Linking human male vocal parameters to perceptions, body morphology, strength and hormonal profiles in contexts of sexual selection

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Sexual selection appears to have shaped the acoustic signals of diverse species, including humans. Deep, resonant vocalizations in particular may function in attracting mates and/or intimidating same-sex competitors. Evidence for these adaptive functions in human males derives predominantly from perception studies in which vocal acoustic parameters were manipulated using specialist software. This approach affords tight experimental control but provides little ecological validity, especially when the target acoustic parameters vary naturally with other parameters. Furthermore, such experimental studies provide no information about what acoustic variables indicate about the speaker—that is, why attention to vocal cues may be favored in intrasexual and intersexual contexts. Using voice recordings with high ecological validity from 160 male speakers and biomarkers of condition, including baseline cortisol and testosterone levels, body morphology and strength, we tested a series of preregistered hypotheses relating to both perceptions and underlying condition of the speaker. We found negative curvilinear and negative linear relationships between male fundamental frequency ($f_o$) and female perceptions of attractiveness and male perceptions of dominance. In addition, cortisol and testosterone negatively interacted in predicting $f_o$, and strength and measures of body size negatively predicted formant frequencies ($F_p$). Meta-analyses of the present results and those from two previous samples confirmed that $f_o$ negatively predicted testosterone only among men with lower cortisol levels. This research offers empirical evidence of possible evolutionary functions for attention to men’s vocal characteristics in contexts of sexual selection.

Acoustic signals comprise a fundamental component of mating competition1–4 and are highly sexually dimorphic in many species, including many anthropoid primates. Humans in particular exhibit strong sexual dimorphism in acoustic signals5, such that the distributions of male and female vocal parameters related to pitch and timbre barely overlap6.

From hearing the voice alone, humans can assess diverse salient social characteristics of a speaker, such biological sex, age and physical strength7–9. Many of these evaluations rely on inter-individual variation in specific sets of vocal parameters, including fundamental frequency and formant frequencies5,10. Fundamental frequency ($f_o$) is the rate of vocal fold vibration during phonation and influences perceptions of pitch. Formant frequencies are resonant frequencies determined by the length and shape of the vocal tract and influence perceptions of vocal timbre.

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Fundamental and formant frequencies are some of the most sexually dimorphic characteristics in humans, suggesting a past influence of sexual selection. Indeed, lower male \( f_0 \) predicts greater perceptions of attractiveness, dominance and masculinity, as well as greater mating success (but see for a null finding) and reproductive success (see also ). Likewise, male formant frequencies influence perceptions of attractiveness, dominance and masculinity.

Despite the abundance of evidence linking acoustic parameters to perceptions relevant in mating competition, a fundamental question remains: Why have humans evolved to attend to these parameters? Costly signaling theory (originally proposed by , but see ) which concerns the transmission of reliable information between signalers and receivers, is a useful theoretical tool to answer this question and helps us understand the maintenance of signal honesty via receiver-independent (production costs, developmental costs, maintenance costs) and receiver-dependent costs (e.g., retaliation costs, vulnerability costs; see for reviews). Recently, some authors have pointed out weak receiver-independent costs associated with men's \( f_0 \) and concluded that men's \( f_0 \) does not signal formidability. Others suggest that men's \( f_0 \) is likely to be partly honest.

Although \( f_0 \) influences perceptions of physical dominance, it correlates only weakly with physical strength (see ) (see for a meta-analysis) and body height. Past research also points to associations with hormonal profiles in males; \( f_0 \) decreases strongly during, and higher circulating testosterone levels predict lower \( f_0 \) in men (see ). Another study that utilized salivary immunoglobulin-A (sIgA; a marker of mucosal immunity) as a measure of immunocompetence reported that sIgA was negatively correlated with \( f_0 \). In a similar vein, listeners assigned higher dominance ratings, but not higher health ratings, to speakers with higher self-reported health. Overall, these studies suggest, that \( f_0 \) may be a partly honest signal of condition. Formants are closely tied to vocal tract length and are therefore indirect, albeit weak, correlates of body size in humans. Additionally, a recent study showed significant correlations with other somatometric measures, such as body mass index and hip circumference. However, links between formants and physical strength are equivocal.

In addition to the paucity of evidence concerning the information content of male voices, there are also significant gaps in knowledge concerning how men's voices may influence social perceptions. For example, because most prior studies manipulated only one acoustic parameter at a time in experimental settings, the relative importance of different parameters in forming social judgments have not been well characterized. Prior research also has primarily investigated linear relationships (Table 1), and thus it remains largely unknown whether acoustic parameters have curvilinear effects on perceptions, which have been predicted in some cases. Vocal stimuli in most prior work are also unnaturally invariant in content and motivation, with all speakers uttering a series of vowels, counting, or speaking precisely the same, often socially irrelevant, phrase; hence, the generalizability and external validity of such results depend on whether the effects they reveal persist in natural speech. Finally, only a few, mostly low-powered studies (Table 1) have simultaneously shown that these acoustic parameters are related to both perceptions of attractiveness and/or dominance on the one hand and indirect measures of mate quality and formidability on the other.

Given the fundamental gaps in knowledge outlined above, we conducted a preregistered study (preregistration: https://osf.io/nrmpf/) to examine (1) how vocal parameters are utilized in assessing dominance, and (2) why using those parameters for judgments could be adaptive insofar as they are associated with indirect measures of mate quality and/or formidability. In contrast to most studies on perceived vocal attractiveness and dominance, which have used standardized voice samples (i.e. counting, vowels or standardized passages), more natural stimuli were used to augment external validity. Importantly, we use a relatively large (N = 160) and rich dataset, which allows relationships between vocal parameters, baseline cortisol and testosterone levels, body morphology and strength to be tested in a single sample.

