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1

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

4 Short title: Sexual selection and primate vocalization frequencies

5

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32 **Abstract**

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

46 **Introduction**

47 Explaining why sexual dimorphisms evolve is central to understanding the evolution of
48 primate mating systems and social organization. In many primate species, the vocalizations of
49 males and females differ dramatically, with male vocalizations and vocal anatomy often seeming
50 to exaggerate the appearance of body size (1-7). Among humans, men's approximately 60%
51 longer vocal folds (8, 9) contribute to an average rate of vocal fold vibration during phonation
52 (fundamental frequency, F_0) that is about five standard deviations below women's (5). To human
53 listeners, utterances lower in F_0 are perceived as being deeper in pitch and as emanating from
54 larger individuals (10, 11). The evolutionary reasons for such apparent size exaggeration have
55 been the subject of speculation since Darwin noted the pubertal enlargement of male vocal
56 structures and their intensified employment during the breeding season in many mammals (12).

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

65 Moreover, it is unclear why F_0 should signal formidability to same-sex competitors or
66 mate value to potential mates; F_0 is only weakly associated with body size (5, 7, 18-20) and
67 perhaps strength (5, 21) in humans, although F_0 may be modulated according to relative
68 formidability (22) and mate quality (23, 24). Steroid hormones may provide a link between F_0
69 and condition. Growing evidence indicates that glucocorticoids such as the stress hormone
70 cortisol negatively interact with testosterone in affecting both immune function and the
71 expression of secondary sex traits (25-27). Infection stimulates cortisol production (28), which

72 downregulates androgen receptors and inhibits the action of testosterone on target tissues (29-
73 33). Hence, testosterone should be more potent in individuals in good condition with low
74 immune system activation. In humans, positive relationships between testosterone and immune
75 response to a vaccine (34), and between testosterone and both facial attractiveness (34) and
76 dominance (35), were stronger in males with low cortisol. Furthermore, the interactive effect of
77 testosterone and cortisol on attractiveness was mediated by immune function, supporting the
78 stress-linked immunocompetence handicap hypothesis (SL-ICHH) that testosterone-related
79 traits that interact with cortisol are linked to immunocompetence (34). Although previous studies
80 have found negative relationships between men's testosterone and F_0 (5, 20), it is unknown
81 whether testosterone and cortisol negatively interact in predicting F_0 , as the SL-ICHH would
82 suggest if F_0 reflects underlying condition.

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

96 Here, we report the results of three studies designed to clarify the evolution of sexual
97 dimorphism in F_0 . In Study 1, we examined the evolution of F_0 dimorphism as a function of

98 mating system, as well as body mass dimorphism and habitat, across anthropoid primates.
99 Studies 2 and 3 focused on humans. Not only are humans of special interest, but they are also
100 highly useful as a model organism: There is strong evidence implicating sexual selection in the
101 evolution of human F_0 (39, 40), as well as a unique richness to the data available for addressing
102 the questions outlined above, as we detail below. In Study 2, we tested the stimulus-response
103 properties of F_0 on intrasexual competitiveness in humans by examining the independent
104 contributions of F_0 and other acoustic parameters related to assessments of attractiveness and
105 dominance. In Study 3, we explored the indexical value of F_0 by testing the SL-ICHH prediction
106 that F_0 will be more strongly linked to testosterone in individuals with low cortisol.

107

108 **Study 1: F_0 across anthropoid primates**

109 **Methods**

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

111 We obtained recordings of nonhuman primate calls from our own fieldwork and by
112 contacting other primatologists. From these, we selected 1721 files, such that each was without
113 substantial background noise and was produced by a single individual of known species, sex,
114 and adult status. The acoustic properties of primate calls vary across call types and contexts
115 (13). We chose to utilize measurements across all available call types (but see also
116 Supplementary Results) rather than, for example, selecting only calls believed to be analogous
117 across species, or only calls shared between males and females. Our reasoning was that
118 averaging across call types should maximize our ability to capture information about the
119 physical properties of the sound source (e.g., vocal fold length and thickness), especially if
120 some call types may provide more information than others. If F_0 is driven by underlying
121 anatomy—as it is fundamentally—then any influence on F_0 should be manifest similarly across
122 call types, even if not specifically adapted to be, because the same anatomy supports the
123 production of all calls. Although it is possible that some other special mechanism of vocal fold

124 action is in play for some calls (e.g., loud calls compared to close calls), this is not a given and
125 certainly cannot be assumed a priori. Moreover, it is unclear whether call types are truly
126 analogous across species, which complicates comparisons of only a particular call type or set of
127 types. In addition, the repertoire shared between males and females can be very limited in some
128 primate species, occasionally down to one call type, as in the orangutan. Finally, we do not
129 know of any reason that our sampling procedures would have systematically biased our sample,
130 and the size of our sample—the largest ever compiled for this type of research—should reduce
131 any bias due to random sampling.

