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Higher fundamental frequency in bonobos is explained by laryngeal morphology, not body size

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Great ape with a tiny voice: higher fundamental frequency in bonobos is explained by laryngeal morphology, not body size.

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In brief

A unique case of positive selection for high voices in both sexes of bonobo? Bonobos have loud calls with nearly double the fundamental frequency and half the vocal length of those of their sister species, chimpanzee, for males and females. Results show partial support of the self-domestication hypothesis.

Acoustic signals, shaped by natural and sexual selection, give insight into ecological and social selection pressures (e.g. Charlton and Reby 2016). Examining acoustic signals together with morphology can be particularly revealing. But this approach has rarely been applied to examine selection pressures in primates, where clues to the evolutionary trajectory of human communication may be found. Across vertebrate species, a close relationship exists between body size and acoustic parameters, such as formant dispersion and fundamental frequency (f0). Deviations from this acoustic allometry usually produce calls with a lower f0 than expected for the body size, often due to morphological adaptations in the larynx or vocal tract (Charlton et al. 2013). An unusual example of an obvious mismatch between fundamental frequency and body size occurs in humans' two closest living relatives, bonobos (*Pan paniscus*) and chimpanzees (*Pan troglodytes*). Although these two ape species overlap in body size (Morbeck and Zilhman 1989), bonobo calls have a strikingly higher f0 than corresponding calls from chimpanzees (de Waal 1988).

Here, we compare acoustic structures of calls from bonobos and chimpanzees in relation to their laryngeal morphology. Most populations of bonobos live in lowland forests of the central Congo basin whereas chimpanzees inhabit diverse habitats from dense lowland forest to open riverine forest and dry savannah.

To assess the extent of between-species differences in f0 we analyzed loud calls with the highest and lowest f0 for each species (high hoots and low hoots of bonobos, pant hoots and roars of chimpanzees) recorded from wild populations of both species (Table S1, Figure S1). Using linear mixed models to test for species and sex differences in the maximum f0 of calls, we found that bonobo vocalizations were close to one octave higher than corresponding chimpanzee calls (full vs null model results: $\chi 2 = 176.73$, df = 3, p<0.0000; Fig. 1, S2 and Table S2). In addition, sex differences were evident in the maximum f0 in chimpanzee but not bonobo calls, with chimpanzee males having a higher f0 than females (Fig. S3 and Table S2).

Across species, the strongest determinant of f0 is vocal fold length (Garcia et al. 2017; Titze et al. 2016). We measured the total vocal fold length tVFL, and effective vocal fold length eVFL (i.e. the anterior membranous portion of the VF that oscillates during vocalization) of larynxes from bonobos (N=7) and chimpanzees (N=7), obtained from zoo facilities (Fig. 1, Table S3) and compared them using unpaired two-tailed t tests. We derived morphometric measures from post mortem µCT scans of extracted larynxes (N=12), or from full body scans (N=2) acquired with a medical CT device. In bonobos, total vocal fold length as well as effective vocal fold length were significantly shorter than those of chimpanzees (tVFL bonobo 22.5 mm ± 2.65 mm *versus* tVFL chimpanzee 33.7 ± 2.54, $t(12)=8.1$, $p<0.001$; eVFL bonobo 15.7 mm± 2.00 mm *versus* eVFL L 26.8 mm ± 2.67 mm, $t(11)=8.5$, $p<0.001$).
Yet, eVFL:tVFL ratios were similar in both species ($p=0.083$) which implies there are no significant shape differences in vocal fold anatomy. The f0 of a call is largely defined by the eVFL, the shorter the eVFL found in bonobos corresponds well with the higher f0, and both measures deviate markedly from the corresponding values of chimpanzees. Given that the relationship between f0 and VFL of other African apes is similar to that of the chimpanzees in our study (Garcia et al. 2017) suggests that the high f0 and the short vocal fold length of bonobos are derived traits.

