

# PROCEEDINGS B

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

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

4 Short title: Sexual selection and primate vocalization frequencies

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31 **Abstract**

32 In many primates, including humans, the vocalizations of males and females differ dramatically,  
33 with male vocalizations and vocal anatomy often seeming to exaggerate size. Males may evolve  
34 low-frequency vocalizations in order to intimidate rivals and/or attract females, but this  
35 hypothesis has not been systematically tested across primates, nor is it clear why competitors  
36 and potential mates should attend to vocalization frequencies. Here we show across  
37 anthropoids that sexual dimorphism in fundamental frequency ( $F_0$ ) increases during evolutionary  
38 transitions toward polygyny, and decreases during transitions toward monogamy. Surprisingly,  
39 humans exhibit greater  $F_0$  sexual dimorphism than any other ape. We also show that low- $F_0$   
40 vocalizations predict perceptions of men's dominance and attractiveness, and hormonal (cortisol  
41 and testosterone) profiles related to immune function. These results suggest that low male  $F_0$   
42 signals condition to competitors and mates, and evolves when male primates compete more  
43 intensely for mating opportunities.

## 44 Introduction

45 Explaining why sexual dimorphisms evolve is central to understanding the evolution of primate  
46 mating systems and social organization. In many primate species, the vocalizations of males  
47 and females differ dramatically, with male vocalizations and vocal anatomy often seeming to  
48 exaggerate size (1-7). Among humans, men's approximately 60% longer vocal folds (12-13)  
49 contribute to an average rate of vocal fold vibration during phonation (fundamental frequency,  
50  $F_0$ ) that is about five standard deviations below women's (5). To human listeners, utterances  
51 lower in  $F_0$  are perceived as being deeper in pitch and as emanating from larger individuals (14-  
52 15). The evolutionary reasons for such apparent size exaggeration have been the subject of  
53 speculation since Darwin noted the pubertal enlargement of male vocal structures and their  
54 deployment during the breeding season in many mammals (16).

55 Some have suggested that masculine vocalizations evolve to intimidate male  
56 competitors and/or attract mates (6, 17). For example, among orangutans, lower-ranking males  
57 avoid long calls given by higher-ranking males (18), indicating that acoustic cues suggest threat-  
58 potential to conspecifics. Several studies in humans suggest that  $F_0$  has relevance under both  
59 inter- and intrasexual competition: experimentally lowering  $F_0$  increases perceptions of men's  
60 dominance and attractiveness (15, 19), and raising  $F_0$  increases women's vocal attractiveness  
61 (20-21). However, little is known about whether these effects persist in unmanipulated speech  
62 when  $F_0$  and other acoustic parameters vary naturally and simultaneously.

63 Moreover, it is unclear why  $F_0$  should signal formidability to same-sex competitors or  
64 mate value to potential mates;  $F_0$  is only weakly associated with body size (5, 7, 22-23) and  
65 perhaps strength (5, 24) in humans, although  $F_0$  may be modulated according to relative  
66 formidability (25) and mate quality (26-27). Steroid hormones may provide a link between  $F_0$  and  
67 condition. Growing evidence indicates that glucocorticoids such as the stress hormone cortisol  
68 (C) negatively interact with testosterone (T) in affecting both immune function and the  
69 expression of secondary sex traits (28-30). Infection stimulates C production (31), which

70 downregulates androgen receptors and inhibits the action of T on target tissues (32-36). Hence,  
71 T should be more potent in individuals in good condition with low immune system activation. In  
72 humans, positive relationships between T and immune response to a vaccine (37), and between  
73 T and both facial attractiveness (37) and dominance (38), were stronger in males with low C.  
74 Furthermore, the interactive effect of T and C on attractiveness was mediated by immune  
75 function, supporting the stress-linked immunocompetence handicap hypothesis (SL-ICHH) that  
76 T-related traits that interact with C are linked to immunocompetence (37). At present, it is  
77 unknown whether T and C negatively interact in predicting  $F_0$ , as the SL-ICHH would suggest if  
78  $F_0$  reflects underlying condition.

79 More generally, scant evidence exists to support a role for sexual selection in shaping  $F_0$   
80 and other vocal sexual dimorphisms across primates (6), and there are plausible alternative  
81 hypotheses:  $F_0$  dimorphism may represent a byproduct of selection for greater male size or  
82 long-distance transmission of male calls (39), or reflect selection for sex identification.

83 Here, we report the results of three studies designed to clarify the evolution of sexual  
84 dimorphism in  $F_0$ . In Study 1, we examined the evolution of  $F_0$  dimorphism as a function of  
85 mating system across anthropoid primates. In Study 2, we tested the stimulus-response  
86 properties of  $F_0$  on intrasexual competitiveness in humans by examining the independent  
87 contributions of  $F_0$  controlling for other acoustic parameters to assessments of attractiveness  
88 and dominance. In Study 3, we explored the indexical value of  $F_0$  by testing the SL-ICHH  
89 prediction that  $F_0$  will be more strongly linked to T in individuals with low C.

90

## 91 **Study 1: $F_0$ across anthropoid primates**

### 92 **Methods**

93 Please refer to *SI Materials and Methods* for additional details.

94 We obtained recordings of nonhuman primate calls from our own fieldwork and by  
95 contacting other primatologists. From these, we selected 1723 files such that each was without

96 substantial background noise and was produced by a single individual of known species, sex,  
97 and adult status. Files were measured as uncompressed .WAV or .AIFF files using the acoustic  
98 analysis software Praat version 5.3.  $F_0$  was measured from each file by identifying in the raw  
99 waveform a segment in which cycles were clearly discernible. Cycles were counted along this  
100 segment up to 20 cycles, and then divided by the duration of the interval to calculate  $F_0$ . This  
101 procedure was repeated for a second segment, if possible (78% of files). Mean  $F_0$  values from  
102 each recording were averaged with all other mean  $F_0$  values per sex to arrive at separate male  
103 and female  $F_0$  averages for each species (Table S2). Between-segment reliability was high for  
104 files with two measurable segments (Cronbach's  $\alpha = 0.973$ ). First segments of a randomly  
105 chosen 11% of files were re-measured to determine intra-measurer reliability, which was very  
106 high (Cronbach's  $\alpha = 1.000$ ). Body size, habitat, and mating system were obtained from the  
107 literature (Table S2). We conducted phylogenetically-informed analyses using a consensus  
108 phylogeny for all species represented in our sample (40) and assessed correlated evolution  
109 among our variables with phylogenetic generalized least squares.