Perceptions of attractiveness and dominance. Because deep male voices may display social power, threat potential, and predict greater anticipated and actual sexual infidelity, there may be costs as well as benefits to mating with males with masculine voices. Further, some studies suggest that the link between mean \( f_0 \) and attractiveness is weaker and rather curvilinear: Very low-pitched voices are not seen as more attractive and sometimes even less attractive as low-pitched voices. In line with the context-dependent nature of costs and benefits and reports from previous literature, we therefore predicted negative linear and negative quadratic relationships between attractiveness ratings and both mean \( f_0 \) (H1) and formant position (\( P_f \)) (H2). \( P_f \) is a measure of formant structure, calculated as the average standardized formant value for the first n (usually four) formants).

Masculine voices (i.e. low \( f_0 \) and \( P_f \)) have been found to be preferred by females to a greater extent in short-term compared to long-term relationship contexts. This might reflect an adaptive trade-off strategy in which a mate's genetic fitness, putatively indicated by masculine traits, is granted greater value in short-term contexts, whereas his expected investment and fidelity are valued more in long-term contexts. Consequently, we predicted stronger relationships between short-term, compared to long-term, attractiveness ratings and both mean \( f_0 \) (H3) and \( P_f \) (H4).

It has been hypothesized that deep voices display threat potential; hence, we predicted negative relationships between dominance ratings and both mean \( f_0 \) (H5) and \( P_f \) (H6). According to the source-filter theory, \( f_0 \) and \( P_f \) are theoretically distinct. They are also only weakly correlated and seem to convey different information about a male speaker. Accordingly, we predicted \( f_0 \) and \( P_f \) to be independent predictors of both attractiveness (H7) and dominance (H8) ratings.
| No | Studies                          | Rater (n) | Vocalizers (n) | Perceptions evaluated | Vocalizer's condition | Natural voices | Cuvilinear tested |
|----|---------------------------------|-----------|----------------|------------------------|------------------------|----------------|------------------|
| 1  | Schild et al.                  | 95        | 181            | Trus                   | True                   | +              | +                |
| 2  | Collins and Missing            | 30        | 30             | Att, Age               | Size                   | +              | +                |
| 3  | Puts et al.                    | 1126      | 548            | Att, Dom               | T; C                   |                | +                |
| 4  | Raine et al.                   | 150       | 61             | Size                   | True                   | +              | +                |
| 5  | Raine et al.                   | 135       | 61             | Size                   | True                   | +              | +                |
| 6  | Rentall et al.                 | 163       | 68             | Size                   | True                   | +              | +                |
| 7  | Rosenfield et al.              | 84        | 4              | Att, Pres, Dom         | MS                     | +              | +                |
| 8  | Sebesta et al.                 | 62        | 93             | Att                    | Size                   | +              | +                |
| 9  | Sebesta et al.                 | 63        | 40             | Dom                    | Size                   | +              | +                |
| 10 | Simmons et al.                 | 30        | 44             | Att, Mas               | Sperm                  | +              | +                |
| 11 | Valenrova et al.               | 203       | 152            | Att                    | Size                   | +              | +                |
| 12 | Armstrong et al.               | 224       | 183            | Dom, Size              | True                   | +              | +                |
| 13 | Feinberg et al.                | 991       | 123            | Age, Att, Fem          | +                      | +              | +                |
| 14 | Babel et al.                   | 30        | 60             | Att                    | +                      | +              | +                |
| 15 | Gregory et al.                 | 118       | 60             | Com Qual               | +                      | +              | +                |
| 16 | Hodges-Simeon et al.           | 350       | 111            | Att, Dom               | +                      | +              | +                |
| 17 | Knowles et al.                 | 180       | 32             | Cop                    | +                      | +              | +                |
| 18 | Mischlshy and Schormann        | 20        | 20             | Att, Like              | +                      | +              | +                |
| 19 | Piotanko and Rentall           | 129       | 89             | Size, Att, Mas, Fem    | +                      | +              | +                |
| 20 | Piotanko et al.                | 48        | 20             | Size, Att, Mas, Fem    | +                      | +              | +                |
| 21 | Sokolowski et al.              | 39        | 51             | Com, Auth              | +                      | +              | +                |
| 22 | Valenrova et al.               | 84        | 30             | Att, Mas               | +                      | +              | +                |
| 23 | Hill et al.                    | 1349      | 471            | Att, Fac, Sym          | +                      | +              | +                |
| 24 | Wolff and Puts                 | 376       | 117            | Dom                    | Size, T, Agg           | +              | +                |
| 25 | Shank et al.                   | 328       | 6              | Att                    | E, P                   |                | +                |
| 26 | Re et al.                      | 39        | 64             | Att, Mas, Fem          | +                      | +              | +                |
| 27 | Saxton et al.                  | 40        | 6              | Att, Dom               | +                      | +              | +                |
| 28 | Apicella and Feinberg          | 88        | 10             | Att                    | +                      | +              | +                |
| 29 | Borkowska and Pawleskowska     | 473       | 58             | Att, Dom               | +                      | +              | +                |
| 30 | Borkert et al.                 | 64        | 55             | Att                    | +                      | +              | +                |
| 31 | Feinberg et al.                | 68        | 5              | Att, Dom               | +                      | +              | +                |
| 32 | Feinberg et al.                | 26        | 8              | Att, Dom               | +                      | +              | +                |
| 33 | Feinberg et al.                | 1759      | 6              | Pref                   | +                      | +              | +                |
| 34 | Feinberg et al.                | 85        | 6              | Att                    | +                      | +              | +                |
| 35 | Tracaron et al.                | 179       | 8              | Att, Dom               | +                      | +              | +                |
| 36 | Hughes et al.                  | 40        | 40             | Att                    | +                      | +              | +                |
| 37 | Jones et al.                   | 800       | 12             | Att, Dom               | +                      | +              | +                |
| 38 | Klotstad et al.                | 382       | 27             | Com, Size, Trus        | +                      | +              | +                |
| 39 | Leaderbrand et al.             | 48        | 4              | Att                    | +                      | +              | +                |
| 40 | O'Connor et al.                | 138       | 6              | Att, Inv               | +                      | +              | +                |
| 41 | Puts et al.                    | 86        | 111            | Dom                    | +                      | +              | +                |
| 42 | Puts et al.                    | 42        | 30             | Dom                    | +                      | +              | +                |
| 43 | Puts et al.                    | 109       | 4              | Att, Flir              | +                      | +              | +                |
| 44 | Puts et al.                    | 142       | 111            | Att                    | +                      | +              | +                |
| 45 | Riding et al.                  | 54        | 9              | Att                    | +                      | +              | +                |
| 46 | Suire et al.                   | 225       | 58             | Att                    | +                      | +              | +                |
| 47 | Tigue et al.                   | 165       | 15             | Int, Prow, Vote        | +                      | +              | +                |
| 48 | Vukovic et al.                 | 70        | 6              | Att, Dom, Trus         | +                      | +              | +                |
| 49 | Widian et al.                  | 50        | 10             | Dom                    | +                      | +              | +                |
| 50 | Xu et al.                      | 42        | 2              | Att, Emo               | +                      | +              | +                |

