of the variance among vocal types (DS1: 83.1%; DS2: 8.8%; DS3: 4.4%; DS4: 3.0%). DS1 correlated most strongly with the third formant (F3, SC = 0.774), DS2 was primarily explained by the second formant (F2, SC = 0.511), DS3 by F0 variables (F0end, SC = – 0.642; F0start, SC = – 0.614; F0 min, SC = – 0.587; F0mean, SC = – 0.567; F0max, SC = – 0.556) and DS4 by duration (SC = – 0.541). Overall correct classification was 92.9% (cross-validated 88.1%; Wilks' lambda = 0.006, $F_{8, 117}$ = 2287.03, P < 0.001). Across the nine vocal types, correct classification ranged in the cross-validated analysis from 57.1% (snorts) to 100% (showed by all other types except the clicks). Clicks and snorts, which appeared the most structurally similar types, were misclassified in each other's group by 25.0 and 42.9%, respectively. The parameters we measured were able to discriminate quantitatively among all the vocal types entered into the DFA better than the 14.0% expected by chance (binomial test,
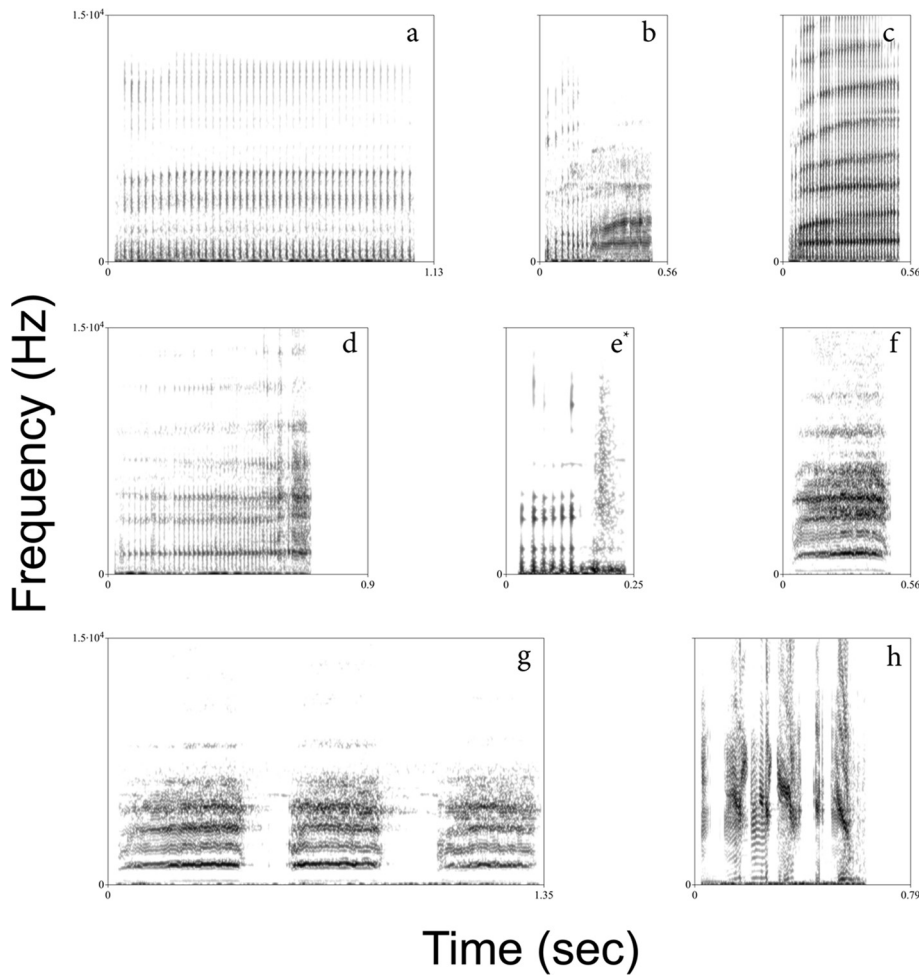
Fig. 2. — Sound spectrograms of the vocal types emitted by *Eulemur mongoz*: (a) long grunt; (b) grunt clear call; (c) alarm long grunt; (d) alarm long grunt clear call; (e) grunt hoot; (f) territorial call; (g) crouicroui; (h) scream. All spectrograms were generated in Praat with the following parameters: window length: 0.01, time range as shown (0.34–1.13 sec); frequency range: 0–15000 Hz; maximum: 100 dB/Hz; dynamic range: 45–30 dB; pre-emphasis: 0.0 dB/Oct. Asterisks denote a different time scale.