110 Mating system was utilized as a proxy for the intensity of sexual selection (41-42) and  
111 was categorized as monogamous, promiscuous, or polygynous (43) rather than using an  
112 interval-level measure such as socionomic sex ratio, as such measures often vary widely within  
113 species and hold uncertain relationships to the intensity of intermale competition (41, 44-45).  
114 Habitat was categorized as arboreal, terrestrial, or arboreal/terrestrial. We conducted  
115 phylogenetically-informed analyses using a consensus phylogeny for all species represented in  
116 our sample (40; Fig. 1) and assessed correlated evolution among our variables with  
117 phylogenetic generalized least squares (46).

118

## 119 **Results**

120 Across analyses,  $F_0$  and  $F_0$  dimorphism exhibited strong phylogenetic signals ( $\lambda > 0.8$ ). In  
121 general, New World primates showed little sexual dimorphism in  $F_0$ , averaging a mean  $F_0$

122 dimorphism of 1.05 across 7 species, while male cercopithecines averaged half of the  $F_0$  of  
123 females (mean  $F_0$  dimorphism = 0.48 across 10 species). With a similar  $F_0$  dimorphism of 0.51,  
124 humans surprisingly exhibited the greatest dimorphism that we measured in any ape.

125 We first tested whether low  $F_0$  predicts greater body size across species for each sex.  
126 Previous tests relied on published acoustic data measured using varying methodologies and  
127 either averaged male and female measurements (47) or included only males (39). In our data,  
128 body mass negatively predicted  $F_0$  (both variables natural log-transformed) in males ( $t_{27} = -3.74$ ,  
129  $p < 0.001$ ; model  $F_{2,27} = 14.01$ ,  $p < 0.0001$ ,  $R^2 = 0.34$ ) and females ( $t_{26} = -2.62$ ,  $p = 0.014$ ; model  
130  $F_{2,26} = 6.88$ ,  $p < 0.001$ ,  $R^2 = 0.18$ ; Table 1). These results suggest that body size constrains the  
131 evolution of primate call frequencies in both sexes (47).

132 We then regressed  $F_0$  dimorphism (male  $F_0$ /female  $F_0$ ) on mating system, controlling for  
133 body size dimorphism (male mass/female mass). Sexual selection tends to be more intense in  
134 polygynous than in monogamous primates, which are less dimorphic in size and weaponry (48).  
135 Although some evidence suggests intermediate levels of male contest competition in  
136 promiscuous species, the ability of males to monopolize females varies widely (49), other  
137 mechanisms of sexual selection such as sperm competition are more salient (48), and the  
138 degree of sexual dimorphism relative to monogamous or polygynous species varies widely by  
139 trait (48). Although such apparent diversity in the mechanisms and intensity of sexual selection  
140 precludes straightforward predictions regarding  $F_0$  dimorphism in promiscuous species, which  
141 were therefore excluded from this analysis, promiscuous species indeed appear intermediate in  
142  $F_0$  dimorphism (see Fig. 2a). We found that greater  $F_0$  dimorphism evolves in transitions to  
143 polygyny than in transitions to monogamy ( $t_{13} = 3.36$ ,  $p = 0.004$ ; model  $F_{3,13} = 6.42$ ,  $p = 0.007$ ,  
144  $R^2 = 0.50$ ; Table 1, Fig. 2). In this model, changes toward greater  $F_0$  dimorphism also tended to  
145 be accompanied by decreases in body size dimorphism ( $t_{13} = 2.62$ ,  $p = 0.021$ ). Humans were  
146 treated as polygynous and exhibited  $F_0$  dimorphism that was outside the range of monogamous



147 species (Fig. 2a); however, we obtained similar results when humans were treated as  
148 monogamous, or excluded from the analysis (Table 1).

149 Finally, we tested the relationship between  $F_0$  dimorphism and habitat. Waves reflected  
150 from the ground produce interference that especially attenuates low frequencies, whereas  
151 greater atmospheric absorption and scattering in arboreal vocalizations particularly attenuate  
152 high frequencies (50). Thus, if male vocalizations are selected primarily to propagate over  
153 distance, then arboreal species should exhibit relatively lower male  $F_0$  than terrestrial species.  
154 We found the reverse: arboreal primates showed less  $F_0$  dimorphism than terrestrial primates  
155 ( $F_0$  dimorphism regressed on habitat and mass dimorphism: model  $F_{4,19} = 3.33$ ,  $p = 0.032$ ,  $R^2 =$   
156  $0.34$ ; arboreal vs. terrestrial  $t_{19} = -2.58$ ,  $p = 0.018$ ; arboreal/terrestrial vs. terrestrial  $t_{19} = -1.37$ ,  $p$   
157  $= 0.118$ ; mass dimorphism  $t_{19} = 1.30$ ,  $p = 0.209$ ; Table 1).

158

## 159 **Study 2: $F_0$ , dominance, and attractiveness in humans**

### 160 **Methods**

161 Please refer to *SI Materials and Methods* for additional details.

162 Two hundred fifty-eight female ( $20.0 \pm 1.6$  y) and 175 male ( $20.1 \pm 1.7$  y) students from  
163 Michigan State University provided written consent to participate in this study approved by the  
164 university's Institutional Review Board. Participants were recorded reading a standard voice  
165 passage (51) in an anechoic, soundproof booth using a Shure SM58 vocal cardioid microphone.  
166 Voices were recorded in mono at a sampling rate of 44,100 Hz and 16-bit quantization, and  
167 saved as uncompressed .WAV files. Recordings were rated by 558 female ( $19.1 \pm 2.4$  y) and  
168 568 male ( $19.4 \pm 1.8$  y) students from The Pennsylvania State University. Each female  
169 recording was rated by 15 men for attractiveness for short- and long-term romantic relationships  
170 using 7-point Likert scales. Each male recording was rated by 15 men for dominance (7-point  
171 scale) and 15 women for short- and long-term attractiveness. Ratings were averaged to produce

172 composite ratings of short- and long-term attractiveness for each recording, and dominance for  
173 each male recording.