Table 1. A non-exhaustive list of studies (n = 50) on human voice perception. A list of 50 studies that relate to mating-relevant perceptions of human voice was obtained via Google Scholar search. Most studies that investigate human voice perceptions tested only on perceptions (n = 35), used manipulated voice stimuli (n = 28), and tested linear relationships (n = 44). Agg = Aggressiveness; Att = Attractiveness; C = Cortisol; Com = Competent; Com Qual = Communication Quality; Cop = Cooperativeness; Dom = Dominance; Emo = Emotions; E = Estradiol; Fac Sym = Facial Symmetry; Flir = Flirtatiousness; Fem = Femininity; Int = Integrity; Inv = Investing; Mas = Masculinity; MS = Mating Success; P = Progesterone; Pref = Preference; Pres = Prestige; Prow = Prowess; T = Testosterone; Trus = Trustworthiness; + = Presence.
Indirect measures of mate quality and formidability. Previous studies linked lower $f_o$ to higher circulating testosterone levels, and more recently this relationship was found to be stronger in men with lower cortisol levels, a result seemingly consistent with the stress-linked immunocompetence handicap hypothesis that $f_o$ honestly signals a speaker’s physical condition. We therefore predicted a negative relationship between mean $f_o$ and testosterone (H9) and predicted that this relationship would be attenuated by high baseline cortisol (H10).

Formants have been shown to relate moderately to body height, a phenotype that is relevant in both intra- and intersexual selective contexts. We therefore predicted a negative relationship between $P_f$ and body height (H11).

Exploratory analyses. In addition to these preregistered predictions, we conducted the following exploratory analyses. First, we examined how vocal parameters related to physical strength and body morphology. Second, we compared whether distinct parameters are used as cues for ratings on social dominance (i.e. being respected) and physical dominance (i.e. fighting ability), as they describe separate aspects of social evaluation.

Third, we explored whether jitter and shimmer influence attractiveness and dominance perceptions, as these acoustic parameters seem to provide information on male body shape. Jitter and shimmer quantify cycle-to-cycle variation in $f_o$ and amplitude, respectively, and influence perceptions of voice roughness. Fourth, we conducted three mediation analyses: (1) a moderated mediation model to test whether $f_o$ mediates the relationship between vocalizers’ testosterone levels (condition) and dominance ratings (perception), and whether this mediation is further moderated by cortisol, (2) a mediation model to test whether $f_o$ and $P_f$ mediate the relationship between vocalizers’ height and dominance ratings, and (3) a mediation model to test whether $f_o$ and $P_f$ mediate the relationship between vocalizers’ composite measure of size (extracted via factor analysis with varimax rotation) and dominance ratings. We conducted a separate mediation model for height, in addition to its inclusion in the factor analysis, as height has been shown to reflect good nutrition and low stress during development, as well as genetic predictors of immune function. Additionally, a recent study reported that $f_o$ mediated the relationship between height and physical dominance ratings in two separate samples. Finally, we conducted three meta-analyses to test: (1) the mediating effect of $f_o$ between height and dominance ratings, (2) whether cortisol and testosterone negatively interact to predict male $f_o$, and (3) whether $f_o$ negatively predicts testosterone levels, especially among men with lower cortisol levels.

