

## Correspondence

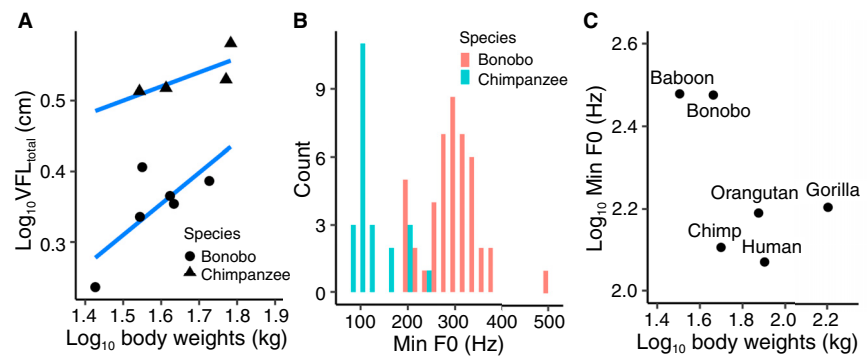
# Response to Garcia and Dunn

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Garcia and Dunn [1] raise some interesting and valuable points regarding our recent paper in *Current Biology* [2]. As Garcia and Dunn [1] point out, cross-species variation in vocal and anatomical relations allows for the identification of relevant outliers from the body size — fundamental frequency ( $f_0$ ) regression. However, this depends on the premise that the chosen or available  $f_0$  and body size values are typical of the species. A motivation for our study [2] was in part to improve the accuracy of such estimates by providing more data per species compared to previous studies. We address each point of their critique by controlling for cross-species body size variation using body weights for chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*), addressing potential call variation in different subspecies of *Pan troglodytes*, measuring minimum  $f_0$  as well as maximum  $f_0$  and possible effects caused by different larynx fixation methods.

First, we plotted the body weights against vocal fold length, where available in our sample (Figure 1A; Table S1). For bonobos and chimpanzees, respectively, a least squares fit shows intercepts of -0.8 and 0.46, and slopes of 0.44 and 0.2. Thus chimpanzees with the same body weight as bonobos have a vocal fold that is 1.8 times longer than that of bonobos. We conclude that indeed bonobo vocal fold lengths are shorter than expected for their body size within the genus *Pan*.

Second, bonobos have longer mean trunk lengths of 59.5 (5.0) cm compared with 55.7 (2.7) cm in chimpanzees [3]. Mean head lengths are 20.3 (1.1) cm and 24.3 (1.3), respectively [3], giving ratios for bonobos and chimpanzees, respectively, for head length of 1:1.2, anterior membranous vocal fold length: 1:1.7; and total vocal fold length: 1:1.5 (Data S1B).



**Figure 1. Comparisons between bonobos and chimpanzees.**

(A) Body weights (kg,  $\log_{10}$ ) of individuals with measured vocal fold length (total length,  $\log_{10}$ ); blue line: least squares fit per species. (B) The loud call with the lowest fundamental frequency ( $f_0$ ) per species, using the minimum  $f_0$  per call. (C) Lowest  $f_0$  in each species' repertoire plotted against body weights.  $f_0$  measures for *Pan* are taken from this paper, and for other species, see [S1–S4]. For body weight measures for *Pan* see Data S1A, and for other species [S5,S6].

Third, subspecies identity is known for three of the subjects in our study (BRI: *P. t. troglodytes*, KAR: *P. t. troglodytes*, MON: *hybrid*) — and these subspecies are not represented in our vocal recordings. Genetic data from sites across Africa strongly suggest that genetic variation is correlated with geographic distance [4]. Given that the geographical range of *P. t. troglodytes* is between that of *P. t. verus* and *P. t. schweinfurthii*, variation in body size or vocal fold length in *P. t. troglodytes* should be expected to be between that of *P. t. verus* and *P. t. schweinfurthii* [4].

Garcia and Dunn [1] argue that subspecies differences may confound acoustic variation. However, when comparing maximum and minimum  $f_0$  across chimpanzee populations, we see that potential subspecies variation in chimpanzee body size is not sufficient to affect  $f_0$  (Table S2: for maximum  $f_0$  in the climax scream of the pant hoot, the same measure as in [2]): the suggested smallest Gombe chimps do not have the highest  $f_0$ . Also, there is minimal variation across subspecies for  $f_0$  of the build-up phase of the chimpanzee pant hoot, which is close to the lowest  $f_0$  for chimpanzees. Nonetheless, in order to account for any acoustic variation related to chimpanzee subspecies, we included vocalisations of both subspecies in our original dataset. In our study [2], Figure 1B shows that maximum  $f_0$  dramatically differs between chimpanzees and bonobos such that any variation in chimpanzee subspecies does not reduce the bonobo–chimpanzee dichotomy.