174 Recordings were analyzed using Praat version 5.3 for mean  $F_0$ , standard deviation in  $F_0$   
175 across the utterance ( $F_0$ -SD), duration, number of voice breaks, harmonics, four measures of  
176 jitter (cycle-to-cycle variation in  $F_0$ ), and five measures of shimmer (cycle-to-cycle variation in  
177 amplitude) using the 'voice report' function in Praat (Table S3). Pitch floors were set to 75 Hz  
178 and 100 Hz, and pitch ceilings were 300 Hz and 500 Hz, for men and women, respectively.  
179 Otherwise, default settings were used. We also measured the first four formant frequencies ( $F_1$ -  
180  $F_4$ , Table S3). Formants were measured at each glottal pulse, averaged across measurements,  
181 and then used to compute formant position ( $P_f$ ), the average standardized formant value for the  
182 first four formants (5).

183 We utilized multiple regression to examine the effects of acoustic parameters on  
184 perceptual variables.

185

## 186 **Results**

187  $F_0$  predicted men's perceived dominance to heterosexual male listeners ( $\beta = -0.43$ ,  $p < 0.0001$ )  
188 and attractiveness to heterosexual female listeners for both prospective short-term ( $\beta = -0.36$ ,  $p$   
189  $< 0.001$ ) and long-term ( $\beta = -0.32$ ,  $p = 0.001$ ) romantic relationships (Table S4). When  
190 perceived dominance and short-term attractiveness were entered into a multiple regression to  
191 predict men's  $F_0$  (model  $F_{2,171} = 12.99$ ,  $p < 0.0001$ ,  $R^2 = 0.13$ ), dominance negatively predicted  
192  $F_0$  ( $\beta = -0.30$ ,  $p = 0.001$ ), but short-term attractiveness did not ( $\beta = -0.09$ ,  $p = 0.314$ ), suggesting  
193 a stronger role for male contests than female choice in shaping men's  $F_0$ .  $F_0$  did not predict  
194 women's attractiveness to men for either short- ( $\beta = 0.03$ ,  $p = 0.695$ ) or long-term ( $\beta = -0.03$ ,  $p =$   
195  $0.722$ ) relationships when other acoustic parameters were statistically controlled (Table S4).  
196 These results are thus more consistent with sexual selection (primarily intrasexual selection) on

197 males, rather intersexual selection on females, influencing the evolution of human  $F_0$   
198 dimorphism.

199

### 200 **Study 3: $F_0$ and hormonal profiles in humans**

#### 201 **Methods**

202 Please refer to *SI Materials and Methods* for additional details.

203 Participants from The Pennsylvania State University provided written consent to  
204 participate in this study approved by the university's Institutional Review Board. Fifty-three  
205 normally-cycling women ( $19.4 \pm 1.6$  y) and 62 men ( $19.9 \pm 2.0$  y) were recorded in an anechoic  
206 recording booth in a quiet room (Sample 1), and 58 men ( $19.9 \pm 1.2$  y) were recorded in a quiet  
207 room (Sample 2), with a Shure SM58 vocal cardioid microphone.

208 Participants rinsed their mouths with water before providing two saliva samples of 1-2 ml  
209 each via passive drool approximately 30 (Sample 1) or 20 (Sample 2) min apart. From each  
210 sample, 0.5 ml of saliva was aliquotted into a third tube, which was shaken and then frozen at -  
211  $20^\circ\text{C}$  until analysis by the Johns Hopkins Center for Interdisciplinary Salivary Bioscience  
212 Research (Baltimore, MD) using Salimetrics® kits. Samples were analyzed in duplicate via  
213 enzyme immunoassay. Duplicates correlated highly for both C and T (all  $r \geq 0.97$ ,  $p < 0.0001$ ),  
214 and were consequently averaged. For cortisol assays, sensitivity is  $<0.003$   $\mu\text{g/dL}$ , and average  
215 intra-assay coefficient of variation is 3.5%. For testosterone assays, sensitivity is  $<1.0$   $\text{pg/mL}$ ,  
216 and average intra-assay coefficient of variation is 4.6%.

217 We utilized multiple regression to examine the effects of C and T on  $F_0$  and statistically  
218 controlled for diurnal decreases in C and T (52), but results were similar without controlling for  
219 these effects (Table S5, Fig. 3).

220

#### 221 **Results**

222 In women,  $F_0$  was unrelated to C, T, and their interaction (Table S5). However, in both male  
223 samples, C and T interacted in predicting  $F_0$  (Sample 1:  $\beta = 0.36$ ,  $p = 0.007$ ; Sample 2:  $\beta = 0.28$ ,  
224  $p = 0.033$ ; Table S5) such that T was negatively related to  $F_0$  only in low-C men (median split for  
225 C; Sample 1: partial  $r = -0.44$ ,  $p = 0.018$ ; Sample 2: partial  $r = -0.40$ ,  $p = 0.034$ ; Fig. S1). This  
226 pattern of relationships between hormones and a putative sexually selected trait has been found  
227 to indicate men's immune function (37), as well as attractiveness (37) and dominance (38), and  
228 is consistent with the SL-ICHH (37).