Our results do not support several hypotheses that might account for species differences in f0. First, differences are unlikely a result of selection for efficient sound propagation in forest habitats where transmission of low f0 calls is more efficient than calls with a high f0 (Morton 1977). Whilst chimpanzees and bonobos both live in dense forest habitats, chimpanzees live also in more open habitat. However, across populations, chimpanzees do not show dramatic differences in maximum f0 (Mitani et al. 1992). Second, it has been proposed that loud calls with a high f0 may signal physical strength and endurance in males (Titze and Riede 2010). While strength may explain sex differences in loud calls of chimpanzees (Fedurek et al. 2016), where male calls reach a higher f0 than female calls (Fig. S3, Table S2), the f0 in corresponding bonobo calls is similar for males and females (Fig. S3; Table S2), suggesting that in bonobos signaling physical strength is not a sexually-selected trait.

The high f0 vocalizations and shorter larynxes in bonobos show partial consistency with the self-domestication hypothesis, which implies the retention of juvenile traits and which has recently been applied to bonobos (Hare et al. 2012). However, in bonobos, high f0 is equally prominent in females and males, suggesting selection for high f0 has occurred in both sexes. Predictions of the self-domestication hypothesis may thus actually apply to both sexes. While acoustic body size exaggeration is well documented in various taxa of vertebrates, including primates (Garcia et al. 2017), the results of our study are novel in representing a case of positive selection for signaling diminution.

Our results show that high f0 calls in both male and female bonobos correspond to short vocal fold length and cannot be fully explained by acoustic hypotheses of environmental influence, sexual selection nor the self- domestication hypothesis. Future studies will need to determine what females and males gain from signalling with a high f0. One possibility is that high f0 determines physical strength and endurance in both sexes and that this gives individuals an advantage when communicating within or between groups, and may facilitate co-dominance between males and females. If this was the case, achieving higher f0 through strength implies the use of greater lung capacity. We suggest that reducing the size of the VFL to achieve higher f0 more likely mimics juvenile vocal quality. We suggest another possibility. Bonobos of both sexes are noticeably more tolerant and less violent to conspecifics than chimpanzees, both within and between groups. Thus, the high f0 may signal social tolerance or appeasement within and between groups.

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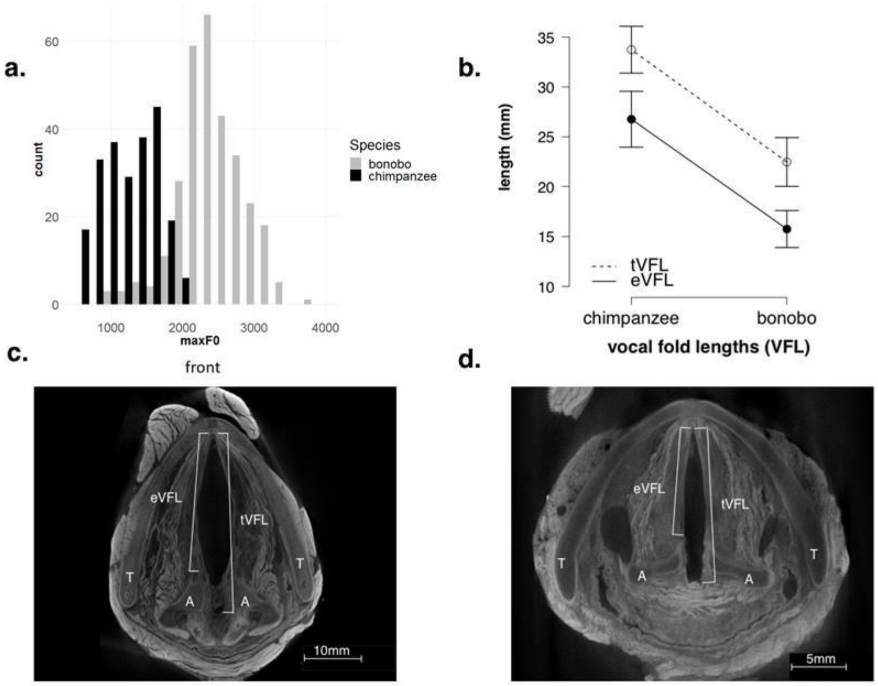
Figure 1. Comparison of chimpanzee and bonobo vocalizations and vocal folds. a) distribution of maximum fundamental frequency values for chimpanzees and bonobos; b) Measures of vocal fold length (VFL) per species: mean of total VFL (tVFL) and effective (anterior membranous) VFL (eVFL) with error bars showing a 95% confidence interval; c) Vocal folds shown in a transverse CT scan for female chimpanzee KAI and d) female bonobo JAS. Labels indicate the arytenoid cartilages (A) and the thyroid cartilage (T).



