PROCEEDINGS B

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

SCHOLARONE™
Manuscripts

1

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

Short title: Sexual selection and primate vocalization frequencies

5

6　David A. Puts[a,b,1], Alexander K. Hill[a], Drew H. Bailey[c], Robert S. Walker[d], Drew Rendall[e], John

7　R. Wheatley[a], Lisa L. M. Welling[f], Khytam Dawood[g], Rodrigo Cárdenas[g], Robert. P. Burriss[h],

8　Nina G. Jablonski[a], Mark D. Shriver[a], Daniel Weiss[g], Adriano R. Lameira[ij], Coren L. Apicella[k],

9　Michael J. Owren[l], Claudia Barelli[m], Mary E. Glenn[n], and Gabriel Ramos-Fernandez[o]

10

11　a.　Department of Anthropology, Pennsylvania State University, University Park, PA 16802

12　b.　Center for Brain, Behavior, and Cognition, Pennsylvania State University, University Park,

13　　　PA 16802

14　c.　School of Education, University of California, Irvine, CA 92697

15　d.　Department of Anthropology, University of Missouri, Columbia, MO 65211

16　e.　Department of Psychology, University of Lethbridge, Lethbridge, Alberta, Canada T1K 3M4

17　f.　Department of Psychology, Oakland University, Rochester, MI 48309

18　g.　Department of Psychology, Pennsylvania State University, University Park, PA 16802

19　h.　Department of Psychology, Northumbria University, Newcastle upon Tyne NE1 8ST, UK

20　i.　Department of Anthropology, Durham University, Durham DH1 3LE, UK

21　j.　Pongo Foundation, Papenhoeflaan 91, 3421XN Oudewater, the Netherlands.

22　k.　Department of Psychology, University of Pennsylvania, Philadelphia, PA 19104

23　l.　Language Research Center, Georgia State University, Decatur, GA 30034

24   m. Sezione di Biodiversità Tropicale, Museo delle Scienze, Trento, Italy 38122

25   n. Department of Anthropology, Humboldt State University, Arcata, CA 95521

26   o. CIIDIR Unidad Oaxaca, Instituto Politecnico Nacional, Mexico and C3-Centro de Ciencias

27   de la Complejidad, Universidad Nacional Autonoma de Mexico, Mexico 04510.

28

29   1. Corresponding author. 218 Carpenter Building, Department of Anthropology, Pennsylvania

30   State University, University Park, PA 16802. Phone: 814-867-0354. Email: dap27@psu.edu

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

4

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

5

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 α = 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 α = 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 (λ > 0.8). In

121   general, New World primates showed little sexual dimorphism in F_0, averaging a mean F_0

6

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 ± 1.6 y) and 175 male (20.1 ± 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 ± 2.4 y) and

168   568 male (19.4 ± 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 (β = -0.43, p < 0.0001)

188   and attractiveness to heterosexual female listeners for both prospective short-term (β = -0.36, p

189   < 0.001) and long-term (β = -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 (β = -0.30, p = 0.001), but short-term attractiveness did not (β = -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- (β = 0.03, p = 0.695) or long-term (β = -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 ± 1.6 y) and 62 men (19.9 ± 2.0 y) were recorded in an anechoic

206   recording booth in a quiet room (Sample 1), and 58 men (19.9 ± 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°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 μg/dL, and average

215   intra-assay coefficient of variation is 3.5%. For testosterone assays, sensitivity is <1.0 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**

10

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: β = 0.36, p = 0.007; Sample 2: β = 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