229

## 230 Discussion

231 Our data supported the sexual selection hypothesis:  $F_0$  dimorphism increased with evolutionary  
232 changes toward polygyny and decreased with transitions toward monogamy across anthropoid  
233 primates. Moreover, the pattern of  $F_0$  dimorphism across mating systems was similar whether  
234 we examined all available calls or only those calls for which we had examples from both sexes  
235 (SI Results, Fig. S2), indicating that the observed pattern does not merely reflect sex differences  
236 in the use of particular calls types, which may differ in  $F_0$ . Our data also indicate that sex  
237 differences in  $F_0$  result primarily from selection on males rather than females: We observed  
238 greater  $F_0$  dimorphism in polygynous species, where male sexual selection is stronger, and  $F_0$   
239 affected components of men's but not women's mating success. These results thus provide a  
240 plausible explanation for the prior finding that  $F_0$  predicted men's but not women's reproductive  
241 success among Hadza foragers (53).

242 By contrast,  $F_0$  dimorphism appears unlikely to be a byproduct of greater male size: With  
243 mating system controlled,  $F_0$  dimorphism decreased with relative male size. Although  $F_0$   
244 dimorphism likely facilitates sex identification, if it evolves primarily for this function, then one  
245 might expect it to be greater in arboreal species where visibility is obscured, and in  
246 monogamous species where the sexes are otherwise less dimorphic (54), yet in both cases we  
247 found the opposite. Our finding that male  $F_0$  is relatively lower in terrestrial species than in

248 arboreal species also challenges the long-distance transmission hypothesis and is more  
249 consonant with elevated male-male competition in terrestrial compared with arboreal species  
250 (55-56).

251 Inspection of Fig. 1 indicates an increase in  $F_0$  dimorphism from the last common  
252 ancestor of the apes to modern humans, culminating in humans exhibiting the greatest  $F_0$   
253 dimorphism of all apes. These results contrast sharply with moderate human body mass  
254 dimorphism and negligible canine length dimorphism, which some have suggested indicate  
255 weak sexual selection in ancestral humans (57). However, unlike other primates, in humans,  
256 female adiposity greatly exceeds that of males, and males fight with handheld weapons and  
257 fists rather than teeth in combat (56, 58). These unique features preclude conclusions about the  
258 strength of human sexual selection based on overall mass or canine size dimorphism (59-60).  
259 Yet, if mating competition also tends to decrease male  $F_0$  relative to female  $F_0$  across primates,  
260 then  $F_0$  dimorphism has the potential to elucidate human sexual selection in ways that  
261 comparisons of body mass or canine size cannot. Our results suggest that, contrary to some  
262 claims (57, 61), ancestral human mating should not be viewed as fundamentally monogamous.

263 When phylogeny and mating system were statistically controlled, evolutionary changes  
264 toward greater  $F_0$  dimorphism were associated with changes toward less body size dimorphism  
265 and vice versa. This suggests that, where costly fights cannot be avoided, males may receive  
266 less benefit from exaggerating size acoustically and instead invest in mass that is useful in  
267 contests. Conversely, where acoustic threats and displays are more effective, perhaps when  
268 female choice is more important to male fitness, there may be lower payoff to investing in mass.  
269 In humans, male  $F_0$  was indeed important in mate attraction, yet  $F_0$  more strongly predicted  
270 perceptions of men's dominance, consistent with previous experimental research (25, 62).  
271 Masculinity in men's faces is similarly perceived as aggressive across human societies,  
272 whereas the influence on attractiveness is more variable in magnitude and direction (63). While  
273 such male traits appear better designed to function in male contests than in female choice (56),

274 it remains possible that female choice is relatively more important in humans compared to other  
275 polygynous primates, and that stronger female choice tends to favor lower male  $F_0$  and more  
276 modest size dimorphism among polygynous primates.

277 In many species, males exaggerate size to intimidate conspecifics, but attention to these  
278 exaggerations is likely maintained by a continued association between apparent size and  
279 formidability (4). Although  $F_0$  decreased with increasing body size in both sexes across primate  
280 species, body size only weakly predicts  $F_0$  in adult humans (5, 7). However, our data show that  
281 C and T interact to predict men's  $F_0$  in a pattern that has previously been found to predict men's  
282 dominance (38), attractiveness (37), and immunocompetence (37), and hence that  $F_0$  is likely to  
283 reveal male condition to same-sex competitors and potential mates.

284 Our results thus not only demonstrate a likely influence of sexual selection in the origins  
285 and maintenance of sexual dimorphism in  $F_0$  across anthropoids, but also suggest that male  
286 contests, and to a lesser degree female mate choice, favor low male  $F_0$  as a signal of condition,  
287 shedding new light on the intensity and mechanisms of sexual selection in humans and other  
288 primates.

289

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295

## 296 **References**

297 1. Harris TR, Fitch WT, Goldstein LM, Fashing PJ. Black and white colobus monkey  
298 (*Colobus guereza*) roars as a source of both honest and exaggerated information about body  
299 mass. *Ethology*. 2006;**112**:911–20.

- 300 2. Schön MA. The anatomy of the resonating mechanism in howling monkeys. *Folia*  
301 *Primatologica*. 1971;**15**:117-32.
- 302 3. Fitch WT, Giedd J. Morphology and development of the human vocal tract: A study using  
303 magnetic resonance imaging. *Journal of the Acoustical Society of America*. 1999 Sep;**106**:1511-  
304 22.
- 305 4. Fitch WT, Reby D. The descended larynx is not uniquely human. *Proc Biol Sci*. 2001  
306 Aug 22;**268**:1669-75.
- 307 5. Puts DA, Apicella CL, Cárdenas RA. Masculine voices signal men's threat potential in  
308 forager and industrial societies. *Proceedings*. 2012 Feb 7;**279**:601-9.
- 309 6. Delgado RA. Sexual selection in the loud calls of male primates: Signal content and  
310 function. *International Journal of Primatology*. 2006;**27**:5-25.
- 311 7. Rendall D, Kollias S, Ney C, Lloyd P. Pitch (F0) and formant profiles of human vowels  
312 and vowel-like baboon grunts: The role of vocalizer body size and voice-acoustic allometry.  
313 *Journal of the Acoustical Society of America*. 2005 Feb;**117**:944-55.
- 314 8. Green SM. Sex differences and age gradations in vocalizations of Japanese and lion-  
315 tailed monkey. *American Zoologist*. 1981;**21**:165-84.
- 316 9. Rendall D, Owren MJ, Weerts E, Hienz RD. Sex differences in the acoustic structure of  
317 vowel-like grunt vocalizations in baboons and their perceptual discrimination by baboon  
318 listeners. *J Acoust Soc Am*. 2004 Jan;**115**:411-21.
- 319 10. Fischer J, Hammerschmidt K, Cheney DL, Seyfarth RM. Acoustic features of male  
320 baboon loud calls: influences of context, age, and individuality. *J Acoust Soc Am*. 2002  
321 Mar;**111**:1465-74.
- 322 11. Mitani JC, Gros-Louis J. Species and sex differences in the screams of chimpanzees  
323 and bonobos. *International Journal of Primatology*. 1995;**16**:393-411.
- 324 12. Fant G. *Acoustic Theory of Speech Production*. The Hague: Mouton; 1960.