Design and methods

Participants. One hundred sixty-five heterosexual males participated in a study on testosterone reactivity and personality state changes, which was conducted at the University of Goettingen, Germany (for details, see). Each participant provided a standardized video recording, saliva samples, body morphology measurements, and handgrip as well as upper-body strength. Data from five individuals could not be used due to technical issues during video recording or because consent for further use of the video material was not given, resulting in a final sample of 160 males (mean age = 24.28, SD = 3.25 years). All participants were at least 18 years old. In a sensitivity power analysis using G*Power, this sample had sufficient power ($>0.80$) to detect an effect size of $r = +/−0.20$, assuming one-tailed alpha = 0.05. All procedures were in accordance with relevant guidelines and regulations, and received ethics approval from the local Ethics Committees at the University of Goettingen and the Pennsylvania State University. Informed consent was obtained from all subjects.

Voice recordings. Standardized video recordings were obtained using a Full-HD camera and Line6 Modell XD-V75 microphones. The participants were instructed to describe what is great about themselves, choosing three domains such as “friendship” or “success in studies/job” from a list of overall eight domains (for details, see). The video clips were cut to a length of 5 s, beginning 5 s after participants had begun to speak, and voice clips were extracted. Five seconds were chosen because vocal parameters usually show strong correlations across different recordings, independent of length and content. And, both attractiveness and dominance ratings are stable and highly correlated across different recordings. Further, the use of relatively brief voice clips allowed us to avoid rater fatigue. The voice clips were analyzed using PRAAT software (Version 6.0.36). The measures obtained were mean $f_o$, the first four formant frequencies ($F_1- F_4$), four measures of jitter and five measures of shimmer. Both jitter (all $r > 0.83$, $p < 0.001$) and shimmer measures (all $r > 0.56$, $p < 0.001$) were highly intercorrelated, a standardized mean was calculated for each perturbation measure. Additionally, $P_f$ was computed for the first four formants. Formants were measured at each glottal pulse using automated detection in PRAAT. Formant measurement across standardized speech samples produces highly similar results to measurement of individual vowels and averaging across these measurements.

It should be noted that different methods of measuring formant structure are used across studies. Formant dispersion ($D_f$), for example, describes the distance between the highest (e.g., $F_3$) and lowest formants (e.g., $F_1$) measured. While $D_f$ is commonly used, it has also been criticized especially for not using information about the middle formants (e.g., $F_2$ and $F_3$). Further, although $D_f$ is theoretically dependent on body height, other measures of formant structure have shown stronger relations with body height. One of these measures is formant position ($P_f$) which describes the average standardized formant value for the first $n$ formants (e.g., $F_n- F_1$) and thus utilizes information of all formants measured. Given these advantages of $P_f$ over $D_f$, $P_f$ was chosen as the relevant measure for formant structure in this study. For further discussion, see.

Saliva samples. Based on previous studies, we controlled for circadian variation in participants’ hormonal reactivity by collecting saliva samples only between 2 and 6 pm. Approximately 12–15 min after each participant arrived at the lab, he rinsed his mouth with water and provided at least 2 ml of saliva via passive drool through a straw, just prior to the video recording. The collected samples were immediately transported.
to an ultra-low temperature freezer (−80 °C), where salivary testosterone is expected to be stable for at least 36 months \(^\text{101}\). At the end of the data collection period (see \(^\text{29}\) for details), saliva samples were shipped on dry ice to the Technical University of Dresden and analyzed using chemiluminescence-immuno- assays with high sensitivity (IBL International, Hamburg, Germany). The intra- and inter-assay coefficients (CVs) for cortisol are below 8% and for testosterone below 11%. Basal cortisol and testosterone outliers were identified and winsorized to 3 SDs \(^\text{102}\). To correct for skewness, we log10-transformed both variables.

**Body morphology and strength measurements.** As this procedure was also reported \(^\text{103}\), procedural and methodological descriptions overlap. Participants were scanned three times using a Vitus Smart XXL 3D body scanner, running AnthroScan software (both Human Solutions GmbH, Kaiserslautern, Germany). Participants wore standardized tight underwear and were instructed to stand upright with legs hip-width apart, arms extended and held slightly away from the body, making a fist with thumbs showing forward, the head positioned in accordance with the Frankfort Horizontal, and to breathe normally during the scanning process. Using AnthroScan's automatic measures (according to ISO 20685), we extracted masculinity-relevant body dimensions from the body scan: body volume, bust-chest girth, buttock girth, chest-to-hip ratio (CHR), forearm girth, lower limb ("leg") length-to-height ratio (LHR), shoulder-to-hip ratio (SHR), thigh girth, upper arm girth, waist girth, waist-to-chest ratio (WCR), and waist-to-hip ratio (WHR). An aggregate indicator of upper body size was calculated by averaging z-standardized shoulder width, bust-chest girth, and upper arm girth \(^\text{104}\). Weight (in kg) was measured as part of the first body scanning process with the integrated SECA 635 scale (SECA, Hamburg, Germany). Body height (in cm) was measured twice using a stadiometer while participants stood barefoot, and the two values were averaged (ICC = 0.996). Body-mass index (BMI) was calculated from average weight and height measures (kg/cm²). Upper body and handgrip strength were measured using a hand dynamometer (Sae- han SH5001). Each measurement was taken three times, starting with handgrip strength, for which participants were asked to use their dominant hand (88.2% used their right). As in \(^\text{105}\), upper body strength was measured by having participants hold the dynamometer in front of their chest with both hands and press both handles toward the middle as strongly as possible. A composite strength measure was formed by averaging the maximum values for each of the three measures of handgrip and upper body strength (ICCs: 0.81 and 0.64, respectively).