132 Files were measured as uncompressed .WAV or .AIFF files using the acoustic analysis
133 software Praat version 5.3. F_0 was measured from each file by identifying in the raw waveform a
134 segment in which cycles were clearly discernible. Cycles were counted along this segment up to
135 20 cycles, and then divided by the duration of the interval to calculate F_0 . This procedure was
136 repeated for a second segment, if possible (78% of files, $n = 1343$). Mean F_0 values from each
137 recording were averaged with all other mean F_0 values per sex to arrive at separate male and
138 female F_0 averages for each species (Table S2). Between-segment reliability was high for files
139 with two measurable segments (Cronbach's $\alpha = 0.973$). First segments of a randomly chosen
140 11% of files ($n = 184$) were re-measured to determine intra-measurer reliability, which was very
141 high (Cronbach's $\alpha = 1.000$). Body size, habitat, and mating system were obtained from the
142 literature (Table S2).

143 Mating system was utilized as a proxy for the intensity of sexual selection (41, 42). We
144 categorized mating system as monogamous, promiscuous, or polygynous (43) rather than using
145 an interval-level measure such as socionomic sex ratio, as such measures often vary widely
146 within species and hold uncertain relationships to the intensity of intermale competition (41, 44,
147 45). Promiscuity differs from monogamy and polygyny in that females far more frequently
148 copulate with multiple males in promiscuous species. Although evidence suggests intermediate
149 levels of male contest competition in promiscuous species, the ability of males to monopolize

150 females varies widely (46), other mechanisms of sexual selection such as sperm competition
151 are more salient (47, 48), and the degree of sexual dimorphism relative to monogamous or
152 polygynous species varies widely by trait (47). Such apparent diversity in the mechanisms and
153 intensity of sexual selection, as well as their influence on sexual dimorphism, precludes
154 straightforward predictions regarding F_0 dimorphism in promiscuous species. By contrast,
155 predictions regarding monogamous and polygynous species are clearer: In polygynous species,
156 some males are able to monopolize multiple mates, whereas in monogamous species, males do
157 not, leaving fewer males unmated. Hence, sexual selection—particularly, intrasexual selection—
158 tends to be more intense in polygynous than in monogamous primates, which are less
159 dimorphic in size and weaponry (47). Dimorphism in F_0 was therefore predicted to increase
160 during evolutionary transitions toward polygyny and decrease during transitions toward
161 monogamy.

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

166

167 **Results**

168 Across analyses, F_0 and F_0 dimorphism exhibited strong phylogenetic signals ($\lambda > 0.8$).
169 In general, New World primates showed little sexual dimorphism in F_0 , averaging a mean F_0
170 dimorphism (male F_0 /female F_0) of 1.05 across 7 species, while male cercopithecines averaged
171 half of the F_0 of females (mean F_0 dimorphism = 0.48 across 10 species). With a similar F_0
172 dimorphism of 0.51, humans surprisingly exhibited the greatest dimorphism that we measured in
173 any ape.

174 We tested whether increases in body size predict decreases in F_0 across species for
175 each sex. Previous studies relied on published acoustic data measured using varying

176 methodologies and either averaged male and female measurements (51) or included only males
177 (36). In our data, body mass negatively predicted F_0 (both variables natural log-transformed) in
178 males and females (Table 1). These results suggest that body size constrains the evolution of
179 primate call frequencies in both sexes (51).

180 We then regressed F_0 dimorphism on mating system, controlling for body size
181 dimorphism (male mass/female mass). Because diversity in the mechanisms and intensity of
182 sexual selection precludes straightforward predictions regarding F_0 dimorphism in promiscuous
183 species (see above), we excluded promiscuous species from this analysis; however,
184 promiscuous species appear intermediate in F_0 dimorphism (Fig. 2a). We found that greater F_0
185 dimorphism evolves in transitions to polygyny than in transitions to monogamy (Table 1, Fig.
186 2c). In this model, changes toward greater F_0 dimorphism also tended to be accompanied by
187 decreases in body size dimorphism. Humans were treated as polygynous (52) and exhibited F_0
188 dimorphism that was outside the range of monogamous species (Fig. 2a); however, we
189 obtained similar results when humans were treated as monogamous, or excluded from the
190 analysis (Table 1).

