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Sexual selection on male vocal fundamental frequency in humans and other anthropoids

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In many primates, including humans, the vocalizations of males and females differ dramatically, with male vocalizations and vocal anatomy often seeming to exaggerate apparent body size. These traits may be favoured by sexual selection because low-frequency male vocalizations intimidate rivals and/or attract females, but this hypothesis has not been systematically tested across primates, nor is it clear why competitors and potential mates should attend to vocalization frequencies. Here we show across anthropoids that sexual dimorphism in fundamental frequency (F_0) increased during evolutionary transitions towards polygyny, and decreased during transitions towards monogamy. Surprisingly, humans exhibit greater F_0 sexual dimorphism than any other ape. We also show that low- F_0 vocalizations predict perceptions of men's dominance and attractiveness, and predict hormone profiles (low cortisol and high testosterone) related to immune function. These results suggest that low male F_0 signals condition to competitors and mates, and evolved in male anthropoids in response to the intensity of mating competition.

1. Introduction

Explaining why sexual dimorphisms evolve is central to understanding the evolution of primate mating systems and social organization. In many primate species, the vocalizations of males and females differ dramatically, with male vocalizations and vocal anatomy often seeming to exaggerate the appearance of body size [1–7]. Among humans, men's approximately 60% longer vocal folds [8,9] contribute to an average rate of vocal fold vibration during phonation (fundamental frequency, F_0) that is about 5 standard deviations below women's [5]. To human listeners, utterances lower in F_0 are perceived as being deeper in pitch and as emanating from larger individuals [10,11]. The evolutionary reasons

for such apparent size exaggeration have been the subject of speculation since Darwin noted the pubertal enlargement of male vocal structures and their intensified employment during the breeding season in many mammals [12].

Some have suggested that male vocalizations evolve to intimidate male competitors and/or attract mates [6,13]. For example, among orang-utans, lower-ranking males avoid long calls given by higher-ranking males [14], suggesting that acoustic cues convey threat potential to conspecifics. Several studies in humans suggest that F_0 has relevance under both inter- and intrasexual competition: experimentally lowering F_0 increases perceptions of men's dominance and attractiveness [11,15], and raising F_0 increases women's vocal attractiveness [16,17]. However, little is known about whether these effects persist in unmanipulated speech when F_0 and other acoustic parameters vary naturally and simultaneously.

Moreover, it is unclear why F_0 should signal formidability to same-sex competitors or mate value to potential mates; F_0 is only weakly associated with body size [5,7,18–20] and perhaps strength [5,21] in humans, although F_0 may be modulated according to relative formidability [22] and mate quality [23,24]. Steroid hormones may provide a link between F_0 and condition. Growing evidence indicates that glucocorticoids such as the stress hormone cortisol negatively interact with testosterone in predicting immune function and influencing the expression of secondary sex traits [25–27]. Infection stimulates cortisol production [28], which downregulates androgen receptors and inhibits the action of testosterone on target tissues [29–33]. Hence, testosterone should be more potent in individuals in good condition with low immune system activation. In humans, positive relationships between testosterone and immune response to a vaccine [34], and between testosterone and both facial attractiveness [34] and dominance [35], were stronger in males with low cortisol. Furthermore, the interactive effect of testosterone and cortisol on attractiveness was mediated by immune function, supporting the stress-linked immunocompetence handicap hypothesis (SL-ICHH) that testosterone-related traits that interact with cortisol are linked to immunocompetence [34]. Although previous studies have found negative relationships between men's testosterone and F_0 [5,20], it is unknown whether testosterone and cortisol negatively interact in predicting F_0 , as the SL-ICHH would suggest if F_0 reflects underlying condition.

More generally, scant evidence exists to support a role for sexual selection in shaping F_0 and other vocal sexual dimorphisms across primates [6], and there are plausible alternative hypotheses: F_0 dimorphism may represent a by-product of selection for greater male size or long-distance transmission of male calls [36], or reflect selection for sex identification. The latter two hypotheses predict relationships between habitat and F_0 dimorphism. In general, open, terrestrial habitats are poor acoustic environments in which sounds greatly attenuate over distance compared with arboreal habitats. This is particularly true for the heights at which each habitat's primate residents tend to communicate and for lower-frequency sounds [37]. Thus, all else equal, selection for long-distance transmission of male calls should tend to produce relatively lower-frequency male calls in arboreal environments than in terrestrial ones (for caveats, see Discussion). Likewise, because primates are both more visible and more sexually dimorphic in terrestrial species than in arboreal ones [38], selection for sex identification should favour greater F_0 dimorphism in arboreal species.

Here, we report the results of three studies designed to clarify the evolution of sexual dimorphism in F_0 . In study 1, we examined the evolution of F_0 dimorphism as a function of mating system, as well as body mass dimorphism and habitat, across anthropoid primates. Studies 2 and 3 focused on humans. Not only are humans of special interest, but they are also highly useful as a model organism: there is strong evidence implicating sexual selection in the evolution of human F_0 [39,40], as well as a unique richness to the data available for addressing the questions outlined earlier, as we detail in the following. In study 2, we tested the stimulus–response properties of F_0 on intrasexual competitiveness in humans by examining the independent contributions of F_0 and other acoustic parameters related to assessments of attractiveness and dominance. In study 3, we explored the indexical value of F_0 by testing the SL-ICHH prediction that F_0 will be more strongly linked to testosterone in individuals with low cortisol.

2. Study 1: F_0 across anthropoid primates

(a) Methods

Please refer to electronic supplementary material, Materials and methods for additional details.