**Attractiveness and dominance ratings.** In exchange for course credit, 120 men (mean age = 19.82, SD = 2.71 years) and 120 women (mean age = 19.90, SD = 3.80 years) participated in a rating study on short- and long-term attractiveness as well as social and physical dominance at the Pennsylvania State University. All raters were at least 18 years old. Raters were equipped with Sennheiser HD 280 Professional Headphones and seated at private workstations. Raters provided demographic data on age, gender, sexual orientation, and relationship status. To control for the influence of semantic content, we also asked raters to indicate their German language comprehension ("How well do you understand German?") on a 7-point Likert scale from 0 ("Not at All") to 6 ("Fluent"). Below, we report results with all participants, but excluding raters score 2 or higher (n = 26) does not change results. Raters were then randomly assigned to one of four rating experiments, each asking for perceptions of either short-term attractiveness, long-term attractiveness, social dominance, or physical dominance of 160 randomly assigned voice files (for specific items see Appendix A). The voice file pool contained 320 voice samples that were taken from the 160 former targets before and after the competitive setting \(^\text{103}\). Raters always rated both files of a target, but both recordings of the same individual were separated by at least ten other voice samples. However, only ratings of the recordings before the competition were used in the present study. To ensure that each file was rated 15 times by each sex, a file was removed from the pool of remaining files to be rated once this criterion was met. The only exception was long-term attractiveness, where one male rater dropped out because of technical issues. Because correlations between male and female ratings were high (all rs > 0.70, ps < 0.001), and intraclass correlations within each rating condition were at least satisfactory (all ICCs > 0.76, ps < 0.001), mean scores were calculated.

**Results**

For tests of directed hypothesis one-tailed tests were used, and for exploratory tests two-tailed tests were used. Analyses were conducted using R \(^\text{106}\).

**Perceptions of Attractiveness and Dominance.** \(^\text{Attractiveness H1}\) Predictions on negative linear and negatively quadratic relationships between attractiveness ratings and mean, \(f_0\) were supported. We found that \(f_0\) negatively linearly predicted both short-term and long-term attractiveness. Furthermore, we found significant negatively quadratic (inverted U-shaped) relationships between \(f_0\) and both short-term (Fig. 1a) and long-term attractiveness (Fig. 1b). Comparisons of linear and curvilinear models showed that the relationship between \(f_0\) and short-term attractiveness was significantly better described by the curvilinear model \(\left(F_{2,157} = 4.38, p = 0.038\right)\), while there was no significant difference between models for long-term attractiveness \(\left(F_{2,157} = 3.76, p = 0.054\right)\).

\(^\text{H2}\) Predictions of negative linear and negative quadratic relationships between attractiveness ratings and \(P_f\) were only partially supported. We found no significant linear relationships between \(P_f\) and either short-term or long-term attractiveness. While the non-linear relationship of \(P_f\) and short-term attractiveness was not significant (Fig. 2a), a significant negative quadratic relationship between \(P_f\) and long-term attractiveness emerged (Fig. 2b).

\(^\text{H3}\) The prediction of a stronger relationship between mean \(f_o\) and short-term, compared to long-term attractiveness ratings was supported. Although both attractiveness ratings were highly correlated \((r = 0.82, p < 0.001)\), the relationship between \(f_o\) and short-term attractiveness was significantly stronger \((z = 2.06, p = 0.020)\) when comparing dependent correlation coefficients \(^\text{108}\).
H4) The prediction of a stronger relationship between Pf and short-term, compared to long-term attractiveness ratings was supported; the relationship between Pf and short-term attractiveness was significantly stronger ($z = -2.00, p = 0.023$) when comparing dependent correlation coefficients.

**Dominance H5** The prediction of a negative relationship between dominance ratings and mean fo was partially supported: fo negatively predicted physical dominance (Fig. 1c), but not social dominance ratings (Fig. 1d).

H6) The prediction of a negative relationship between dominance ratings and Pf was supported. Pf negatively predicted perceptions of both physical (Fig. 2c) and social (Fig. 2d) dominance ratings.

**Independent Predictors H7** The prediction that mean fo and Pf are independent predictors of attractiveness ratings was partially supported. When fo and Pf were included in a multiple regression ($F_{2,157} = 16.78, p < 0.001, R^2 = 0.17$), fo negatively predicted short-term attractiveness ($\beta = -0.40, p < 0.001$), but Pf did not ($\beta = -0.08, p = 0.132$). Similarly, fo negatively predicted long-term attractiveness ($\beta = -0.32, p < 0.001$) in a multiple regression ($F_{2,157} = 8.94, p < 0.001, R^2 = 0.09$), but Pf did not ($\beta = 0.01, p = 0.471$). Because the curvilinear relationship between long-term attractiveness and Pf was significant, we investigated whether the linear term of fo and the quadratic term of Pf were independent predictors of long-term attractiveness. Indeed, adding the quadratic term of Pf explained significantly more variance in long-term attractiveness ratings ($F_{2,157} = 3.15, p = 0.045$), with both predictors remaining significant. H8) The prediction that mean fo and Pf are independent predictors of dominance ratings was partially supported. Multiple regressions with fo and Pf as predictors ($F_{2,157} = 31.73, p < 0.001, R^2 = 0.28$) showed that both independently predicted physical dominance ($\beta = -0.35, p < 0.001$ for fo; $\beta = -0.37, p < 0.001$ for Pf). For social dominance ($F_{2,157} = 5.12, p = 0.007, R^2 = 0.05$), Pf was a significant predictor ($\beta = -0.25, p < 0.001$), but fo was not ($\beta = 0.02, p = 0.391$).