Figure

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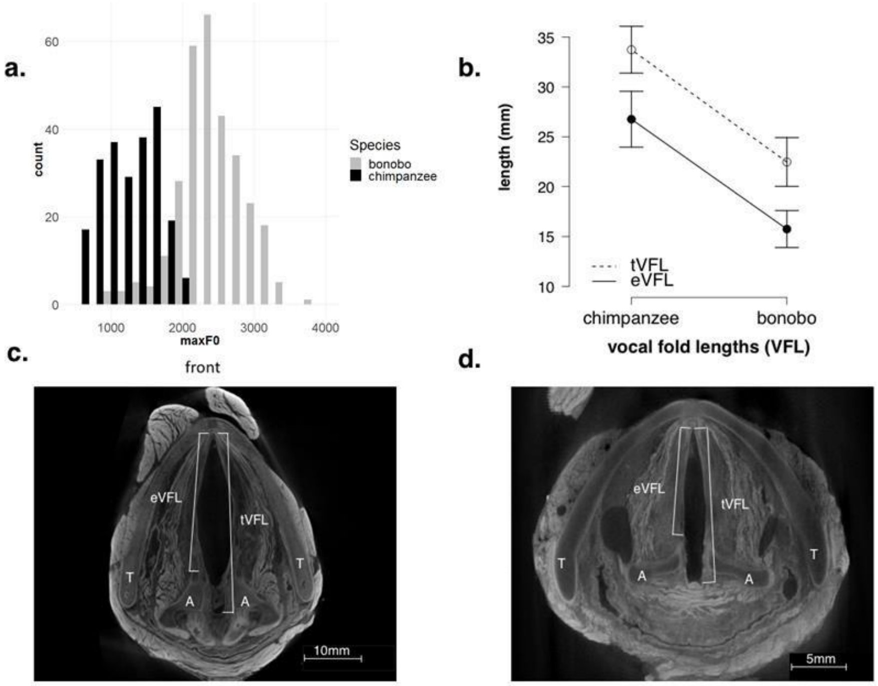

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Supplementary information

Methods

(1) Sound recordings of loud calls

We included bonobos and chimpanzees from different field sites with existing audio recordings. To consider the variation of spectral distribution of the vocal repertoires of both species, we selected loud calls that are representative of the highest fundamental frequency (the bonobo high hoot and the chimpanzee pant hoot) as well as a loud call representing one of the lowest fundamental frequency (low hoot of bonobos and roars of chimpanzees). We followed Mitani and Gros-Louis (1995) to identify acoustic features likely to discriminate well between the species-typical loud calls, the bonobo high hoot and the chimpanzee pant hoot.

Study sites, subjects, audio recordings: Audio recordings of bonobo calls came from the Eyengo community at Lomoko (21º05'E, 00º50'N) collected by GH between 1990 and 1996, and from the West community at Lui Kotale (2º45.610'S, 20º22.723'E) collected by ZC in 2013 and 2014. At both sites, bonobos were fully habituated to the presence of researchers and recordings were made from close distances of 7-20m. The Lomako forest is characterised by terra firma with some swamp forest (Boubli et al 2004 whereas the LuiKotale forest includes also other forest types such as natural secondary, temporarily and permanently inundated forest (Fruth 2011). Both sites are low altitude areas receiving high rainfall and moderate seasonal variation in climate (for Lomako see Boubli et al. 2004, for LuiKotale see Hohmann et al 2006, and Beaune et al. 2013). Calls from bonobos included those recorded during focal follows or ad libitum recordings. Bonobos emit loud calls in various contexts making context assignment often difficult (Hohmann and Fruth 1994, .Schamberg et al. 2016). At both sites, emission of loud calls increases in the late afternoon when dispersed party members coordinate their travel. The recordings from Lomako are biased to this time. However at LuiKotale, calls were collected more evenly throughout the day between dawn and dusk.

