Modeling individual vocal differences in group-living lemurs using vocal tract morphology

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Abstract

Vocal individuality is widespread in social animals. Individual variation in vocalizations is a prerequisite for discriminating among conspecifics and may have facilitated the evolution of large complex societies. Ring-tailed lemurs Lemur catta live in relatively large social groups, have conspicuous vocal repertoires, and their species-specific utterances can be interpreted in light of source-filter theory of vocal production. Indeed, their utterances allow individual discrimination and even recognition thanks to the resonance frequencies of the vocal tract. The purpose of this study is to determine which distinctive vocal features can be derived from the morphology of the upper vocal tract. To accomplish this, we built computational models derived from anatomical measurements collected on lemur cadavers and compared the results with the spectrographic output of vocalizations recorded from ex situ live individuals. Our results demonstrate that the morphological variation of the ring-tailed lemur vocal tract explains individual distinctiveness of their species-specific utterances. We also provide further evidence that vocal tract modeling is a powerful tool for studying the vocal output of non-human primates.

Key words: formants, indexical cues, Lemur catta, nasal resonance, ring-tailed lemur.

The capacity to emit and recognize individually distinctive vocalizations is considered to be a crucial prerequisite for the evolution of complex animal and human societies (Tibbetts and Dale 2007). Thus, in recent years, individual recognition mediated by vocal signals has received increasing attention due to the importance of understanding the cognitive and physiological processes underlying these abilities (Pollard and Blumstein 2011). Nonhuman primates (hereafter primates), because of the complexity of their social interactions and the large groups some of them live in, have been targeted as model systems for investigating individual recognition (Rendall et al. 1996, 1998).

The morphology of speech organs is a critical source of interspeaker variation in the human voice (Titze 1994). In line with the source-filter theory of speech production (Fant 1971; Flanagan 1972), the length of the vocal tract affects the resonance of the signal produced by the larynx (Dellwo et al. 2007). Moreover, the vast amount of information yielded by phonetic studies has shown that vocal tract resonance is crucial in encoding individually distinctive features of the human voice (Daqrouq and Tutunji 2015). Vocal production in nonhuman animals can similarly be interpreted using the source-filter theory (e.g. Taylor and Reby 2010; Gamba et al. 2011; Favaro et al. 2015).

The salience of vocal tract filtering in primate communication has been investigated in several species. Historically, Rendall and colleagues (1998) found that the coos of rhesus monkeys Macaca mulatta could be classified by caller identity with high correct classification rates using vocal tract resonances. Evidence that formants play a major role in primate communication can be derived from studies of call production in baboons (Rendall et al. 2005) and macaques (Fitch 1997), and from the spontaneous abilities of macaques to perceive
formants (Fitch and Fritz 2006). However, studies of strepsirhine pri-
mates are still limited. Gamba and colleagues (2012a) found that the 
formants comprising the low-pitched grunts of red-bellied lemurs Eulemur rubriventer were markedly more individually specific when 
compared to larynx-related aspects and were potentially informative 
as to individual identity. Recently, computational models have been 
used to simulate resonance in lemur vocal tracts (Gamba et al. 2012b). In particular, the acoustic output of models built using anatomic 
measurements of the vocal tract showed the same species-
specific features observed in wild animal calls, providing evidence 
that these vocal-tract modeling techniques provide powerful and reli-
able tools for studying the vocal output of primates (Gamba et al. 2012b).

The fact that vocal tract morphology plays a key role in explaining 
interspecific and inter-individual acoustic variation invites questions 
about the degree of inter-individual difference in the vocal apparatus, 
and the effects that changes in a particular part of the vocal tract may 
have on the acoustic properties of vocalizations. Because individuality 
information could be encoded in various acoustic parameters of the 
vocal signal (e.g. Gustison et al. 2012; Scheumann et al. 2012), we 
chose to investigate whether variation in vocal tract morphology could 
yield insights into the sources of variation in resonance. Recent 
research has demonstrated that nasal sounds play a significant role in 
the vocal communication of many species (Lapshina et al. 2012; 
Sibiryakova et al. 2015). The frequencies of short vocalizations 
released via the nasal regions are also particularly interesting to study 
the impact of morphology on vocal output, in that these calls are pro-
duced without articulation of the vocal apparatus.

