

Correspondence

Higher fundamental frequency in bonobos is explained by larynx morphology

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Acoustic signals, shaped by natural and sexual selection, reveal ecological and social selection pressures [1]. Examining acoustic signals together with morphology can be particularly revealing. But this approach has rarely been applied to primates, where clues to the evolutionary trajectory of human communication may be found. Across vertebrate species, there is a close relationship between body size and acoustic parameters, such as formant dispersion and fundamental frequency (f_0). Deviations from this acoustic allometry usually produce calls with a lower f_0 than expected for a given body size, often due to morphological adaptations in the larynx or vocal tract [2]. An unusual example of an obvious mismatch between fundamental frequency and body size is found in the two closest living relatives of humans, bonobos (*Pan paniscus*) and chimpanzees (*Pan troglodytes*). Although these two ape species overlap in body size [3], bonobo calls have a strikingly higher f_0 than corresponding calls from chimpanzees [4]. Here, we compare acoustic structures of calls from bonobos and chimpanzees in relation to their larynx morphology. We found that shorter vocal fold length in bonobos compared to chimpanzees accounted for species differences in f_0 , showing a rare case of positive selection for signal diminution in both bonobo sexes.

To assess the extent of between-species differences in f_0 , we analyzed loud calls with the highest and lowest f_0 for each species (high hoots and low hoots of bonobos, pant hoots and roars of chimpanzees) recorded

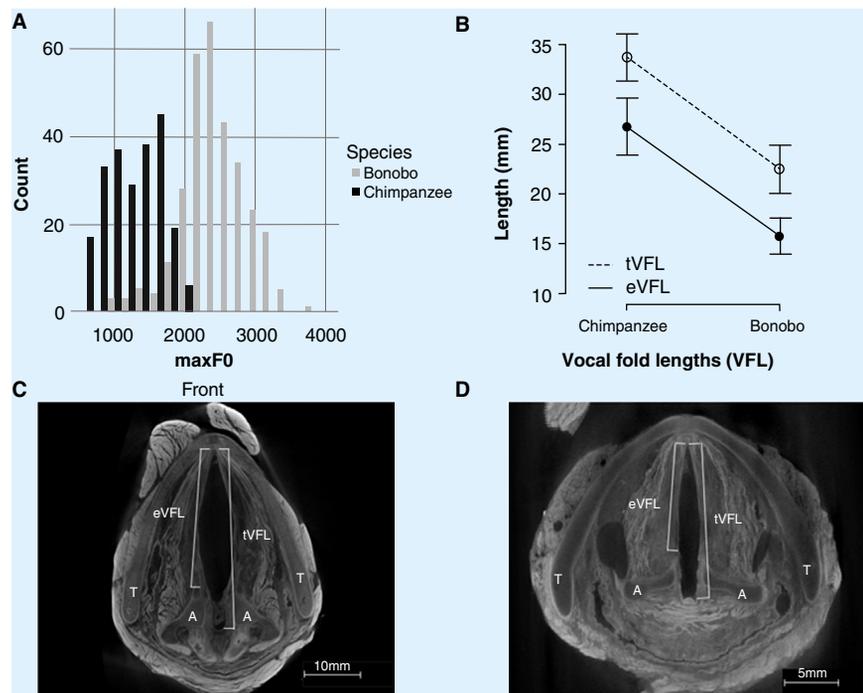


Figure 1. Comparison of chimpanzee and bonobo vocalizations and vocal folds.

(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,D) Vocal folds shown in a transverse CT scan for (C) female chimpanzee KAI and (D) female bonobo JAS. Labels indicate the arytenoid cartilages (A) and the thyroid cartilage (T).

from wild populations of both species (Supplemental Information; Data S1). Using linear mixed models to test for species and sex differences in the maximum f_0 of calls, we found that bonobo vocalizations were close to one octave higher than corresponding chimpanzee calls (full vs null model results: $\chi^2 = 176.73$, $df = 3$, $p < 0.0000$; Figure 1; Supplemental Information; Data S1). In addition, sex differences were evident in the maximum f_0 in chimpanzee but not bonobo calls, with chimpanzee males having a higher f_0 than females (Supplemental Information; Data S1).