Chimpanzees calls were recorded from four communities of *Pan troglodytes verus*, in the Tai Forest, Ivory Coast (see Boesch and Boesch-Achermann 2000 for geographic and climate details) between 1998-2001 (Period 1 by CC and Ilka Herbinger) and between 2011-2012 (Period 2 by Ammie Kalan), from individuals habituated to human presence. For the female analysis, due to low numbers of recordings for female pant hoots in Tai, we included female pant hoots from a second population, Sonso community, Budongo Forest , Uganda (*Pan troglodytes schweinfurthii*) collected by CC from 2008-2010 (see Reynolds 2005 for geographic and climate details). Likewise, due to the low rates at which all chimpanzees, especially females, produce low frequency roars, this analysis was conducted on male calls only, and included roars from males from both Tai and Sonso communities. Tai Forest is a high rainfall, low altitude, mainly primary forest habitat whilst Budongo Forest is mid rainfall, higher altitude, secondary forest. The chimpanzees in all populations in this study are wholly forest-dwelling, suggesting that any acoustic adaptation to habitat will have been shaped by the tropical forest environment.

All calls were recorded ab libitum when the identity and context of calling could be clearly identified. To limit variability of pant hoot climax screams, CC selected those produced only during one context (travelling). Roars were included from two contexts: travel and intergroup encounter.

We included pant hoots from 18 male bonobos (N = 160 total male bonobo calls) and 16 male chimpanzees (N = 120 total male chimpanzee calls). For the analyses including females, we included 23 female bonobos (N = 143 total female bonobo calls) and 29 female chimpanzees (N = 105 total female chimpanzee calls). See **Table S1** for distribution of calls across groups and individuals.

Table S1. Distribution of calls across species, groups and individuals.

Species	Bonobos		IDs	Calls/ID		Chimpanzees				IDs	Calls/ID
Group	Lomako	LK			North	South	Middle	r	so		
Males:											
High hoot/Pant hoot	86	75	18	8.9±4.6	25	48	34	30	-	17	9.1±8.5
Low hoots/Roars	32	14	13	2±2.3	1	6	-	1	15	10	1±1.47
Females:											
High hoot/Pant hoot	94	49	24	6±3.3	65	-	3	-	37	29	3.6±2.6

Legend: LK: Lui Kotale; Guir: Guiroutou. Chimpanzees: *P. t. versus*: Tai Forest Groups: north, south, middle, Guiroutou; *P. t. schweinfurthii*: Budongo Forest Group: Sonso. IDs: number of individuals that have contributed calls; Calls/ID: mean±SD calls per individual.