Vocal tract modelling (Zhang and Espy-Wilson 2004; Pruthi et al. 2007; Zhou et al. 2008) has proven reliable in describing indi-
vidual variation in vocal tract morphology and its impact on the for-
nants. Accordingly, this approach holds considerable promise in 
providing insights into vocal production mechanisms of nonhuman 
animals (Gamba and Giacoma 2006; Gamba et al. 2012b).

The ring-tailed lemur Lemur catta is a gregarious strepsirhine with 
a conspicuous vocal repertoire that includes oral and nasal calls (Macedonia 1993). This species lives in large multi-male/multi-female 
groups and their social interactions involve a complex balance 
between cooperation and competition (Palagi and Noscia 2015) 
where individual recognition plays a crucial role (Macedonia 1986; 
was 2-fold. First, we aimed to establish whether inter-individual var-
ation in the length and shape of the nasal tract was demonstrable in 
ring-tailed lemurs. Previous research has indicated that differences in 
the vocal tract length are common among conspecifics, even of the same 
sex. Fitch (1997) found that nasal tract length in male rhesus maca-
ques could vary between 6.74 and 10.89 cm (N = 20). If such varia-
tion was present, we predicted that it should be reflected in the 
acoustic signals emitted by the different tracts. Our second goal was 
an investigation of the potential of formants to provide clues for indi-
vidual recognition within small groups of conspecifics (Fitch 2000; Ey 
et al. 2007). We asked whether individuality in lemurs is encoded 
exclusively through changes in the length of the nasal tract (which 
changes in accordance with body size), or whether the shape of the 
tract may play a role in individual differences in vocalizations. It has 
been demonstrated that species-specific formant patterns in lemurs 
(Eulemur spp.; Gamba et al. 2012b) are influenced by both shape and 
length of the vocal tract, hence, we predicted that changes in both of 
these aspects have the potential to encode individual recognition. 
Finally, we measured formants of live lemur calls to understand 
whether formant variation was present in their nasal utterances.

Materials and Methods
Casting and modeling of the vocal tract
We made silicone casts of the vocal tracts of the cadavers of three 
adult male ring-tailed lemurs Lemur catta at the Parc Botanique et 
Zoologique Tsimbazaza (Antananarivo, Madagascar) that had been 
frozen shortly after death. Vocal tract casting is an effective means 
of reproducing in detail the structures of cavities (Riede et al. 2005), 
and can be performed in Madagascar (Gamba and Giacoma 2006) 
where no medical imaging is available. We cut the trachea 3–4 cm 
below the hyoid bone and injected high-speed catalysed silicone rub-
ber (Blue Star Silcones Rhodorsil® RTV) before closing the tracheal 
tube using surgical clamps. This procedure gave us a flexible cast 
that we extracted as a single piece through the mouth.

We then measured the silicone cast to build the computational 
model. Vocal tract modeling (Zhang and Espy-Wilson 2004; Pruthi 
et al. 2007; Zhou et al. 2008) is a technique for characterizing indi-
vidual variation in vocal tract morphology and its impact on the for-
nants produced, and has previously provided important insights 
to animal phonation (Gamba and Giacoma 2006; Gamba et al. 2012b). All length and volume measurements of the casts were taken 
with Mitutoyo digital calipers (accurate to 0.01 mm) in 0.2 cm incre-
ments moving from the vocal folds toward the nostrils. To create the 
vocal tract models, we calculated cross-sectional area functions, 
from the glottal constriction to the nostrils, such that the virtual

Figure 1. An old silicone cast of the nasal tract of a male Lemur catta and its 3D model. (A) Dorsal view of the silicone cast stretched on a plane. (B) A 3D rendering of the concatenated tubes model. The luminal areas of the tract are labeled with the corresponding anatomical parts: Trach., trachea; Glot., glottis; Epigl., epiglot-
tis; Nasophar., nasopharynx; Turb., turbinates; Nostr., nostril. Scale bar, 10 mm.
tract consisted of many elliptical segments of equal lengths but different cross-sectional areas (Figure 1). The vocal tract area function serves as the input for a customised version of VTAR (Vocal Tract Acoustic Response) modeling software (Zhang and Espy-Wilson 2004; Zhou et al. 2008) that calculates the acoustic response of each model. Because in primates the column of air passes the glottis and then resonates either solely in the oral or exclusively in the nasal tract (Fitch 2000, 2006), we did not consider resonance in the oral cavity for the lemur nasal grunts. We modelled the double intracranial nasal tract as a singular entity.