$P < 0.001$). The plot in Fig. 4 shows that DS1, which correlated most strongly with F3, clearly separates clusters corresponding to the average individual means of hoots, clicks and snorts from all other vocal types. Territorial calls, tonal calls and croui-croui calls cluster with negative DS1 scores and high, positive DS2 scores. Pulse trains showed negative DS1 and lower DS2 scores, with grunts forming a distinct cluster from long grunts and alarm long grunts. The high rate of correct classifications validated our a priori identification of vocal types.
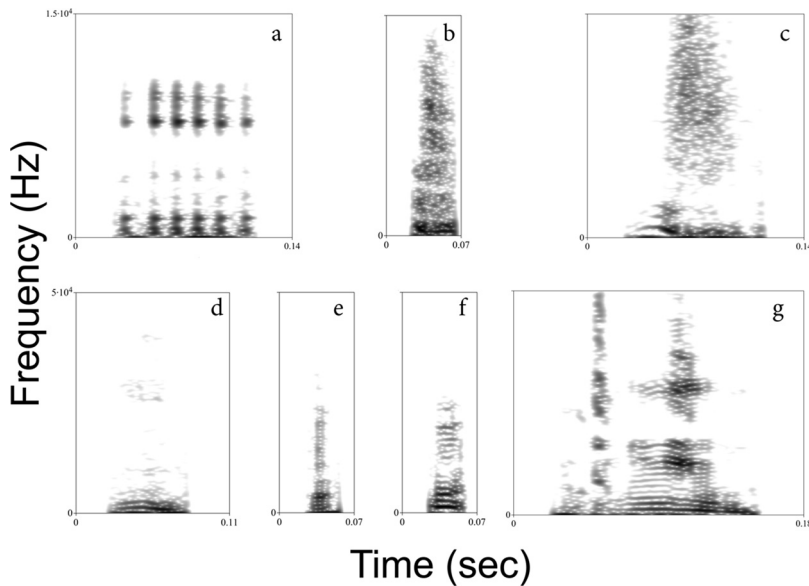
Fig. 3. — Sound spectrograms of the vocal types emitted by *Eulemur mongoz*: (a) grunt; (b) click; (c) snort; (d) hoot; (e) aerial alarm call; (f) tonal call; (g) chatter. All spectrograms were generated in Praat with the following parameters: window length: 0.01, time range as shown (0.07–0.18 sec); frequency range: 0–15000 Hz; maximum: 100 dB/Hz; dynamic range: 45–30 dB; pre-emphasis: 0.0 dB/Oct.

DISCUSSION

Our investigation confirmed the hypothesis that the mongoose lemur has a repertoire that exceeds estimates obtained by previous studies. We identified 15 categories of vocalisations, in addition to the infant call recorded by PETTER & CHARLES-DOMINIQUE (1979). All of the calls can be distinguished by ear and on the basis of their acoustic structure. Previous publications described most of the calls, but each paper contributed only a partial inventory of different categories based on qualitative evaluation. Our analysis critically revises the vocal types found in previous studies in the light of a quantitative analysis of acoustic structure. We also give a well-founded estimate of within-species variability, as our samples of calls and individuals were much larger than those studied previously (e.g. compare Table 4 in MACEDONIA & STANGER 1994 with Tables 2 and 3 in this study).

As other studies have observed for diverse primate species, differences between captive and wild populations are limited in terms of vocal repertoire, but the frequency of occurrence of a particular display may differ depending on the environment (KEITH-LUCAS et al. 1999; HOSEY 2005). The differences we found, such as the lack of territorial and aerial alarm calls emitted by captive animals, are likely to be due to the absence of the proper contexts under captive conditions. The aerial alarm calls were emitted in nature in response to the presence of predators and were rare even in our field recordings: they were sampled only at Bombetoka-Belemboka, probably because of the locally high density of aerial raptors and because the forest there is less dense than at our other recording sites. Chatters, grunt clear calls and grunt hoots, which are shared across

Table 1.

Definition of the vocal types including synonyms used in previous studies of *Eulemur mongoz,* context of emission, description of the call usage and phonation mechanics [(1) ANDREW (1963); (2) TATTERSALL & SUSSMAN (1975); (3) PETTER & CHARLES-DOMINIQUE (1979); (4) MACEDONIA & STANGER (1994); (5) CURTIS & ZARAMODY (1999)]. Italic font denotes vocal types not included in the discriminant function analysis.

Vocal types	Synonyms	Contexts	Phonation mechanism and posture
Long grunt	Creeeeeeeeee (3) Long grunts (4) creak (5)	Group-cohesion, alert.	Nasal call. Quadrupedal or sitting posture.
Grunt clear call	–	Alert.	Mouth barely closed mouth. Quadrupedal standing posture.
Alarm long grunt	Creaking door (2), Greeee (3), Open mouth grunts, (4), Long creak (5)	Terrestrial anti-predator alarm, territorial defence.	Open mouth. Quadrupedal posture.
Alarm long grunt clear call	Closed open-mouth grunts (4)	Terrestrial anti-predator alarm, alert.	Open mouth. Quadrupedal posture.
Grunt	Grunt (2), short grunt (4) Grunt agitated, grunt soft (5)	Group-cohesion, alert, territorial defence, aggression	Nasal call. Quadrupedal posture with head and tail movements.
Grunt hoot	Click-grunt (1), explosive grunt (2), grunt sneeze (5)	Alert	Mouth closed. Quadrupedal standing posture.
Click	Click (4)	Group-cohesion, alert	Mouth closed. Various postures.
Snort	Snort (3, 5)	Group-cohesion, alert	Nasal call. Various postures.
Territorial call	Creeee (3), terrestrial disturbance/ advertisement (4), screech (5)	Territorial defence	Open mouth. Quadrupedal posture.
Croui-croui	–	Territorial advertisement	Open mouth. Quadrupedal standing posture.
Hoot	Sneeze (3, 5), hoots (4)	Alert	Emitted with mouth closed; quadrupedal or sitting posture.
Aerial alarm call	Cak (5)	Aerial anti-predator alarm	Mouth closed. Crouched posture.
Tonal call	Hon (3), clear call (4), hmm (5)	Group-cohesion	Emitted with closed mouth; sitting position or while moving.