**Indirect measures of mate quality and formidability.** Testosterone, cortisol and fo Testosterone levels were not significantly related to fo ($r = -0.07, p = 0.18$). However, cortisol and testosterone interacted in predicting fo ($\beta = 0.16, p = 0.024$) (Fig. 3a). While these results do not support H9) a negative relationship between mean fo and testosterone, they supported H10) a negative relationship between mean fo and testosterone, which is attenuated by high baseline cortisol.

**Body Morphology and Pf** A significant relationship between Pf and body height was found ($r = -0.13, p = 0.046$), supporting H11).
**Exploratory analyses.** Strength and \( P_f \). Additional exploratory analyses showed significant negative relationships between \( P_f \) and strength (\( r = -0.25, p = 0.002 \)). Furthermore, \( P_f \) was significantly correlated with multiple body morphology measures related to volume and mass (Table 2).

**Perturbation measures, vocal perception and target parameters** Pearson correlations showed significant negative relationships between shimmer and both social (\( r = -0.31, p < 0.001 \)) and physical dominance (\( r = -0.31, p < 0.001 \)). No significant relationships were found between shimmer and short-term (\( r = -0.14, p = 0.076 \)) or long-term attractiveness (\( r = -0.12, p = 0.122 \)). Jitter showed no significant relationship to any of the four ratings (all \( rs < +/− 0.11, ps > 0.16 \)). Moreover, the only significant relationship between perturbation measures and any of the target parameters was a significant negative correlation between shimmer and baseline cortisol (\( r = -0.21, p = 0.006 \)). Multiple regressions with \( f_o \), \( P_f \), jitter and shimmer as predictors and all ratings as outcomes can be found in Tables S1–S4.

**Mediation models** In this analysis (model 7)\(^{111} \), cortisol level was recoded into two categories (median split), and their interaction term was computed by multiplying testosterone levels with dichotomized cortisol category. In this model, we found that testosterone levels (\( \beta = -0.09; p = 0.321 \)), cortisol category (\( \beta = 0.07; p = 0.367 \)) and their interaction term (\( \beta = 0.135; p = 0.119 \)) did not predict \( f_o \). Adjusting for \( P_f \) (\( \beta = -0.39; p < 0.001 \)), testosterone (\( \beta = 0.15; p = 0.028 \)) and \( f_o \) (\( \beta = -0.34; p < 0.001 \)) significantly predicted physical dominance ratings. The indirect effect of testosterone on dominance ratings via \( f_o \) was not significant (\( \beta = 0.06; p = 0.344 \)), and no significant indirect effect was observed among men with lower cortisol (\( \beta = 0.04; p = 0.227 \)), or men with higher cortisol levels (\( \beta = 0.02; p = 0.832 \)).

We ran two additional mediation models: (1) \( f_o \) and \( P_f \) were entered as mediators between height and physical dominance ratings, (2) \( f_o \) and \( P_f \) were entered as mediators between physical strength and dominance ratings. A composite measure of physical size was extracted from a factor analysis (Fig. 4d) on the following body morphology measures that significantly correlated with \( P_f \) (Table 2): height, weight, body volume, bust-chest girth, buttock girth, forearm girth, physical strength, thigh girth, upper body size, upper arm girth, and waist girth. In model 1, \( f_o \) and \( P_f \) were entered as mediators between height and physical dominance ratings (Fig. 4a). Neither \( f_o \) nor \( P_f \) was a significant mediator. In model 2, we found evidence that \( P_f \) mediated the relationship between physical strength condition and physical dominance ratings (Fig. 4b).

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**Figure 2.** Relationships between male formant position (\( P_f \)) and perceptions. We observed negative curvilinear relationships between \( P_f \) and (a) short-term attractiveness and (b) long-term attractiveness, (c) a negative linear relationship with physical dominance ratings, and (d) social dominance ratings. All panels were plotted using the “ggplot2” package.\(^{60} \)
Figure 3. Negative interaction between testosterone and cortisol on male fundamental frequency ($f_o$). (a) A combination of higher testosterone and lower cortisol levels predict lower male $f_o$ in this study. (b) A meta-analysis on the interaction effects across studies, using a random-effects model yielded a significant overall effect. Follow-up meta-analyses on simple slopes of (c) lower cortisol levels yielded a significant negative relationship between testosterone and $f_o$, and (d) higher cortisol levels yielded null results. Panel b was plotted via the "rsm" package109, and meta-analyses were conducted via the "metaphor" package110.

Table 2. Means, standard deviations, and correlations of body morphology measures with $P_x$. $M$ and $SD$ are used to represent mean and standard deviation. Values in square brackets indicate the confidence interval for each correlation. ** indicates $p < .01$; *** indicates $p < .001$. 