According to the aims of the study, we modified the vocal tract models to determine (a) whether lengthening of the vocal tract may affect individual recognition, and (b) to what extent changing length influenced formant structure. To estimate how length variation affected the formant pattern, we generated 180 models (60 per original VT model) where the length of all segments was decreased or increased by 0.5% over a range of ± 15%. This variation was calculated based on the variation in vocal tract length measured by Fitch (1997) in the Rhesus macaque Macaca mulatta. To investigate the effect of changes in cross-sectional areas, we used a different design to accommodate high inter-individual variability. The random module (a set of classes and functions from the python3 language) was used to generate random cross-sectional areas within a range of variation of 31%, which was based on the variation of the vocal tract cross-sectional areas of the study specimens.

While running the computations, we extracted the length and volume of each model and the first five formants of the acoustic response ($F_1$–$F_5$). All vocal tract geometries were also extracted and we divided the results into three groups. The first group (Anatomical) includes the original models of the three specimens. The second group (Length-variation) presents the results of the models in which vocal tract length was varied, and the third group (Shape-variation) shows the results of those models in which length was kept constant and the cross-sectional areas were modified.

Acoustic recording and analysis of the vocalizations
We recorded nasal click grunts of four male individuals (Figure 2) in captivity at the Parco Natura Viva (Bussolengo, Verona, Italy; July–August 2008) and Zoom Torino (Piscina, Torino, Italy; September–October 2013). All subjects were members of social groups ranging from 6 to 14 individuals. All individuals received a daily diet consisting mainly of vegetables and fruits with water supplied ad libitum and were maintained on a natural light/dark cycle. Vocalizations were recorded in outdoor enclosures using a SoundDevices 702 solid-state recorder and a Sennheiser K6/ME66 microphone (sampling rate of 44.1 kHz, digitized at 16 bits). Lemurs produced grunts in a range of contexts. We recorded the click grunts while the animals were moving around the enclosure, during solitary exploration, or interactions with conspecifics or visitors.

We estimated formants using Linear Predictive Coding (LPC) in Praat (Boersma 2014; see also Gamba et al. 2015). LPC estimates the frequency values corresponding to the first five formants (Figure 2). In particular, we used the PRAAT function LPC [To Formant (burg)...] all along the signal frames and then extracted the minimum frequency of each formant. Depending on the acoustic characteristics of the click grunt, we used a window length of 0.025–0.035 s. We detected five to six formants in the frequency range 0–8,500 Hz while searching for 5.5 formants (for details, see Gamba and Giacoma 2007). Frequency spectra were then superimposed on the signal spectrogram to verify the goodness of the LPC analysis (Nadhurou et al. 2016). A custom-built

![Figure 2. Spectrogram (A) and linear predictive coding analysis (B) of a ring-tailed lemur click grunt. Formants F1–F5 are indicated on the respective LPC peaks.](https://academic.oup.com/cz/article-abstract/63/4/467/3091898)

script was used to automate file opening and saving of the measurements.

Statistical analyses
We used the lme4 package (Bates et al. 2015) in R (R Core Team, 2013; version 3.2.0) to run the Linear Mixed Models (LMMs). We used a series of LMMs to investigate formant variation under different values of vocal tract length and volume. We included the log-transformed formant frequency ($F_1$–$F_5$) as the response variable, length or volume as predictors and (individual) model ID as a random factor.