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 proceptivity 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 phylogenic 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).
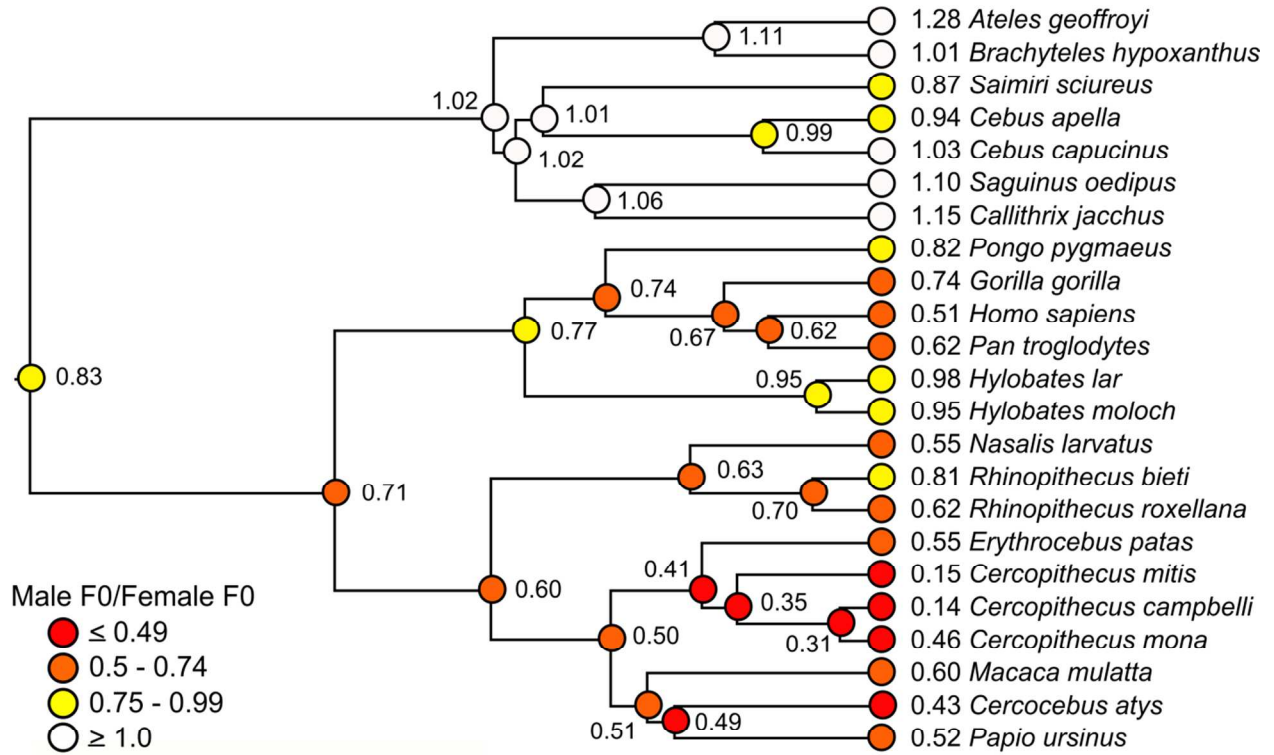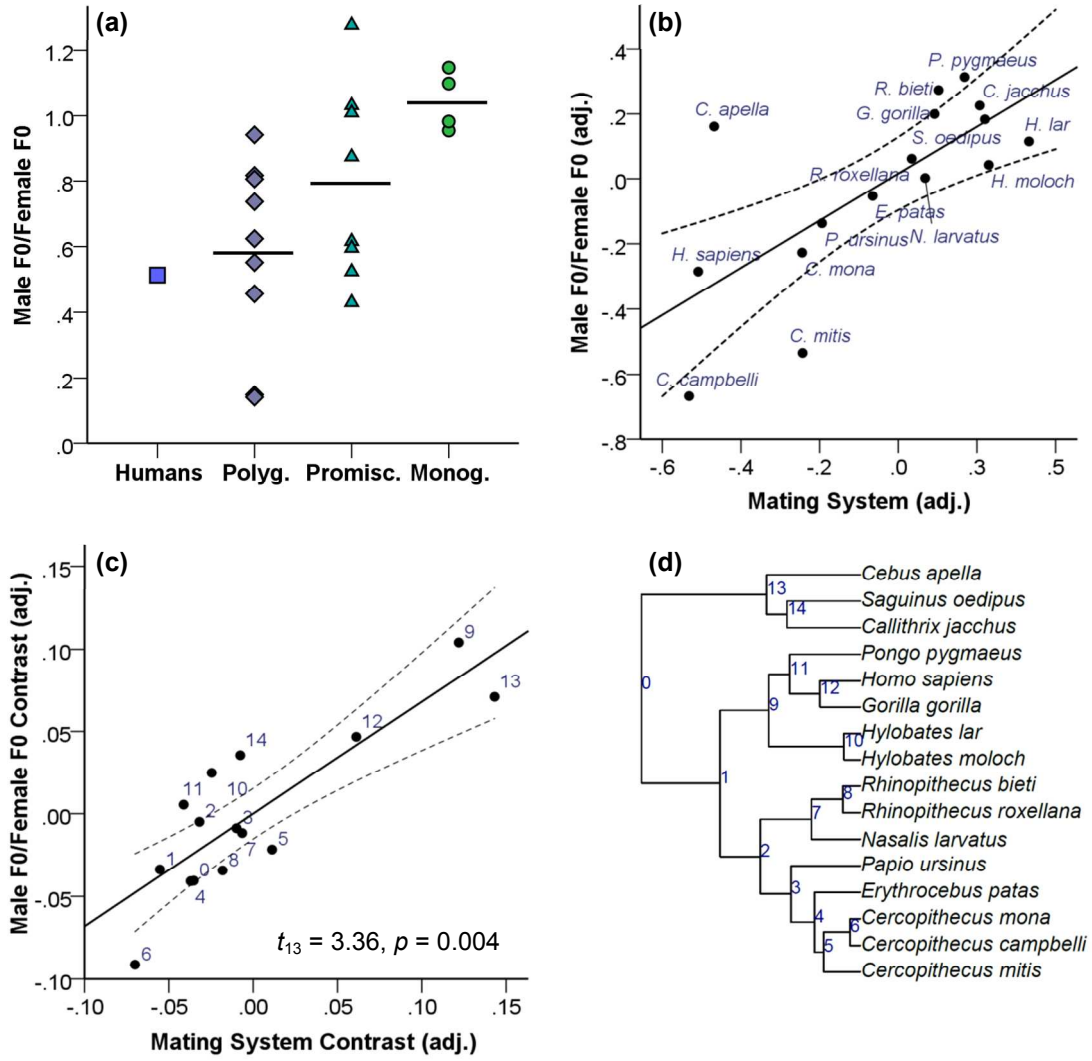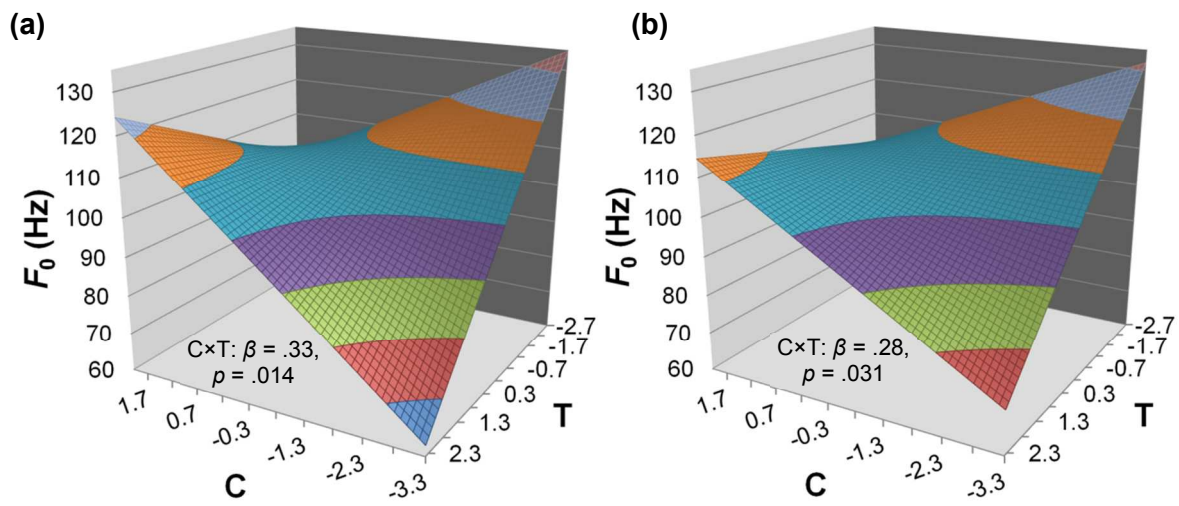
Fig. 1

Fig. 2

Fig. 3

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

		F	df	R^2	λ	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[1]	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[2]	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[3]	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.

1