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RESEARCH ARTICLE

Honest signaling in domestic piglets (*Sus scrofa domesticus*): vocal allometry and the information content of grunt calls

Maxime Garcia[1,*], Marianne Wondrak[2,3], Ludwig Huber[2,3] and W. Tecumseh Fitch[1]

ABSTRACT

The information conveyed in acoustic signals is a central topic in mammal vocal communication research. Body size is one form of information that can be encoded in calls. Acoustic allometry aims to identify the specific acoustic correlates of body size within the vocalizations of a given species, and formants are often a useful acoustic cue in this context. We conducted a longitudinal investigation of acoustic allometry in domestic piglets (*Sus scrofa domesticus*), asking whether formants of grunt vocalizations provide information concerning the caller's body size over time. On four occasions, we recorded grunts from 20 kunekune piglets, measured their vocal tract length by means of radiographs (X-rays) and weighed them. Controlling for effects of age and sex, we found that body weight strongly predicts vocal tract length, which in turn determines formant frequencies. We conclude that grunt formant frequencies could allow domestic pigs to assess a signaler's body size as it grows. Further research using playback experiments is needed to determine the perceptual role of formants in domestic pig communication.

KEY WORDS: Domestic pig, Acoustic allometry, Longitudinal study, Formants, Size information, Vocal communication

INTRODUCTION

Identifying the type of information conveyed by animal acoustic signals is a central research focus in the field of bioacoustics (Bradbury and Vehrencamp, 1998). Studies conducted on different model species have shown that diverse information concerning a caller's traits may be encoded within the acoustic signal it produces. Vocalizations may thus allow receivers to evaluate many relevant attributes of the caller, including body size (Charlton et al., 2009a; Pitcher et al., 2012; Reby and McComb, 2003; Vannoni and McElligott, 2008), sex (Charlton et al., 2009a; Vignal and Kelley, 2007), age (Charlton et al., 2009a; Reby and McComb, 2003), individual identity (Charlton et al., 2011a, 2009b; Reby et al., 1998; Robisson et al., 1993), group membership (Boughman, 1997; Randall et al., 2005), geographical origin (Catchpole and Armanda, 1993), motivational state (Kreutzer et al., 1999), physical condition (Wyman et al., 2008), hormone levels (Charlton et al., 2011c; Koren and Geffen, 2009) and emotional state (Briefer, 2012).

[1]Department of Cognitive Biology, University of Vienna, Althanstrasse 14, Vienna 1090, Austria. [2]Comparative Cognition, Messerli Research Institute, University of Veterinary Medicine Vienna, Medical University of Vienna, University of Vienna, Veterinaerplatz 1, Vienna 1210, Austria. [3]Haidlhof Research Station, 2540 Bad Vöslau, Austria.

*Author for correspondence (maxime.garcia@univie.ac.at)

M.G., 0000-0003-2014-7387

Received 28 January 2016; Accepted 29 March 2016

Among these topics, the particular study of 'acoustic allometry' has recently emerged, focusing on identifying the vocal correlates of a caller's body size (Fitch, 2000c; Reby and McComb, 2003; Rendall et al., 2005). Because body size has a fundamental influence on animal ecology (Peters, 1983), physiology (Taylor et al., 1982) and social behavior (Clutton-Brock et al., 1979; Ryan, 1980), accurate acoustic cues to body size should be biologically relevant, and not only perceived but also interpreted and utilized by receivers.

In birds and mammals, early work suggested that fundamental frequency (hereafter F_0), a key component in many acoustic signals, might be negatively correlated with body size, and thus that an impression of bigger size would be conveyed by a lower F_0 (Morton, 1977). This suggestion seems plausible based on the anatomical–physical description of sound production: F_0 corresponds to the rate of vibration of the vocal folds, and longer, thicker vocal folds vibrate at a lower rate (Titze, 1994). If vocal fold length correlated with body size, it would thus be possible to predict a caller's body size based on F_0. However, this acoustic feature has been shown to poorly reflect the caller's body size in various mammalian species (Lass and Brown, 1978; Masataka, 1994; Pfefferle et al., 2007; Rendall et al., 2005), probably due to the absence of strict anatomical constraints on the size of the larynx, which can thus grow with relative independence from overall body size (Fitch and Hauser, 1995).

Unlike the laryngeal structures, the dimensions of the supralaryngeal vocal tract (hereafter simply 'vocal tract') are often more closely linked to those of the rest of the body (Fitch and Hauser, 1995). The shape and length of the volume of air within the vocal tract enhance certain resonant frequencies, called formants, and both formants and formant spacing (the mean frequency spacing between consecutive formants) are inversely correlated with vocal tract length (VTL). Formant-related features have been shown to be a good indicator of body size in multiple species (Charlton et al., 2011b, 2009a; Fitch, 1997; Harris et al., 2006; Reby and McComb, 2003). Even when particular adaptations have led to an exaggerated VTL (Fitch and Reby, 2001), formant characteristics can still correlate with VTL and remain a robust and honest indicator of body size within the species because all individuals are subject to the same physical limits imposed by body size (Reby and McComb, 2003).

Research investigating acoustic allometry typically involves cross-sectional studies, sampling a specific group of subjects at a fixed point in time (Evans et al., 2006; Fitch, 1997; Hauser, 1993; Rendall et al., 2005; Riede and Fitch, 1999). For example, a cross-sectional study conducted on humans (Fitch and Giedd, 1999) looked at vocal allometry at different life stages (childhood, puberty and adulthood) and showed that key differences between VTL in males and females arose at puberty, caused by a male-specific laryngeal descent. Although a descended larynx is not typically found in mammals and was previously thought to be uniquely human (Lieberman, 1984), it has recently been reported in non-human primates (chimpanzee; Nishimura et al., 2003), artiodactyls

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List of symbols and abbreviations

AIC	Akaike information criterion
B	basion
BW	body weight
E	base of the epiglottis
Fn	PCA component on F_1 and F_2
F_0	fundamental frequency
F_1	first formant
F_2	second formant
I	incision
P	prosthion
PCA	principal component analysis
S	intersection between nasal tract and apical segment of the piglet snout
VF	vocal folds
VTL	vocal tract length (PCA component on skull length, nasal tract length and oral tract length)
ΔF	formant spacing

(red and fallow deer; Fitch and Reby, 2001), Mongolian gazelle (Frey and Gebler, 2003), goitered gazelle (Frey et al., 2011), marsupials (koala; Charlton et al., 2011b) and some carnivores (lion, tiger, jaguar, leopard and snow leopard; Hast, 1989; Weissengruber et al., 2002). Additionally, cineradiographic observations on several mammalian species have shown that the larynx is more mobile than previously thought (Fitch, 2000b). Allometric relationships between body size and formants may be affected by larynx descent, whether it occurs at a given point in life or while an animal is vocalizing. However, the importance of acoustic allometry in relation to vocal ontogeny and laryngeal descent/position remains little explored.

In this context, domestic pigs (*Sus scrofa domesticus*) represent an excellent model species to examine acoustic allometry, because they are extremely vocal and social, and produce abundant low-frequency and relatively broadband grunts (Kiley, 1972) (ideal for formant salience; Fitch and Hauser, 1995). Within a pig group, size and dominance status are normally strongly correlated (Jensen, 2002), so if cues to body size are present in the formants of pig grunts, they should be highly relevant for receivers. In the present study, we investigated acoustic allometry longitudinally in domestic piglets from the kunekune breed as they grew, making multiple measurements of the same individuals at different life stages. To our knowledge, this is the first longitudinal acoustic allometry study. We captured radiographs (X-rays) of awake piglets and collected body weight data and acoustic recordings of grunts as they aged in order to quantify the anatomical–acoustical correlations relevant to allometric relationships, focusing on formants. As cineradiography data previously collected on a domestic piglet showed only a slight variation of the larynx position while emitting grunts (as opposed to piglet screams, which typically involve laryngeal retraction; Fitch, 2000b), we expected a close relationship between VTL and overall body size, and we predicted that formant characteristics in grunts would provide reliable information regarding the caller's body size in this species. We discuss our findings in relation to the domestic pig's complex communication system, and consider the potential selective advantages of cue extraction in acoustic signals for the receiver.

MATERIALS AND METHODS

Study site and animals

The subjects were 20 kunekune piglets (*Sus scrofa domesticus* Erxleben 1777) from three different litters [litter B: *N*=7 (3 females, 4 males); litter R: *N*=6 (4 females, 2 males); litter Z: *N*=7 (2 females, 5 males)] at the Haidlhof Research Station in Bad Vöslau, Austria. Subjects were between 8 and 131 days old during the course of the study. They were housed in semi-natural free-ranging conditions in an 8 ha pasture and a forested patch where five A-shaped huts, a muddy wallow and the water supply were located. The animals had continuous free access to pasture and forest where they spent the nights or found shelter. The pigs lived together in a stable natural social structure, consisting of sounders of three sows and their offspring of two consecutive years, 41 pigs altogether (22 females, 19 males). The subjects of this study were the youngest three litters. Animals were fully habituated to humans (a high number of interactions on a daily basis) and had *ad libitum* water and grass to graze. Additionally, they were fed daily with a diverse mixture of fruits, vegetables, bread and grain.

Data collection

Piglets were born on 20 June 2015 (litters B and Z) and 22 June 2015 (litter R). Data collection occurred on four different occasions (hereafter 'series'), namely when piglets were on average 9, 43, 72 and 130 days old (weaning occurred at about 80 days). Body weight (BW) curves from the previous generation were used to evaluate variation in growth rate and select appropriate dates to capture the measurement series. The first three series covered the pre-weaning period, when the piglets' BW increase was not linear, whereas the fourth series occurred after weaning when the piglets' BW increase was stable over time. All piglets were weighed on each of the four series with a My Weigh WR-12K Washdown Scale (reading accuracy, ±20 g) when they were less than 10 kg (series 1–2), and later with a Soehnle 7858 Veterinary scale (reading accuracy, ±100 g accuracy) as soon as some of the piglets weighed more than 10 kg (series 3–4).

Acoustic recordings

Vocalizations were recorded 10 cm to 1.5 m away from the subjects with a Sennheiser ME-66 directional microphone (frequency response, 40–20,000 Hz ±2.5 dB; Sennheiser Electronic GmbH & Co. KG, Wedemark, Germany) powered by an LR6 battery, and connected to a Zoom H4N digital recorder (48 kHz sampling frequency and 16-bit quantization; Zoom Corporation, Tokyo, Japan). These recordings were stored as uncompressed WAV files. For shock and wind-noise reduction, the microphone was mounted on a Rycote Modular Windshield (Stroud, UK) WS 7 Kit for Shotgun Microphones. Recordings were carried out in a sheltered hut regularly used by the animals, which provided ideal recording conditions (minimal wind and background noise). All 20 individuals were led individually to the hut and had their calls recorded on each of the four series. Recordings were obtained either on the same day or 1 day prior to or following radiograph collection; time constraints prevented collection of both types of data in a single day.