We also used LMMs to explore the relationship between formant variation and the shape of the vocal tract. To reduce the number of predictors, we performed a Principal Components Analysis (PCA) including all the cross-sectional areas of segments that had been increased or decreased randomly within a range of 31% (see Supplementary Materials), while the length was kept constant. The first two PCs represented the final predictors in the LMM models, while the log-transformed formant frequency ($F_1$–$F_5$) was the response variable. Finally, the model ID was included as a random factor. For all models, we verified the assumptions that the residuals were normally distributed and homogeneous (see Gamba et al. 2016 for details) and avoided collinearity among variables (e.g. vocal tract volume was not tested together with PCs). We then tested the full model against a null model comprising only the random factors (see Estienne et al. 2017) and we calculated the $P$ values using the R-function “drop1” (Barr 2013).

To evaluate the potential for distinguishing individual identities, we calculated the variation of formants within and among models, and within and among individuals. Individual discrimination using vocalizations is possible when a character shows low intra-individual variation and high inter-individual variation in acoustic parameters. Thus, we calculated within- (CVi) and between-model (CVb) coefficients of variation (Sokal and Rohlf 1995) and the potential for individual identity coding (PIC) as the CVb/CVi ratio.
(Mathevon et al. 2003) for the models. We applied the same calculation to the click grunt acoustic parameters (Gamba et al. 2012b).

Results

Original vocal tract transfer-functions and acoustic response

The three specimens measured had nasal tract lengths of 9.2, 9.4, and 9.6 cm, which were divided into 46, 47, and 48 segments, respectively, rendered as a series of concatenated 0.2 cm tubes. The specimens showed clear differences in their cross-sectional area functions (Figure 3). We observed an average coefficient of variation of 31% (± 15%) in the areas of the elliptical cross-sections that we used to discretize the vocal tracts. The actual measurements were used to generate a first set of computational vocal tract models, and the formants predicted from the models showed differences among individuals. The coefficient of variation of F1 was 18.81%, 6.10% for F2, 2.96% for F3, 6.17% for F4 and 0.83% for F5 (Table 1).

Effects of lengthening the vocal tract

The variation in vocal tract length recorded from our three lemur cadavers was 2.13%. It was considerably lower than the 15% reported by Fitch (1997) for his larger sample of 20 Rhesus macaques. Using the three models based on the original casts but standardized to the length of 9.6 cm, we altered the lengths within a range of 15%, generating models of an average length of 9.58 ± 0.84 cm and volumes of 3.52 ± 0.31 cm³, 3.21 ± 0.28 cm³, 2.38 ± 0.21 cm³. The effects produced on the vocal tract acoustics when the length of each segment was changed are shown in Figure 4, for each of the three models. Formants predicted from these computational models showed an average variation of 8.44 ± 0.14% within model across formants and 8.44 ± 0.49% between models across formants (Table 1 shows the variation for each model and formant). All formants scaled inversely with length, but not with volume, of the vocal tract model (Table 2). The PICs of formants ranged between 1.88 for F1 and 1.47 for F4, to 1.08 for F3, 1.05 for F2, and 1.01 for F5.

Effects of modifying the cross-sectional shape

The PCA of cross-sectional areas generated two components exceeding an eigenvalue = 1. PC1 and PC2 explained 43% and 15% of the total variance, respectively. All other PCs accounted for <2% variation and thus were not included in further analyses. In Figure 5, we report the variation in volume observed when the shape of the segments was modified, and the respective vocal tract acoustics in Table 1.

All formants were significantly influenced by PC1 and PC2, except F4 which showed significant values for PC1 only (Table 2). All formants also scaled inversely with the volume of the vocal tract model (18.708 < χ² < 1302.573, all P’s < 0.001). Formants predicted from the computational models showed higher PICs for F1 and F4 (3.47 and 4.13, respectively), and lower potential for the other formants (Table 1).