(*Continued*)

Table 1.

(*Continued*)

Vocal types	Synonyms	Contexts	Phonation mechanism and posture
Chatter	Contact-rejection (3)	Aggression	Emitted with open mouth articulation; usually crouched or jumping between branches.
Scream	Shriek in fear (1), distress calls (3), warble (5)	Physical fight, manipulation	Given with open mouth.

most Lemuridae (see PEREIRA et al. 1988; MACEDONIA & STANGER 1994; GAMBA & GIACOMA 2005, 2007), were not recorded in all the sites, probably because of limited sampling. Screams were rare: they were recorded in captivity only during manipulation of the animals, but were also emitted by injured animals in the wild.

Our findings are in agreement with most of the contextual observations mentioned in previous studies and for each vocal type. Nine vocal types (croui-croui, chatter, scream, aerial alarm, terrestrial alarm, alarm long grunt, alarm long grunt clear call, territorial call, click, tonal call) are context-typical emissions that are likely to show various degrees of referentiality (HOLLÉN & RADFORD 2009; GAMBA & GIACOMA 2010).

The mongoose lemurs' repertoire includes four loud vocalisations that are likely to play a role in long-distance communication for regrouping (croui-croui) or for alerting the group to possible danger (territorial call, alarm long grunt, alarm long grunt clear call). Concerning the croui-croui, several factors favour its long-range propagation, such as its repetitive emission of units and its acoustic structure, characterised by repetitive amplitude modulation and low mean frequency (WILEY & RICHARDS 1982). As in other lemur species (FICHTEL & KAPPELER 2002; SEILER et al. 2013) aerial and terrestrial alarm vocalisations differed strongly in phonation mechanisms and acoustic structure. Unlike other lemur species (*Eulemur macaco*, GOSSET et al. 2001; *Indri indri*, MARETTI et al. 2010), *Eulemur mongoz* emits the aerial alarm call with its mouth closed. The alarm long grunt, which was emitted when a potential terrestrial predator was nearby, retained the typical pulse train structure of other congeneric species' signals (GAMBA & GIACOMA 2005, 2008), but was emitted with an open mouth.

Calls used to maintain group cohesion (e.g. grunt, grunt clear call, grunt hoot, snort and hoot), present a shorter pulse train or a harmonic structure and were emitted in several contexts, i.e. when animals were disturbed, or travelling and/or to maintain contact. The utterance of one of these calls appeared to depend more on the degree of arousal than on a particular situation. They can also be structurally similar, as the DFA showed for click and snorts. These calls are widespread and given by most species across the genus *Eulemur* (GAMBA & GIACOMA 2005, 2010). Selection apparently favoured low-pitched qualities that reflect body size better than high-pitched calls (OWINGS & MORTON 1998). Size- and individual-related cues are, in fact, better projected in the signals in which, because of the low fundamental frequency, formants are

Table 2.

Mean and standard deviation calculated from individual mean values of acoustic parameters per vocal type. The parameters measured were: call duration (DUR), average fundamental frequency (MeF0), maximum fundamental frequency (F0max), minimum fundamental frequency (F0min), start fundamental frequency (F0start), final fundamental frequency (F0end), RangeF0 (F0max–F0 min), EnstF0 (EndF0–StartF0), average first formant (F1), average second formant (F2), average third formant (F3), percentage of time required to reach F0 min (Pt2 min), percentage of time required to reach F0max (Pt2max).

Types	No. of vocalisations	DUR (sec)	MeF0 (Hz)	F0min (Hz)	F0max (Hz)	F0start (Hz)	F0end (Hz)	RangeF0 (Hz)	EnstF0 (Hz)	F1 (Hz)	F2 (Hz)	F3 (Hz)	Pt2min (%)	Pt2max (%)
Long grunt	34	0.95	55	42	70	60	55	27	21	1232	3064	4673	54	45
		± 0.31	± 23	± 20	± 23	± 26	± 23	± 16	± 17	± 237	± 371	± 293	± 26	± 34
Grunt clear call	26	0.33	78	73	83	75	84	11	12	1202	2876	4509	46	55
		± 0.12	± 25	± 27	± 23	± 28	± 23	± 9	± 11	± 258	± 495	± 354	± 41	± 43
Alarm long grunt	105	0.50	78	69	87	76	82	18	19	1271	3049	4564	46	54
		± 0.17	± 21	± 23	± 20	± 23	± 22	± 12	± 14	± 180	± 390	± 276	± 23	± 27
Alarm long grunt clear call	15	0.68	84	67	100	72	95	32	35	1348	3096	4622	49	60
		± 0.14	± 19	± 24	± 15	± 27	± 16	± 24	± 25	± 43	± 331	± 375	± 33	± 35
Grunt	2310	0.10	61	59	63	62	62	4	9	958	2779	4625	46	53
		± 0.03	± 15	± 15	± 16	± 15	± 15	± 3	± 5	± 33	± 48	± 48	± 22	± 20
Grunt hoot	41	0.29	43	43	60	56	49	15	19	1037	2841	4657	40	58
		± 0.14	± 23	± 19	± 28	± 28	± 22	± 9	± 19	± 133	± 304	± 230	± 42	± 45
Click	270	0.02	212	214	215	212	212	1	2	1236	4600	9935	50	56
		± 0.01	± 19	± 39	± 27	± 27	± 28	± 1	± 2	± 114	± 317	± 745	± 35	± 36
			±27,73											

Table 3.