The typical vocalizations recorded from piglets were grunts, as these common low-frequency calls highlight formants better than squeals. For the first series, grunt vocalizations were elicited by preventing the piglets from exiting the hut (blocking the way with the experimenter's hand) or by holding them briefly (which at first elicited squeals, followed by grunts upon their return to the floor). Once piglets were old enough to feed on solid food (from the second series onwards), food was presented as a stimulus to which piglets would produce grunts. This food reward was used in addition to the daily food supply and the *ad libitum* grazing possibility provided by the pasture (no food restriction was imposed, and only the piglets' preference for particular foods was utilized to obtain recordings of

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grunts, which were then rewarded by several food items during a given recording series).

Radiographs

Animals were placed in a restrainer, made of Plexiglas for the first series and a hand-made piece of fabric for the following three series (to avoid discomfort as piglets grew older and heavier). Mid-sagittal radiographs of the head and neck region were made with a mobile digital X-ray system, using a full bridge inverter (Physia Gamma light AD 100/120) with different acquisition settings depending on animal size and tissue thickness (series 1: 64 kV, 2.8 mA; series 2: 68 kV, 3.2 mA; series 3: 68 kV, 3.6 mA; series 4: 74 kV, 3.2 mA). Scaling was automatically recorded on the digital radiograph imaging plates used for image capture. All 20 individuals were radiographed on the first and last series. Because of time and logistic constraints, half of the individuals (N=10) were radiographed in series 2, and the other half in series 3 (piglet selection was based on BW distribution, chosen to span a measurement range representative of the entire group).

Data analysis

Acoustic measures

All acoustical analyses were made in Praat (P. Boersma and D. Weenink 2014: http://www.praat.org/). Based on both visual inspection of spectrograms and listening, only high-quality grunts (i.e. those deemed to have a high enough signal-to-noise ratio and visible formants) were annotated with 'Individual' and 'Series' using the 'Annotate: To TextGrid' function. Care was taken to identify true grunts clearly, as opposed to 'grunt–squeals' which have quite different acoustic characteristics (Garcia et al., 2016). Annotated grunts were extracted and average formant values were retrieved from each call via a custom-written Praat script (M.G.) that used linear predictive coding (LPC) via the 'LPC: To Formants (Burg)' function and allowed editing of the formant contour via the 'Down to FormantGrid' function. Formant editing allowed us to remove sections to which Praat automatically attributed a formant value to background noise although the section actually lacked vocalization. Our analysis parameters differed across series and were based on visual inspection of the spectrograms [window of analysis: 0.025 s; time step: 0.00625 s (one-quarter of window length); maximum number of formants: series 1=3, series 2=4, series 3=4, series 4=2, maximum formant frequency, series 1=4500 Hz, series 2=4500 Hz, series 3=4000 Hz, series 4=1500 Hz]. These input settings were adjusted so that formants 1 (F_1) and 2 (F_2) could be distinctly identified and extracted for each series (Fig. 1).

Higher formants were not extracted as they could not reliably be clearly identified in most cases (at least 89%), for two reasons. First, higher formants did not appear to be consistently as well defined as F_1 and F_2. Second, tracking accuracy for higher formants appeared to be affected by slight vocal tract adjustments (both by potentially changing formant contours and spacing and/or by introducing 'nasal zeros' or 'antiformants', such as seen in humans (Kurowski and Blumstein, 1987)). Ultimately, we retained five grunts per series and per individual, from which we extracted F_1 and F_2 and calculated the average F_1, F_2 (Table S1A–D) and formant spacing (defined here as the average spacing between F_1 and F_2; hereafter, ΔF) for each individual within each series. Whenever more than five calls per individual and per series were available, we performed a second, stricter quality assessment and if this was not sufficient to narrow the sample down to five, we made a random selection of five calls among the remaining highest quality files. Overall, only three individuals in series 1 did not have sufficient good quality recordings to reach the criterion of five calls; these cases were therefore excluded from the analysis.

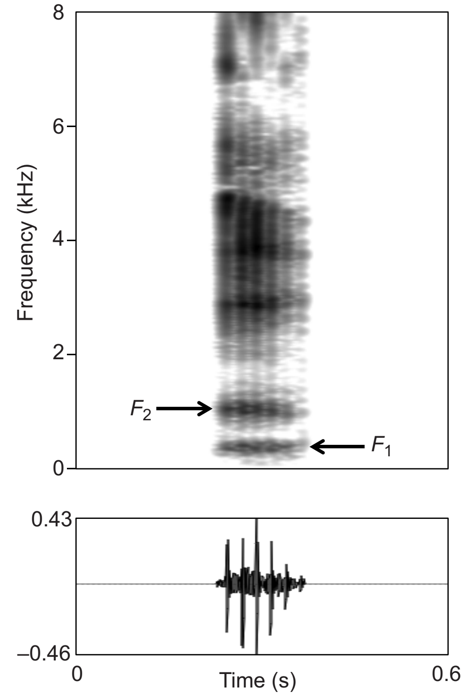

Fig. 1. Spectrogram of a grunt showing its first two formants. Individual: Baldur; series 4; F_1=409 Hz; F_2=1052 Hz. In most cases (unlike this grunt), formants higher than F_2 could not be clearly distinguished. Visualization settings: view range, 0–8 kHz; window length, 0.04 s; time steps, 700, frequency steps, 250, Gaussian window; dynamic range=40 dB.

Radiographic measurements

VTL was measured from lateral radiographs obtained from the piglets (Table S1A–D). For each radiograph, three types of measurements were carried out based on several cranial and soft-tissue landmarks (see illustrations and definitions in Fig. 2): the first measurement, skull length, is based on traditional skull morphometry and corresponds to the distance between the prosthion (P) and the basion (B) (Fitch, 2000c). The two other measurements of VTL aim to evaluate the piglets' airway length anterior to the larynx (following the path of sound emitted from the vocal folds). Here, nasal tract length corresponds to the distance between the tip of the snout (S, defined as the projection from the nasal airway onto a line connecting the two apexes of the piglet snout: see Fig. 2C) following the upper jaw dorsally and then the airway down to the base of the epiglottis (E) within the larynx, which marks a clear sharp inflexion point in the airway between the pharynx and the tracheal portion of the airway. Oral tract length corresponds to the distance between the lower incision (I) following dorsally the teeth of the lower jaw and then the airway down to the same E.

In order to account for the uncertainty sometimes caused by low absorbance and scan blurriness (due to slight animal movements during radiograph capture), a quality assessment was made for each radiograph (1: certain, 2: intermediate, 3: unclear), providing a way to easily search for potential outliers and/or errors in the later statistical analysis.

All measurements from radiographs were made using ImageJ (v2.0.0-rc-15-1.49k). DICOM files were loaded in ImageJ, fine-

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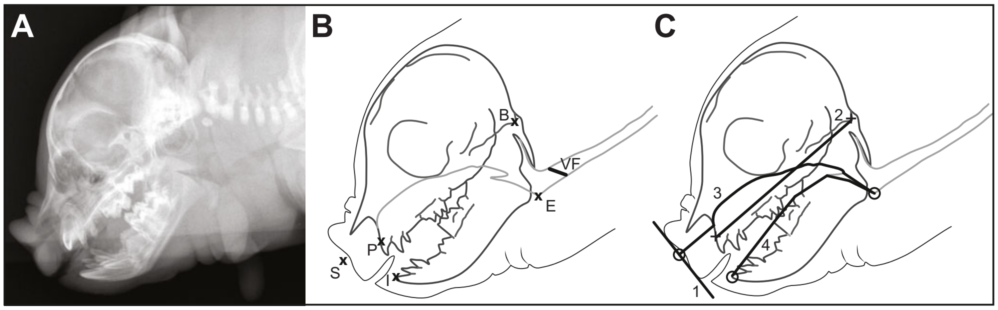

Fig. 2. Illustration of the measurements obtained from landmarks placed on radiographic images. (A) Radiograph of a domestic piglet (individual: Bolero; first series). (B) Landmarks used to measure vocal tract length (VTL) from radiographs. P, prosthion, the most anterior portion of the maxilla between the incisor roots; I, incision, located at the incisal level of the lower central incisors; B, basion, the midline anterior margin of the foramen magnum; E, base of the epiglottis; S, projection from the nasal airway onto the snout apical line (see C); VF, position of the vocal folds as estimated from anatomical data. 'I' was chosen over the lower jaw equivalent of the prosthion because the latter point could not always be identified. 'E' was chosen over the location of the vocal folds themselves, as they were rarely clearly observed on radiographs because of the low absorbance difference between soft and calcified tissues in these young animals (although their expected position is indicated in B, based on anatomical images of sectioned piglet heads (W.T.F., unpublished data). (C) Illustration of the measurement taken from radiographs: 1, apical line; 2, proxy of skull length (straight-line distance between P and B); 3, nasal tract length (segmented line between S and E following the upper jaw dorsally); 4, oral tract length (segmented line between I and E following dorsally the teeth of the lower jaw).

scaled based on DICOM metadata, adjusted for optimal visualization of the landmarks, and measurements were made on segments (PB) or segmented lines (SE and IE). A second measurement session, blind to the first session, was conducted on 10% of the data (based on a random selection excluding the scans labeled with 'quality 3' during the first session, as the quality bias is taken into account by the statistical analysis – see below). This resulted in an overall agreement of 99.9% (Pearson's r=0.9993), illustrating the reliability of this measurement procedure. The accuracy of the measurements was very high: the mean absolute measurement error ranged from 0.046 to 2.48 mm (mean=0.8 mm) and represented between 0.03% and 1.6% (mean=0.6%) of the overall length, which is negligible compared with the average variation found between individuals of the same age (coefficient of variation ranging from 4.2% to 9.5%) and between series (coefficient of variation ranging from 10.3% to 36.2%).

Statistical analysis

Prior to analyses, all parameter units were chosen to avoid scaling issues (all frequency parameters are expressed in kHz, length parameters are in cm and weight is in kg). Data normality was assessed using a Shapiro–Wilk test; afterwards, pairwise correlations were computed. Principal component analyses (PCA) were run on groups of variables that were highly correlated and thus redundant with respect to the acoustic and anatomical measurements. Two different PCA were run, one grouping skull, nasal tract and oral tract length into a single VTL component (eigenvalue=2.96, explaining 98.7% of the variance), the other grouping F_1 and F_2 into one 'formant' or Fn component (eigenvalue=1.93, explaining 96.8% of the variance). VTL and Fn components were also assessed for normality and then correlations among all variables were computed. ΔF was maintained as an individual measurement as it represents a relative measure of F_1 and F_2 variation and could give insight into how evenly/differently formants change through time.

Three types of analysis were conducted, respectively on purely anatomical correlations (testing the effect of BW on VTL), anatomical–acoustical correlations (testing the effect of VTL on formant characteristics) and acoustic allometry (testing the effect of BW on formant characteristics).