We obtained the recordings of non-human primate calls from our own fieldwork and by contacting other primatologists. From these, we selected 1721 files, such that each was without substantial background noise and was produced by a single individual of known species, sex and adult status. The acoustic properties of primate calls vary across call types and contexts [13]. We chose to use measurements across all available call types (but see also electronic supplementary material, Results) rather than, for example, selecting only calls believed to be analogous across species, or only calls shared between males and females. Our reasoning was that averaging across call types should maximize our ability to capture information about the physical properties of the sound source (e.g. vocal fold length and thickness), especially if some call types may provide more information than others. If F_0 is driven by underlying anatomy—as it is fundamentally—then any influence on F_0 should be manifest similarly across call types, even if not specifically adapted to be, because the same anatomy supports the production of all calls. Although it is possible that some other special mechanism of vocal fold action is in play for some calls (e.g. loud calls compared with close calls), this is not a given and certainly cannot be assumed *a priori*. Moreover, it is unclear whether call types are truly analogous across species, which complicates comparisons of only a particular call type or set of types. In addition, the repertoire shared between males and females can be very limited in some primate species, occasionally down to one call type, as in the orang-utan. Finally, we do not know of any reason that our sampling procedures would have systematically biased our sample, and the size of our sample—the largest ever compiled for this type of research—should reduce any bias owing to random sampling.

Files were measured as uncompressed .wav or .aiff files using the acoustic analysis software PRAAT v. 5.3. F_0 was measured from each file by identifying in the raw waveform a segment in which cycles were clearly discernible. Cycles were counted along this segment up to 20 cycles, and then divided by the duration of the interval to calculate F_0 . This procedure was repeated for a second segment, if possible

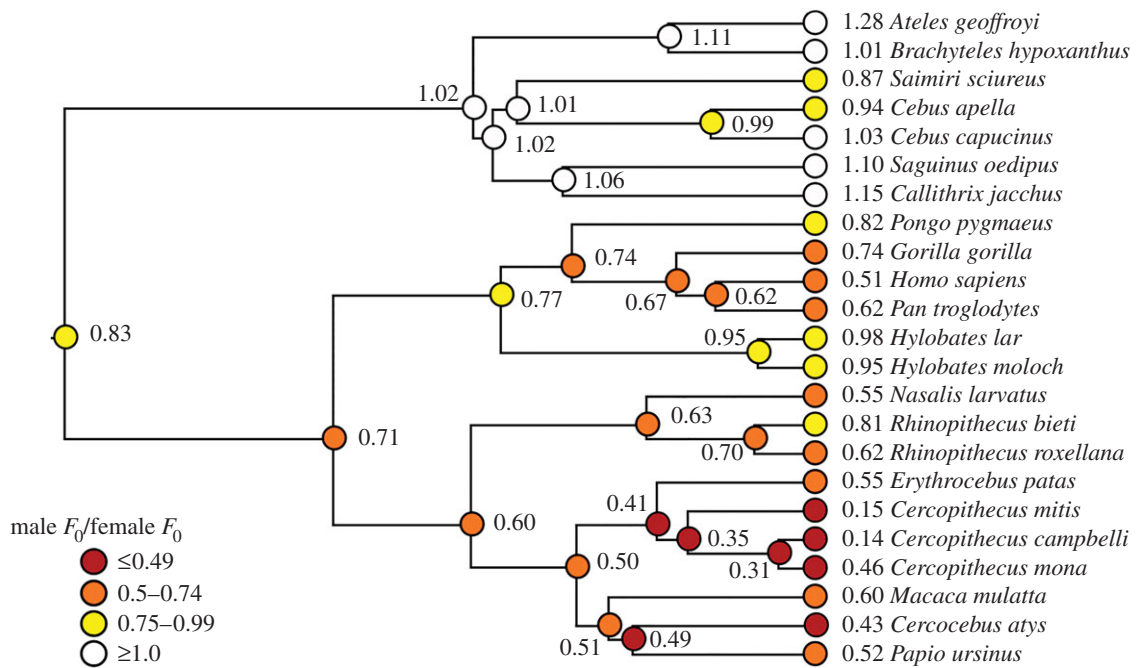


Figure 1. Phylogenetic tree of anthropoid primates included in study 1 for which data were available on at least two vocalizations from each sex (mean number of vocalizations: females = 38.6, males = 22.1; max: females = 181, males = 155; electronic supplementary material, table S1). Tree was constructed using a consensus phylogeny for all species in our sample from the 10kTrees website (<http://10ktrees.fas.harvard.edu/>). Sexual dimorphism (male/female) in F_0 is shown in the column to the left of species names. Inferred ancestral states were determined using squared change parsimony and are shown at nodes on the tree (coloured to highlight evolutionary trends). (Online version in colour.)

(78% of files, $n = 1343$). Mean F_0 values from each recording were averaged with all other mean F_0 values per sex to arrive at separate male and female F_0 averages for each species (electronic supplementary material, table S2). Between-segment reliability was high for files with two measurable segments (Cronbach's $\alpha = 0.973$). First segments of a randomly chosen 11% of files ($n = 184$) were re-measured to determine intrameasurer reliability, which was very high (Cronbach's $\alpha = 1.000$). Body size, habitat and mating system were obtained from the literature (electronic supplementary material, table S2).

Mating system was used as a proxy for the intensity of sexual selection [41,42]. We categorized mating system as monogamous, promiscuous or polygynous [43] rather than using an interval-level measure such as socioeconomic sex ratio [44], as such measures often vary widely within species and hold uncertain relationships to the intensity of intermale competition [41,44,45]. Promiscuity differs from monogamy and polygyny in that females far more frequently copulate with multiple males in promiscuous species. Although evidence suggests intermediate levels of male contest competition in promiscuous species, the ability of males to monopolize females varies widely [46]; other mechanisms of sexual selection (such as sperm competition) are more salient [47,48], and the degree of sexual dimorphism relative to monogamous or polygynous species varies widely by trait [47]. Such apparent diversity in the mechanisms and intensity of sexual selection, as well as their influence on sexual dimorphism, precludes straightforward predictions regarding F_0 dimorphism in promiscuous species. By contrast, predictions regarding monogamous and polygynous species are clearer: in polygynous species, some males are able to monopolize multiple mates, whereas in monogamous species, males do not, leaving fewer males unmated. Hence, sexual selection—particularly intrasexual selection—tends to be more intense in polygynous

than in monogamous primates, which are less dimorphic in size and weaponry [47]. Dimorphism in F_0 was therefore predicted to increase during evolutionary transitions towards polygyny and decrease during transitions towards monogamy.