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

197

198 **Study 2: F_0 , dominance, and attractiveness in humans**

199 **Methods**

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

201 Two hundred fifty-eight female (mean age \pm s.d. = 20.0 \pm 1.6 y) and 175 male (20.1 \pm
202 1.7 y) students from Michigan State University provided written consent to participate in this
203 study approved by the university's Institutional Review Board. Participants were recorded
204 reading a standard voice passage (53) in an anechoic, soundproof booth using a Shure SM58
205 vocal cardioid dynamic microphone (frequency response: 50-15,000 Hz) positioned at
206 approximately 30 degrees and 9.5 cm from the speaker's mouth, and connected to a desktop
207 computer via a Sound Devices USBPre 2 preamplifier. Voices were recorded in mono at a
208 sampling rate of 44,100 Hz and 16-bit quantization, and saved as uncompressed .WAV files.
209 Recordings were rated by 558 female (19.1 \pm 2.4 y) and 568 male (19.4 \pm 1.8 y) students from
210 The Pennsylvania State University. Each female recording was rated by 15 men for
211 attractiveness for short- and long-term romantic relationships using 7-point Likert scales. Each
212 male recording was rated by 15 men for dominance (7-point scale) and 15 women for short- and
213 long-term attractiveness. Ratings were averaged to produce composite ratings of short- and
214 long-term attractiveness for each recording, and dominance for each male recording.

215 Recordings were analyzed using Praat version 5.3 for mean F_0 , standard deviation in F_0
216 across the utterance (F_0 -SD), duration, number of voice breaks, harmonics, four measures of
217 jitter (cycle-to-cycle variation in F_0), and five measures of shimmer (cycle-to-cycle variation in
218 amplitude) using the "voice report" function in Praat (Table S3). Pitch floors were set to 75 Hz
219 and 100 Hz, and pitch ceilings were 300 Hz and 500 Hz, for men and women, respectively.
220 Otherwise, default settings were used. We also measured the first four formant frequencies (F_1 -
221 F_4 , Table S3). Formants were measured at each glottal pulse, averaged across measurements,
222 and then used to compute formant position (P_f), the average standardized formant value for the
223 first four formants (5).

224 Using SPSS v.22, we performed a separate male and female principal components
225 analyses to reduce the number of acoustic control variables (SI Materials and Methods, Table

226 S4), and we utilized multiple regression to examine the effects of acoustic parameters on
227 perceptual variables.

228

229 **Results**

230 F_0 predicted men's perceived dominance to heterosexual male listeners ($\beta = -0.43, p <$
231 0.0001) and attractiveness to heterosexual female listeners for both prospective short-term ($\beta =$
232 $-0.36, p < 0.001$) and long-term ($\beta = -0.32, p = 0.001$) romantic relationships (Table S5). When
233 perceived dominance and short-term attractiveness were entered into a multiple regression to
234 predict men's F_0 (model $F_{2,171} = 12.99, p < 0.0001, R^2 = 0.13$), dominance negatively predicted
235 F_0 ($\beta = -0.30, p = 0.001$), but short-term attractiveness did not ($\beta = -0.09, p = 0.314$), suggesting
236 a stronger role for male contests than female choice in shaping men's F_0 . F_0 did not predict
237 women's attractiveness to men for either short- ($\beta = 0.03, p = 0.695$) or long-term ($\beta = -0.03, p =$
238 0.722) relationships when other acoustic parameters were statistically controlled (Table S5).
239 These results are thus more consistent with sexual selection (primarily intrasexual selection) on
240 males, rather than intersexual selection on females, influencing the evolution of human F_0
241 dimorphism.

242

243 **Study 3: F_0 and hormonal profiles in humans**

244 **Methods**

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

246 Participants from The Pennsylvania State University provided written consent to
247 participate in this study approved by the university's Institutional Review Board. Fifty-three
248 normally-cycling women (mean age \pm s.d. = 19.4 ± 1.6 y) and 62 men (19.9 ± 2.0 y) were
249 recorded in an anechoic recording booth in a quiet room (Sample 1), and 58 men (19.9 ± 1.2 y)
250 were recorded in a quiet room (Sample 2) using the equipment and methods in Study 2 above.