Acoustic analysis of the nasal click grunts

The formants estimated from the click grunts of male ring-tailed lemurs showed a within-individual coefficient of variation of 19.56% for F1, 13.15% for F2, 6.98% for F3, 5.59% and 4.68% for F4 and F5, respectively (Figure 6). When we compared these values with variation among individuals, we obtained PICs ranging from 1.25 (F4) to 0.91 (F5, Table 1).
Table 1. First five formant frequencies for the different vocal tract models and the vocalisations. Lengths and cross-sectional areas measured from the cadavers (Anatomical) were then standardised in length to 9.60 cm (*) to simulate changes in length (Length variation) and shape (Shape-variation). Formants measured on the click grunts are presented for each male specimen we recorded. The potential for individuality coding (PIC) is also reported.

<table>
<thead>
<tr>
<th>Method</th>
<th>Vocal tract model</th>
<th>Length (cm)</th>
<th>Volume (cm³)</th>
<th>F1 (Hz)</th>
<th>F2 (Hz)</th>
<th>F3 (Hz)</th>
<th>F4 (Hz)</th>
<th>F5 (Hz)</th>
<th>N</th>
</tr>
</thead>
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<tr>
<td>Anatomical</td>
<td>g1</td>
<td>9.6</td>
<td>3.481</td>
<td>532</td>
<td>1943</td>
<td>4238</td>
<td>6432</td>
<td>8224</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>g2</td>
<td>9.4</td>
<td>3.117</td>
<td>629</td>
<td>1961</td>
<td>4373</td>
<td>6055</td>
<td>8104</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>g3</td>
<td>9.2</td>
<td>2.322</td>
<td>773</td>
<td>2165</td>
<td>4122</td>
<td>5684</td>
<td>8109</td>
<td>1</td>
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<tr>
<td>Length variation (+15%)</td>
<td>g1*</td>
<td>9.58 ± 0.84</td>
<td>3.52 ± 0.310</td>
<td>595 ± 490</td>
<td>1967 ± 172</td>
<td>4078 ± 357</td>
<td>6472 ± 568</td>
<td>7955 ± 555</td>
<td>60</td>
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<tr>
<td></td>
<td>g2*</td>
<td>9.58 ± 0.85</td>
<td>3.21 ± 0.280</td>
<td>828 ± 700</td>
<td>2102 ± 181</td>
<td>4317 ± 378</td>
<td>6422 ± 556</td>
<td>7846 ± 607</td>
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<tr>
<td></td>
<td>g3*</td>
<td>9.58 ± 0.86</td>
<td>2.38 ± 0.210</td>
<td>721 ± 620</td>
<td>1987 ± 170</td>
<td>3966 ± 345</td>
<td>5242 ± 453</td>
<td>7763 ± 652</td>
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<td>PIC</td>
<td></td>
<td>1.88</td>
<td>1.05</td>
<td>1.08</td>
<td>1.48</td>
<td>1.48</td>
<td>1.01</td>
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<td>Shape variation (+31%)</td>
<td>g1*</td>
<td>9.6</td>
<td>3.49 ± 0.110</td>
<td>576 ± 400</td>
<td>1913 ± 510</td>
<td>3964 ± 940</td>
<td>6293 ± 136</td>
<td>7964 ± 180</td>
<td>5000</td>
</tr>
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<td></td>
<td>g2*</td>
<td>9.6</td>
<td>3.19 ± 0.100</td>
<td>807 ± 200</td>
<td>2048 ± 480</td>
<td>4200 ± 920</td>
<td>6248 ± 132</td>
<td>7742 ± 196</td>
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<td></td>
<td>g3*</td>
<td>9.6</td>
<td>2.36 ± 0.070</td>
<td>701 ± 200</td>
<td>1933 ± 54</td>
<td>3862 ± 105</td>
<td>5108 ± 139</td>
<td>7538 ± 210</td>
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<td>3.47</td>
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<td>Click grunts</td>
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<td></td>
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<tr>
<td>Male 1</td>
<td></td>
<td>657 ± 710</td>
<td>2623 ± 381</td>
<td>4790 ± 359</td>
<td>6169 ± 437</td>
<td>7592 ± 233</td>
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<td>Male 2</td>
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<td>2665 ± 286</td>
<td>4588 ± 287</td>
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<td>7271 ± 229</td>
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<tr>
<td>Male 3</td>
<td></td>
<td>564 ± 161</td>
<td>2734 ± 434</td>
<td>4612 ± 298</td>
<td>5999 ± 198</td>
<td>7383 ± 314</td>
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<tr>
<td>Male 4</td>
<td></td>
<td>693 ± 114</td>
<td>2907 ± 305</td>
<td>4580 ± 330</td>
<td>6321 ± 516</td>
<td>7518 ± 592</td>
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<tr>
<td>PIC</td>
<td></td>
<td>1.05</td>
<td>1.03</td>
<td>1.15</td>
<td>1.25</td>
<td>0.91</td>
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Figure 4. Variation of formant frequencies F1–F5 in the models corresponding to PBZTXY1 (A), PBZTXY2 (B), and PBZTA1 (C). Vocal tract length was standardized across models and then gradually increased and decreased within a 15% range of variation.
Table 2. Influences of the predictors on formant frequencies; results of the full models (full versus null)