| Variable                  | $M$   | $SD$   | $r$     | 95% CI        |
|--------------------------|-------|--------|---------|---------------|
| BMI                      | 23.98 | 3.83   | $-0.23^{***}$ | $[-.37, -.08]$ |
| Body volume              | 79.88 | 14.03  | $-0.27^{***}$ | $[-.41, -.12]$ |
| Bust-chest girth         | 101.67| 8.81   | $-0.29^{***}$ | $[-.43, -.14]$ |
| Buttock girth            | 100.18| 7.25   | $-0.26^{***}$ | $[-.40, -.11]$ |
| Forearm girth            | 27.00 | 1.93   | $-0.28^{***}$ | $[-.42, -.13]$ |
| Physical strength        | 48.40 | 7.99   | $-0.25^{**}$  | $[-.39, -.09]$ |
| Thigh girth              | 57.58 | 4.97   | $-0.22^{**}$  | $[-.37, -.07]$ |
| Upper body size          | 56.96 | 4.13   | $-0.31^{***}$ | $[-.44, -.16]$ |
| Upper arm girth          | 30.20 | 2.67   | $-0.25^{**}$  | $[-.39, -.09]$ |
| Waist girth              | 84.63 | 9.86   | $-0.24^{**}$  | $[-.39, -.09]$ |
| Weight                   | 78.68 | 13.96  | $-0.27^{***}$ | $[-.41, -.12]$ |
| Chest-to-hip ratio (CHR) | 1.02  | 0.05   | $-0.13$     | $[-.28, .02]$  |
| Waist-to-hip ratio (WHR) | 1.21  | 0.07   | 0.03      | $[-.13, .18]$  |
| Waist-to-hip ratio (WHR) | 0.84  | 0.05   | $-0.15$     | $[-.30, .00]$  |
| Leg length-to-height ratio (LHR) | 0.40   | 0.01   | 0.12       | $[-.03, .27]$  |
| Shoulder-to-hip ratio (SHR) | 0.39  | 0.02   | 0.08       | $[-.08, .23]$  |
We combined results of the present study with prior results in a meta-analysis to assess the strength of the mediating effect of \( f_o \) on the relationship between height and perceptions of physical dominance. We found a significant overall mediating effect of \( f_o \), independent of \( P_f \) (Fig. 4c); \( f_o \) mediated about 44% the relationship between height and physical dominance ratings. We also conducted a meta-analysis of the interaction of testosterone and cortisol in predicting \( f_o \). For this analysis, the \( t \)-value and degrees of freedom (\( df \)) of the overall interaction effect were transformed into a correlation. The effect of the testosterone and cortisol interaction on male \( f_o \) (\( k = 3, n = 279 \)) was significant: \( r = 0.23, p = 0.001, 95\% \) CI \([0.12, 0.34]\) (Fig. 3b). In follow-up analyses, the relationship between testosterone and \( f_o \) was significant in men with low cortisol levels (Fig. 3c), but not in those with high cortisol levels (Fig. 3d).

Finally, Fig. 5 provides a lens model overview of the key relations between perceptions, vocal cues and target parameters found in this study.

**Discussion**

We investigated the role of vocal parameters in perceptions of male attractiveness and found that \( f_o \) was the strongest predictor of short- and long-term attractiveness among the vocal parameters measured (\( P_f \), shimmer, and jitter). Consistent with previous studies, the relationship between \( f_o \) and male vocal attractiveness was both negatively linear and negatively curvilinear, the latter suggesting that women’s voice preferences may reflect a tradeoff between the potential genetic or other benefits versus the potential costs of mating with masculine males. Such costs may include lower investment and perhaps risk of interpersonal violence. Low male \( f_o \) has previously been linked to sexual infidelity, and several lines of evidence suggest that phenotypic masculinity—and vocal masculinity in particular—indicate threat potential not only to same-sex competitors but also to potential mates. For example, images of male-on-female violence disrupted U.S. women’s preferences for both masculine voices and faces, and Colombian women with perceptions of greater local domestic violence...
preferred less masculine male faces\textsuperscript{118}. In another study, Filipino women who were younger and rated themselves as less attractive tended to prefer feminized male $f_0$, again suggesting that women’s $f_0$ preferences may in part reflect their own perceived vulnerability\textsuperscript{62}. In our data, $f_0$ was a stronger predictor of short-term than long-term attractiveness, once again supporting the notion of a mate choice trade-off in which putative indicators of genetic fitness are prioritized in short-term contexts, and expected investment and fidelity are prioritized in long-term contexts\textsuperscript{90}.

Although $P_f$ predicted strength and body morphology in our study and predicted ratings of attractiveness in some prior studies\textsuperscript{13,21}, it did not predict attractiveness in another large sample\textsuperscript{5} and was unrelated to short-term attractiveness and only weakly negatively curvilinearly linked to long-term attractiveness in the present study. These lines of evidence suggest that the information provided by formant frequencies may be less relevant to mate quality than that provided by $f_0$. By contrast, shimmer negatively predicted both short- and long-term attractiveness ratings. Shimmer is utilized to assess vocal quality in clinical contexts, such that pathological voices show higher shimmer levels than those of healthy individuals\textsuperscript{119–121}; however, a composite of shimmer and harmonics-to-noise ratio (which were highly correlated) showed no relationship to dominance or attractiveness perception in a recent study\textsuperscript{5}. These divergent findings may be explained by the fact that the latter study used voice samples in which male individuals read a standardized voice passage, while our study used more natural but less standardized stimuli that might have been influenced more strongly by the speaker’s affective state.

Importantly, a Fisherian mate choice model via runaway sexual selection has also been suggested as a possible driver favoring low male $f_0$\textsuperscript{14,122}. A Fisherian model would suggest that female choice primarily drives and exaggerates the evolution of male traits; hence, the model predicts that females prefer males with the lowest $f_0$. However, evidence from the current study and previous studies\textsuperscript{11,62,65} (suggests a general preference for lower $f_0$ by women, but also a relatively stronger negative linear relationship between $f_0$ and dominance perceptions by men across studies\textsuperscript{29}.