Mean and standard deviation of the acoustic parameters per vocal type. The parameters measured were: call duration (DUR), average fundamental frequency (MeF0), maximum fundamental frequency (F0max), minimum fundamental frequency (F0 min), start fundamental frequency (F0start), final fundamental frequency (F0end), RangeF0 (F0max–F0 min), EnstF0 (EndF0–StartF0), average first formant (F1), average second formant (F2), average third formant (F3), percentage of time required to reach F0 min (Pt2 min), percentage of time required to reach F0max (Pt2max).

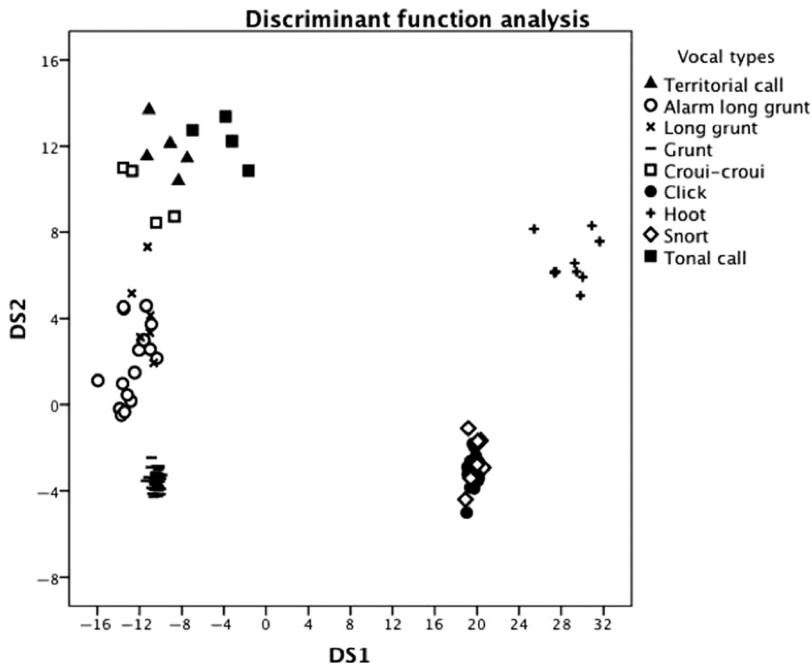| Types	No. of vocalisations	DUR (sec)	MeF0 (Hz)	F0min (Hz)	F0max (Hz)	F0start (Hz)	F0end (Hz)	RangeF0 (Hz)	EnstF0 (Hz)	F1 (Hz)	F2 (Hz)	F3 (Hz)	Pt2min (%)	Pt2max (%)
Snort	52	0.03	199	198	200	198	200	2	3	1219	4664	10063	34	64
		± 0.01	± 45	± 6	± 43	± 45	± 45	± 4	± 6	± 85	± 84	± 106	± 37	± 34
Territorial call	76	0.63	255	237	276	261	255	42	26	1683	3763	5154	67	39
		± 0.17	± 22	± 27	± 24	± 28	± 30	± 9	± 9	± 167	± 209	± 156	± 20	± 22
Croui-croui	29	1.34	128	117	140	126	130	23	18	1654	3806	5058	46	61
		± 0.25	± 8	± 10	± 9	± 11	± 15	± 8	± 7	± 130	± 137	± 243	± 38	± 38
Hoot	80	0.07	306	301	311	301	296	9	18	1398	7072	10378	66	27
		± 0.03	± 96	± 96	± 97	± 92	± 90	± 16	± 25	± 125	± 311	± 736	± 30	± 24
Aerial alarm call	5	0.04	388	386	390	387	389	5	2	1584	4827	6925	39	54
		± 0.02	± 122	± 120	± 125	± 121	± 124	± 5	± 3	± 50	± 129	± 193	± 48	± 44
Tonal call	29	0.12	581	575	587	581	580	12	8	1366	3794	5826	54	44
		± 0.08	± 102	± 101	± 103	± 103	± 101	± 16	± 12	± 130	± 377	± 372	± 38	± 36
Chatter	21	0.36	1906	1846	1958	1912	1921	115	63	3915	6321	9867	53	32
		± 0.39	± 307	± 367	± 262	± 293	± 290	± 112	± 53	± 212	± 2662	± 4228	± 27	± 37
Scream *	21	0.32	586	549	640	606	589	90	64	1724	3345	4819	55	49
		± 0.18	± 128	± 147	± 112	± 122	± 148	± 72	± 65	± 718	± 610	± 333	± 40	± 48

Note: * Only one individual was recorded.

Fig. 4. — Distribution of the discriminant scores (DS) for the vocalisation types along the first two canonical discriminant functions. The highest correlation between discriminating variables and standardised canonical discriminant functions for DS1 (which explained 83.1% of the variance) is the third formant (F3, 0.774); for DS2 (8.8%), it is the second formant (F2, 0.511). Overall correct classification was 92.9% (cross-validated 88.1%; Wilks' lambda = 0.006, F8, 117 = 2287.03, $P < 0.001$).

spectrally prominent (for a theoretical framework see FITCH 1997; REBY & MCCOMB 2003; TAYLOR & REBY 2010). In this manner, vocal communication may regulate social interactions by informing receivers about body size and identity, as well as by indicating the ability to control territory and resources (OWINGS & MORTON 1998). Thus, the high number of grunts exchanged among the mongoose lemurs can provide conspecifics with information about emitter identity (GAMBA et al. 2012a). Viewing mongoose lemur vocal communication from the perspective of motivation-structural principles (MORTON 1977; OWINGS & MORTON 1998), we conclude that the wideband (usually low-pitched) sounds serve for alert, territorial advertisement, anti-predator alarm and aggression (e.g. territorial calls, long grunts, alarm long grunts and multi-unit emissions including low-pitched pulse trains). Higher frequency calls such as the scream and chatter denote distress and occurred during physical interactions.