(2) Acoustic analysis

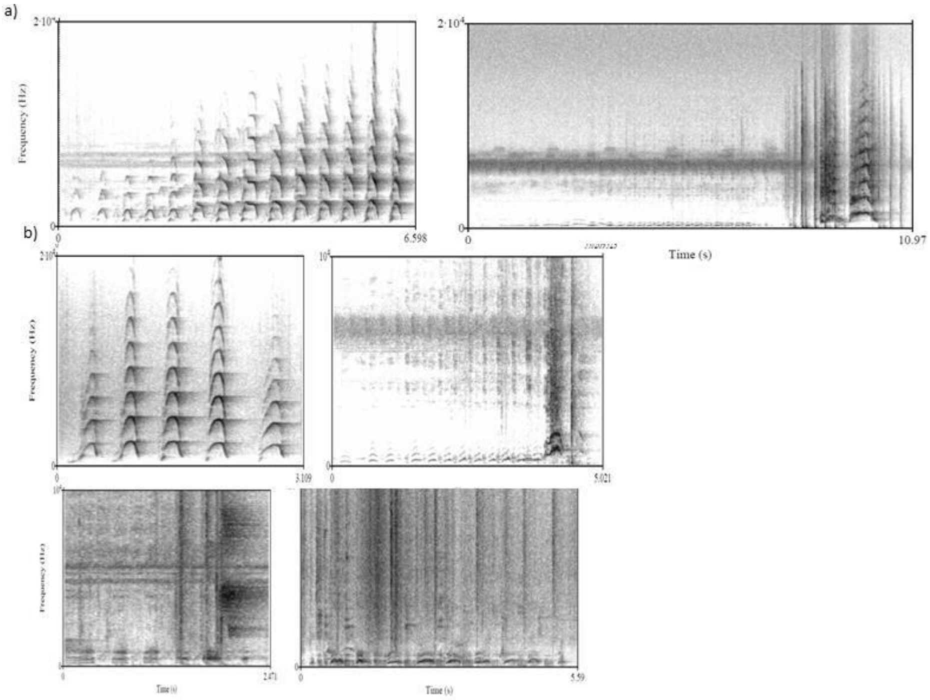
We selected single call elements from the respective long calls with little background noise and without overlap from conspecific vocalisations. Loud calls are emitted as bouts with multiple units and for this comparison we selected one call unit per long call. In bonobos, high hoots are often introduced with whistles that have a higher fundamental frequency than high hoots (Schamberg et al. 2016). For this analysis, we selected the first unit of high hoot within a bout which tends to be lower in frequency than the following units (Hohmann and Fruth 1994). In chimpanzee pant hoots, the f0 varies considerably within call bouts (Riede et al. 2007). We selected the climax scream with the highest fundamental frequency in each recording. Thus, whilst our selection criteria for calls across species was not identical, if anything it should minimize rather than accentuate species differences in f0, thus making our calculation of species differences in f0 a conservative one. In addition, we also examined the lowest long call for each species, in chimpanzees, the roar, and in bonobos the low hoot call. As this call is rare in females of both species, this analysis was limited to males **(Fig. S1**).

Sound recordings at Lomako were taken at a distance between 5 and20 m, using a Sony tape recorder (DAT PCM- 2000), Sennheiser directional microphone (ME88, module K3N), and Sony audio tapes (DT-60P). Audio-recordings were analyzed with a FFT digital real-time analyzer (MEDAV MOSIP 2000N-2.5) using a Hanning 512 window and a 10-kHz frequency scale. Measures of the fundamental frequency

were made on a 5-kHz scale with a Hanning 512 window, providing a sampling rate of 12.8 kHz and a frequency resolution of 25 Hz.

Sound recordings from LuiKotale bonobos were taken at distances of 7–20 m using a Marantz PMD661 solid-state recorder and a Sennheiser MKH816T directional microphone and (Microphone frequency response: 50–20,000 Hz, ±3.5 dB; sampling rate of 44.1 kHz, 16 bits accuracy). Structural analyzes were conducted with Praat acoustic analysis software (v6.0.16; Boersma & Weenink 2006) optimized for voice analysis with a Gaussian window, analysis window length 0.05s, 250 frequency steps, dynamic range 70 dB, 10kz frequency scale with a spectrogram view window 0–10 kHz). We performed pitch analysis using a script (SourceEditor) written by M. Owren (personal communication), and verified the generated values using the harmonic cursor. Spectral measurements were taken from the fundamental frequency (f0).

Figure S1. Spectrogams showing typical examples of loud call types from each species and sex used in the analysis.