<table>
<thead>
<tr>
<th>Length</th>
<th>$\chi^2$</th>
<th>df</th>
<th>$P$</th>
<th>Estimate</th>
<th>SE</th>
<th>df</th>
<th>$\chi^2$</th>
<th>$P$</th>
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<td>1493.238</td>
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<td>&lt;0.001</td>
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<td>0.145</td>
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<td>a</td>
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<td></td>
<td></td>
<td></td>
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<td></td>
<td>Volume</td>
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<td>F2</td>
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<td>&lt;0.001</td>
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<td>0.066</td>
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<td></td>
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<td>169.226</td>
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<td>0.212</td>
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<td>10.554</td>
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<tr>
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<td>&lt;0.001</td>
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<td></td>
<td>Length</td>
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<td>Volume</td>
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<tr>
<td>F5</td>
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<td>&lt;0.001</td>
<td>Intercept</td>
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<td>0.027</td>
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* Data not shown as not having a meaningful interpretation.

Figure 5. Average (+ standard deviation) shape variation (bars) estimated from 15,000 computational vocal tract models. The traces below represent the loading of each segment on the Principal Components (PC1 in black, PC2 in gray).
Observations are in agreement with acoustic analyses of frequencies, exceeding 18% for F1 and 6% for F2 and F4. These morphological differences correspond to variation in formant luminal area of the tracts. According to our computational models, actual lengths and realistic cross-sectional areas to estimate differences in the vocal tracts of three adult male ring-tailed man primates is even scarcer. In this study, we quantified morphological differences in the vocal tracts of three adult male ring-tailed lemurs using silicone casts, and derived computational models to understand whether variation observed in the vocal tracts of these specimens could account for acoustical variations we recorded in the vocalizations of this species.

We built anatomical models resembling the vocal tracts of the cadavers from measurements taken from silicone casts. We used actual lengths and realistic cross-sectional areas to estimate differences in the formant patterns likely to have been emitted by the specimens before death. We found 2% variation in vocal tract length among the three specimens, and 20% variation in the volume of the luminal area of the tracts. According to our computational models, these morphological differences correspond to variation in formant frequencies, exceeding 18% for F1 and 6% for F2 and F4. These observations are in agreement with acoustic analyses of Eulemur fulvus, E. macaco, and E. rubriventer, in which F1, F2, and F4 were more variable than the other formants making up the nasal grunts (Gamba et al. 2012b). Our results imply that formants contribute not only to the encoding of species identity in vocal emissions, but also to individual identification as well. The degree of variation in individual formant patterns estimated from model-derived acoustic responses was similar to that observed in individually distinguishable vocalizations in other lemur species (Gamba et al. 2012b).

Our results demonstrate, in agreement with previous studies involving primates (Fitch 1997), canids (Riede and Fitch 1999), and birds (Fitch and Kelley 2000), that formants in lemur calls are inversely scaled with the length of the vocal tract. Model volume did not show a statistically significant influence on determining the location of formants in the acoustic response.