Qualitatively speaking, the vocal repertoire of the mongoose lemur comprises a mix of discrete and graded calls (MARLER 1976). At least three vocal types showed multi-unit structures, where units were clearly distinguishable in terms of their spectrographic characteristics (grunt clear call, alarm long grunt clear call and grunt hoot). In lemurs, the units within a vocalisation (Fig. 2) are usually recognisable on the basis of their spectral structure, but they are not separated by silent intervals (EENS et al. 1989). Single units (grunt, clear (or tonal) call, hoot) often occurred as 'stand-alone' calls, but were sometimes associated to form composite vocal types, similarly to the repertoires of

Table 4.

Occurrence of vocal types in sampling sites in Madagascar and the Comoros, and in zoo populations. Total time = total recording time for each site. LG = long grunt; GC = grunt clear call; AL = alarm long grunt; AC = alarm long grunt clear call; GR = grunt; GH = grunt hoot; CL = click; SN = snort; TE = territorial call; CR = croui-croui; HO = hoot; AA = aerial alarm call; TC = tonal call; CH = chatter; SR = scream. Symbols indicate presence (+) or absence (–) of a vocal type in a particular site.

Site	Total time	LG	GC	AL	AC	GR	GH	CL	SN	TE	CR	HO	AA	TC	CH	SR
Bombetoka	25 hr 20 min	+	+	+	–	+	+	+	+	+	+	+	+	+	+	–
Antsilaiza	11 hr 25 min	+	–	+	–	+	–	+	+	+	+	+	–	+	+	–
Analabe-Ankatsabe	5 hr 30 min	+	–	+	+	+	–	+	+	+	+	+	–	+	–	–
Comoros	3 hr 50 min	+	–	+	+	+	–	+	+	+	+	+	–	+	+	–
Zoos	14 hr 00 min	+	+	+	+	+	+	+	+	–	–	+	–	+	+	+
Total	60 hr 05 min	34	26	105	15	2310	41	270	52	76	29	80	5	29	21	21

other congeneric species (GAMBA & GIACOMA 2005, 2007). In these composite calls, units are arranged in vocal type-specific order and combinations, but the patterns according to which mongoose lemurs recombine units to form calls are limited. Low-pitched pulse trains (grunts, long grunts, alarm long grunts) are present in six composite types (either as the first or as a single unit), while suffixation mainly involves relatively short harmonic elements (tonal calls or clear calls). OUTTARA et al. (2009) have demonstrated that, in *Cercopithecus campbelli campbelli*, suffixation is associated with different contexts of emission. In *E. mongoz*, as in *E. coronatus* (GAMBA & GIACOMA 2007), detailed analysis is required to test the hypothesis that suffixation appears to be associated with the degree of arousal as in *E. coronatus* (GAMBA & GIACOMA 2007).

At least the nine vocal types tested by a multivariate statistical model were discriminated significantly and with a high percentage of correct assignment to groups. The two canonical dimensions (DS1 and DS2) explaining most of the variability (91.9%) relied heavily on the third and the second formants (F3 and F2). This supports evidence from previous analyses indicating that formants higher than F1 correlate more strongly with vocal tract length (GAMBA et al. 2012b). Studies of auditory sensitivity by RAMSIER et al. (2012; see also RAMSIER et al. 2013) have shown that the greatest auditory sensitivity in *Eulemur mongoz* ranges between 4 and 20 kHz (optimal sensitivity at 8 kHz). This range contains the values of the second and third formants in the vast majority of the vocal types we recorded.

The number of audibly distinct calls given by mongoose lemurs is similar to the average reported for other lemur species ($n = 15 + 7$, MCCOMB & SEMPLE 2005) and in particular to those observed in the crowned lemur (GAMBA & GIACOMA 2007). Since the size and complexity of a species' vocal repertoire is the compound result of its ecological and social needs for functionally meaningful vocal signals, animals living in the same environment may show similarities in their vocal repertoires, both in terms of acoustic structure of vocal types and of their usage. Thus, the most obvious comparison for mongoose lemur repertoires is with those of sympatric congeneric species (MARKOLF & KAPPELER 2013). Despite potential differences deriving from the methods used in other studies, two sympatric species, *E. rufus* ($n = 13$, possibly 14; FICHTEL 2004; MACEDONIA & STANGER 1994) and *E. fulvus* ($n = 11$; MACEDONIA & STANGER 1994), showed similar numbers of vocalisations to those we found in mongoose lemurs (MACEDONIA & STANGER 1994).

We hope that the comprehensive description of the mongoose lemurs' vocal repertoire provided in this paper will encourage further comparative studies of other lemur populations and taxa. Fruitful avenues for future work include possible differences between age classes or individuals, and whether calls are sexually dimorphic (GIACOMA et al. 2010; GAMBA et al. 2012b). It would also be very interesting to investigate whether particular vocalisations differ when uttered in different behavioural contexts, as has been demonstrated in other primate species (CHENEY & SEYFARTH 1982; RENDALL et al. 1999).