- 325 13. Titze IR. Principles of Voice Production. Iowa City, Iowa: National Center for Voice and  
326 Speech; 2000.
- 327 14. Eitan Z, Schupak A, Gotler A, Marks LE. Lower pitch is larger, yet falling pitches shrink:  
328 Interaction of pitch change and size change in speeded discrimination. *Experimental*  
329 *Psychology*. 2014;**61**:273-84.
- 330 15. Feinberg DR, Jones BC, Little AC, Burt DM, Perrett DI. Manipulations of fundamental  
331 and formant frequencies affect the attractiveness of human male voices. *Animal Behaviour*.  
332 2005;**69**:561-8.
- 333 16. Darwin C. *The Descent of Man, and Selection in Relation to Sex*. London: Murray; 1871.
- 334 17. Snowdon CT. Sexual selection and communication. In: Kappeler P, van Schaik CP,  
335 editors. *Sexual Selection in Primates: New and Comparative Perspectives*. Cambridge, UK:  
336 Cambridge University Press; 2004. p. 57–70.
- 337 18. Mitani JC. Sexual selection and adult male orangutan long calls. *Animal Behavior*.  
338 1985;**33**:272–83.
- 339 19. Puts DA, Hodges C, Cárdenas RA, Gaulin SJC. Men's voices as dominance signals:  
340 vocal fundamental and formant frequencies influence dominance attributions among men.  
341 *Evolution and Human Behavior*. 2007;**28**:340-4.
- 342 20. Puts DA, Barndt JL, Welling LLM, Dawood K, Burriss RP. Intrasexual competition among  
343 women: Vocal femininity affects perceptions of attractiveness and flirtatiousness. *Personality*  
344 *and Individual Differences*. 2011;**50**:111-5.
- 345 21. Apicella CL, Feinberg DR. Voice pitch alters mate-choice-relevant perception in hunter-  
346 gatherers. *Proceedings*. 2009 Mar 22;**276**:1077-82.
- 347 22. Pisanski K, Mishra S, Rendall D. The evolved psychology of voice: evaluating  
348 interrelationships in listeners' assessments of the size, masculinity, and attractiveness of  
349 unseen speakers. *Evolution and Human Behavior*. 2012;**33**:509-19.



- 350 23. Pisanski K, Fraccaro PJ, Tigue CC, O'Connor JJM, Röder S, Andrews PW, et al. Vocal  
351 indicators of body size in men and women: a meta-analysis. *Animal Behaviour*. 2014;**95**:89-99.
- 352 24. Sell A, Bryant GA, Cosmides L, Tooby J, Sznycer D, von Rueden C, et al. Adaptations in  
353 humans for assessing physical strength from the voice. *Proceedings*. 2010 Nov 22;**277**:3509-  
354 18.
- 355 25. Puts DA, Gaulin SJC, Verdolini K. Dominance and the evolution of sexual dimorphism in  
356 human voice pitch. *Evolution and Human Behavior*. 2006;**27**:283-96.
- 357 26. Leongómez JD, Binter J, Kubicová L, Stolařová P, Klapilová K, Havlíček J, et al. Vocal  
358 modulation during courtship increases perceptivity even in naive listeners. *Evolution and Human  
359 Behavior*. [doi: 10.1016/j.evolhumbehav.2014.06.008]. 2014;**35**:489-96.
- 360 27. Weusthoff S, Baucom BR, Hahlweg K. The siren song of vocal fundamental frequency  
361 for romantic relationships. *Frontiers in Psychology*. 2013;**4**:439.
- 362 28. Roberts ML, Buchanan KL, Hasselquist D, Evans MR. Effects of testosterone and  
363 corticosterone on immunocompetence in the zebra finch. *Hormones and Behavior*.  
364 2007;**51**:126-34.
- 365 29. Bortolotti GR, Mougeot F, Martinez-Padilla J, Webster LM, Piertney SB. Physiological  
366 stress mediates the honesty of social signals. *PloS one*. 2009;**4**:e4983.
- 367 30. Moore FR, Cornwell RE, Smith MJ, Al Dujaili EA, Sharp M, Perrett DI. Evidence for the  
368 stress-linked immunocompetence handicap hypothesis in human male faces. *Proceedings*.  
369 2011 Mar 7;**278**:774-80.
- 370 31. Sapolsky RM, Romero LM, Munck AU. How Do Glucocorticoids Influence Stress  
371 Responses? Integrating Permissive, Suppressive, Stimulatory, and Preparative Actions. *Endocr  
372 Rev*. 2000;**21**:55-89.
- 373 32. Burnstein KL, Maiorino CA, Dai JL, Cameron DJ. Androgen and glucocorticoid regulation  
374 of androgen receptor cDNA expression. *Molecular and cellular endocrinology*. 1995 Dec  
375 **29**;**115**:177-86.

