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

Short title: Sexual selection and primate vocalization frequencies

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Abstract

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

Introduction

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

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

Moreover, it is unclear why F_0 should signal formidability to same-sex competitors or mate value to potential mates; F_0 is only weakly associated with body size (5, 7, 22-23) and perhaps strength (5, 24) in humans, although F_0 may be modulated according to relative formidability (25) and mate quality (26-27). Steroid hormones may provide a link between F_0 and condition. Growing evidence indicates that glucocorticoids such as the stress hormone cortisol (C) negatively interact with testosterone (T) in affecting both immune function and the expression of secondary sex traits (28-30). Infection stimulates C production (31), which downregulates androgen receptors and inhibits the action of T on target tissues (32-36). Hence, T should be more potent in individuals in good condition with low immune system activation. In humans, positive relationships between T and immune response to a vaccine (37), and between T and both facial attractiveness (37) and dominance (38), were stronger in males with low C. Furthermore, the interactive effect of T and C on attractiveness was mediated by immune function, supporting the stress-linked immunocompetence handicap hypothesis (SL-ICHH) that T-related traits that interact with C are linked to immunocompetence (37). At present, it is unknown whether T and C negatively interact in predicting F_0, as the SL-ICHH would suggest if F_0 reflects underlying condition.

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

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

Study 1: F_0 across anthropoid primates

Methods

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

We obtained recordings of nonhuman primate calls from our own fieldwork and by contacting other primatologists. From these, we selected 1723 files such that each was without substantial background noise and was produced by a single individual of known species, sex, and adult status. Files were measured as uncompressed .WAV or .AIFF files using the acoustic analysis software Praat version 5.3. F_0 was measured from each file by identifying in the raw waveform a segment in which cycles were clearly discernible. Cycles were counted along this segment up to 20 cycles, and then divided by the duration of the interval to calculate F_0. This procedure was repeated for a second segment, if possible (78% of files). Mean F_0 values from each recording were averaged with all other mean F_0 values per sex to arrive at separate male and female F_0 averages for each species (Table S2). Between-segment reliability was high for files with two measurable segments (Cronbach's $\alpha = 0.973$). First segments of a randomly chosen 11% of files were re-measured to determine intra-measurer reliability, which was very high (Cronbach's $\alpha = 1.000$). Body size, habitat, and mating system were obtained from the literature (Table S2). We conducted phylogenetically-informed analyses using a consensus phylogeny for all species represented in our sample (40) and assessed correlated evolution among our variables with phylogenetic generalized least squares.

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

Results

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

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

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

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

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

Study 2: F_0, dominance, and attractiveness in humans

Methods

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

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

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

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

Results

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

Study 3: F_0 and hormonal profiles in humans

Methods

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

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

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

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

Results

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

Discussion

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

By contrast, F_0 dimorphism appears unlikely to be a byproduct of greater male size: With mating system controlled, F_0 dimorphism decreased with relative male size. Although F_0 dimorphism likely facilitates sex identification, if it evolves primarily for this function, then one might expect it to be greater in arboreal species where visibility is obscured, and in monogamous species where the sexes are otherwise less dimorphic (54), yet in both cases we found the opposite. Our finding that male F_0 is relatively lower in terrestrial species than in arboreal species also challenges the long-distance transmission hypothesis and is more consonant with elevated male-male competition in terrestrial compared with arboreal species (55-56).

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

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

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

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

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Figure Legends:

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

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

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

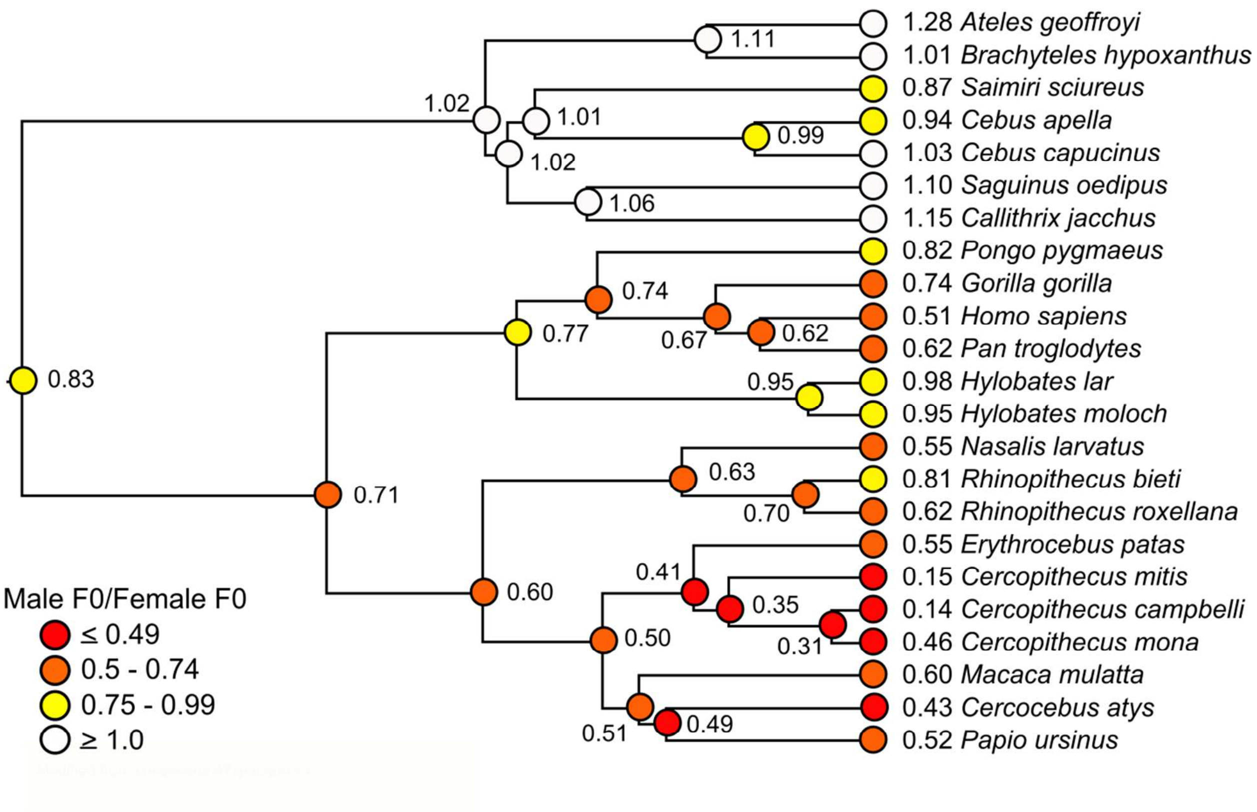
1.28 Ateles geoffroyi
1.01 Brachyteles hypoxanthus
0.87 Saimiri sciureus
0.94 Cebus apella
1.03 Cebus capucinus
1.10 Saguinus oedipus
1.15 Callithrix jacchus
0.82 Pongo pygmaeus
0.74 Gorilla gorilla
0.51 Homo sapiens
0.62 Pan troglodytes
0.98 Hylobates lar
0.95 Hylobates moloch
0.55 Nasalis larvatus
0.81 Rhinopithecus bieti
0.62 Rhinopithecus roxellana
0.55 Erythrocebus patas
0.15 Cercopithecus mitis
0.14 Cercopithecus campbelli
0.46 Cercopithecus mona
0.60 Macaca mulatta
0.43 Cercocebus atys
0.52 Papio ursinus
1.11
1.02
1.01
0.99
1.02
1.06
0.74
0.77
0.67
0.62
0.95
0.83
0.71
0.63
0.70
0.41
0.35
0.31
0.60
0.50
0.51
0.49
Male F0/Female F0
≤ 0.49
0.5 - 0.74
0.75 - 0.99
≥ 1.0