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No potential conflict of interest was reported by the authors.

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REFERENCES

ALTMANN J. 1974. Observational study of behavior: sampling methods. *Behaviour* 49: 227–266. doi:10.1163/156853974X00534.

ANDREW R.J. 1963. The origin and evolution of the calls and facial expressions of the primates. *Behaviour* 20: 1–107. doi:10.1163/156853963X00220.

ANDRIAHOLINIRINA N., FAUSSER J.L., ROOS C., ZINNER D., THALMANN U., RABARIVOLA C., RAVOARIMANANA I. et al. 2006. Molecular phylogeny and taxonomic revision of the sportive lemurs (*Lepilemur*, Primates). *BMC Evolutionary Biology* 6: 1–13.

ASAB (Association for the Study of Animal Behaviour). 2012. Guidelines for the treatment of animals in behavioural research and teaching. *Animal Behaviour* 83: 301–309. doi:10.1016/j.anbehav.2011.10.031.

AZA (Prosimian Taxon Advisory Group). 2013. *Eulemur* care manual. Silver Spring: Association of Zoos and Aquariums.

BAKER M.C. 2004. The chorus song of cooperatively breeding laughing kookaburras (Coraciiformes, Halcyonidae: *Dacelo novaeguineae*): characterization and comparison among groups. *Ethology* 110: 21–35. doi:10.1046/j.1439-0310.2003.00941.x.

BOERSMA P. & WEENINK D. 2006. Praat: doing phonetics by computer (Version. 5.3.4). Available at: http://www.praat.org.

CHENEY D.L. & SEYFARTH R.M. 1982. How vervet monkeys perceive their grunts: field playback experiments. *Animal Behaviour* 30: 739–751. doi:10.1016/S0003-3472(82)80146-2.

CURTIS D.J. 1997. The mongoose lemur (*Eulemur mongoz*). A study in behaviour and ecology. *Ph. D. Thesis, Zurich University*.

CURTIS D.J. & ZARAMODY A. 1998. Group size, home range use, and seasonal variation in the ecology of *Eulemur mongoz*. *International Journal of Primatology* 19: 811–835. doi:10.1023/A:1020341312735.

CURTIS D.J. & ZARAMODY A. 1999. Social structure and seasonal variation in the behaviour of *Eulemur mongoz*. *Folia Primatologica* 70: 79–96. doi:10.1159/000021679.

EENS M., PINXTEN R. & VERHEYEN R.F. 1989. Temporal and sequential organisation of song bouts in the starling. *Ardea* 77: 75–86.

FANT G. 1960. Acoustic theory of speech production. *The Hague*: *Mouton*.

FICHTEL C. 2004. Reciprocal recognition of sifaka (*Propithecus verreauxi verreauxi*) and redfronted lemur (*Eulemur fulvus rufus*) alarm calls. *Animal Cognition* 7: 45–52. doi:10.1007/s10071-003-0180-0.

FICHTEL C. & KAPPELER P.M. 2002. Anti-predator behavior of group-living Malagasy primates: mixed evidence for a referential alarm call system. *Behavioral Ecology and Sociobiology* 51: 262–275. doi:10.1007/s00265-001-0436-0.

FISCHER J. & HAMMERSCHMIDT K. 2002. An overview of the Barbary macaque, *Macaca sylvanus*, vocal repertoire. *Folia Primatologica* 73: 32–45. doi:10.1159/000060417.

FITCH W.T. 1997. Vocal tract length and formant frequency dispersion correlate with body size in rhesus macaques. *Journal of the Acoustical Society of America* 102: 1213–1222.

FITCH W.T., NEUBAUER J. & HERZEL H. 2002. Calls out of chaos: the adaptive significance of nonlinear phenomena in mammalian vocal production. *Animal Behaviour* 63: 407–418. doi:10.1006/anbe.2001.1912.

GAMBA M., COLOMBO C. & GIACOMA C. 2012b. Acoustic cues to caller identity in lemurs: a case study. *Journal of Ethology* 30: 191–196. doi:10.1007/s10164-011-0291-z.

GAMBA M., FRIARD O. & GIACOMA C. 2012a. Vocal tract morphology determines species-specific features in vocal signals of lemurs (*Eulemur*). *International Journal of Primatology* 33: 1453–1466. doi:10.1007/s10764-012-9635-y.

GAMBA M. & GIACOMA C. 2005. Key issues in the study of primate acoustic signals. *Journal of Anthropological Sciences* 83: 61–87.

GAMBA M. & GIACOMA C. 2006. Vocal tract modeling in a prosimian primate: the black and white ruffed lemur. *Acta Acustica United with Acustica* 92: 749–755.

GAMBA M. & GIACOMA C. 2007. Quantitative acoustic analysis of the vocal repertoire of the crowned lemur. *Ethology Ecology & Evolution* 19: 323–343. doi:10.1080/08927014.2007.9522555.

GAMBA M. & GIACOMA C. 2008. Subspecific divergence in the black lemur's low-pitched vocalizations. *The Open Acoustics Journal* 1: 49–53. doi:10.2174/1874837600801010049.

GAMBA M. & GIACOMA C. 2010. Key issues in the study of primate acoustic signals, an update. *Journal of Anthropological Sciences* 88: 215–220.