Habitat was categorized as arboreal, terrestrial or arboreal/terrestrial. We conducted phylogenetically informed analyses using a consensus phylogeny for all species represented in our sample [49] (figure 1) and assessed correlated evolution among our variables with phylogenetic generalized least-squares regression using the caper package, v. 0.5.2, in R [50].

(b) Results

Across analyses, F_0 and F_0 dimorphism exhibited strong phylogenetic signals ($\lambda > 0.8$). In general, New World primates showed little sexual dimorphism in F_0 , averaging a mean F_0 dimorphism (male F_0 /female F_0) of 1.05 across seven species, whereas male cercopithecines averaged half of the F_0 of females (mean F_0 dimorphism = 0.48 across 10 species). With a similar F_0 dimorphism of 0.51, humans surprisingly exhibited the greatest dimorphism that we measured in any ape.

We tested whether increases in body size predict decreases in F_0 across species for each sex. Previous studies relied on published acoustic data measured using varying methodologies, and either averaged male and female measurements [51] or included only males [36]. In our data, body mass negatively predicted F_0 (both variables natural log-transformed) in males and females (table 1). These results suggest that body size constrains the evolution of primate call frequencies in both sexes [51].

We then regressed F_0 dimorphism on mating system, controlling for body size dimorphism (male mass/female mass). Because diversity in the mechanisms and intensity of sexual selection precludes straightforward predictions regarding F_0 dimorphism in promiscuous species (see above), we excluded promiscuous species from this analysis; however, promiscuous

Table 1. Phylogenetic generalized least-squares regression models predicting evolutionary changes in F_0 (body mass models) or F_0 dimorphism (mating system and habitat models). In both sexes, evolutionary increases in body mass predicted decreases in F_0 (body mass models). Consequently, changes in body mass dimorphism were statistically controlled in models showing that F_0 dimorphism increases during transitions from monogamy to polygyny (mating system models), and from arboreality to terrestriality (habitat model).

		<i>F</i>	d.f.	<i>R</i> ²	λ	est.	<i>t</i>	<i>p</i>
body mass	model (males)	14.01	2.27	0.32	1.00			<0.0001
	ln(mass)					-0.74	-3.74	<0.001
	model (females)	6.88	2.26	0.21	0.98			
	ln(mass)					-0.56	-2.62	0.014
mating system	model ^a	6.42	3.13	0.50	0.82			0.007
	polygyny versus monogamy					0.55	3.51	0.004
	male/female mass					0.16	2.62	0.021
	model ^b	6.31	3.13	0.49	1.00			0.007
	polygyny versus monogamy					0.58	2.89	0.013
	male/female mass					0.30	3.55	0.004
	model ^c	6.03	3.12	0.50	0.85			<0.01
	polygyny versus monogamy					0.56	3.40	0.005
habitat	model	3.33	4.19	0.34	1.00			0.032
	terrestrial versus arboreal					-0.18	-2.58	0.018
	terrestrial versus arb./terr.					-0.16	-1.37	0.188
	male/female mass					0.06	1.30	0.209

^aHumans treated as polygynous.

^bHumans treated as monogamous.

^cHumans excluded.

species appear intermediate in F_0 dimorphism (figure 2*a*). We found that greater F_0 dimorphism evolves in transitions to polygyny than in transitions to monogamy (table 1 and figure 2*c*). In this model, changes towards greater F_0 dimorphism also tended to be accompanied by decreases in body size dimorphism. Humans were treated as polygynous [52] and exhibited F_0 dimorphism that was outside the range of monogamous species (figure 2*a*); however, we obtained similar results when humans were treated as monogamous, or excluded from the analysis (table 1).

Finally, we tested the relationship between F_0 dimorphism and habitat. If male vocalizations are selected primarily to propagate over distance, or if F_0 dimorphism evolves primarily for sex discrimination, then arboreal species should tend to exhibit relatively lower male F_0 than terrestrial species. We found the reverse: arboreal primates showed less F_0 dimorphism than terrestrial primates when F_0 dimorphism was regressed on habitat and mass dimorphism (table 1).

3. Study 2: F_0 , dominance and attractiveness in humans

(a) Methods

Please refer to electronic supplementary material, Materials and methods for additional details.

Two hundred and fifty-eight female (mean age \pm s.d. = 20.0 ± 1.6 years) and 175 male (20.1 ± 1.7 years) students from Michigan State University provided written consent to

participate in this study approved by the university's institutional review board. Participants were recorded reading a standard voice passage [53] in an anechoic, soundproof booth using a Shure SM58 vocal cardioid dynamic microphone (frequency response: 50–15 000 Hz) positioned at approximately 30° and 9.5 cm from the speaker's mouth, and connected to a desktop computer via a Sound Devices USBPre 2 preamplifier. Voices were recorded in mono at a sampling rate of 44 100 Hz and 16-bit quantization, and saved as uncompressed .wav files. Recordings were rated by 558 female (19.1 ± 2.4 years) and 568 male (19.4 ± 1.8 years) students from Pennsylvania State University. Each female recording was rated by 15 men for attractiveness for short- and long-term romantic relationships using seven-point Likert scales. Each male recording was rated by 15 men for dominance (seven-point scale) and 15 women for short- and long-term attractiveness. Ratings were averaged to produce composite ratings of short- and long-term attractiveness for each recording, and dominance for each male recording.