Fig. 1

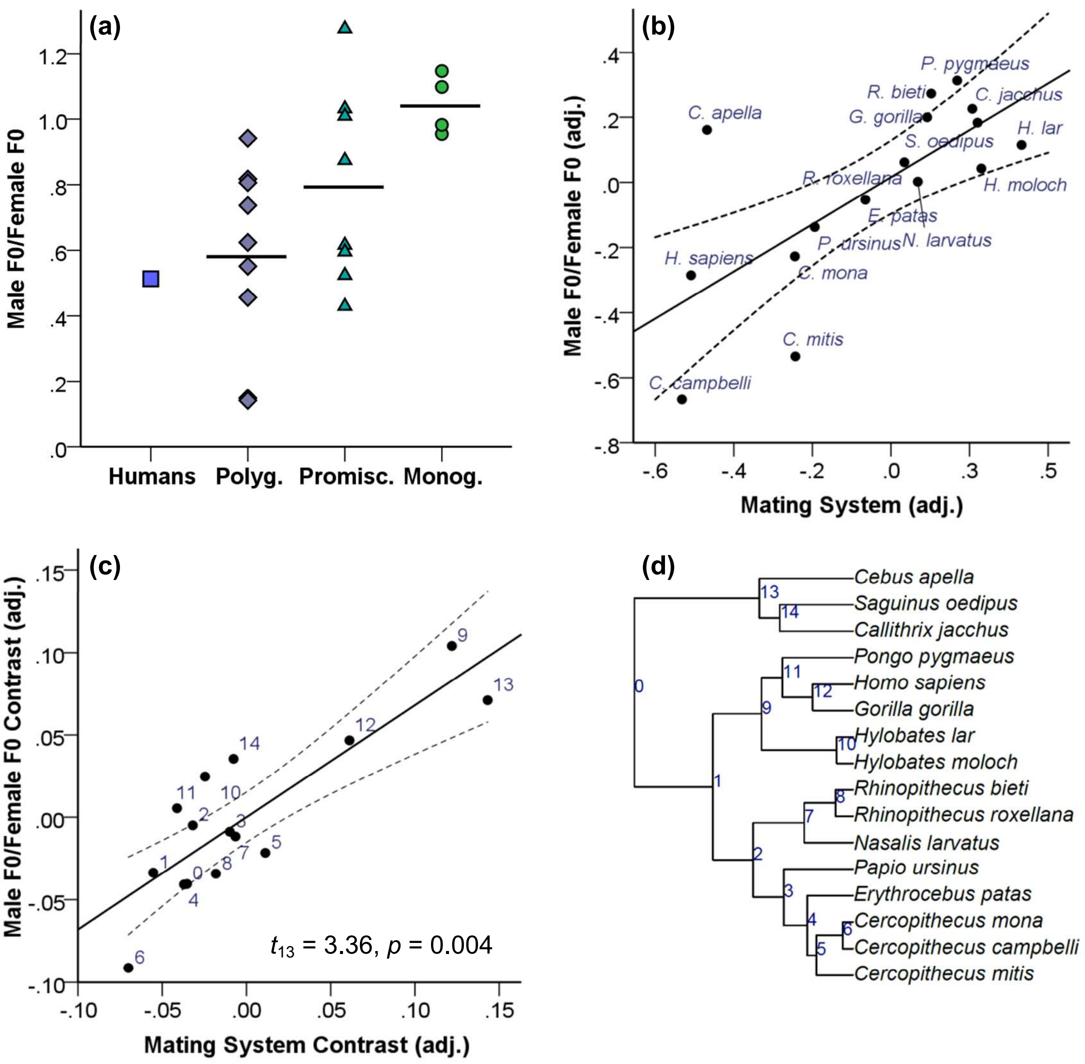
(a)
Male F0/Female F0
1.2
1.0
.8
.6
.4
.2
.0
Humans
Polyg.
Promisc.
Monog.
(b)
Male F0/Female F0 (adj.)
.4
.2
.0
-.2
-.4
-.6
-.8
-.6
-.4
-.2
.0
.3
.5
Mating System (adj.)
P. pygmaeus
R. bieti
C. jacchus
C. apella
G. gorilla
H. lar
S. oedipus
R. roxellana
H. moloch
E. patas
P. ursinus
N. larvatus
H. sapiens
C. mona
C. mitis
C. campbelli
(c)
Male F0/Female F0 Contrast (adj.)
.15
.10
.05
.00
-.05
-.10
-.10
-.05
.00
.05
.10
.15
Mating System Contrast (adj.)
t_{13} = 3.36, p = 0.004
(d)
Cebus apella
Saguinus oedipus
Callithrix jacchus
Pongo pygmaeus
Homo sapiens
Gorilla gorilla
Hylobates lar
Hylobates moloch
Rhinopithecus bieti
Rhinopithecus roxellana
Nasalis larvatus
Papio ursinus
Erythrocebus patas
Cercopithecus mona
Cercopithecus campbelli
Cercopithecus mitis

Fig. 2

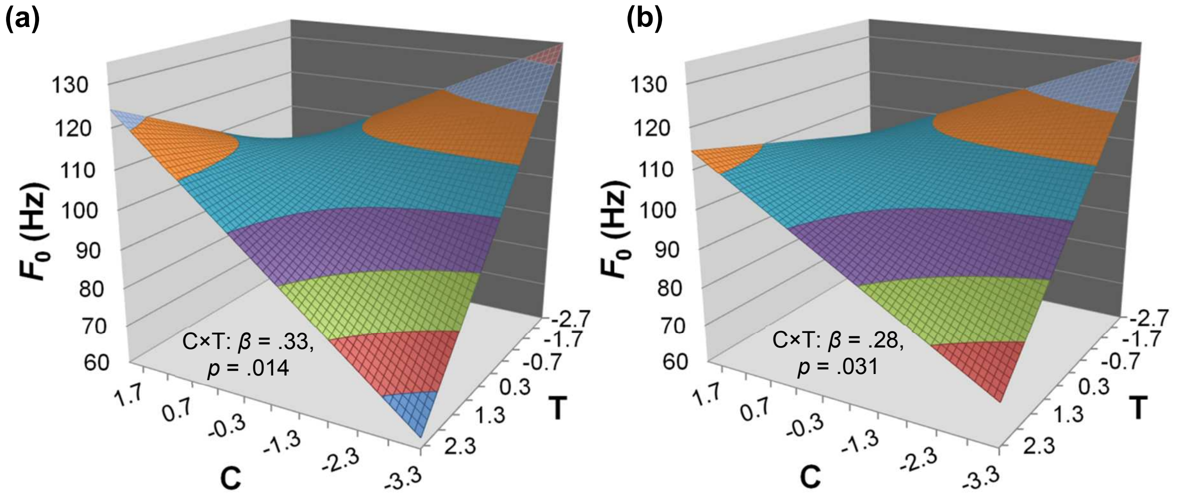
(a)
130
120
110
100
90
80
70
60
F_0 (Hz)
C×T: β = .33,
p = .014
1.7
0.7
-0.3
-1.3
-2.3
-3.3
C
-2.7
-1.7
-0.7
0.3
1.3
2.3
T
(b)
130
120
110
100
90
80
70
60
F_0 (Hz)
C×T: β = .28,
p = .031
1.7
0.7
-0.3
-1.3
-2.3
-3.3
C
-2.7
-1.7
-0.7
0.3
1.3
2.3
T

Fig. 3

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

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