In the models in which we imposed random variation in the shape of the vocal tract, PC1 significantly influenced variation of F1, F2, F3, F4, and F5. PC2 had a significant effect on all but F4. The model volume, which could not be tested together with PC1 and PC2 in the LMMs to avoid variance inflation, had a significant effect on all formants. In agreement with the findings on Eulemur spp. (Gamba et al. 2012b), where the shape of the cross-section of the vocal tract had a dramatic effect on the formant pattern. When comparing the effect of length variation (which we set at 15% instead of the 2% observed in the three cadavers) against shape variation (31% but randomized across the cross-sections), we showed that shape changes accounted for a greater degree of variation in formant structure, implying a higher potential for encoding individuality.

Most of the formants estimated from the recorded vocalizations showed higher intra-individual variation than predicted by the models. The PIC of F4 was greater than that of the other formants measured from the click grunts. It is interesting to note that the PIC of F4 was also the highest of those calculated from the models in which we altered vocal tract shape, and one of the highest (with F1) in the models in which length was changed.

The morphology of the larynx and the nasal airways is relevant in determining differences in formant location in ring-tailed lemur click grunts. Using vocal tract models and acoustic analysis, we provide clear evidence that lemur nasal grunts have the potential to allow individual recognition. Accordingly, higher among individual variation is in agreement with previous findings interpreting resonance frequencies as critical clues for individual discrimination (Rendall et al. 1998; Rendall 2003).

We can also interpret our results with respect to the perceptual abilities of lemurs. Within-species formant variation in Eulemur spp. has been estimated at 8% (Gamba et al. 2012a). Formant variation in Lemur catta appears to be slightly higher on average, around 11% (Table 1). We observed that, according to the audiogram published by Gillette and colleagues (1973, but see also Heffner 2014), the lowest perceptible frequency for L. catta is 67 Hz, and the species has a maximum sensitivity range between 5,700 Hz and 16,000 Hz (Ramsier and Dominy 2010). These values roughly comprise the frequency range of the formants we have estimated from our study of calls and from the computational models.

Our study also has potential limitations. First, recent research suggests that primate vocal tracts are more flexible than what we can reconstruct from investigations of post-mortem anatomy (Fitch et al. 2016). Although we think that this applies in particular to those calls that show oral tract articulation, we cannot rule out the possibility that future research using digital imaging techniques would reveal more complex vocal tract dynamics involved in the production of lemur click grunts. Second, we assumed that nasal resonance took place without the involvement of the oral cavity, as we have observed the air stream flowing out from nostrils. The fact that click grunts resonate solely in the nasal tract is feasible in the light of the anatomy of the lemur vocal tract. However, we cannot exclude that discrepancy between the formants derived from the vocal tract models and those measured on the click grunts can be due to resonance in the oral tract before the column of air exits from the nose (Riede and Zuberbühler 2006). The difference between formants calculated from the vocal tract models and those measured on the grunts can also result from our choice to model the double intracranial nasal vocal tract as a uniform entity. However, our tests showed that the effect of using this simplification is a shift ranging between 1.4% and 2.0% (Gamba and Friard, unpublished data).

The high intra-individual variation we observed in the recordings may also derive from the fact that the click grunts are short and thus the analysis may be less efficient in estimating formants. This fact, combined with the restriction of our sample to lemur males and that we started from only three vocal tracts, has likely limited the potential to describe the morphological variation at a species level. As a
consequence, the study of the individual formant patterns and vocal tract morphology in lemurs deserves further examination, both using larger samples of calls and specimens and considering other vocalization types.

Previous studies suggested that lemur societies are not as sophisticated as those of haplorhine primates (see Byrne and Whiten 1988). However, our results demonstrated that group-living lemurs show similar abilities to identify individuals as social haplorhines do. Such abilities can be associated with the establishment of cohorts and alliances (Soma and Koyama 2013).

Individual variation in lemur calls can also play a role in the non-invasive monitoring of wild populations and, more generally, contribute to the conservation of these endangered primates (Terry et al. 2005). The integration between acoustic analysis and computational modeling of the vocal apparatus is a promising field of modern zoology and bioacoustics. Increasing knowledge on the anatomical diversity of the lemur vocal tracts would be of interest to facilitate understanding of the evolution of lemur communication and the importance of acoustic cues in the process of lemur speciation.

Acknowledgments

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References