Across species, a strong determinant of f_0 is vocal fold length [5,6]. We measured the total vocal fold length (tVFL) and effective vocal fold length (the anterior membranous portion of the vocal fold that oscillates during vocalization; eVFL) of larynxes from bonobos ($n = 7$) and chimpanzees ($n = 7$), obtained from zoo facilities (Figure 1; Data S1), and compared them using unpaired two-tailed t tests, adjusted using Bonferroni correction. We derived morphometric measures

from post mortem μ CT 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 (Figure 1, Data S1; tVFL bonobo $22.5 \text{ mm} \pm 2.65 \text{ mm}$ versus tVFL chimpanzee 33.7 ± 2.54 , $t(12) = 8.12$, $df = 11$, $p < 0.001$; eVFL bonobo $15.7 \text{ mm} \pm 2.00 \text{ mm}$ versus eVFL L $26.8 \text{ mm} \pm 2.67 \text{ mm}$, $t(11) = 8.50$, $df = 11$, $p < 0.001$). 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 f_0 of a call is largely defined by the eVFL, the shorter the eVFL found in bonobos corresponds well with the higher f_0 , and both measures deviate markedly from the corresponding values of chimpanzees. The relationship between f_0 and vocal fold length of other African apes is similar to that of the chimpanzees in our study [5]. This suggests that the high f_0 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 f_0 . First, differences are unlikely a result of selection for efficient sound propagation in forest habitats where transmission of low f_0 calls is more efficient than calls with a high f_0 [7]. Whilst chimpanzees and bonobos both live in dense forest habitats, chimpanzees are also found in more open habitat. However, comparisons of chimpanzee populations living in these different habitats do not show dramatic differences in maximum f_0 [8]. Second, it has been proposed that loud calls with a high f_0 may signal physical strength and endurance in males [6]. While strength may explain sex differences in loud calls of chimpanzees [9], where male calls reach a higher f_0 than female calls (Supplemental Information; Data S1), the f_0 in corresponding bonobo calls is similar for males and females (Supplemental Information; Data S1), suggesting that in bonobos signaling physical strength is not a sexually-selected trait.

The high f_0 vocalizations and shorter larynxes in bonobos show partial consistency with the self-domestication hypothesis, which implies the retention of juvenile traits in adults and has recently been suggested for bonobos [10]. However, in bonobos, high f_0 is equally prominent in females and males, suggesting selection for high f_0 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 [5], the results of our study are novel in representing a case of positive selection for signaling diminution.

Our results show that high f_0 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 male bonobos gain from signalling with a high f_0 . One possibility is that high f_0 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 f_0 through strength implies the use of greater lung capacity rather than vocal fold length reduction. We argue that reducing vocal fold length to achieve higher f_0 more likely mimics juvenile vocal quality. We suggest an alternative explanation. Bonobos of both sexes are noticeably more tolerant and less violent to conspecifics than chimpanzees, both within and between groups. Thus, the high f_0 may signal social tolerance or appeasement within and between groups.

SUPPLEMENTAL INFORMATION

Supplemental Information including experimental procedures, one figure and one table can be found with this article online at <https://doi.org/10.1016/j.cub.2018.09.030>.

ACKNOWLEDGEMENTS

Sincere thanks go to the staff of the zoos in Frankfurt am Main, Gossau (Walter Zoo), Leipzig, Magdeburg, Planckendael, Romagne (La Vallée de Singes), Stuttgart, Twycross, and Wuppertal for providing access to material for morphometric measures. Collection of audio-recordings in the field was strictly non-invasive and approved by the following authorities: The Ministry of Research and Environment of Côte d'Ivoire, Office Ivoirien des Parcs et Réserves, the Ugandan Authorities (UWA, UNCST), and the Institut Congolais pour la Conservation de la Nature (ICCN). We thank the Royal Zoological Society of Antwerp (KMDA/RZSA), the Centre Suisse de Recherches Scientifiques, and the Budongo Conservation Field Station. This paper is number 5 in a series of studies conducted at the University of Antwerp, as part of the Bonobo Morphology Initiative 2016. For help with sample collection, sample preparation, and scanning we thank Jahmaira Archbold, Verena Behringer, Romain David, Barbara Fruth, Ilka Herbing, Kerstin Mätz-Renzig, Sandra Nauwelaerts, David Plotzki, Isaac Schamberg, Heiko Temming, and Klaus Zuberbühler. We also thank two anonymous referees for their helpful and constructive comments on an earlier draft. The institutional support from Christophe Boesch, Jean-Jaques Hublin, Zjef Pereboom and Richard McElreath is gratefully acknowledged. This research was funded by the Max Planck Society. C.C. received funding from the European Research Council (ERC) under the European Union's Horizon 2020 research and innovation programme (Grant Agreement No 679787). The work of G.H. in Lomako was supported by the Deutsche Forschungsgemeinschaft.

Z.C. received funding from the L.S.B. Leakey Foundation; the National Geographic Society: Committee for Research and Exploration Grant; the British Academy: Small Research Grants and from private donors associated with the British Academy and the Leakey Foundation.

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