Recordings were analysed using PRAAT v. 5.3 for mean F_0 , standard deviation in F_0 across the utterance (F_0 -SD), duration, number of voice breaks, harmonics, four measures of jitter (cycle-to-cycle variation in F_0) and five measures of shimmer (cycle-to-cycle variation in amplitude) using the 'voice report' function in PRAAT (electronic supplementary material, table S3). Pitch floors were set to 75 and 100 Hz, and pitch ceilings were 300 and 500 Hz, for men and women, respectively. Otherwise, default settings were used. We also measured the first four formant frequencies (F_1 – F_4 , electronic supplementary material, table S3). Formants were measured at each glottal pulse, averaged across measurements and

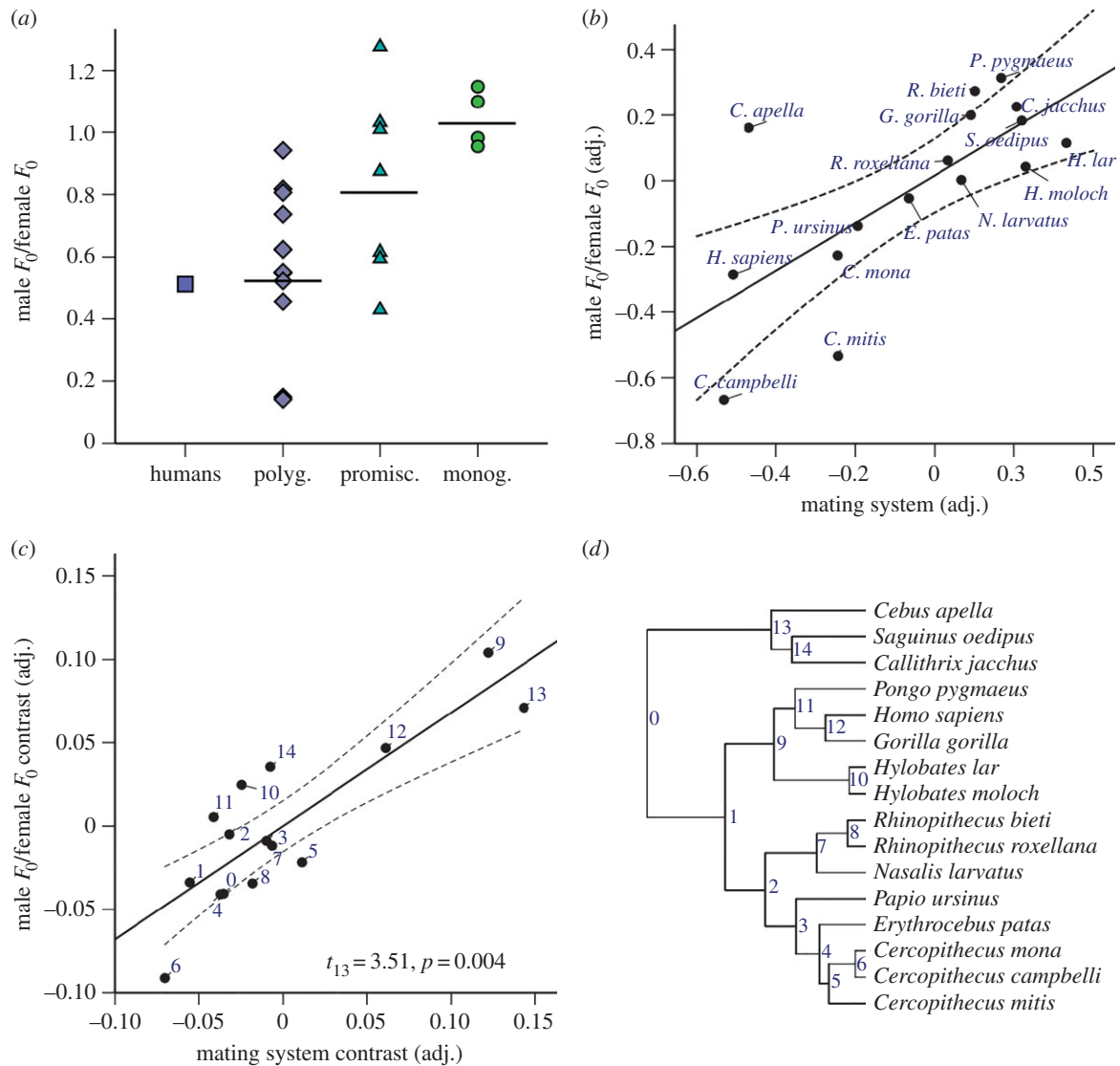


Figure 2. Sexual dimorphism in vocal F_0 as a function of mating system. In panel (a), data points represent individual species, and horizontal bars represent mean F_0 dimorphism for each mating system. Sexual dimorphism in F_0 is most extreme in polygynous anthropoid primates and lowest in monogamous species. This remains true after adjusting for body mass dimorphism (b), and after adjusting for both body mass dimorphism and phylogenetic non-independence (c). Panel (c) shows results from phylogenetic generalized least-squares regression with statistics for the effect of mating system on F_0 dimorphism. In panels (b) and (c), least-squares regression lines with 95% CI are plotted, mating system refers to polygyny (coded as -1) versus monogamy (coded as 1), and adjusted values are residuals after each variable was regressed on body mass dimorphism. The key for independent contrasts in panel (c) is shown in panel (d). (Online version in colour.)

then used to compute formant position (P_f), the average standardized formant value for the first four formants [5].

Using SPSS v. 22, we performed separate male and female principal components analyses to reduce the number of acoustic control variables (electronic supplementary material, Materials and methods and table S4), and we used multiple regression to examine the effects of acoustic parameters on perceptual variables.

(b) Results

F_0 predicted men's perceived dominance to heterosexual male listeners ($\beta = -0.43, p < 0.0001$) and attractiveness to heterosexual female listeners for both prospective short-term ($\beta = -0.36, p < 0.001$) and long-term ($\beta = -0.33, p = 0.001$) romantic relationships (electronic supplementary material, table S5). When perceived dominance and short-term attractiveness were entered into a multiple regression to predict men's F_0 (model $F_{2,171} = 12.36, p < 0.0001, R^2 = 0.13$), dominance negatively predicted F_0 ($\beta = -0.28, p = 0.002$), but short-term attractiveness did not ($\beta = -0.10, p = 0.259$),

suggesting a stronger role for male contests than female choice in shaping men's F_0 . F_0 did not predict women's attractiveness to men for either short- ($\beta = -0.03, p = 0.650$) or long-term ($\beta = -0.03, p = 0.652$) relationships when other acoustic parameters were statistically controlled (electronic supplementary material, table S5). These results are thus more consistent with sexual selection (primarily intrasexual selection) on males, rather than intersexual selection on females, influencing the evolution of human F_0 dimorphism.