To evaluate statistical significance and relative predictive power, data were analyzed by means of model selection using linear mixed models (LMMs) with restricted maximum likelihood estimation (REML) and/or generalized linear mixed models (GLMMs). Models were computed including non-intercorrelated fixed effects and random effect intercepts. Based on visual inspection of the data, models were also run including random slopes for the effect of the main factor of interest (VTL for the anatomical–acoustical dependency, and BW for the anatomical and acoustic allometry dependencies). Our model selection procedure followed a stepwise removal of fixed effects, evaluating a decrease in Akaike information criterion (AIC) scores (corresponding to an improvement of the model), to reach the best model with the lowest AIC. Statistical significance of the final models was evaluated using likelihood ratio tests (final model versus null model, excluding the fixed effect for which significance was being tested; following Winter, 2013). Provided residuals were normally distributed, this model was considered to be validated. Otherwise, a GLMM fitting the dependent data distribution was computed, including the same fixed and random effects/slopes as in the LMM (see Table S2 for details on initial model composition).

To control for the effect of potentially significant errors in the measurements, the same overall analysis was conducted on a reduced sample, excluding the cases in which the quality of one of the three measurements was ranked as low with '3'. Data was prepared in SPSS Statistics (v21.0) and statistical analyses were conducted using SPSS and R (http://www.R-project.org/) with the R-package lme4 (Bates et al., 2015). Two-tailed P-values are reported with the significance level set at 0.05.

Ethical note

All procedures were approved by the institutional ethics committee in accordance with GSP guidelines and national legislation (ref. 12/07/97/2014).

RESULTS

Examination of normality revealed that all variables measured were non-normally distributed. Therefore, non-parametric Spearman rank correlations were computed, which showed that all measured variables were significantly intercorrelated (P<0.001

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Table 1. Spearman correlation coefficients between the anatomical and acoustic variables measured in the study

	F_1	F_2	ΔF	Fn	Skull	Nasal tract	Oral tract	VTL	BW	log BW
F_1	**1.000**	0.954	0.861	0.987	−0.922	−0.917	−0.926	−0.931	−0.954	−0.954
F_2	0.954	**1.000**	0.967	0.985	−0.935	−0.928	−0.940	−0.942	−0.955	−0.955
ΔF	0.861	0.967	**1.000**	0.919	−0.884	−0.877	−0.892	−0.890	−0.891	−0.891
Fn	0.987	0.985	0.919	**1.000**	−0.936	−0.932	−0.943	−0.946	−0.963	−0.963
Skull	−0.922	−0.935	−0.884	−0.936	**1.000**	0.974	0.978	0.990	0.955	0.955
Nasal tract	−0.917	−0.928	−0.877	−0.932	0.974	**1.000**	0.980	0.990	0.954	0.954
Oral tract	−0.926	−0.940	−0.892	−0.943	0.978	0.980	**1.000**	0.993	0.955	0.955
VTL	−0.931	−0.942	−0.890	−0.946	0.990	0.990	0.993	**1.000**	0.964	0.964
BW	−0.954	−0.955	−0.891	−0.963	0.955	0.954	0.955	0.964	**1.000**	1.000
log BW	−0.954	−0.955	−0.891	−0.963	0.955	0.954	0.955	0.964	1.000	**1.000**

F_1 and F_2, first and second formant; ΔF, formant spacing; Fn, PCA component on F_1 and F_2; PCA, principal component analysis; VTL, vocal tract length; BW, body weight.
All correlations are significant at the P<0.001 level.

for all correlations; Table 1). Overall, the two components resulting from the PCA have higher correlations with other variables than variables singled out from the components [e.g. Fn correlates better than F_1 and F_2 with VTL and $\log_{10}$ of body weight (hereafter, log BW)], justifying the use of the PCA variables. Because we were generally interested in determining the predictability of one variable by another, and because when compared with Fn, ΔF showed less strong correlations with both BW and VTL (Table 1), Fn was the only frequency-related variable retained for further analysis (moreover, formant dispersion is usually based on an average of more than three formants, and cannot be appropriately calculated here as only F_1 and F_2 could be clearly distinguished). Finally, log BW was used rather than BW because volume is proportional to the cube of a linear dimension (BW was the only variable log-transformed as the relationships between log BW and VTL and between log BW and Fn appeared to be linear after visual inspection).

Anatomical dependencies: BW predicts VTL

Because log BW and VTL were strongly and positively correlated (r=0.964, P<0.001; Fig. 3A), we further examined the dependence of VTL on log BW with linear models. log BW, Litter (B, R or Z) and Sex (male or female) were entered as fixed effects whereas Individual and Series (1, 2, 3 or 4) were entered as random effects. Two types of model were calculated, either specifying random slopes for the by-Individual and by-Series effect of log BW, or only for the by-Series effect of log BW (based on visual inspection of the data prior to running the analysis; see Table S2 for initial model composition). After stepwise removal of the fixed effects based on a decrease in AIC scores, the best-fitting model was a GLMM (because the residuals from the LMM were non-normally distributed) with a gamma distribution and an inverse link function, including only log BW as fixed effect and random slope only for the by-Series effect of log BW (Table 2). We thus found that BW was the only significant predictor of VTL (N=60; predictions not back transformed: β=−1.515, s.e.m.=0.48, t=−3.158, P=0.002), excluding an effect of sexual dimorphism on this relationship. Inspection of the initial GLMM confirmed the selection of our final model, as neither sex nor litter effects were significant (P>0.9). The same analysis was conducted controlling for Age instead of Series and produced the same final model (which is not surprising considering that series number increased in time and was tightly linked to age). Because this study is a longitudinal sampling of the same individuals, our analysis shows that in domestic pigs, the growth of the vocal tract is dependent on BW entirely with no additional significant effects of Sex or Age.

Acoustical dependencies: VTL predicts formants

VTL and Fn were strongly negatively correlated (r=−0.946, P<0.001; Fig. 3B), as predicted based on acoustic principles, and we thus further examined the dependence of Fn on VTL (an anatomical-to-acoustic relationship) in a similar way to the previous analysis (Table S2). Our best-fitting model revealed that VTL is the only significant determinant (N=57; β=−0.574, s.e.m.=0.15, t=−3.955, P=0.006) of Fn (Table 2), including when Age is controlled for instead of Series. Likelihood ratio

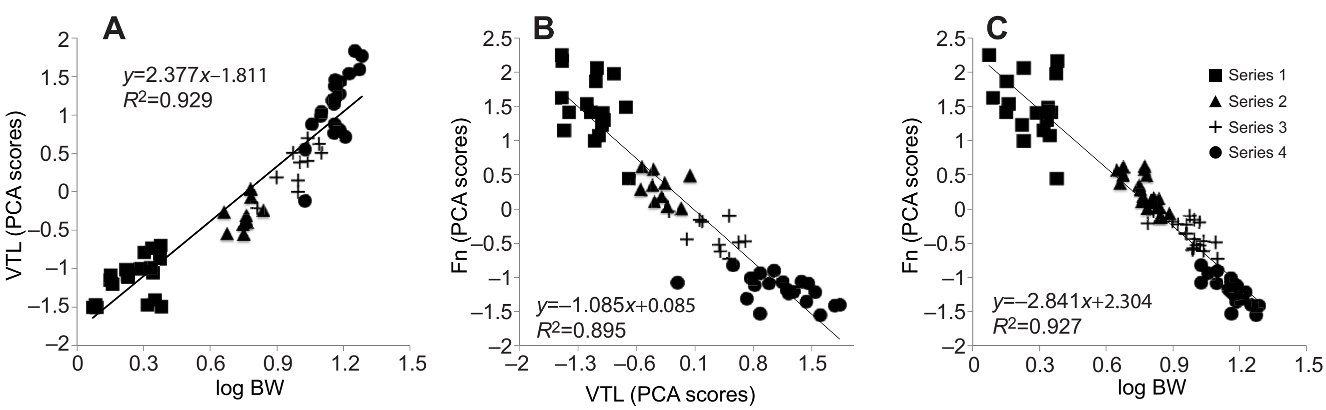

Fig. 3. Bivariate plots illustrating intercorrelations of body weight, VTL and formants. (A) VTL (PCA scores from a PCA on skull length, nasal tract length and oral tract length) against log body weight (BW, in kg); N=60. (B) Formants (Fn; PCA scores from a PCA on F_1 and F_2) against VTL; N=57. (C) Fn against log BW (in kg); N=77.

Table 2. Details of the best-fitting models for each of the main three analyses

Analysis	Type	Final model formula	AIC	β	s.e.m.	*t*	*P*
Anatomical	GLMM	VTL~log BW+(1|Individual)+(1+log BW|Series)	140.5	−1.51	0.48	−3.16	0.002*
Anatomical–acoustical	LMM	Fn~VTL+(1+VTL|Individual)+(1+VTL|Series)	49.2	−0.57	0.15	−3.96	0.006*
Acoustic allometry	LMM	Fn~log BW+(1+log BW|Individual)+(1+log BW|Series)	10.6	−2.19	0.42	−5.18	<0.001*

Best-fitting models were obtained after model reduction based on inspection of the Akaike information criterion (AIC) scores. *Significant *P*-values.

tests on initial models excluding one main factor at a time (Winter, 2013) confirmed the selection for our final model, as neither sex nor litter effects were significant (respectively, $P>0.9$ and $P>0.8$). This analysis shows that the observed decrease in formant frequencies with body size (Table 1) depends only on the increase in VTL; again, no sex differences were significant.

Acoustical allometry: BW predicts formants

Finally, looking at acoustic allometric correlations, Fn depended strongly and negatively upon log BW ($r=-0.963$, $P<0.001$; Fig. 3C), as expected based on the previous two correlations. Following the same procedure for model selection (see Table S2 for initial model), the best-fitting model for this analysis only included a significant effect of log BW ($N=77$; $\beta=-2.191$, s.e.m.=0.42, $t=-5.178$, $P<0.001$) on Fn (Table 2). This was again confirmed by likelihood ratio tests on initial models, showing non-significant effects of sex ($P>0.6$) and litter ($P>0.7$). As for the two previous analyses, replacing Series by Age yielded the same final model. This result therefore shows that formants are tightly determined by BW, via the intervening variable of VTL, with no additional significant dependence upon age, litter or sex.

These anatomical and anatomical–acoustical analyses were run a second time, removing all cases where VTL measurements from the radiographs included at least one uncertain measurement (quality ‘3’). While AIC scores and significance values differed slightly from the main analyses, all best-fitting models were the same, indicating that measurements potentially involving greater uncertainty did not affect the fundamental relationships found in the analyses reported above.