Legend: Bonobo loud calls (left) and chimpanzee loud calls (right): a) bonobo male high hoots and chimpanzee male pant hoot climax respectively; b) bonobo female high hoot and chimpanzee female pant hoot climax respectively; c) bonobo male low hoot and chimpanzee male roars. a) frequency windows of 20,000Hz; b) and c) frequency windows of 10,000 Hz. Time (s) is shown on each X axis. For chimpanzee male and female calls in a) and b) the last vocal element is the climax element in each case (also visible are other phases of the pant hoot- the initial build up phase and then buttress drums overlapping with the climax phase in each case).

(3) Statistical Analysis

To determine the discriminatory impact of species and sex differences on variation in the maximum fundamental frequency (f0), we ran linear mixed models for both high and low frequency loud calls. The

acoustic variable was the response variable in each model. The test predictor was species or sex. To control for the model containing more than one call per individual, individual identity was entered as a random factor (Schielzeth & Forstmeier 2009). To control for variation that may occur from individuals belonging to different groups, we also entered group as a random factor. Another reason to control for variation at the group level is that for some groups the acoustic measures were derived using slightly different methods. We used LMMs with Gaussian error structure and identity link using R version 3.2.5 (Team RC 2017) and function glmer of the package lme4 (Bates et al. 2014). We tested the significance of each fixed effect by comparing the full model (comprising all fixed and random effects) with a respective reduced model (not comprising the test predictor) using likelihood ratio tests (Dobson 2002). We only considered model estimates if the full-null model comparison was significant. We assessed model stability for all models by excluding the random effects one at a time and then comparing the estimates for these data with those for the full data set. This showed no influential subjects or groups.

Table S2. LMMs showing species and sex differences with respect to maximum fundamental frequency for high and low frequency loud calls.

Predictor variable	***Bonobo B***		***Chimp C***		***ß***	***SE***	***x2***	***p***
	mean	***sd***	***mean***	***sd***				
High Hoots/Pant hoot screams								
<u>Across Species</u>:								
Maximum F0 (Hz)	2478	466	1488	290				
Intercept					2401	122	-	-
Species (chimpanzee)					**-1380**	**139.4**	**19.9**	**<0.0000**
Sex (male)					118.3	70.3	2.7	0.099
<u>Bonobo only</u>								
Intercept					2421.7	51	-	-
Sex (male)					82.2	73.7	1.12	0.54
<u>Chimpanzee only</u>								
Intercept					887.2	75.6	-	-
Sex (male)					**479.1**	**79**	**23.1**	**<0.0000**
<u>Low Hoots and Roars</u>								
Max F0	425	86	289	49				
Intercept					427.31	18.29		
Species (chimpanzee)					**-127.98**	**28.58**	**-4.48**	**0.0001**

Acoustic variables approximated normal distributions without requiring transformation. Full v null model results: High hoots and Pant hoot climax screams Maximum F0: 1) across species: Max F0: $\chi 2$ = 176.73, df = 3, p<0.0000; 2) Bonobos only: $\chi 2$ = 1.24, df = 2, p<0.543; Chimpanzees only: $\chi 2$ = 26.57, df = 2, p<0.0000. Subject and group identity were included as random factors in each model.

Low Hoots and Roars: Max F0: $\chi 2 = 13.97$, df = 1, $p < 0.0000$; Call Duration: $\chi 2 = 0.45$, df = 1, $p = 0.5$.
Bold indicates P values below 0.05.

Figure S2. Low f0 loud calls comparison between bonobos (low hoots) and chimpanzees (roar).