251 Participants rinsed their mouths with water before providing two saliva samples of 1-2 ml
252 each via passive drool approximately 30 (Sample 1) or 20 (Sample 2) min apart. From each
253 sample, 0.5 ml of saliva was aliquotted into a third tube, which was shaken and then frozen at -
254 20°C until analysis by the Johns Hopkins Center for Interdisciplinary Salivary Bioscience
255 Research (Baltimore, MD) using Salimetrics® kits. Samples were analyzed in duplicate via
256 enzyme immunoassay. Duplicates correlated highly for both cortisol and testosterone (all $r \geq$
257 0.97, $p < 0.0001$), and were consequently averaged. For cortisol assays, sensitivity is <0.003
258 $\mu\text{g/dL}$, and average intra-assay coefficient of variation is 3.5%. For testosterone assays,
259 sensitivity is <1.0 pg/mL, and average intra-assay coefficient of variation is 4.6%.

260 Hormone data were natural log-transformed to correct skew prior to analysis. We utilized
261 multiple regression to examine the effects of cortisol and testosterone on F_0 and statistically
262 controlled for diurnal decreases in cortisol and testosterone (54), but results were similar without
263 controlling for these effects (Table S6, Figs. S1, S2).

264

265 Results

266 In women, F_0 was unrelated to cortisol, testosterone, and their interaction (Table S6).
267 However, in both male samples, cortisol and testosterone interacted in predicting F_0 (Sample 1:
268 $\beta = 0.36$, $p = 0.007$; Sample 2: $\beta = 0.28$, $p = 0.033$; Table S6) such that testosterone was
269 negatively related to F_0 only in low-cortisol men (median split for cortisol; Sample 1: partial $r = -$
270 0.44, $p = 0.018$; Sample 2: partial $r = -0.40$, $p = 0.034$; see also Fig. S2). This pattern of
271 relationships between hormones and a putative sexually selected trait has been found to
272 indicate men's immune function (34), as well as attractiveness (34) and dominance (35), and is
273 consistent with the SL-ICHH (34).

274

275 Discussion

276 Our data supported the sexual selection hypothesis: F_0 dimorphism increased with
277 evolutionary changes toward polygyny and decreased with transitions toward monogamy across
278 anthropoid primates. Although our primary analyses averaged across call types in order to
279 maximize data, we also examined patterns of F_0 dimorphism across mating systems using only
280 those calls for which we had examples from both sexes (SI Results, Fig. S3). Patterns were
281 similar across analyses, indicating that the observed pattern in our primary results does not
282 merely reflect sex differences in the use of particular call types, which may differ in F_0 . Our data
283 also indicate that sex differences in F_0 result mainly from selection on males rather than
284 females: We observed greater F_0 dimorphism in polygynous species, where male sexual
285 selection is stronger, and F_0 affected components of men's but not women's mating success.
286 These results thus provide a plausible explanation for the prior finding that F_0 predicted men's
287 but not women's reproductive success among Hadza foragers (55). If low F_0 augments male
288 reproductive success by increasing access to mates in some other anthropoids, as appears to
289 be the case in humans, then we would expect males to evolve relatively lower F_0 when mating
290 competition intensifies during transitions to polygyny, as we found.

291 By contrast, F_0 dimorphism appears unlikely to be a byproduct of greater male size: With
292 mating system controlled, F_0 dimorphism decreased with relative male size. Although F_0
293 dimorphism likely facilitates sex identification, if it evolves primarily for this function, then one
294 might expect it to be greater in arboreal species where visibility is obscured, and in
295 monogamous species where the sexes are otherwise less dimorphic (38), yet in both cases we
296 found the opposite.