Predictive relationships between VTLs and formants

To evaluate the fit between measured formant frequencies and those predicted for a simple uniform tube closed at one end and open at the other, we compared predicted and measured F_1 and F_2 values. From each average individual F_1 (Table S3A–C) and F_2 (Table S4A–C), the predicted VTL was calculated based on the following equations:

$$F_1 = c/4L, \quad (1)$$

$$F_2 = 3c/4L, \quad (2)$$

where c is the approximate speed of sound in the warm, moist air of a mammalian vocal tract ($350\ \mathrm{m\ s^{-1}}$) and L is the length of the supralaryngeal tract when considered as a half-open resonant tube (Titze, 1994). Wilcoxon signed-rank tests indicated that the measured nasal tract length and oral tract length were significantly different from the predicted VTL calculated from F_1 (nasal tract length: $Z=-6.018$, $P<0.001$; oral tract length: $Z=-6.567$, $P<0.001$) and F_2 (nasal tract length: $Z=-6.567$, $P<0.001$; oral tract length: $Z=-6.567$, $P<0.001$). Most of our nasal measurements were shorter than predicted from F_1 ($N=49/57$) and all were shorter than predicted from F_2 ($N=57/57$); all of our oral measurements were shorter than predicted from F_1 and F_2. Although highly correlated, measured nasal and oral tract length also significantly differed, and nasal tract length was always longer than oral tract length (F_1: $Z=-6.567$, $P<0.001$; F_2: $Z=-6.567$, $P<0.001$). Thus, although apparently underestimating VTL, our measured nasal tract length was consistently closer to the VTL predicted from F_1 and F_2 than our measured oral tract length [based on the differences between expected values and nasal or oral tract measurements: F_1: $Z=-6.567$, $P<0.001$; F_2 (paired sample *t*-test): $t_{56}=-35.23$, $P<0.001$].

Because the vocal folds were not visible in our radiographs, our tracing of nasal and oral tracts stopped at the base of the epiglottis (E), and the full VTL was thus not included. Specifically, the distance between E and the vocal folds (VF, taken at their mid-point) was not included in our measurements, which thus represent a small but consistent underestimate. From digital images of a cross-section of a domestic piglet (W.T.F., unpublished data), we estimated this distance and calculated the resulting increase in VTL. The distance ‘E–VF’ represented, respectively, 8.15% and 9.68% of the nasal and oral tract length stopping at E.

In order to compensate for this additional portion of the vocal tract, we therefore increased our measured nasal and oral tract lengths by 8.15% and 9.68%, respectively (see corrected nasal and oral tract length, Tables S3 and S4) and ran the above analyses again. Nonetheless, as before, the corrected measurements differed from VTL predicted from F_1 (corrected nasal tract length: $Z=-4.024$, $P<0.001$; corrected oral tract length: $Z=-6.567$, $P<0.001$) and F_2 (corrected nasal tract length: $Z=-6.567$, $P<0.001$; corrected oral tract length: $Z=-6.567$, $P<0.001$). Most of the corrected nasal measurements were still shorter than predicted (F_1: $N=42/57$; F_2: $N=59/57$) and all corrected oral measurements were shorter than predicted from F_1 and F_2. Corrected nasal tract length was always longer than corrected oral tract length (F_1: $Z=-6.567$, $P<0.001$; F_2: $Z=-6.567$, $P<0.001$) and thus also closer than corrected oral tract length to the predictions from F_1 ($Z=-6.567$, $P<0.001$) and F_2 ($t_{56}=-32.52$, $P<0.001$).

DISCUSSION

While acoustic cues to adult male quality have been shown to vary over time (see Briefer et al., 2010), the data collected in this study represent, to our knowledge, the first attempt at a longitudinal investigation of acoustic allometry. We found that formants measured in grunt vocalizations provide a reliable cue to body size (assessed by BW) in growing domestic piglets. The very strong correlations between VTL, formants and body size (Table 1, Fig. 3), together with the predictive models that we have computed (Table 2), leave little doubt that formants contain accurate information regarding body size, because increasing BW strongly predicts increasing VTL, which in turn predicts decreasing formant frequencies. Crucially, by resampling the same individuals on four occasions and controlling for age and sex, we could disentangle the specific roles of these parameters in pig vocal allometry. We found that formant frequencies were predicted by body size rather than age, and found no suggestions of potential acoustic sexual dimorphism, or vocal tract modification specifically dependent on age in this species and stage of development. Grunt formants could therefore provide relevant information to listeners, provided that

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these acoustic cues to body size are perceived and used by conspecifics.

On the origin of formant frequencies within grunts

Estimations of VTL based on F_1 and F_2 (Tables S3 and S4) were invariably closer to the measured nasal tract length than to the measured oral tract length. Measured nasal and oral tract length were always shorter than predicted by F_2 (Table S4A–C). Regarding the VTL predicted by F_1, measured nasal tract length was shorter than predicted in most individuals (N=49/57), while measured oral tract length was always shorter than predicted (Table S3A–C). We therefore suggest that grunts for our sample were mostly produced nasally, in accordance with previous cineradiographic observations of grunts by a vocalizing piglet (Fitch, 2000b).

The fact that predicted VTLs do not perfectly match nasal tract measurements can be explained by several factors. First, our calculations and predictions for expected VTL were based on a quarter-wave resonance tube model, which assumes a closed end (at the glottis) and an open end (the mouth for the oral tract, the nostrils for the nasal tract; Titze, 1994). This does not take into account the changing cross-sectional area (or 'shape') of the vocal tract, which is also important in determining formant frequencies and could partly explain the difference between observed and expected VTLs. However, we expect the effect of vocal tract shape to be negligible based on these and previous X-ray observations (Fitch, 2000a,b); furthermore, the effect, if present, would equally concern the nasal and oral airways and thus does not modify our analysis and conclusion. Second, VTL measurements were made down to the base of the epiglottis, which was clearly visible in our radiographs. However, according to the source-filter theory of voice production (Fant, 1960), sound is produced by the vibrating vocal folds (whose vibration rate defines F_0) and then filtered by the supralaryngeal tract (enhancing formants). When correcting our initial measurements for the missing distance between the base of the epiglottis and the vocal folds, we reached similar conclusions, with measurements still typically shorter than predicted. Another potential reason is that laryngeal position in domestic pigs is not as static as previously thought (Fitch, 2000b) and larynx position could thus descend during vocalization (and thus contain lower formants) when piglets produce grunts compared with when they remain silent (which was typically the case during radiographs). Finally, in a few cases nasal tract length was longer than predicted by F_1: this could also be explained by laryngeal mobility and our experimental setup. Although we tried to keep piglets as calm as possible while proceeding with radiographs, in some cases piglets produced squeals while being scanned. Squeals in the domestic pig are very loud calls, which involve retracting the larynx down from the nasopharyngeal region (Fitch, 2000b), in turn leading to a fully extended supralaryngeal tract. Measurements of radiographs of the VTL in this configuration would therefore exceed that characteristic of a grunt call and could explain these isolated observations.

It should be noted that in this study we investigated how formants, instead of formant dispersion, predict body size. These measures are of course intimately related, and it has been suggested that while individual formants could provide information regarding VTL, they are more liable to uncontrolled variability due either to movements or to deviations from the uniform tube assumption (Fitch, 1997; Owren et al., 1997); formant dispersion, in contrast, relies on the redundancy of formant spacing pattern and is thus expected to be more robust (Fitch, 1997). As a result, rather than focusing on individual formant measurements (Owren et al., 1997), most studies investigating formant-related characteristics in mammal vocal communication have used some variant of formant dispersion (Charlton et al., 2011b, 2009a; Fischer et al., 2004; Fitch, 1997; Reby and McComb, 2003; Sanvito et al., 2007). In the present study, information redundancy was low because we were only able to measure the first two formants consistently. Furthermore, the grunts extracted from our labeling were chosen to be as stable and consistent as possible, minimizing the problem raised by formant variability through time. Finally, because grunts appeared to be produced nasally, acoustic attenuation could have occurred as a result of higher sound absorbance from nasal cavities (Fitch, 2000b) or the generation of antiformants by the closed mouth cavity (Kurowski and Blumstein, 1987), explaining why only two formants were clearly distinguishable.

Selection pressures and grunt-specific cues

Previous work has shown that two main call types, grunts and squeals, could be consistently identified while investigating the vocal repertoires of both domestic pigs (Kiley, 1972; Tallet et al., 2013) and wild boars (Garcia et al., 2016; Klingholz et al., 1979). Unlike squeals, the acoustic characteristics of grunts make them particularly well suited for highlighting formants because of their low F_0 (Fitch and Hauser, 1995; Ryalls and Lieberman, 1982), even though the nasal production typical of this call type might slightly impair our ability to track formants compared with formants from calls of other mammalian species (Charlton et al., 2011b; Reby and McComb, 2003).

Grunts are produced across various contexts in which extracting information about the caller might prove beneficial to the receiver. Grunts are, for instance, produced by male domestic (Kiley, 1972) and wild (Meynhardt, 1990) boars as a courtship display, and as an alarm signal in female wild boars (Klingholz and Meynhardt, 1979; Klingholz et al., 1979). It has been shown in various taxa that body size often plays a major role in sexual selection (Carranza, 1996; Clutton-Brock, 2009; Clutton-Brock et al., 2006; Hedrick and Temeles, 1989; Ryan, 1985), and body size influences resource holding potential and fighting ability in mammals on both a within-species and a between-species level (Clutton-Brock et al., 1979; Morton, 1977; Persson, 1985), including in domestic pigs (Jensen, 2002). Advertising body size in such contexts may be beneficial for large individuals, and the results of the current study suggest that, presumably originating in wild boar vocalizations, the domestic pig grunt can provide a cue to the signaler's body size. Furthermore, retrieval of this information should be biologically relevant to conspecifics (both in sexual competition and in agonistic group encounters, as documented by Meynhardt, 1990), which suggests that pigs should both perceive and attend to formants in conspecific vocalizations. Playback experiments, preferably using resynthesized grunts in which the formants are shifted to simulate different phenotypes, would be necessary to test this prediction.

In several mammalian species, the selective pressures on body size advertisement appear to have led to specific vocal tract adaptations that allow exaggeration of the acoustic impression of body size via formant lowering. Some examples include laryngeal retraction down to the sternum (Fitch and Reby, 2001) or possibly even into the thoracic chamber (Charlton et al., 2011b), the presence and inflation of vocal air sacs (Harris et al., 2006) and rostral extension of a nasal vestibulum (Frey et al., 2007). Our results combined with previous radiographic observations strongly suggest that domestic pig grunts are produced nasally. Because measured nasal tract length was consistently longer than measured oral tract length, this implies that lower formants would be produced from nasal grunts than expected from grunts produced orally, potentially indicating a mild form of body size exaggeration.

We note a previous speculation that the sound source in at least some grunts could be a dorsal velar closure ('snoring') rather than vocal fold vibrations (Klingholz et al., 1979). We know of no data relevant to this speculation. Whether such a non-standard production mechanism would have an effect on formants in the context of size exaggeration would require further in-depth investigation of the production mechanisms of this vocalization.