GIACOMA C., SORRENTINO V., RABARIVOLA C. & GAMBA M. 2010. Sex differences in the song of Indri indri. *International Journal of Primatology* 31: 539–551. doi:10.1007/s10764-010-9412-8.

GOSSET D., FORNASIERI I. & ROEDER J.-J. 2001. Acoustic structure and contexts of emission of vocal signals by black lemurs. *Evolution of Communication an International Multidisciplinary Journal* 4: 225–251. doi:10.1075/eoc.4.2.

HARRIS T.R., FITCH W.T., GOLDSTEIN L.M. & FASHING P.J. 2006. Black and white colobus monkey (*Colobus guereza*) roars as a source of both honest and exaggerated information about body mass. *Ethology* 112: 911–920. doi:10.1111/eth.2006.112.issue-9.

HAUSER M.D. 1996. The evolution of communication. *Cambridge, MA*: *MIT Press*.

HOLLÉN L.I. & RADFORD A.N. 2009. The development of alarm call behaviour in mammals and birds. *Animal Behaviour* 78: 791–800. doi:10.1016/j.anbehav.2009.07.021.

HOSEY G. 2005. How does the zoo environment affect the behaviour of captive primates? *Applied Animal Behaviour Science* 90: 107–129. doi:10.1016/j.applanim.2004.08.015.

KEITH-LUCAS T., WHITE F., KEITH-LUCAS L. & VICK L.G. 1999. Changes in behavior in free ranging *Lemur catta* following release in a natural habitat. *American Journal of Primatology* 47: 15–28. doi:10.1002/(ISSN)1098-2345.

LAIOLO P. 2010. The emerging significance of bioacoustics in animal species conservation. *Biological Conservation* 143: 1635–1645. doi:10.1016/j.biocon.2010.03.025.

LELIVELD L., SCHEUMANN M. & ZIMMERMANN E. 2011. Acoustic correlates of individuality in the vocal repertoire of a nocturnal primate (*Microcebus murinus*). *Journal of the Acoustical Society of America* 129: 2278–2288. doi:10.1121/1.3559680.

LEMASSON A. & HAUSBERGER M. 2011. Acoustic variability and social significance of calls in female Campbell's monkeys (*Cercopithecus campbelli campbelli*). *Journal of the Acoustical Society of America* 129: 3341–3352.

MACEDONIA J.M. 1993. The vocal repertoire of the ring-tailed lemur (*Lemur catta*). *Folia Primatologica* 61: 186–217. doi:10.1159/000156749.

MACEDONIA J.M. & STANGER K.F. 1994. Phylogeny of the Lemuridae revisited: evidence from communication signals. *Folia Primatologica* 63: 1–43. doi:10.1159/000156787.

MARETTI G., SORRENTINO V., FINOMANA A., GAMBA M. & GIACOMA C. 2010. Not just a pretty song: *An Overview of the Vocal Repertoire of Indri Indri*. *Journal of Anthropological Science* 88: 151–165.

MARKEL J.D. & GRAY A.H. 1976. Linear prediction of speech. Communication and cybernetics Vol. 12. *New York, NY*: *Springer-Verlag*.

MARKOLF M. & KAPPELER P.M. 2013. Phylogeographic analysis of the true lemurs (*genus Eulemur*) underlines the role of river catchments for the evolution of micro-endemism in Madagascar. *Frontiers in Zoology* 10: 70.

MARLER P. 1976. Social organization, communication and graded signals: the chimpanzee and gorilla, pp. 239–280. In: Bateson P.P.G. & Hinde R.A., Eds. Growing points in ethology. *Cambridge*: *Cambridge University Press*.

MCCOMB K. & SEMPLE S. 2005. Coevolution of vocal communication and sociality in primates. *Biology Letters* 1: 381–385.

MCGREGOR P.K. & DABELSTEEN T. 1996. Communication networks, pp. 409–425. In: Kroodsma D.E. & Miller E.H., Eds. Ecology and evolution of acoustic communication among birds. *New York, NY*: *Cornell University Press*.

MITTERMEIER R.A., LOUIS E.E., RICHARDSON M., SCHWITZER C., LANGRAND O., RYLANDS A.B., HAWKINS F. et al. 2010. Lemurs of Madagascar (3rd ed.) *Washington, DC*: *Conservation International*.

MORTON E.S. 1977. On the occurrence and significance of motivation-structural rules in some bird and mammal sounds. *The American Naturalist* 111: 855–869.

NADHUROU B. 2014. Ecology, behaviour and conservation of the mongoose lemur (*Eulemur mongoz*). *Ph.D. Thesis*, *University of Torino*.

ODA R. 2002. Individual distinctiveness of the contact calls of ring tailed lemurs. *Folia Primatologica* 73: 132–136. doi:10.1159/000064785.

OLIVIERI G., CRAUL M. & RADESPIEL U. 2005. Inventaire des lémuriens dans 15 fragments de forêt de la province de Mahajanga. *Lemur News* 10: 11–16.

OUTTARA K., LEMASSON A. & ZUBERBÜHLER K. 2009. Campbell's monkeys use affixation to alter call meaning. *PloS ONE* 4 (11): e7808. doi:10.1371/journal.pone.0007808.

OWINGS D.H. & MORTON E.S. 1998. Animal vocal communication: a new approach (1st ed.) *Cambridge*: *Cambridge University Press*.