- 376 33. Chen S, Wang J, Yu G, Liu W, Pearce D. Androgen and glucocorticoid receptor  
377 heterodimer formation. A possible mechanism for mutual inhibition of transcriptional activity. *J*  
378 *Biol Chem.* 1997 May 30;**272**:14087-92.
- 379 34. Smith RG, Syms AJ, Nag A, Lerner S, Norris JS. Mechanism of the glucocorticoid  
380 regulation of growth of the androgen-sensitive prostate-derived R3327H-G8-A1 tumor cell line. *J*  
381 *Biol Chem.* 1985 Oct 15;**260**:12454-63.
- 382 35. Johnson EO, Kamilaris TC, Chrousos GP, Gold PW. Mechanisms of stress: a dynamic  
383 overview of hormonal and behavioral homeostasis. *Neurosci Biobehav Rev.* 1992  
384 Summer;**16**:115-30.
- 385 36. Tilbrook AJ, Turner AI, Clarke IJ. Effects of stress on reproduction in non-rodent  
386 mammals: the role of glucocorticoids and sex differences. *Rev Reprod.* 2000 May;**5**:105-13.
- 387 37. Rantala MJ, Moore FR, Skrinda I, Krama T, Kivleniece I, Kecko S, et al. Evidence for the  
388 stress-linked immunocompetence handicap hypothesis in humans. *Nature Communications.*  
389 2012;**3**:694-8.
- 390 38. Mehta PH, Josephs RA. Testosterone and cortisol jointly regulate dominance: evidence  
391 for a dual-hormone hypothesis. *Horm Behav.* 2010 Nov;**58**:898-906.
- 392 39. Mitani JC, Stuht J. The evolution of nonhuman primate loud calls: Acoustic adaptation  
393 for long-distance transmission. *Primates.* 1998;**39**:171-82.
- 394 40. Arnold C, Matthews LJ, Nunn CL. The 10k Trees Website: A New Online Resource for  
395 Primate Phylogeny. *Evolutionary Anthropology.* 2010 May-Jun;**19**:114-8.
- 396 41. Leutenegger W, Cheverud J. Correlates of sexual dimorphism in primates: ecological  
397 and size variables. *International Journal of Primatology.* 1982;**3**:387-402.
- 398 42. Wade MJ, Shuster SM. Sexual selection: Harem size and the variance in male  
399 reproductive success. *The American Naturalist.* 2004;**164**:E83-E9.
- 400 43. Clutton-Brock TH. Mammalian mating systems. *Proc R Soc Lond B Biol Sci.* 1989 May  
401 22;**236**:339-72.

- 402 44. Clutton-Brock TH, Harvey PH. Primate Ecology and Social-Organization. *J Zool.*  
403 1977;**183**:1-39.
- 404 45. Clutton-Brock TH, Harvey PH, Rudder B. Sexual dimorphism, socionomic sex ratio and  
405 body weight in primates. *Nature.* 1977 Oct 27;**269**:797-800.
- 406 46. Orme D, Freckleton R, Thomas G, Petzoldt T, Fritz S, Isaac N, et al. caper: Comparative  
407 Analyses of Phylogenetics and Evolution in R. R package version 0.5.2 ed2013.
- 408 47. Hauser MD. The evolution of nonhuman primate vocalizations: Effects of phylogeny,  
409 body weight and social-context. *American Naturalist.* 1993;**142**:528–42.
- 410 48. Clutton-Brock TH, Harvey PH. Comparative approaches to investigating adaptation. In:  
411 Krebs JR, Davies NB, editors. *Behavioral Ecology: A Evolutionary Approach.* 2nd ed. Oxford:  
412 Blackwell; 1984. p. 7-29.
- 413 49. Emlen ST, Oring LW. Ecology, sexual selection, and the evolution of mating systems.  
414 *Science.* 1977 Jul 15;**197**:215-23.
- 415 50. Wiley RH, Richards D. Adaptations for acoustic communication in birds: sound  
416 transmission and signal detection. In: Kroodsma D, Miller EH, editors. *Acoustic Communication*  
417 *in Birds.* New York: Academic Press; 1982. p. 131-81.
- 418 51. Fairbanks G. *Voice and articulation drillbook.* 2nd ed. New York: Harper & Row; 1960.
- 419 52. Mrosovsky N. Beyond the suprachiasmatic nucleus. *Chronobiol Int.* 2003 Jan;**20**:1-8.
- 420 53. Apicella CL, Feinberg DR, Marlowe FW. Voice pitch predicts reproductive success in  
421 male hunter-gatherers. *Biology Letters.* 2007 Dec 22;**3**:682-4.
- 422 54. Mitani JC, Gros-Louis J, Richards AF. Sexual dimorphism, the operational sex ratio, and  
423 the intensity of male competition in polygynous primates. *American Naturalist.* 1996;**147**:966-80.
- 424 55. Cheverud JM, Dow MM, Leutenegger W. The Quantitative Assessment of Phylogenetic  
425 Constraints in Comparative Analyses - Sexual Dimorphism in Body-Weight among Primates.  
426 *Evolution.* 1985;**39**:1335-51.

- 427 56. Puts DA. Beauty and the beast: Mechanisms of sexual selection in humans. *Evolution*  
428 and *Human Behavior*. 2010;**31**:157-75.
- 429 57. Lovejoy CO. Reexamining human origins in light of *Ardipithecus ramidus*. *Science*. 2009  
430 Oct 2;**326**:74e1-8.
- 431 58. Carrier DR, Morgan MH. Protective buttressing of the hominin face. *Biological reviews of*  
432 *the Cambridge Philosophical Society*. 2014 Jun 9.
- 433 59. Marlowe FW, Berbesque JC. The human operational sex ratio: effects of marriage,  
434 concealed ovulation, and menopause on mate competition. *Journal of human evolution*. 2012  
435 Dec;**63**:834-42.
- 436 60. Plavcan JM. Sexual size dimorphism, canine dimorphism, and male-male competition in  
437 primates: where do humans fit in? *Hum Nat*. 2012 Mar;**23**:45-67.
- 438 61. Stanyon R, Bigoni F. Sexual selection and the evolution of behavior, morphology,  
439 neuroanatomy and genes in humans and other primates. *Neurosci Biobehav Rev*. 2014;**46, Part**  
440 **4**:579-90.
- 441 62. Puts DA, Jones BC, DeBruine LM. Sexual selection on human faces and voices. *Journal*  
442 *of Sex Research*. 2012;**49**:227-43.
- 443 63. Scott IM, Clark AP, Josephson SC, Boyette AH, Cuthill IC, Fried RL, et al. Human  
444 preferences for sexually dimorphic faces may be evolutionarily novel. *Proc Natl Acad Sci U S A*.  
445 2014 Oct 7;**111**:14388-93.
- 446
- 447

448 **Figure Legends:**

449

450 Fig. 1. Phylogenetic tree of anthropoid primates included in Study 1, for which data were  
451 available on at least 2 vocalizations from each sex (mean number of vocalizations: females =  
452 38.6, males = 22.1; max: females 181, males = 155; Table S1). Sexual dimorphism  
453 (male/female) in  $F_0$  is shown in the column to the left of species names, and inferred ancestral  
454 states are shown at nodes on the tree using squared change parsimony.