In addition to the agonistic or courtship contexts mentioned above, grunts are also used more generally as contact calls, noticeably occurring during foraging and nursing events in domestic pigs (Kiley, 1972) and wild boars (Klingholz et al., 1979). In both of these contexts, individuality appears to be another type of potentially useful acoustic information. It has indeed been shown in several species that contact calls contain cues to individual identity (Favaro et al., 2015; Jansen et al., 2012; Müller and Manser, 2008; Shapiro, 2009; Townsend et al., 2010). In meerkats and banded mongooses for instance, individual-specific information is used by conspecifics during foraging for vigilance and coordination purposes (for a review, see Manser et al., 2014). Given the strong similarities with the social and vocal communication system found in pigs and meerkats and banded mongooses (also highly social and vocal mammals; Manser et al., 2014), it is reasonable to suggest that cues to individual identity might be perceived and used by other conspecifics in domestic pigs. Parent–offspring recognition is another situation typical of the socio-communicative system characterizing this species where cues to individuality could exist, as such recognition relies on vocal communication in other mammalian species (Briefer and McElligott, 2011; Charrier et al., 2001; Fischer, 2004; Insley, 2001). Previous work on domestic pigs indeed reported that grunts produced during nursing allowed litter discrimination by sows (Illmann et al., 2002) and suggested mother recognition by piglets based on formant-related acoustic features (Schön et al., 1999). Together with our results, this suggests that grunt formants have the potential for carrying multiple messages, as seen in other mammals [rhesus macaques (Fitch, 1997; Rendall, 1996), koalas (Charlton et al., 2012, 2011a)]. Again, playback studies would be required to test this hypothesis.

In conclusion, our results show that formants in domestic piglet grunts are a reliable indicator of body size throughout piglet development. These acoustic cues are available and would in theory be useful to the receiver in various contexts such as sexual selection and agonistic interactions. However, whether information related to vocal tract filtering is perceived and used by conspecifics, including in the case of multi-message signaling, remains unknown. Future research involving playback experiments combined with formant manipulation and signal re-synthesis should improve our understanding of the mechanisms involved in perception and interpretation of domestic pig grunts by their conspecifics. This would in turn provide additional insight regarding the selective pressures, such as sexual selection and/or size exaggeration, acting upon this species' communication system. Because domestic pigs are common, highly vocal and easy to work with, they provide excellent potential as a study species for future bioacoustics research, especially given that their wild progenitors, wild boars, still exist and remain both widespread and relatively accessible.

Acknowledgements
We are especially grateful to Ariane Veit for her essential contribution to the diverse data acquisition. We are thankful to Larissa Kawasch, Sarah Deventer, Martina Schiestl and Andrius Pasukonis for their help with data collection. We thank Nadja Kavcik for figure editing, Riccardo Hofer for advice on the experimental design and Christian Tanczos for X-ray capture. Finally, we thank Benjamin D. Charlton and an anonymous reviewer for valuable comments on the manuscript.

Competing interests
The authors declare no competing or financial interests.

Author contributions
M.G. designed the study, collected acoustic, weight and radiographic data, processed and analyzed the data, created the figures and wrote the manuscript; M.W. helped design the study, provided daily care to the animals and helped collect weight and radiographic data; L.H. provided the research facility and helped design the study; W.T.F. helped conceive and design the study and data analysis, and helped write the manuscript. All authors gave final approval for publication.

Funding
This research was funded by the University of Vienna (Universität Wien; M.G. and W.T.F.). Financial support to L.H. and M.W. came from the Messerli Foundation (project grant: 'Socio-cognitive abilities of domestic pigs, their ethical implications, and indicators of well-being'). Deposited in PMC for immediate release.

Supplementary information
Supplementary information available online at
http://jeb.biologists.org/lookup/suppl/doi:10.1242/jeb.138255/-/DC1

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Table S1. Raw data including general information on the subjects, acoustic and X-ray measurements. A- First series; B- Second series; C- Third series; D- Fourth series.

S1A-

	General information				Acoustic analysis		X-ray measurements			Quality assessment		
Individual	Sex	Series	Age (days)	Weight (Kg)	Formant1	Formant2	Skull (Prosthion-Basion)	Nasal tract (mm)	Vocal tract (mm)	Skull	Nasal	Oral
Baldur	Male	1	10	1.66	664.13	1758.26	83.646	118.407	85.450	1	1	1
Barbarossa	Male	1	10	2.08	678.93	1674.67	70.370	103.969	75.661	1	2	2
Belana	Female	1	10	2.17	691.50	1848.78	87.075	126.535	98.720	1	1	1
Bernadette	Female	1	10	2.21	712.28	1551.88	83.790	113.029	87.138	1	1	2
Blossom	Female	1	10	2.25	748.02	1673.72	69.322	105.853	80.934	1	2	1
Bolero	Male	1	10	2.145	668.20	1791.82	83.309	116.864	89.742	1	1	1
Bruno	Male	1	10	2.39	605.67	1422.14	88.168	127.514	99.057	1	1	1
Zafran	Male	1	10	2.37	797.26	1896.05	84.752	122.310	92.816	1	2	2
Zardoz	Male	1	10	1.93	701.00	1775.36	80.920	118.665	89.612	1	2	2
Zeppelin	Male	1	10	2.4	790.74	2019.54	71.725	101.736	74.171	1	2	2
Zeus	Male	1	10	2.015			84.767	128.892	94.219	1	1	2
Zirbe	Female	1	10	1.69	670.68	1606.16	78.266	113.658	88.911	1	2	1
Zita	Female	1	10	1.18	869.05	1897.06	72.303	100.085	74.344	1	2	1
Zoltan	Male	1	10	1.7			83.518	115.299	89.242	1	2	1
Radischen	Female	1	8	1.413	819.39	1512.40	80.051	111.853	84.004	1	2	1
Radomir	Male	1	8	1.445	806.21	1613.57	81.159	111.600	78.969	1	2	1
Raya	Female	1	8	1.69	799.02	1940.02	80.327	113.472	88.876	1	2	1
Ronon	Male	1	8	1.21			72.139	103.986	73.246	1	2	2
Rosine	Female	1	8	1.23	727.74	1848.02	71.444	99.234	76.170	1	1	1
Rubina	Female	1	8	1.42	833.53	1749.00	81.080	113.958	86.511	1	3	2

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S1B-

Individual	General information				Acoustic analysis		X-ray measurements			Quality assessment		
	Sex	Series	Age (days)	Weight (Kg)	Formant1	Formant2	Skull (Prosthion-Basion)	Nasal tract (mm)	Vocal tract (mm)	Skull	Nasal	Oral
Baldur	Male	2	44	4.58	560.96	1486.08	91.435	148.730	113.324	1	3	2
Barbarossa	Male	2	44	5.79	556.34	1381.19	98.059	137.683	111.972	1	1	1
Belana	Female	2	44	5.64	555.17	1447.78	92.622	128.234	106.202	1	2	1
Bernadette	Female	2	44	6.35	566.69	1303.74						
Blossom	Female	2	44	6.49	553.56	1378.20						
Bolero	Male	2	44	7.03	503.05	1321.98						
Bruno	Male	2	44	7.62	510.18	1340.08						
Zafran	Male	2	44	6.88	521.85	1375.07	102.712	134.194	115.952	2	3	2
Zardoz	Male	2	44	5.59	555.23	1481.89	98.692	130.438	108.513	1	2	1
Zeppelin	Male	2	44	6.07	551.17	1290.92	107.662	139.401	119.893	1	1	1
Zeus	Male	2	44	6.32	557.55	1347.55						
Zirbe	Female	2	44	4.44	609.48	1494.06						
Zita	Female	2	44	4.75	650.02	1426.11	83.325	138.541	108.679	2	3	3
Zoltan	Male	2	44	4.73	569.06	1542.14						
Radischen	Female	2	42	5.94	626.76	1484.93						
Radomir	Male	2	42	6.89	531.56	1257.17						
Raya	Female	2	42	6.83	542.62	1397.85						
Ronon	Male	2	42	6.03	614.86	1432.39	109.204	145.293	121.290	1	2	1
Rosine	Female	2	42	5.73	530.36	1399.55	98.896	135.883	105.523	1	1	2
Rubina	Female	2	42	5.87	621.42	1471.98	98.228	133.135	107.981	1	2	1

S1C-

Individual	General information				Acoustic analysis		X-ray measurements			Quality assessment		
	Sex	Series	Age (days)	Weight (Kg)	Formant1	Formant2	Skull (Prosthion-Basion)	Nasal tract (mm)	Vocal tract (mm)	Skull	Nasal	Oral
Baldur	Male	3	73	6.1	494.42	1289.94						
Barbarossa	Male	3	73	9	536.76	1106.86						
Belana	Female	3	73	9.1	490.24	1207.15						
Bernadette	Female	3	73	9.9	493.73	1153.83	109.183	147.655	115.642	1	1	2
Blossom	Female	3	73	9.9	548.48	1198.46	110.630	157.838	116.943	1	2	2
Bolero	Male	3	73	10.9	482.02	1162.49	122.682	171.397	137.686	3	3	3
Bruno	Male	3	73	12.3	457.79	1208.22	122.216	173.353	129.544	1	2	2
Zafran	Male	3	73	10.5	454.94	1188.22						
Zardoz	Male	3	73	8.3	493.64	1285.93						
Zeppelin	Male	3	73	9.7	467.72	1117.74						
Zeus	Male	3	73	10.9	480.74	1077.87	111.333	163.997	133.015	1	2	1
Zirbe	Female	3	73	6.5	532.97	1304.85	98.162	138.069	119.632	1	3	2
Zita	Female	3	73	7	524.78	1305.11						
Zoltan	Male	3	73	7.9	493.51	1306.05	108.382	150.513	130.552	1	1	1
Radischen	Female	3	71	9.4	532.11	1266.10	116.832	164.515	134.877	1	2	1
Radomir	Male	3	71	12.6	443.96	1094.49	118.680	161.182	135.940	1	1	1
Raya	Female	3	71	10.1	441.40	1224.28	116.096	155.489	133.885	1	2	1
Ronon	Male	3	71	10.4	517.49	1247.94						
Rosine	Female	3	71	9.8	457.27	1159.31						
Rubina	Female	3	71	9.1	525.61	1204.32						

S1D-

	General information				Acoustic analysis		X-ray measurements			Quality assessment		
Individual	Sex	Series	Age (days)	Weight (Kg)	Formant1	Formant2	Skull (Prosthion-Basion)	Nasal tract (mm)	Vocal tract (mm)	Skull	Nasal	Oral
Baldur	Male	4	131	11.4	408.56	1052.32	125.728	171.480	150.461	1	1	1
Barbarossa	Male	4	131	14.1	392.93	942.50	133.951	181.848	157.785	1	2	2
Belana	Female	4	131	14.4	425.60	934.07	130.850	181.462	157.357	1	1	1
Bernadette	Female	4	131	15.3	392.02	986.49	122.974	176.080	142.707	2	3	3
Blossom	Female	4	131	14.5	400.89	998.46	139.894	188.397	159.600	1	1	1
Bolero	Male	4	131	16.8	404.59	894.81	143.516	193.793	164.872	1	1	1
Bruno	Male	4	131	19.2	360.94	878.60	144.303	205.770	172.869	1	2	2
Zafran	Male	4	131	16.2	366.00	931.81	120.092	171.646	142.473	3	3	3
Zardoz	Male	4	131	12.6	433.10	1016.43	134.348	171.495	154.420	1	1	1
Zeppelin	Male	4	131	15.3	371.46	890.85	142.507	186.494	163.508	1	1	1
Zeus	Male	4	131	17.8	360.02	891.22	151.286	206.186	168.956	1	2	2
Zirbe	Female	4	131	10.6	454.78	1016.59	112.709	163.600	145.414	2	1	1
Zita	Female	4	131	10.6	387.59	1017.10	104.430	141.312	117.729	2	3	3
Zoltan	Male	4	131	12.5	379.46	1032.51	124.723	180.392	151.988	1	1	1
Radischen	Female	4	129	14.6	406.22	969.82	141.477	189.400	164.369	1	1	1
Radomir	Male	4	129	18.7	345.89	833.80	146.427	188.054	172.062	1	2	1
Raya	Female	4	129	14.5	340.73	858.49	129.170	169.083	148.241	1	1	1
Ronon	Male	4	129	15.3	384.00	949.79	134.231	184.834	162.115	1	2	1
Rosine	Female	4	129	14.6	399.55	896.01	134.539	180.046	161.344	1	2	2
Rubina	Female	4	129	14.4	414.67	993.89	119.579	172.965	146.201	2	3	1

Table S2. Detailed composition of the initial models used in the analyses conducted on anatomical correlations, anatomical-acoustical correlations and acoustic allometry.