297 Previous work indicates that lower frequency male loud calls are selected for
298 propagation over distance (36), but our finding that male F_0 is relatively lower in terrestrial
299 species than in arboreal species suggests that selection for long-distance male calls is not the
300 only or primary influence on F_0 dimorphism across species' vocal repertoires. Lower frequencies
301 should, *ceteris paribus*, aid long-distance transmission to a greater degree in arboreal habitats

302 than in terrestrial ones for the heights at which primates normally communicate. Although we
303 view our measure of environmental influence on acoustic transmission (arboreal vs. terrestrial)
304 as a safe parsing for such a broad sample encompassing a panoply of subtly different habitat
305 types, it is admittedly crude, and environmental effects on acoustic transmission are complex.
306 Other variables such as type of call, location in an arboreal environment, and ambient noise are
307 likely to play a role (37), and an exploration of these influences should be taken up more fully as
308 more precise data accumulate. However, such possible environmental influences might be
309 expected to weaken any relationship between F_0 dimorphism and arboreal vs. terrestrial habitat
310 rather than producing an effect that is opposite the predicted direction. Our results thus
311 challenge the hypothesis that overall F_0 dimorphism primarily evolves when male calls are
312 selected for long-distance transmission, and our findings are more consonant with elevated
313 male-male competition in terrestrial compared with arboreal species (56, 57).

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

328 When phylogeny and mating system were statistically controlled, evolutionary changes
329 toward greater F_0 dimorphism were associated with changes toward less body size dimorphism
330 and vice versa. Perhaps where mates are won mainly through direct fighting, males receive less
331 benefit from exaggerating size acoustically and must instead invest in mass that is useful in
332 contests. Conversely, acoustic threats and displays may be more effective when body mass or
333 fights are especially costly, or where female choice is more important to male fitness. In
334 humans, male F_0 was indeed important in mate attraction, yet F_0 more strongly predicted
335 perceptions of men's dominance, consistent with previous experimental evidence (22, 39).
336 Masculinity in men's faces is similarly perceived as aggressive across human societies,
337 whereas the influence on attractiveness is more variable in magnitude and direction (63). While
338 such male traits appear better designed to function in male contests than in female choice (57),
339 it remains possible that female choice is relatively more important in humans compared to other
340 polygynous primates, and that stronger female choice tends to favor lower male F_0 and more
341 modest size dimorphism among polygynous primates. It is also possible that the unprecedented
342 lethality imbued to human fighting with the advent of handheld and projectile weapons elevated
343 the importance of threats and deference in relation to physical attacks (52, 57). Finally, in
344 arboreal primates, large body mass may impose additional energetic costs, as well as
345 increasing the risk of injury from falls. Although the relatively limited number of species in our
346 sample prohibited exploring interactions between mating system, habitat, and body mass
347 dimorphism, we note that the single species in our sample with the greatest F_0 dimorphism,
348 *Cercopithecus campbelli*, is polygynous, partly arboreal, and exhibits body mass dimorphism
349 comparable to that of humans. In other words, one can speculate that male *C. campbelli*
350 achieve polygyny partly via acoustic threats and/or mate attraction while body mass is
351 constrained by partial arboreality.

352 In many species, males exaggerate size to intimidate conspecifics, but attention to these
353 exaggerations is likely maintained by a continued association between apparent size and

354 formidability (4). Although F_0 decreased with increasing body size in both sexes across primate
355 species, body size only weakly predicts F_0 in adult humans (5, 7). However, our data show that
356 cortisol and testosterone interact to predict men's F_0 in a pattern that has previously been found
357 to predict men's dominance (35), attractiveness (34), and immunocompetence (34), and hence
358 that F_0 is likely to reveal male condition to same-sex competitors and potential mates.

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

366

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

370

371 **Data accessibility.** Data deposited in Dryad Digital Repository:

372 <http://datadryad.org/submit?journalID=RSPB&manu=RSPB-2015-2830>

373

374 **Authors' contributions.** Conception and design of the experiments: DAP, AKH, RAC, RPB;
375 collection, analysis, and interpretation of data: DAP, AKH, DHB, RSW, DR, JRW, LLMW, RPB,
376 ARL, CLA, MJO, CB, MEG, GR-F; drafting the article or revising it for important intellectual
377 content: DAP, AKH. All authors approved the final version of the manuscript.

378

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380

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532

533 **Figure Legends:**

534

535 Fig. 1. Phylogenetic tree of anthropoid primates included in Study 1 for which data were
536 available on at least 2 vocalizations from each sex (mean number of vocalizations: females =
537 38.6, males = 22.1; max: females 181, males = 155; Table S1). Tree was constructed using a
538 consensus phylogeny for all species in our sample from the 10kTrees website
539 (<http://10ktrees.fas.harvard.edu/>). Sexual dimorphism (male/female) in F_0 is shown in the
540 column to the left of species names. Inferred ancestral states were determined using squared
541 change parsimony and are shown at nodes on the tree (colored to highlight evolutionary trends).

542

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

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