PAILLETTE M. & PETTER J.J. 1978. Vocal repertoire of *Lemur fulvus albifrons*, pp. 831–834. In: Chivers D.J. & Herbert J., Eds. Recent advances in primatology. *London*: *Academic Press*.

PASTORINI J., THALMANN U. & MARTIN R.D. 2003. A molecular approach to comparative phylogeography of extant Malagasy lemurs. *Proceedings of National Academy of Science of the United States of America* 100: 5879–5884. doi:10.1073/pnas.1031673100.

PEREIRA M.E., SEELIGSON M.L. & MACEDONIA J.M. 1988. The behavioral repertoire of the black-and-white ruffed lemur, *Varecia variegata variegata* (Primates: Lemuridae). *Folia Primatologica* 51: 1–32. doi:10.1159/000156353.

PETTER J.J., ALBIGNAC R. & RUMPLER Y. 1977. Faune de Madagascar, Vol. 44. Mammifères lémuriens *Paris*: *Orstom, CNRS*.

PETTER J.J. & CHARLES-DOMINIQUE P. 1979. Vocal communication in prosimians, pp. 247–305. In: Doyle G.A. & Martin R.D., Eds. The study of prosimian behavior. *New York, NY*: *Academic Press*.

RAMSIER M.A. 2013. Evolution of auditory sensitivity among strepsirhine primates, pp. 265–270. In: Masters J.D. et al., Eds. Leaping ahead: advances in prosimian biology. *New York, NY*: *Springer*.

RAMSIER M.A., CUNNINGHAM A.J., FINNERAN J.J. & DOMINY N.J. 2012. Social drive and the evolution of primate hearing. *Philosophical Transactions of the Royal Society (B)* 367: 1860–1868.

RASMUSSEN M. 1998. Mongoose lemurs at Ampijoroa, Madagascar: Notes on behavior, ecology and activity cycle. In: Bettinger T., Ed. Mongoose lemur (*Eulemur mongoz*), SSP Masterplan. *Cleveland*: *Cleveland Metroparks Zoo*.

REBY D. & MCCOMB K. 2003. Anatomical constraints generate honesty: acoustic cues to age and weight in the roars of red deer stags. *Animal Behaviour* 65: 519–530. doi:10.1006/anbe.2003.2078.

RENDALL D., CHENEY D.L., SEYFARTH R.M. & OWREN M.J. 1999. The meaning and function of grunt variants in baboons. *Animal Behaviour* 57: 583–592. doi:10.1006/anbe.1998.1031.

RENDALL D., KOLLIAS S., NEY C. & LLOYD P. 2005. Pitch (F0) and formant profiles of human vowels and vowel-like baboon grunts: the role of vocalizer body size and voice-acoustic allometry. *Journal of the Acoustical Society of America* 117: 944–955.

RENDALL D., OWREN M.J., WEERTS E. & HIENZ R.D. 2004. Sex differences in the acoustic structure of vowel-like grunt vocalizations in baboons and their perceptual discrimination by baboon listeners. *Journal of the Acoustical Society of America* 115: 411–421.

SCHWITZER C., MITTERMEIER R.A., DAVIES N., JOHNSON S., RATSIMBAZAFY J., RAZAFINDRAMANANA J., LOUIS JR E.E. & RAJAOBELINA S. 2013. Lemurs of Madagascar: A strategy for their conservation 2013-2016. *Bristol*: *IUCN SSC Primate Specialist Group, Bristol Conservation and Science Foundation, and Conservation International*.

SEILER M., SCHWITZER C. & HOLDERIED M. 2013. Anti-predator behaviour of Sahamalaza sportive lemurs, *Lepilemur sahamalazensis*, at diurnal sleeping sites. *Contributions to Zoology* 82: 131–143.

STANGER K.F. & MACEDONIA J.M. 1994. Vocalizations of aye-ayes *(Daubentonia madagascariensis)* in captivity. *Folia Primatologica* 62: 160–169. doi:10.1159/000156773.

TATTERSALL I. 1982. The primates of Madagascar. *New York, NY*: *Columbia University Press*.

TATTERSALL I. & SUSSMAN R.W. 1975. Observation on the ecology and behaviour of the mongoose lemur *Lemur mongoz mongoz* Linnaeus (Primates, Lemuriformes, at Ampijoroa, Madagascar. *Anthropological Papers of the American Museum of Natural History* 52: 193–216.

TAYLOR A.M. & REBY D. 2010. The contribution of source-filter theory to mammal vocal communication research. *Journal of Zoology* 280: 221–236. doi:10.1111/j.1469-7998.2009.00661.x.

TERRY A.M.R., PEAKE T.M. & MCGREGOR P.K. 2005. The role of vocal individuality in conservation. *Frontiers in Zoology* 2: 10.

WILEY R.H. & RICHARDS D.G. 1982. Adaptations for acoustic communication in birds: sound propagation and signal detection, pp. 131–181. In: Kroodsma D.E. & Miller E.H., Eds. Acoustic communication in birds, Vol. 1. *New York, NY*: *Academic Press*.

ZIMMERMANN E. 2009. Vocal expression of emotion in a nocturnal prosimian primate group, mouse lemurs, pp. 215–225. In: Brudzynski S.M., Ed. Handbook of mammalian vocalizations: an integrative neuroscience approach. *Oxford*: *Academic Press*.