Analysis	**Type**	**Predicted variable**	**Fixed effect**	**Random effect**	**Effect for which random slope is created**
Anatomical dependence	LMM	Vocal Tract Length (VTL)	Weight (Log Wt) + Sex + Litter	Individual + Series	Weight (Log Wt)
Anatomical-acoustical dependence	LMM	Formant frequencies (Fn)	Vocal tract length (VTL) + Sex + Litter	Individual + Series	Vocal Tract Length (VTL)
Acoustic allometry	LMM	Formant frequencies (Fn)	Weight (Log Wt) + Sex + Litter	Individual + Series	Weight (Log Wt)

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Table S3. Difference between expected vocal tract length (based on first formant value) and measured (both corrected and non-corrected) nasal and oral tract length. A – First series; B – Second and third series; C – Fourth series.

S3A-

Series	Individual	F1 (Hz)	Expected vocal tract length (mm)	Measured Nasal tract length (mm)	Corrected (+8.15%) Nasal tract length (mm)	Measured Oral tract length (mm)	Corrected (+9.68%) Oral tract length (mm)	Difference Nasal / Expected (mm)	Difference Nasal / Expected (%)	Difference Corrected Nasal/ Expected (mm)	Difference Corrected Nasal/ Expected (%)	Difference Oral / Expected (mm)	Difference Oral / Expected (%)	Difference Corrected Oral/ Expected (mm)	Difference Corrected Oral/ Expected (%)
1	Baldur	664.13	131.752	118.407	128.057	85.450	93.722	13.345	10.13	3.695	2.80	46.302	35.14	38.030	28.87
1	Barbarossa	678.93	128.880	103.969	112.442	75.661	82.985	24.911	19.33	16.437	12.75	53.219	41.29	45.895	35.61
1	Belana	691.50	126.537	126.535	136.848	98.720	108.276	0.002	< 0.01	-10.311	-8.15	27.817	21.98	18.261	14.43
1	Bernadette	712.28	122.846	113.029	122.241	87.138	95.573	9.817	7.99	0.605	0.49	35.708	29.07	27.273	22.20
1	Blossom	748.02	116.975	105.853	114.480	80.934	88.768	11.122	9.51	2.495	2.13	36.041	30.81	28.207	24.11
1	Bolero	668.20	130.948	116.864	126.388	89.742	98.429	14.084	10.76	4.560	3.48	41.206	31.47	32.519	24.83
1	Bruno	605.67	144.468	127.514	137.906	99.057	108.646	16.954	11.74	6.562	4.54	45.411	31.43	35.822	24.80
1	Zafran	797.26	109.751	122.310	132.278	92.816	101.801	-12.559	-11.44	-22.528	-20.53	16.935	15.43	7.950	7.24
1	Zardoz	701.00	124.822	118.665	128.336	89.612	98.286	6.157	4.93	-3.514	-2.82	35.210	28.21	26.536	21.26
1	Zeppelin	790.74	110.656	101.736	110.027	74.171	81.351	8.920	8.06	0.629	0.57	36.485	32.97	29.306	26.48
1	Zeus			128.892	139.397	94.219	103.339								
1	Zirbe	670.68	130.465	113.658	122.921	88.911	97.518	16.807	12.88	7.544	5.78	41.554	31.85	32.947	25.25
1	Zita	869.05	100.685	100.085	108.242	74.344	81.540	0.600	0.60	-7.557	-7.51	26.341	26.16	19.145	19.01
1	Zoltan			115.299	124.696	89.242	97.881								
1	Radischen	819.39	106.787	111.853	120.969	84.004	92.136	-5.066	-4.74	-14.182	-13.28	22.783	21.34	14.652	13.72
1	Radomir	806.21	108.532	111.600	120.695	78.969	86.613	-3.068	-2.83	-12.163	-11.21	29.563	27.24	21.919	20.20
1	Raya	799.02	109.509	113.472	122.720	88.876	97.479	-3.963	-3.62	-13.211	-12.06	20.633	18.84	12.030	10.99
1	Ronon			103.986	112.461	73.246	80.336								
1	Rosine	727.74	120.236	99.234	107.322	76.170	83.543	21.002	17.47	12.914	10.74	44.066	36.65	36.693	30.52
1	Rubina	833.53	104.975	113.958	123.246	86.511	94.885	-8.983	-8.56	-18.271	-17.40	18.464	17.59	10.090	9.61
	Mean	**740.20**	**119.343**	**113.346**	**122.584**	**85.390**	**93.655**	**6.475**	**5.14**	**-2.723**	**-2.92**	**33.985**	**28.09**	**25.722**	**21.13**
	SD	**74.07**	**12.063**	**8.927**	**9.655**	**8.000**	**8.775**	**10.961**	**9.20**	**11.161**	**9.73**	**10.693**	**7.11**	**10.854**	**7.80**
	Min	**605.67**	**100.685**	**99.234**	**107.322**	**73.246**	**80.336**	**-12.559**	**-11.44**	**-22.528**	**-20.53**	**16.935**	**15.43**	**7.950**	**7.24**
	Max	**869.05**	**144.468**	**128.892**	**139.397**	**99.057**	**108.646**	**24.911**	**19.33**	**16.437**	**12.75**	**53.219**	**41.29**	**45.895**	**35.61**

S3B-

Series	Individual	F1 (Hz)	Expected vocal tract length (mm)	Measured Nasal tract length (mm)	Corrected (+8.15%) Nasal tract length (mm)	Measured Oral tract length (mm)	Corrected (+9.68%) Oral tract length (mm)	Difference Nasal / Expected (mm)	Difference Nasal / Expected (%)	Difference Corrected Nasal/ Expected (mm)	Difference Corrected Nasal/ Expected (%)	Difference Oral / Expected (mm)	Difference Oral / Expected (%)	Difference Corrected Oral/ Expected (mm)	Difference Corrected Oral/ Expected (%)
2	Baldur	560.96	155.982	148.730	160.851	113.324	124.294	7.252	4.65	-4.869	-3.12	42.658	27.35	31.688	20.32
2	Barbarossa	556.34	157.279	137.683	148.904	111.972	122.811	19.596	12.46	8.375	5.32	45.307	28.81	34.468	21.92
2	Belana	555.17	157.608	128.234	138.685	106.202	116.482	29.374	18.64	18.923	12.01	51.406	32.62	41.126	26.09
2	Zafran	521.85	167.672	134.194	145.131	115.952	127.176	33.478	19.97	22.541	13.44	51.720	30.85	40.495	24.15
2	Zardoz	555.23	157.593	130.438	141.069	108.513	119.017	27.155	17.23	16.525	10.49	49.080	31.14	38.576	24.48
2	Zeppelin	551.17	158.753	139.401	150.762	119.893	131.499	19.352	12.19	7.991	5.03	38.860	24.48	27.254	17.17
2	Zita	650.02	134.612	138.541	149.832	108.679	119.199	-3.929	-2.92	-15.220	-11.31	25.933	19.27	15.413	11.45
2	Ronon	614.86	142.308	145.293	157.134	121.290	133.031	-2.985	-2.10	-14.827	-10.42	21.018	14.77	9.277	6.52
2	Rosine	530.36	164.981	135.883	146.957	105.523	115.738	29.098	17.64	18.023	10.92	59.458	36.04	49.243	29.85
2	Rubina	621.42	140.807	133.135	143.986	107.981	118.434	7.672	5.45	-3.179	-2.26	32.826	23.31	22.373	15.89
	Mean	**571.74**	**153.759**	**137.153**	**148.331**	**111.933**	**122.768**	**16.606**	**10.32**	**5.428**	**3.01**	**41.827**	**26.86**	**30.991**	**19.78**
	SD	**42.14**	**10.836**	**6.313**	**6.828**	**5.586**	**6.127**	**13.761**	**8.54**	**14.098**	**9.24**	**12.208**	**6.48**	**12.466**	**7.11**
	Min	**521.85**	**134.612**	**128.234**	**138.685**	**105.523**	**115.738**	**-3.929**	**-2.92**	**-15.220**	**-11.31**	**21.018**	**14.77**	**9.277**	**6.52**
	Max	**650.02**	**167.672**	**148.730**	**160.851**	**121.290**	**133.031**	**33.478**	**19.97**	**22.541**	**13.44**	**59.458**	**36.04**	**49.243**	**29.85**
3	Bernadette	493.73	177.223	147.655	159.689	115.642	126.836	29.568	16.68	17.534	9.89	61.581	34.75	50.387	28.43
3	Blossom	548.48	159.532	157.838	170.702	116.943	128.263	1.694	1.06	-11.170	-7.00	42.589	26.70	31.269	19.60
3	Bolero	482.02	181.528	171.397	185.366	137.686	151.014	10.131	5.58	-3.838	-2.11	43.842	24.15	30.514	16.81
3	Bruno	457.79	191.135	173.353	187.481	129.544	142.084	17.782	9.30	3.654	1.91	61.591	32.22	49.051	25.66
3	Zeus	480.74	182.010	163.997	177.363	133.015	145.891	18.013	9.90	4.647	2.55	48.995	26.92	36.119	19.84
3	Zirbe	532.97	164.174	138.069	149.322	119.632	131.212	26.105	15.90	14.853	9.05	44.542	27.13	32.962	20.08
3	Zoltan	493.51	177.301	150.513	162.780	130.552	143.189	26.788	15.11	14.521	8.19	46.749	26.37	34.112	19.24
3	Radischen	532.11	164.439	164.515	177.923	134.877	147.933	-0.076	-0.05	-13.484	-8.20	29.562	17.98	16.506	10.04
3	Radomir	443.96	197.091	161.182	174.318	135.940	149.099	35.909	18.22	22.772	11.55	61.151	31.03	47.992	24.35
3	Raya	441.40	198.234	155.489	168.161	133.885	146.845	42.745	21.56	30.073	15.17	64.349	32.46	51.389	25.92
	Mean	**490.67**	**179.267**	**158.401**	**171.310**	**128.772**	**141.237**	**20.866**	**11.33**	**7.956**	**4.10**	**50.495**	**27.97**	**38.030**	**21.00**
	SD	**37.61**	**13.647**	**10.897**	**11.785**	**8.245**	**9.044**	**14.072**	**7.38**	**14.473**	**7.98**	**11.295**	**4.88**	**11.363**	**5.35**
	Min	**441.40**	**159.532**	**138.069**	**149.322**	**115.642**	**126.836**	**-0.076**	**-0.05**	**-13.484**	**-8.20**	**29.562**	**17.98**	**16.506**	**10.04**
	Max	**548.48**	**198.234**	**173.353**	**187.481**	**137.686**	**151.014**	**42.745**	**21.56**	**30.073**	**15.17**	**64.349**	**34.75**	**51.389**	**28.43**