In sum, although we agree with Garcia and Dunn [1] regarding the importance of controlling for body size across subspecies, the available vocal data strongly indicate that if vocal folds generally scale with body size, any body size differences between chimpanzee subspecies do not substantially affect vocal fold length.

As requested by Garcia and Dunn [1], we measured the minimum  $f_0$  of the loud call in each species' vocal repertoire which has the lowest  $f_0$  (bonobos: low hoot; chimpanzee: pant roar) in a linear mixed model, using the same model structure as in [2]. As predicted by vocal fold ratios across species, chimpanzees have a significantly lower minimum  $f_0$  than bonobos (Full vs null model comparison:  $\chi^2 = 15.3$ ,  $df = 1$ ,  $P = 0.0001$ ; mean  $\pm$  SD: chimpanzee =  $128 \pm 45.5$  Hz; Bonobo =  $299 \pm 54$  Hz, with ratio of means 1:2.33; Figure 1B; Videos S1 and S2).

We agree that it is important to measure minimum  $f_0$  given potential disparity in morphological measurements of relaxed vocal folds. Human voice research, however, also considers  $f_0$  maxima in order to characterize human voices (e.g. soprano, baritone, bass), which are known to be based on vocal fold length, with for example, basses having longer vocal fold lengths than tenors (e.g., [5]). Thus maximum  $f_0$ , and the highest used  $f_0$ , may not be ideal but are certainly not misleading parameters to examine.

Of the twelve larynxes extracted during autopsy only one specimen was fixed

in formaldehyde solution 4%, buffered while all remaining specimens were fixed using Bouin's solution. After fixation, larynxes were washed, dehydrated and stored in 70% alcohol. Placing samples in formaldehyde can sometimes lead to tissue volume increase while Bouin's solution has the opposite effect. However, as shown in the reference given by Garcia and Dunn [1,6], washing and dehydration using Bouin's solution and formaldehyde solution has a similar effect on tissue volume changes. Consequently, fixing one specimen with formaldehyde solution while using Bouin's solution for the others should thus have no significant effect on the results presented in [2].

Our results show that bonobos have shorter vocal folds compared to chimpanzees, given their respective body sizes. A phylogenetic analysis is needed, however, to determine which species is the outlier. Garcia and Dunn [1] present a regression of logged body size and vocal fold length across mammals which suggests that neither bonobos nor chimpanzees are outliers. We advocate caution with this interpretation. While considerable effort was obviously required in acquiring larynxes from many species, the data are scarce and not well defined, potentially introducing considerable unaccounted for variation into the regression. Body weight and vocal fold length data come from separate papers [7,8] and separate sources, and each species is often represented by only a single individual. Also, the sex of the individuals sampled is not always indicated, even in species with considerable body size sexual dimorphism. With such variation in the referenced sources, it is difficult to ascertain where the regression line should fall, and where bonobos and chimpanzees would lie relative to this line. Whilst acquiring more larynxes will be slow, given there is a direct influence of vocal fold length on minimum  $f_0$  [9], we contrast body weight with the minimum  $f_0$  in the vocal repertoire of each great ape species, and of an old world monkey, chacma baboons (*Papio ursinus*), representing a deeper evolutionary trajectory (Figure 1C; Data S1C). We show that bonobos stand out amongst the great apes as having a higher  $f_0$  for their body size, again supporting our original claim that the vocal fold length of bonobos is likely to be unusually short within the apes.

In sum, while we appreciate the valuable points made by Garcia and Dunn [1], we do not find robust support their concerns. Specifically, after including all published and our own data on body weights, we find that body sizes for chimpanzees and bonobos overlap, with bonobo body weights being 10% less than those of chimpanzees (Data S1A). Vocal fold length, using allometric scaling principles in contrast to body weight, for bonobos is shorter than would be expected for their body size (Data S1B). Scaling the minimum  $f_0$  in the vocal repertoire for each ape species against their respective body weights shows that the minimum  $f_0$  for bonobos is considerably higher than expected for their body size (Figure 1C; Data S1C; Videos S1 and S2). Thus our original conclusions are again supported by the additional analyses presented here, showing a likely rare case of positive selection for shorter vocal folds and strikingly higher voices in bonobos than in the other ape species.

#### SUPPLEMENTAL INFORMATION

Supplemental Information including two tables, one data file, and two videos can be found with this article online at <https://doi.org/10.1016/j.cub.2019.06.023>.

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