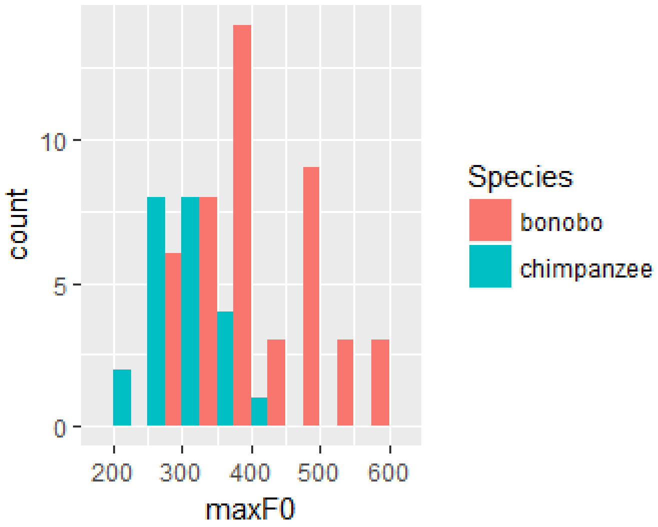
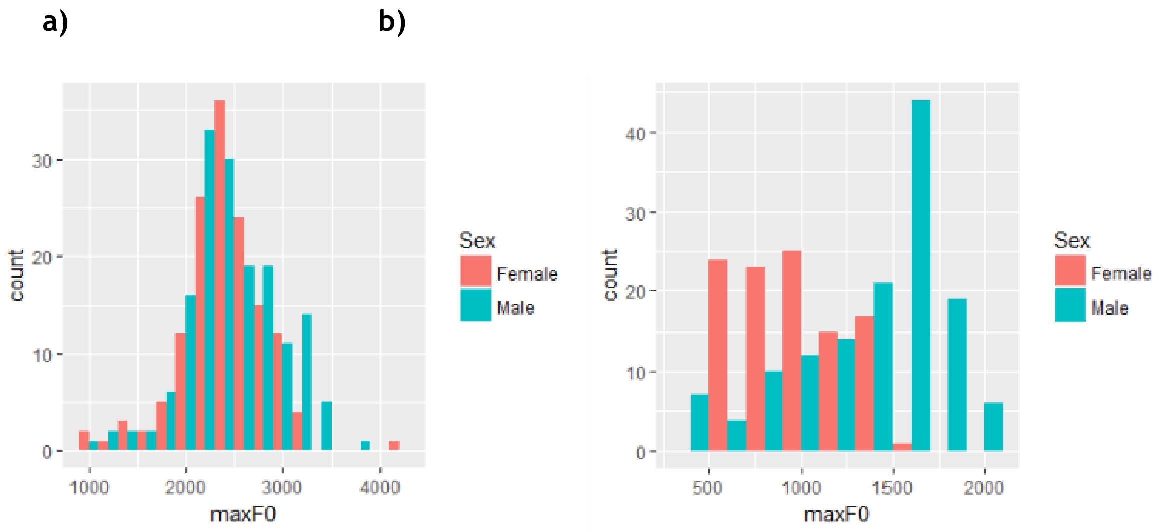


Figure S3. Variation in maximum f0 across sexes shown for a) bonobos and b) chimpanzees.



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(4)Laryngeal Morphology

We selected parameters based on their putative functional relevance for registers (Figure 1). The cardinal parameter that has an immediate effect on register is the effective vocal fold (VF) length, that is, the anterior membranous portion of the VF (mVF). The anterior membranous VF length determines the effective oscillating tissue mass (Titze, 2000). Following similar studies on human larynx morphology e.g. by Eckel et al. (1994) and Jotz (2014) we included anterior and posterior vocal fold length as length of the entire glottis. Vocal fold length measures were taken always in the transverse plane with reference to the base of the arytenoid cartilage as level between *processus vocalis* and insertion at the interior thyroid wall.

(4) Subjects and samples

Analyses of laryngeal morphology are based on data from corpses of 7 chimpanzees (3 male /4 female) and 7 bonobos (5 male / 2 female). Measures were taken either from samples that were stored frozen in the collections of the respective zoo facility, or from scans that had been produced by the zoo for other purposes. After extraction of the larynxes and before scanning, they were stored in Bouin' solution or in 4% Formaldehyd. All measurements were done by means of the *Avizo* visualization software (version 9.3 by FEI Visualization Sciences Group). If available the measures were taken from both sides (left/right), repeated twice for consistency and averaged over all for providing one measure per specimen.