S3C-

Series	Individual	F1 (Hz)	Expected vocal tract length (mm)	Measured Nasal tract length (mm)	Corrected (+8.15%) Nasal tract length (mm)	Measured Oral tract length (mm)	Corrected (+9.68%) Oral tract length (mm)	Difference Nasal / Expected (mm)	Difference Nasal / Expected (%)	Difference Corrected Nasal/ Expected (mm)	Difference Corrected Nasal/ Expected (%)	Difference Oral / Expected (mm)	Difference Oral / Expected (%)	Difference Corrected Oral/ Expected (mm)	Difference Corrected Oral/ Expected (%)
4	Baldur	408.56	214.167	171.480	185.456	150.461	165.026	42.687	19.93	28.712	13.41	63.706	29.75	49.142	22.95
4	Barbarossa	392.93	222.688	181.848	196.669	157.785	173.059	40.840	18.34	26.019	11.68	64.903	29.15	49.629	22.29
4	Belana	425.60	205.590	181.462	196.251	157.357	172.589	24.128	11.74	9.339	4.54	48.233	23.46	33.001	16.05
4	Bernadette	392.02	223.204	176.080	190.431	142.707	156.521	47.124	21.11	32.773	14.68	80.497	36.06	66.683	29.88
4	Blossom	400.89	218.266	188.397	203.751	159.600	175.049	29.869	13.68	14.515	6.65	58.666	26.88	43.217	19.80
4	Bolero	404.59	216.270	193.793	209.587	164.872	180.832	22.477	10.39	6.682	3.09	51.398	23.77	35.438	16.39
4	Bruno	360.94	242.426	205.770	222.540	172.869	189.603	36.656	15.12	19.885	8.20	69.557	28.69	52.823	21.79
4	Zafran	366.00	239.073	171.646	185.635	142.473	156.264	67.427	28.20	53.438	22.35	96.600	40.41	82.809	34.64
4	Zardoz	433.10	202.030	171.495	185.472	154.420	169.368	30.535	15.11	16.558	8.20	47.610	23.57	32.662	16.17
4	Zeppelin	371.46	235.557	186.494	201.693	163.508	179.336	49.063	20.83	33.863	14.38	72.049	30.59	56.221	23.87
4	Zeus	360.02	243.043	206.186	222.990	168.956	185.311	36.857	15.16	20.053	8.25	74.087	30.48	57.732	23.75
4	Zirbe	454.78	192.402	163.600	176.933	145.414	159.490	28.802	14.97	15.468	8.04	46.988	24.42	32.911	17.11
4	Zita	387.59	225.757	141.312	152.829	117.729	129.125	84.445	37.41	72.928	32.30	108.028	47.85	96.631	42.80
4	Zoltan	379.46	230.593	180.392	195.094	151.988	166.700	50.201	21.77	35.499	15.39	78.605	34.09	63.892	27.71
4	Radischen	406.22	215.402	189.400	204.836	164.369	180.280	26.002	12.07	10.566	4.91	51.033	23.69	35.122	16.31
4	Radomir	345.89	252.967	188.054	203.380	172.062	188.718	64.913	25.66	49.587	19.60	80.905	31.98	64.250	25.40
4	Raya	340.73	256.801	169.083	182.863	148.241	162.591	87.718	34.16	73.938	28.79	108.560	42.27	94.210	36.69
4	Ronon	384.00	227.867	184.834	199.898	162.115	177.808	43.033	18.89	27.969	12.27	65.752	28.86	50.060	21.97
4	Rosine	399.55	218.994	180.046	194.720	161.344	176.962	38.948	17.78	24.274	11.08	57.650	26.32	42.032	19.19
4	Rubina	414.67	211.009	172.965	187.062	146.201	160.353	38.044	18.03	23.948	11.35	64.808	30.71	50.656	24.01
	Mean	**391.45**	**224.705**	**180.217**	**194.905**	**155.224**	**170.249**	**44.488**	**19.52**	**29.801**	**12.96**	**69.482**	**30.65**	**54.456**	**23.94**
	SD	**29.13**	**16.716**	**14.507**	**15.689**	**12.834**	**14.076**	**18.602**	**7.17**	**19.236**	**7.75**	**18.583**	**6.68**	**19.215**	**7.33**
	Min	**340.73**	**192.402**	**141.312**	**152.829**	**117.729**	**129.125**	**22.477**	**10.39**	**6.682**	**3.09**	**46.988**	**23.46**	**32.662**	**16.05**
	Max	**454.78**	**256.801**	**206.186**	**222.990**	**172.869**	**189.603**	**87.718**	**37.41**	**73.938**	**32.30**	**108.560**	**47.85**	**96.631**	**42.80**
All series	**Mean**	**544.50**	**172.863**	**147.113**	**159.103**	**120.322**	**131.969**	**24.115**	**12.30**	**11.992**	**4.92**	**50.712**	**28.75**	**38.888**	**21.85**
	SD	**151.69**	**45.685**	**30.233**	**32.697**	**30.649**	**33.616**	**21.648**	**9.82**	**20.404**	**10.67**	**20.474**	**6.51**	**18.844**	**7.14**
	Min	**340.73**	**100.685**	**99.234**	**107.322**	**73.246**	**80.336**	**-12.559**	**-11.44**	**-22.528**	**-20.53**	**16.935**	**14.77**	**7.950**	**6.52**
	Max	**869.05**	**256.801**	**206.186**	**222.990**	**172.869**	**189.603**	**87.718**	**37.41**	**73.938**	**32.30**	**108.560**	**47.85**	**96.631**	**42.80**

Table S4. Difference between expected vocal tract length (based on second formant value) and measured (both corrected and non-corrected) nasal and oral tract length. A – First series; B – Second and third series; C – Fourth series.

S4A-

Series	Individual	F2 (Hz)	Expected vocal tract length (mm)	Measured Nasal tract length (mm)	Corrected (+8.15%) Nasal tract length (mm)	Measured Oral tract length (mm)	Corrected (+9.68%) Oral tract length (mm)	Difference Nasal / Expected (mm)	Difference Nasal / Expected (%)	Difference Corrected Nasal/ Expected (mm)	Difference Corrected Nasal/ Expected (%)	Difference Oral / Expected (mm)	Difference Oral / Expected (%)	Difference Corrected Oral/ Expected (mm)	Difference Corrected Oral/ Expected (%)
1	Baldur	1758.26	149.295	118.407	128.057	85.450	93.722	30.888	20.69	21.238	14.23	63.845	42.76	55.574	37.22
1	Barbarossa	1674.67	156.747	103.969	112.442	75.661	82.985	52.778	33.67	44.305	28.27	81.086	51.73	73.762	47.06
1	Belana	1848.78	141.986	126.535	136.848	98.720	108.276	15.451	10.88	5.138	3.62	43.266	30.47	33.710	23.74
1	Bernadette	1551.88	169.149	113.029	122.241	87.138	95.573	56.120	33.18	46.909	27.73	82.011	48.48	73.576	43.50
1	Blossom	1673.72	156.836	105.853	114.480	80.934	88.768	50.983	32.51	42.356	27.01	75.902	48.40	68.068	43.40
1	Bolero	1791.82	146.499	116.864	126.388	89.742	98.429	29.635	20.23	20.111	13.73	56.757	38.74	48.070	32.81
1	Bruno	1422.14	184.581	127.514	137.906	99.057	108.646	57.067	30.92	46.674	25.29	85.524	46.33	75.935	41.14
1	Zafran	1896.05	138.446	122.310	132.278	92.816	101.801	16.136	11.66	6.168	4.45	45.630	32.96	36.645	26.47
1	Zardoz	1775.36	147.857	118.665	128.336	89.612	98.286	29.192	19.74	19.521	13.20	58.245	39.39	49.571	33.53
1	Zeppelin	2019.54	129.980	101.736	110.027	74.171	81.351	28.244	21.73	19.953	15.35	55.809	42.94	48.629	37.41
1	Zeus			128.892	139.397	94.219	103.339								
1	Zirbe	1606.16	163.433	113.658	122.921	88.911	97.518	49.775	30.46	40.512	24.79	74.522	45.60	65.916	40.33
1	Zita	1897.06	138.372	100.085	108.242	74.344	81.540	38.287	27.67	30.130	21.77	64.028	46.27	56.832	41.07
1	Zoltan														
1	Radischen	1512.40	173.566	111.853	120.969	84.004	92.136	61.713	35.56	52.597	30.30	89.562	51.60	81.430	46.92
1	Radomir	1613.57	162.683	111.600	120.695	78.969	86.613	51.083	31.40	41.988	25.81	83.714	51.46	76.070	46.76
1	Raya	1940.02	135.308	113.472	122.720	88.876	97.479	21.836	16.14	12.588	9.30	46.432	34.32	37.829	27.96
1	Ronon														
1	Rosine	1848.02	142.044	99.234	107.322	76.170	83.543	42.810	30.14	34.722	24.44	65.874	46.38	58.501	41.18
1	Rubina	1749.00	150.086	113.958	123.246	86.511	94.885	36.128	24.07	26.841	17.88	63.575	42.36	55.201	36.78
	Mean	**1739.91**	**152.169**	**113.757**	**123.029**	**85.850**	**94.161**	**39.302**	**25.33**	**30.103**	**19.25**	**66.811**	**43.54**	**58.548**	**38.08**
	SD	**163.13**	**14.794**	**9.138**	**9.883**	**7.859**	**8.620**	**14.769**	**7.84**	**14.985**	**8.48**	**14.731**	**6.52**	**14.943**	**7.15**
	Min	**1422.14**	**129.980**	**99.234**	**107.322**	**74.171**	**81.351**	**15.451**	**10.88**	**5.138**	**3.62**	**43.266**	**30.47**	**33.710**	**23.74**
	Max	**2019.54**	**184.581**	**128.892**	**139.397**	**99.057**	**108.646**	**61.713**	**35.56**	**52.597**	**30.30**	**89.562**	**51.73**	**81.430**	**47.06**