4. Study 3: F_0 and hormonal profiles in humans

(a) Methods

Please refer to electronic supplementary material, Materials and methods for additional details.

Participants from Pennsylvania State University provided written consent to participate in this study approved by the university's institutional review board. Fifty-three normally cycling women (mean age \pm s.d. = 19.4 ± 1.6 years) and 62

men (19.9 ± 2.0 years) were recorded in an anechoic recording booth in a quiet room (sample 1), and 58 men (19.9 ± 1.2 years) were recorded in a quiet room (sample 2) using the equipment and methods in study 2 above.

Participants rinsed their mouths with water before providing two saliva samples of 1–2 ml each via passive drool approximately 30 (sample 1) or 20 (sample 2) min apart. From each sample, 0.5 ml of saliva was aliquotted into a third tube, which was shaken and then frozen at -20°C until analysis by the Johns Hopkins Center for Interdisciplinary Salivary Bioscience Research (Baltimore, MD) using Salimetrics kits. Samples were analysed in duplicate via enzyme immunoassay. Duplicates correlated highly for both cortisol and testosterone (all $r \geq 0.97$, $p < 0.0001$), and were consequently averaged. For cortisol assays, sensitivity is less than $0.003 \mu\text{g dl}^{-1}$, and average intra-assay coefficient of variation is 3.5%. For testosterone assays, sensitivity is less than 1.0 pg ml^{-1} , and average intra-assay coefficient of variation is 4.6%.

We used multiple regression to examine the effects of cortisol and testosterone (natural log-transformed to correct skew) on F_0 , and statistically controlled for diurnal decreases in cortisol and testosterone [54], but results were similar without controlling for these effects (electronic supplementary material, table S6, figures S1 and S2).

(b) Results

In women, F_0 was unrelated to cortisol, testosterone, and their interaction (electronic supplementary material, table S6). However, in both male samples, cortisol and testosterone interacted in predicting F_0 (sample 1: $\beta = 0.36$, $p = 0.007$; sample 2: $\beta = 0.28$, $p = 0.033$; electronic supplementary material, table S6) such that testosterone was negatively related to F_0 only in low-cortisol men (median split for cortisol; sample 1: partial $r = -0.44$, $p = 0.018$; sample 2: partial $r = -0.40$, $p = 0.034$; see also electronic supplementary material, figure S2). This pattern of relationships between hormones and a putative sexually selected trait has been found to indicate men's immune function [34], as well as attractiveness [34] and dominance [35], and is consistent with the SL-ICHH [34].

5. Discussion

Our data supported the sexual selection hypothesis: F_0 dimorphism increased with evolutionary changes towards polygyny and decreased with transitions towards monogamy across anthropoid primates. Although our primary analyses averaged across call types in order to maximize data, we also examined the patterns of F_0 dimorphism across mating systems using only those calls for which we had examples from both sexes (electronic supplementary material, Results and figure S3). Patterns were similar across analyses, indicating that the observed pattern in our primary results does not merely reflect sex differences in the use of particular call types, which may differ in F_0 . Our data also indicate that sex differences in F_0 result mainly from selection on males rather than females: we observed greater F_0 dimorphism in polygynous species, where male sexual selection is stronger, and F_0 affected components of men's but not women's mating success. These results thus provide a plausible explanation for the prior finding that F_0 predicted men's but not women's reproductive success among Hadza foragers [55]. If low F_0 augments male reproductive success by increasing

access to mates in some other anthropoids, as appears to be the case in humans, then we would expect males to evolve relatively lower F_0 when mating competition intensifies during transitions to polygyny, as we found.

By contrast, F_0 dimorphism appears unlikely to be a by-product of greater male size: with mating system controlled, F_0 dimorphism decreased with relative male size. Although F_0 dimorphism probably facilitates sex identification, if it evolves primarily for this function, then one might expect it to be greater in arboreal species, where visibility is obscured, and in monogamous species, where the sexes are otherwise less dimorphic [38], yet in both cases we found the opposite.

Previous work indicates that lower-frequency male loud calls are selected for propagation over distance [36], but our finding that male F_0 is relatively lower in terrestrial species than in arboreal species suggests that selection for long-distance male calls is not the only or primary influence on F_0 dimorphism across species' vocal repertoires. Lower frequencies should, *ceteris paribus*, aid long-distance transmission to a greater degree in arboreal habitats than in terrestrial ones for the heights at which primates normally communicate. Although we view our measure of environmental influence on acoustic transmission (arboreal versus terrestrial) as a safe parsing for such a broad sample encompassing a panoply of subtly different habitat types, it is admittedly crude, and environmental effects on acoustic transmission are complex. Other variables such as type of call, location in an arboreal environment and ambient noise are likely to play a role [37], and an exploration of these influences should be taken up more fully as more precise data accumulate. However, such possible environmental influences might be expected to weaken any relationship between F_0 dimorphism and arboreal versus terrestrial habitat rather than producing an effect that is opposite the predicted direction. Our results thus challenge the hypothesis that overall F_0 dimorphism primarily evolves when male calls are selected for long-distance transmission, and our findings are more consonant with elevated male–male competition in terrestrial compared with arboreal species [56,57].

Inspection of figure 1 indicates an increase in F_0 dimorphism from the last common ancestor of the apes to modern humans, culminating in humans exhibiting the greatest F_0 dimorphism of all apes. These results contrast sharply with moderate human body mass dimorphism and negligible canine length dimorphism, which some have suggested indicate weak sexual selection in ancestral humans [58]. However, unlike other primates, in humans, female adiposity greatly exceeds that of males, producing modest overall mass dimorphism despite the fact that males possess 60% more muscle mass, and men fight with hand-held weapons and fists rather than teeth in combat [57,59]. These unique features preclude conclusions about the strength of human sexual selection based on overall mass or canine size dimorphism [60,61]. Yet, if mating competition also tends to decrease male F_0 relative to female F_0 across primates, then F_0 dimorphism has the potential to elucidate human sexual selection in ways that comparisons of body mass or canine size cannot. Our results suggest that, despite widespread pair bonding and contrary to some claims [58,62], ancestral human mating should not be viewed as fundamentally monogamous [52].