455

456 Fig. 2. Sexual dimorphism in vocal  $F_0$  as a function of mating system. Sexual dimorphism in  $F_0$   
457 is most extreme in polygynous anthropoid primates and lowest in monogamous species (a).  
458 This remains true after adjusting for body mass dimorphism (b), and after adjusting for both  
459 body mass dimorphism and phylogenetic non-independence (c). Least-squares regression lines  
460 with 95% CI are plotted for species with monogamous or polygynous mating systems in (b) and  
461 (c); monogamy increases from left to right. Key for independent contrasts in (c) is shown in (d).

462

463 Fig. 3. Relationships of vocal fundamental frequency ( $F_0$ ) with cortisol (C) and testosterone (T)  
464 in men from (a) Sample 1 and (b) Sample 2. Hormone concentrations are natural log-  
465 transformed, then standardized to reduce collinearity with interaction terms. In both samples,  
466 cortisol and testosterone negatively interacted, such that testosterone was significantly  
467 negatively related to  $F_0$  only in men with low cortisol levels (see also Fig. S1, Table S6).

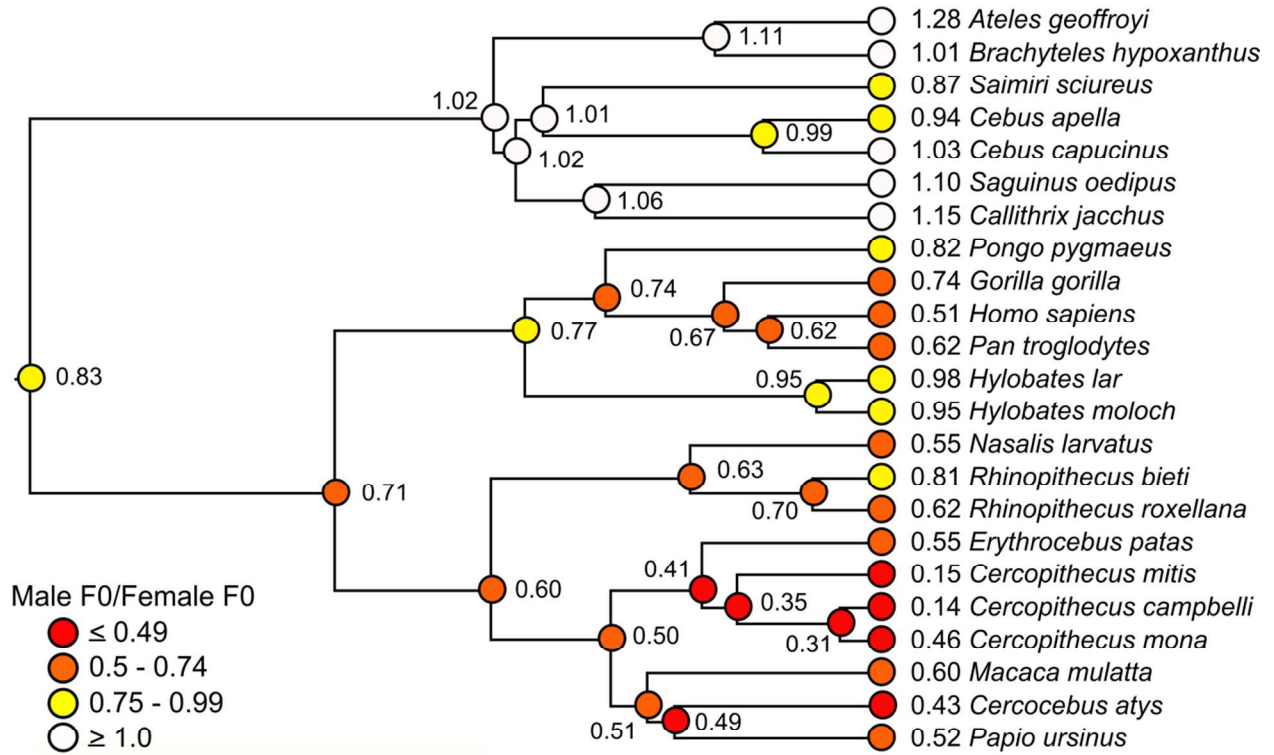


Fig. 1

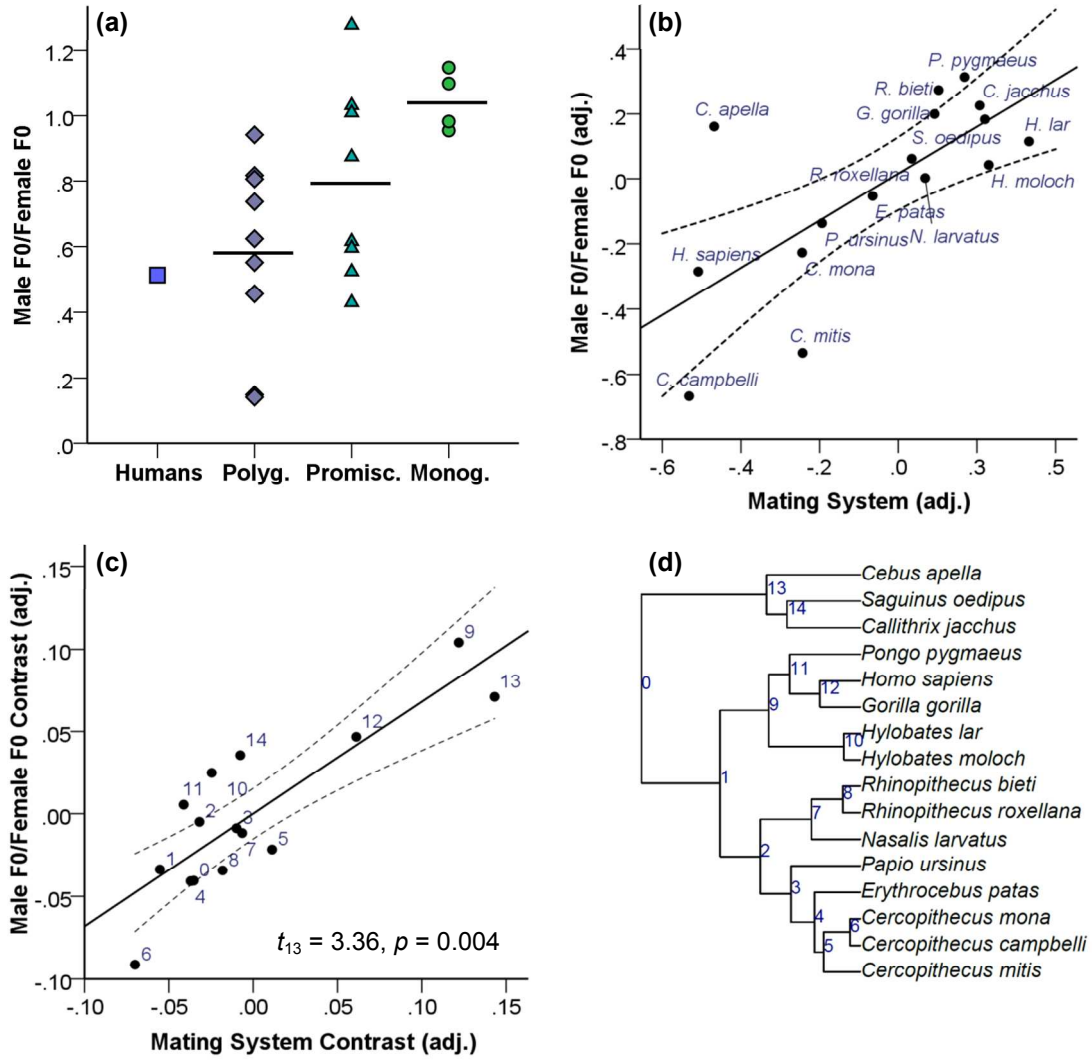


Fig. 2

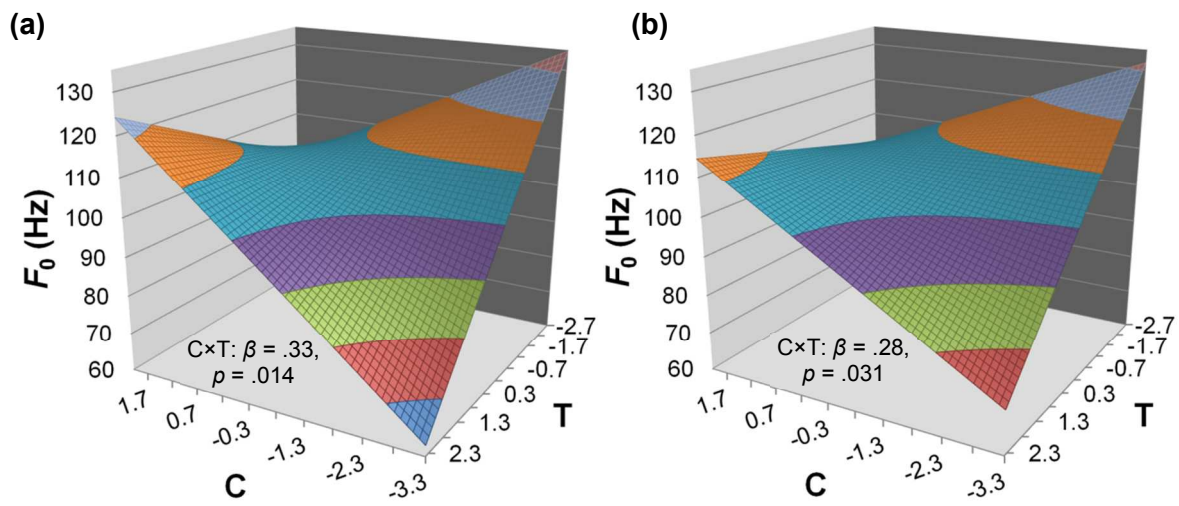


Fig. 3



1 Table 1. PGLS regression models predicting evolutionary changes in  $F_0$ 

		$F$	df	$R^2$	$\lambda$	Est.	$t$	$p$
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)					-.56	-2.62	0.014
Mating system	Model <sup>1</sup>	6.42	3,13	0.50	0.82			0.007
	Polygyny vs. monogamy					0.55	3.51	0.004
	Male/female mass					0.16	2.62	0.021
	Model <sup>2</sup>	6.31	3,13	0.49	1.00			0.007
	Polygyny vs. monogamy					0.58	2.89	0.013
	Male/female mass					0.30	3.55	0.004
	Model <sup>3</sup>	6.03	3,12	0.50	0.85			<0.01
	Polygyny vs. monogamy					0.56	3.40	0.005
	Male/female mass					0.17	2.50	0.028
Habitat	Model	3.33	4,19	0.34	1.00			0.032
	Terrestrial vs. arboreal					-0.18	-2.58	0.018
	Terrestrial vs. arb./terr.					-0.16	-1.37	0.188
	Male/female mass					0.06	1.30	0.209

2

3 1. Humans treated as polygynous. 2. Humans treated as monogamous. 3. Humans excluded.