S4B-

Series	Individual	F2 (Hz)	Expected vocal tract length (mm)	Measured Nasal tract length (mm)	Corrected (+8.15%) Nasal tract length (mm)	Measured Oral tract length (mm)	Corrected (+9.68%) Oral tract length (mm)	Difference Nasal / Expected (mm)	Difference Nasal / Expected (%)	Difference Corrected Nasal/ Expected (mm)	Difference Corrected Nasal/ Expected (%)	Difference Oral / Expected (mm)	Difference Oral / Expected (%)	Difference Corrected Oral/ Expected (mm)	Difference Corrected Oral/ Expected (%)
2	Baldur	1486.08	176.639	148.730	160.851	113.324	124.294	27.909	15.80	15.788	8.94	63.315	35.84	52.346	29.63
2	Barbarossa	1381.19	190.054	137.683	148.904	111.972	122.811	52.371	27.56	41.150	21.65	78.082	41.08	67.243	35.38
2	Belana	1447.78	181.313	128.234	138.685	106.202	116.482	53.079	29.27	42.627	23.51	75.111	41.43	64.830	35.76
2	Zafran	1375.07	190.899	134.194	145.131	115.952	127.176	56.705	29.70	45.768	23.98	74.947	39.26	63.723	33.38
2	Zardoz	1481.89	177.139	130.438	141.069	108.513	119.017	46.701	26.36	36.070	20.36	68.626	38.74	58.122	32.81
2	Zeppelin	1290.92	203.343	139.401	150.762	119.893	131.499	63.942	31.45	52.581	25.86	83.450	41.04	71.844	35.33
2	Zita	1426.11	184.067	138.541	149.832	108.679	119.199	45.526	24.73	34.235	18.60	75.388	40.96	64.868	35.24
2	Ronon	1432.39	183.260	145.293	157.134	121.290	133.031	37.967	20.72	26.125	14.26	61.970	33.82	50.229	27.41
2	Rosine	1399.55	187.560	135.883	146.957	105.523	115.738	51.677	27.55	40.603	21.65	82.037	43.74	71.823	38.29
2	Rubina	1471.98	178.331	133.135	143.986	107.981	118.434	45.196	25.34	34.346	19.26	70.350	39.45	59.898	33.59
	Mean	**1419.30**	**185.260**	**137.153**	**148.331**	**111.933**	**122.768**	**48.107**	**25.85**	**36.929**	**19.81**	**73.328**	**39.54**	**62.492**	**33.68**
	SD	**60.06**	**8.140**	**6.313**	**6.828**	**5.586**	**6.127**	**10.045**	**4.63**	**10.356**	**5.01**	**7.236**	**2.89**	**7.370**	**3.17**
	Min	**1290.92**	**176.639**	**128.234**	**138.685**	**105.523**	**115.738**	**27.909**	**15.80**	**15.788**	**8.94**	**61.970**	**33.82**	**50.229**	**27.41**
	Max	**1486.08**	**203.343**	**148.730**	**160.851**	**121.290**	**133.031**	**63.942**	**31.45**	**52.581**	**25.86**	**83.450**	**43.74**	**71.844**	**38.29**
3	Bernadette	1153.83	227.504	147.655	159.689	115.642	126.836	79.849	35.10	67.815	29.81	111.862	49.17	100.668	44.25
3	Blossom	1198.46	219.030	157.838	170.702	116.943	128.263	61.192	27.94	48.328	22.06	102.087	46.61	90.767	41.44
3	Bolero	1162.49	225.809	171.397	185.366	137.686	151.014	54.412	24.10	40.443	17.91	88.123	39.03	74.795	33.12
3	Bruno	1208.22	217.261	173.353	187.481	129.544	142.084	43.908	20.21	29.780	13.71	87.717	40.37	75.177	34.60
3	Zeus	1077.87	243.536	163.997	177.363	133.015	145.891	79.539	32.66	66.173	27.17	110.521	45.38	97.645	40.09
3	Zirbe	1304.85	201.172	138.069	149.322	119.632	131.212	63.103	31.37	51.851	25.77	81.540	40.53	69.960	34.78
3	Zoltan	1306.05	200.988	150.513	162.780	130.552	143.189	50.475	25.11	38.208	19.01	70.436	35.04	57.798	28.76
3	Radischen	1266.10	207.330	164.515	177.923	134.877	147.933	42.815	20.65	29.407	14.18	72.453	34.95	59.397	28.65
3	Radomir	1094.49	239.838	161.182	174.318	135.940	149.099	78.656	32.80	65.519	27.32	103.898	43.32	90.739	37.83
3	Raya	1224.28	214.411	155.489	168.161	133.885	146.845	58.922	27.48	46.250	21.57	80.526	37.56	67.566	31.51
	Mean	**1199.66**	**219.688**	**158.401**	**171.310**	**128.772**	**141.237**	**61.287**	**27.74**	**48.378**	**21.85**	**90.916**	**41.20**	**78.451**	**35.50**
	SD	**79.48**	**14.730**	**10.897**	**11.785**	**8.245**	**9.044**	**14.125**	**5.21**	**14.442**	**5.63**	**15.241**	**4.84**	**15.524**	**5.31**
	Min	**1077.87**	**200.988**	**138.069**	**149.322**	**115.642**	**126.836**	**42.815**	**20.21**	**29.407**	**13.71**	**70.436**	**34.95**	**57.798**	**28.65**
	Max	**1306.05**	**243.536**	**173.353**	**187.481**	**137.686**	**151.014**	**79.849**	**35.10**	**67.815**	**29.81**	**111.862**	**49.17**	**100.668**	**44.25**

S4C-

Series	Individual	F2 (Hz)	Expected vocal tract length (mm)	Measured Nasal tract length (mm)	Corrected (+8.15%) Nasal tract length (mm)	Measured Oral tract length (mm)	Corrected (+9.68%) Oral tract length (mm)	Difference Nasal / Expected (mm)	Difference Nasal / Expected (%)	Difference Corrected Nasal/ Expected (mm)	Difference Corrected Nasal/ Expected (%)	Difference Oral / Expected (mm)	Difference Oral / Expected (%)	Difference Corrected Oral/ Expected (mm)	Difference Corrected Oral/ Expected (%)
4	Baldur	1052.32	249.450	171.480	185.456	150.461	165.026	77.970	31.26	63.994	25.65	98.989	39.68	84.424	33.84
4	Barbarossa	942.50	278.514	181.848	196.669	157.785	173.059	96.666	34.71	81.846	29.39	120.729	43.35	105.456	37.86
4	Belana	934.07	281.029	181.462	196.251	157.357	172.589	99.567	35.43	84.778	30.17	123.672	44.01	108.440	38.59
4	Bernadette	986.49	266.094	176.080	190.431	142.707	156.521	90.014	33.83	75.663	28.43	123.387	46.37	109.573	41.18
4	Blossom	998.46	262.904	188.397	203.751	159.600	175.049	74.507	28.34	59.152	22.50	103.304	39.29	87.855	33.42
4	Bolero	894.81	293.358	193.793	209.587	164.872	180.832	99.565	33.94	83.771	28.56	128.486	43.80	112.526	38.36
4	Bruno	878.60	298.771	205.770	222.540	172.869	189.603	93.001	31.13	76.231	25.51	125.902	42.14	109.168	36.54
4	Zafran	931.81	281.711	171.646	185.635	142.473	156.264	110.065	39.07	96.075	34.10	139.238	49.43	125.446	44.53
4	Zardoz	1016.43	258.256	171.495	185.472	154.420	169.368	86.761	33.59	72.784	28.18	103.836	40.21	88.888	34.42
4	Zeppelin	890.85	294.662	186.494	201.693	163.508	179.336	108.168	36.71	92.969	31.55	131.154	44.51	115.327	39.14
4	Zeus	891.22	294.540	206.186	222.990	168.956	185.311	88.354	30.00	71.549	24.29	125.584	42.64	109.229	37.08
4	Zirbe	1016.59	258.215	163.600	176.933	145.414	159.490	94.615	36.64	81.282	31.48	112.801	43.68	98.725	38.23
4	Zita	1017.10	258.086	141.312	152.829	117.729	129.125	116.774	45.25	105.257	40.78	140.357	54.38	128.960	49.97
4	Zoltan	1032.51	254.234	180.392	195.094	151.988	166.700	73.842	29.04	59.140	23.26	102.246	40.22	87.534	34.43
4	Radischen	969.82	270.668	189.400	204.836	164.369	180.280	81.268	30.03	65.832	24.32	106.299	39.27	90.388	33.39
4	Radomir	833.80	314.825	188.054	203.380	172.062	188.718	126.771	40.27	111.445	35.40	142.763	45.35	126.108	40.06
4	Raya	858.49	305.771	169.083	182.863	148.241	162.591	136.688	44.70	122.907	40.20	157.530	51.52	143.180	46.83
4	Ronon	949.79	276.378	184.834	199.898	162.115	177.808	91.544	33.12	76.480	27.67	114.263	41.34	98.570	35.67
4	Rosine	896.01	292.966	180.046	194.720	161.344	176.962	112.920	38.54	98.246	33.53	131.622	44.93	116.004	39.60
4	Rubina	993.89	264.115	172.965	187.062	146.201	160.353	91.150	34.51	77.053	29.17	117.914	44.64	103.761	39.29
	Mean	**949.28**	**277.727**	**180.217**	**194.905**	**155.224**	**170.249**	**97.510**	**35.01**	**82.823**	**29.71**	**122.504**	**44.04**	**107.478**	**38.62**
	SD	**63.72**	**18.874**	**14.507**	**15.689**	**12.834**	**14.076**	**16.820**	**4.75**	**17.190**	**5.14**	**15.530**	**4.02**	**15.733**	**4.41**
	Min	**833.80**	**249.450**	**141.312**	**152.829**	**117.729**	**129.125**	**73.842**	**28.34**	**59.140**	**22.50**	**98.989**	**39.27**	**84.424**	**33.39**
	Max	**1052.32**	**314.825**	**206.186**	**222.990**	**172.869**	**189.603**	**136.688**	**45.25**	**122.907**	**40.78**	**157.530**	**54.38**	**143.180**	**49.97**
All series	**Mean**	**1311.47**	**213.875**	**148.405**	**160.500**	**121.669**	**133.447**	**65.128**	**29.24**	**53.005**	**23.47**	**91.725**	**42.60**	**79.900**	**37.04**
	SD	**342.72**	**54.710**	**29.900**	**32.337**	**30.244**	**33.171**	**28.947**	**7.21**	**27.238**	**7.80**	**27.873**	**5.08**	**25.686**	**5.57**
	Min	**833.80**	**129.980**	**99.234**	**107.322**	**74.171**	**81.351**	**15.451**	**10.88**	**5.138**	**3.62**	**43.266**	**30.47**	**33.710**	**23.74**
	Max	**2019.54**	**314.825**	**206.186**	**222.990**	**172.869**	**189.603**	**136.688**	**45.25**	**122.907**	**40.78**	**157.530**	**54.38**	**143.180**	**49.97**