When phylogeny and mating system were statistically controlled, evolutionary changes towards greater F_0 dimorphism were associated with changes towards less body size dimorphism and vice versa. Perhaps where mates are won mainly through direct fighting, males receive less benefit from exaggerating size

acoustically and must instead invest in mass that is useful in contests. Conversely, acoustic threats and displays may be more effective when body mass or fights are especially costly, or where female choice is more important to male fitness. In humans, male F_0 was indeed important in mate attraction, yet F_0 more strongly predicted perceptions of men's dominance, consistent with previous experimental evidence [22,39]. Masculinity in men's faces is similarly perceived as aggressive across human societies, whereas the influence on attractiveness is more variable in magnitude and direction [63]. While such male traits appear better designed to function in male contests than in female choice [57], it remains possible that female choice is relatively more important in humans compared with other polygynous primates, and that stronger female choice tends to favour lower male F_0 and more modest size dimorphism among polygynous primates. It is also possible that the unprecedented lethality imbued to human fighting with the advent of handheld and projectile weapons elevated the importance of threats and deference in relation to physical attacks [52,57]. Finally, in arboreal primates, large body mass may impose additional energetic costs, as well as increasing the risk of injury from falls. Although the relatively limited number of species in our sample prohibited exploring interactions between mating system, habitat and body mass dimorphism, we note that the single species in our sample with the greatest F_0 dimorphism, *Cercopithecus campbelli*, is polygynous, partly arboreal and exhibits body mass dimorphism comparable to that of humans. In other words, one can speculate that male *C. campbelli* achieve polygyny partly via acoustic threats and/or mate attraction, whereas body mass is constrained by partial arboreality.

In many species, males exaggerate size to intimidate conspecifics, but attention to these exaggerations is likely to be maintained by a continued association between apparent size and formidability [4]. Although F_0 decreased with increasing body size in both sexes across primate species, body size only

weakly predicts F_0 in adult humans [5,7]. However, our data show that cortisol and testosterone interact to predict men's F_0 in a pattern that has previously been found to predict men's dominance [35], attractiveness [34] and immunocompetence [34], and hence that F_0 is likely to reveal male condition to same-sex competitors and potential mates.

Our results thus not only demonstrate a likely influence of sexual selection in the origins and maintenance of sexual dimorphism in F_0 across anthropoids, but also suggest that male contests, and to a lesser degree female mate choice, favour low male F_0 as a signal of condition, shedding new light on the intensity and mechanisms of sexual selection in humans and other primates. Future research should extend these comparative investigations to vocal tract resonance frequencies, which have been implicated in mating competition and size exaggeration in several mammals [1,4,7], including humans [11,15].

Ethics. Participants provided informed written consent. The ethics committees of Michigan State University and Pennsylvania State University approved these studies, and all procedures adhered to the Declaration of Helsinki.

Data accessibility. Data available from the Dryad Digital Repository: <http://doi.org/10.5061/dryad.r0160>.

Authors' contributions. Conception and design of the experiments: D.A.P., A.K.H., R.C., R.P.B.; collection, analysis and interpretation of data: D.A.P., A.K.H., D.H.B., R.S.W., D.R., J.R.W., L.L.M.W., R.P.B., A.R.L., C.L.A., M.J.O., C.B., M.E.G., G.R-F.; drafting the article or revising it for important intellectual content: D.A.P., A.K.H. All authors approved the final version of the manuscript.

Competing interests. We declare we have no conflict of interest.

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References

- Harris TR, Fitch WT, Goldstein LM, Fashing PJ. 2006 Black and white colobus monkey (*Colobus guereza*) roars as a source of both honest and exaggerated information about body mass. *Ethology* **112**, 911–920. (doi:10.1111/j.1439-0310.2006.01247.x)
- Schön MA. 1971 The anatomy of the resonating mechanism in howling monkeys. *Folia Primatol.* **15**, 117–132. (doi:10.1159/000155371)
- Fitch WT, Giedd J. 1999 Morphology and development of the human vocal tract: a study using magnetic resonance imaging. *J. Acoust. Soc. Am.* **106**, 1511–1522. (doi:10.1121/1.427148)
- Fitch WT, Reby D. 2001 The descended larynx is not uniquely human. *Proc. R. Soc. Lond. B* **268**, 1669–1675. (doi:10.1098/rspb.2001.1704)
- Puts DA, Apicella CL, Cárdenas RA. 2012 Masculine voices signal men's threat potential in forager and industrial societies. *Proc. R. Soc. B* **279**, 601–609. (doi:10.1098/rspb.2011.0829)
- Delgado RA. 2006 Sexual selection in the loud calls of male primates: signal content and function. *Int. J. Primatol.* **27**, 5–25. (doi:10.1007/s10764-005-9001-4)
- Rendall D, Kollias S, Ney C, Lloyd P. 2005 Pitch (F_0) and formant profiles of human vowels and vowel-like baboon grunts: the role of vocalizer body size and voice-acoustic allometry. *J. Acoust. Soc. Am.* **117**, 944–955. (doi:10.1121/1.1848011)
- Fant G. 1960 *Acoustic theory of speech production*. The Hague: Mouton.
- Titze IR. 2000 *Principles of voice production*. Iowa City, IA: National Center for Voice and Speech.
- Eitan Z, Schupak A, Gotler A, Marks LE. 2014 Lower pitch is larger, yet falling pitches shrink: interaction of pitch change and size change in speeded discrimination. *Exp. Psychol.* **61**, 273–284. (doi:10.1027/1618-3169/a000246)
- Feinberg DR, Jones BC, Little AC, Burt DM, Perrett DI. 2005 Manipulations of fundamental and formant frequencies affect the attractiveness of human male voices. *Anim. Behav.* **69**, 561–568. (doi:10.1016/j.anbehav.2004.06.012)
- Darwin C. 1871 *The descent of man, and selection in relation to sex*. London, UK: Murray.
- Snowdon CT. 2004 Sexual selection and communication. In *Sexual selection in primates: new and comparative perspectives* (eds P Kappeler, CP van Schaik), pp. 57–70. Cambridge, UK: Cambridge University Press.
- Mitani JC. 1985 Sexual selection and adult male orangutan long calls. *Anim. Behav.* **33**, 272–283. (doi:10.1016/S0003-3472(85)80141-X)
- Puts DA, Hodges C, Cárdenas RA, Gaulin SJC. 2007 Men's voices as dominance signals: vocal fundamental and formant frequencies influence dominance attributions among men. *Evol. Hum. Behav.* **28**, 340–344. (doi:10.1016/j.evolhumbehav.2007.05.002)
- Puts DA, Barndt JL, Welling LLM, Dawood K, Burriss RP. 2011 Intrasexual competition among women: vocal femininity affects perceptions of attractiveness and flirtatiousness. *Pers. Individ. Diff.* **50**, 111–115. (doi:10.1016/j.paid.2010.09.011)
- Apicella CL, Feinberg DR. 2009 Voice pitch alters mate-choice-relevant perception in hunter-gatherers. *Proc. R. Soc. B* **276**, 1077–1082. (doi:10.1098/rspb.2008.1542)
- Pisanski K, Mishra S, Rendall D. 2012 The evolved psychology of voice: evaluating interrelationships in