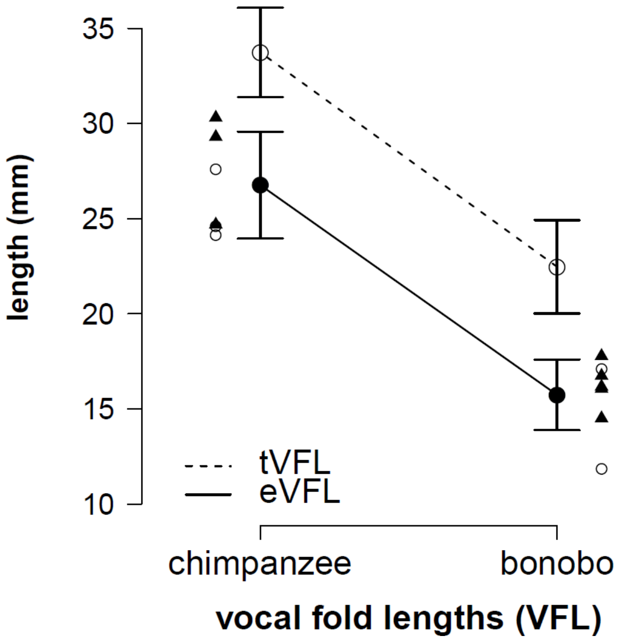
Table S3. Information on the subjects used in this study.

Individual	Species	Sex	Provenance	Weight (kg)	Age (years)
HER	Paniscus	female	Stuttgart	35.5	38.00
JAS	Paniscus	female	Planckendael	26.7	8.00
KAK	Paniscus	male	Twycross	43.0	36.00
KID	Paniscus	male	Planckendael	35.0	25.00
KIR	Paniscus	male	Romagne	NA	24.00
LUD	Paniscus	male	Frankfurt	53.3	32.00
LUS	Paniscus	male	Wuppertal	42.0	34.00
BRI	Troglodytes	female	Leipzig	60.7	49.00
CHO	Troglodytes	female	Twycross	41.0	46.00
KAI	Troglodytes	female	Planckendael	NA	27.00
NIK	Troglodytes	female	Gossau	NA	NA
FLI	Troglodytes	male	Planckendael	NA	45.00
KAR	Troglodytes	male	Magdeburg	34.9	37.00
MON	Troglodytes	male	Twycross	59.0	21.11

Legend: Figures in the second last column are mean values of adult body weight (in kg) that were taken prior to the death and represent body weights when subjects were in healthy conditions. Figures in the last column refer to the chronologic age (in full years) of the subject at the time of death, or at the time when the scan was taken.

For specimens KAR and NIK, we used full body scans (voxel size 1mm) which were taken for medical care reasons. With the exception of one subadult female bonobo (JAS), all remaining subjects were adult when they died (age at time of scan: 32.47± 11.4 yrs). Out of the 14 specimens available for this study, 11 scans were carried out on *post mortem* excised larynxes as 3D micro-CT-scans (18-42µm resolution) using *diondo d3* at MPI EVA, Leipzig.

Figure S4. Vocal fold length by sex per species. Same plot as shown in Fig. 1, here with individual eVFL measures illustrated in addition: Black triangles: males. Open circles: females.



(5) Statistical Analysis

The current sample size allows only for statistical testing at the species level. The distribution of total VFL values in chimpanzees (33.7±2.54 mm) seems to be concordant with that presented by Garcia et al. (2017), although their specimen (38.25mm) appears at the upper tail of our sample. After visual checking for normality, mean comparisons were done by means of an unpaired Students t-test assuming similar variance based on Levene test. In order to adjust for multiple testing we report adjusted p-values using the family-wise error rate correction by Bonferroni, i.e. division by number of tests. (s. Table S3).

Table S4: Vocal fold measures compared across species using unpaired t-tests.

Measure	df	Chimp mean	chimp sd	bonobo mean	bonobo sd	t value	adj p-val
eVFL	11	26.8	2.67	15.7	2.00	8.501	< 0.001
tVFL	12	33.7	2.54	22.5	2.65	8.122	< 0.001

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