- listeners' assessments of the size, masculinity, and attractiveness of unseen speakers. *Evol. Hum. Behav.* **33**, 509–519. (doi:10.1016/j.evolhumbehav.2012.01.004)
19. Pisanski K *et al.* 2014 Vocal indicators of body size in men and women: a meta-analysis. *Anim. Behav.* **95**, 89–99. (doi:10.1016/j.anbehav.2014.06.011)
20. Cartei V, Bond R, Reby D. 2014 What makes a voice masculine: physiological and acoustical correlates of women's ratings of men's vocal masculinity. *Horm. Behav.* **66**, 569–576. (doi:10.1016/j.yhbeh.2014.08.006)
21. Sell A, Bryant GA, Cosmides L, Tooby J, Szyner D, von Rueden C, Krauss A, Gurven M. 2010 Adaptations in humans for assessing physical strength from the voice. *Proc. R. Soc. B* **277**, 3509–3518. (doi:10.1098/rspb.2010.0769)
22. Puts DA, Gaulin SJC, Verdolini K. 2006 Dominance and the evolution of sexual dimorphism in human voice pitch. *Evol. Hum. Behav.* **27**, 283–296. (doi:10.1016/j.evolhumbehav.2005.11.003)
23. Leongómez JD, Binter J, Kubicová L, Stolařová P, Klapiřová K, Havlíček J, Roberts SC. 2014 Vocal modulation during courtship increases perceptivity even in naive listeners. *Evol. Hum. Behav.* **35**, 489–496. (doi:10.1016/j.evolhumbehav.2014.06.008)
24. Weusthoff S, Baucom BR, Hahlweg K. 2013 The siren song of vocal fundamental frequency for romantic relationships. *Front. Psychol.* **4**, 439. (doi:10.3389/fpsyg.2013.00439)
25. Roberts ML, Buchanan KL, Hasselquist D, Evans MR. 2007 Effects of testosterone and corticosterone on immunocompetence in the zebra finch. *Horm. Behav.* **51**, 126–134. (doi:10.1016/j.yhbeh.2006.09.004)
26. Bortolotti GR, Mougeot F, Martínez-Padilla J, Webster LM, Piertney SB. 2009 Physiological stress mediates the honesty of social signals. *PLoS ONE* **4**, e4983. (doi:10.1371/journal.pone.0004983)
27. Moore FR, Cornwell RE, Smith MJ, Al Dujaili EA, Sharp M, Perrett DI. 2011 Evidence for the stress-linked immunocompetence handicap hypothesis in human male faces. *Proc. R. Soc. B* **278**, 774–780. (doi:10.1098/rspb.2010.1678)
28. Sapolsky RM, Romero LM, Munck AU. 2000 How do glucocorticoids influence stress responses? Integrating permissive, suppressive, stimulatory, and preparative actions. *Endocr. Rev.* **21**, 55–89.
29. Burnstein KL, Maiorino CA, Dai JL, Cameron DJ. 1995 Androgen and glucocorticoid regulation of androgen receptor cDNA expression. *Mol. Cell. Endocrinol.* **115**, 177–186. (doi:10.1016/0303-7207(95)03688-1)
30. Chen S, Wang J, Yu G, Liu W, Pearce D. 1997 Androgen and glucocorticoid receptor heterodimer formation. A possible mechanism for mutual inhibition of transcriptional activity. *J. Biol. Chem.* **272**, 14 087–14 092. (doi:10.1074/jbc.272.22.14087)
31. Smith RG, Syms AJ, Nag A, Lerner S, Norris JS. 1985 Mechanism of the glucocorticoid regulation of growth of the androgen-sensitive prostate-derived R3327H-G8-A1 tumor cell line. *J. Biol. Chem.* **260**, 12 454–12 463.
32. Johnson EO, Kamilaris TC, Chrousos GP, Gold PW. 1992 Mechanisms of stress: a dynamic overview of hormonal and behavioral homeostasis. *Neurosci. Biobehav. Rev.* **16**, 115–130. (doi:10.1016/S0149-7634(05)80175-7)
33. Tilbrook AJ, Turner AI, Clarke IJ. 2000 Effects of stress on reproduction in non-rodent mammals: the role of glucocorticoids and sex differences. *Rev. Reprod.* **5**, 105–113. (doi:10.1530/ror.0.0050105)
34. Rantala MJ, Moore FR, Skrinda I, Krama T, Kivleniece I, Kecko S, Krams I. 2012 Evidence for the stress-linked immunocompetence handicap hypothesis in humans. *Nat. Commun.* **3**, 694–698. (doi:10.1038/ncomms1696)
35. Mehta PH, Josephs RA. 2010 Testosterone and cortisol jointly regulate dominance: evidence for a dual-hormone hypothesis. *Horm. Behav.* **58**, 898–906. (doi:10.1016/j.yhbeh.2010.08.020)
36. Mitani JC, Stuht J. 1998 The evolution of nonhuman primate loud calls: acoustic adaptation for long-distance transmission. *Primates* **39**, 171–182. (doi:10.1007/BF02557729)
37. Waser PM, Brown CH. 1986 Habitat acoustics and primate communication. *Am. J. Primatol.* **10**, 135–154. (doi:10.1002/ajp.1350100205)
38. Mitani JC, Gros-Louis J, Richards AF. 1996 Sexual dimorphism, the operational sex ratio, and the intensity of male competition in polygynous primates. *Am. Nat.* **147**, 966–980. (doi:10.1086/285888)
39. Puts DA, Jones BC, DeBruine LM. 2012 Sexual selection on human faces and voices. *J. Sex Res.* **49**, 227–243. (doi:10.1080/00224499.2012.658924)
40. Puts D, Doll L, Hill A. 2014 Sexual selection on human voices. In *Evolutionary perspectives on human sexual psychology and behavior* (eds V Weekes-Shackelford, T Shackelford), pp. 69–86. Berlin, Germany: Springer.
41. Leutenegger W, Cheverud J. 1982 Correlates of sexual dimorphism in primates: ecological and size variables. *Int. J. Primatol.* **3**, 387–402. (doi:10.1007/BF02693740)
42. Wade MJ, Shuster SM. 2004 Sexual selection: harem size and the variance in male reproductive success. *Am. Nat.* **164**, E83–E99. (doi:10.1086/424531)
43. Clutton-Brock TH. 1989 Mammalian mating systems. *Proc. R. Soc. Lond. B* **236**, 339–372. (doi:10.1098/rspb.1989.0027)
44. Clutton-Brock TH, Harvey PH, Rudder B. 1977 Sexual dimorphism, socioeconomic sex ratio and body weight in primates. *Nature* **269**, 797–800. (doi:10.1038/269797a0)
45. Clutton-Brock TH, Harvey PH. 1977 Primate ecology and social organization. *J. Zool.* **183**, 1–39. (doi:10.1111/j.1469-7998.1977.tb04171.x)
46. Emlen ST, Oring LW. 1977 Ecology, sexual selection, and the evolution of mating systems. *Science* **197**, 215–223. (doi:10.1126/science.327542)
47. Clutton-Brock TH, Harvey PH. 1984 Comparative approaches to investigating adaptation. In *Behavioral ecology: a evolutionary approach* (eds JR Krebs, NB Davies), pp. 7–29, 2nd edn. Oxford, UK: Blackwell.
48. Harcourt AH, Purvis A, Liles L. 1995 Sperm competition: mating system, not breeding season, affects testes size of primates. *Funct. Ecol.* **9**, 468–476. (doi:10.2307/2390011)
49. Arnold C, Matthews LJ, Nunn CL. 2010 The 10 k trees website: a new online resource for primate phylogeny. *Evol. Anthropol.* **19**, 114–118. (doi:10.1002/evan.20251)
50. Orme D, Freckleton R, Thomas G, Petzoldt T, Fritz S, Isaac N, Pearse W. 2013 Caper: comparative analyses of phylogenetics and evolution in R. R package version 0.5.2 ed. See <http://CRAN.R-project.org/package=caper>.
51. Hauser MD. 1993 The evolution of nonhuman primate vocalizations: effects of phylogeny, body weight and social-context. *Am. Nat.* **142**, 528–542. (doi:10.1086/285553)
52. Puts D. 2016 Human sexual selection. *Curr. Opin. Psychol.* **7**, 28–32. (doi:10.1016/j.copsyc.2015.07.011)
53. Fairbanks G. 1960 *Voice and articulation drillbook*, 2nd edn. New York, NY: Harper & Row.
54. Mrosovsky N. 2003 Beyond the suprachiasmatic nucleus. *Chronobiol. Int.* **20**, 1–8. (doi:10.1081/CBI-120017811)
55. Apicella CL, Feinberg DR, Marlowe FW. 2007 Voice pitch predicts reproductive success in male hunter-gatherers. *Biol. Lett.* **3**, 682–684. (doi:10.1098/rsbl.2007.0410)
56. Cheverud JM, Dow MM, Leutenegger W. 1985 The quantitative assessment of phylogenetic constraints in comparative analyses: sexual dimorphism in body-weight among primates. *Evolution* **39**, 1335–1351. (doi:10.2307/2408790)
57. Puts DA. 2010 Beauty and the beast: mechanisms of sexual selection in humans. *Evol. Hum. Behav.* **31**, 157–175. (doi:10.1016/j.evolhumbehav.2010.02.005)
58. Lovejoy CO. 2009 Reexamining human origins in light of *Ardipithecus ramidus*. *Science* **326**, 74e1–74e8. (doi:10.1126/science.1175834)
59. Carrier DR, Morgan MH. 2014 Protective buttressing of the hominin face. *Biol. Rev. Camb. Phil. Soc.* **90**, 330–346. (doi:10.1111/brv.12112)
60. Marlowe FW, Berbesque JC. 2012 The human operational sex ratio: effects of marriage, concealed ovulation, and menopause on mate competition. *J. Hum. Evol.* **63**, 834–842. (doi:10.1016/j.jhevol.2012.09.004)
61. Plavcan JM. 2012 Sexual size dimorphism, canine dimorphism, and male–male competition in primates: where do humans fit in? *Hum. Nat.* **23**, 45–67. (doi:10.1007/s12110-012-9130-3)
62. Stanyon R, Bigoni F. 2014 Sexual selection and the evolution of behavior, morphology, neuroanatomy and genes in humans and other primates. *Neurosci. Biobehav. Rev.* **46**, 579–590. (doi:10.1016/j.neubiorev.2014.10.001)
63. Scott IM *et al.* 2014 Human preferences for sexually dimorphic faces may be evolutionarily novel. *Proc. Natl Acad. Sci. USA* **111**, 14 388–14 393. (doi:10.1073/pnas.1409643111)