While $f_0$ predicted both short- and long-term attractiveness, it predicted physical dominance but not social dominance, in line with previous studies\textsuperscript{13,25}. $P_f$ and shimmer were linked to both social and physical dominance ratings. A possible explanation for this pattern of results is that social dominance is influenced less by threat potential and more by other qualities, such as competence, communication and cooperation skills, or leadership qualities. These attributes might be more strongly associated with $P_f$ and shimmer than with $f_0$.

The other aim of this study was to explore whether attention to vocal cues is adaptive by investigating the information content of acoustic parameters. We replicated a negative relationship between $P_f$ and height\textsuperscript{33} and found that $P_f$ negatively predicted strength and several body morphology measures. Men with lower $P_f$ were taller, stronger, and had larger bodies in general. Further, our mediation analysis indicated that $P_f$, independently of $f_0$, mediated the relationship between a composite measure of body size and physical dominance ratings.

Importantly, baseline cortisol and testosterone levels interacted in predicting $f_0$, such that testosterone levels more strongly negatively predicted $f_0$ as cortisol levels decreased across participants. When we entered the interaction term between testosterone and median-split cortisol levels into our exploratory moderated mediation analyses, the interaction effect became non-significant, likely due to reduced statistical power\textsuperscript{125} from dichotomizing a continuous variable (cortisol). Nevertheless, the overall interaction between testosterone and cortisol in predicting male $f_0$ was confirmed in a meta-analysis (Fig. 3b). Male $f_0$ was negatively correlated with

**Figure 5.** Lens model overview of the study results. Connections indicate significant relations ($p < .05$).
testosterone when cortisol was low, whereas no significant relationship was observed between male \( f_o \) and testosterone when cortisol was high (Fig. 3c). These patterns of relationships may help clarify why dose-dependent effects of androgen levels on the intensity of elaborate male traits are sometimes undetected, and why \( f_o \) is only weakly correlated with testosterone when cortisol is not considered. Across a variety of species, testosterone and cortisol are linked to measures of physical condition, including disease, stress, and diet. The interaction between testosterone and cortisol, in particular, has been tied to immune function in birds, but the functional and behavioral correlates of this hormonal interaction in humans are not yet clear, and most studies are arguably underpowered. Further, a recent meta-analysis found only modest support for an interactive relationship between testosterone and cortisol in predicting status-relevant behavior (e.g., dominance & risk taking) and suggested that this association could be driven by publication bias and flexibility in data analysis. Although only one paper besides the current one has reported the specific interaction effect of testosterone and cortisol on male \( f_o \), the meta-analysis reported here suggests that the interaction is robust.

There is widespread agreement that low male \( f_o \) evolved to exaggerate apparent size by leveraging a predisposition to perceive low frequencies as emanating from large sound sources. Phylogenetic reconstruction suggests that relatively male \( f_o \) evolved in the common ancestor of the catarrhine primates after their divergence from platyrrhines approximately 43.5mya. Given the weak correspondence between \( f_o \) and body size, some have argued that \( f_o \) is purely deceptive and is not an honest indicator of physical dominance. Others have suggested that \( f_o \) may reliably correlate with other salient speaker characteristics such as status, threat, and dominance, and that these dimensions may overlap with, and hence intrude onto impressions of, size. Our results better comport with the latter possibility. Indeed, relatively low male \( f_o \) tends to be lost in primate species in which male-male mating competition is reduced, suggesting that there are costs associated with low \( f_o \) that cause this trait to be selected against when compensatory benefits are absent.

Defence to male \( f_o \) is demonstrably costly in human terms of social status, mates, and reproduction, and thus attention to \( f_o \) would seemingly be selected against if \( f_o \) did not provide valid information about male condition. However, this does not mean that \( f_o \) is cheat-proof, or that the assessment of condition or formidability from \( f_o \) is largely accurate. Honest signals are often corrupted into conventional signals where cheating is common because the assessment of the signal itself is costly to the receiver. Although we did not find support for the cortisol-moderated mediation role of \( f_o \) between testosterone levels and physical dominance ratings in the present sample, this may be explained by reduced statistical power due to dichotomized cortisol levels and reduced sample sizes for testing two separate indirect effects. Indeed, we found a strong meta-analytic support for an overall interaction between testosterone and cortisol in predicting male \( f_o \), suggesting that \( f_o \) conveys underlying endocrine state, if imprecisely, and lower male \( f_o \) has consistently been shown to predict perceptions of physical dominance across multiple studies. Likewise, a recent study reported that \( f_o \) mediated the relationship between developmental condition (measured via height) and physical dominance ratings in two separate samples with different types of vocal stimuli. Although we did not find that \( f_o \) significantly mediated the relationship between height and physical dominance ratings in our data, our meta-analysis suggests that \( f_o \) mediates about 44% of the relationship between height and physical dominance ratings. Collectively, our findings support the hypothesis that, while the correlation between \( f_o \) and underlying quality is imperfect, \( f_o \) might be utilized as one of many cues for assessing competitors and potential mates because it communicates the quality of the signaler significantly better than chance.

Shimmer also negatively predicted social and physical dominance ratings, as well as lower cortisol levels. The latter finding is consistent with prior evidence that shimmer is reduced when stress is induced experimentally or when the speaker is under high tension. However, the other perturbation measure, jitter, showed no such associations. Future research should continue to explore the relevance of jitter and shimmer to human sexual selection (see also), as they have been shown to be associated with pathological voice quality and body shape in men and might therefore be relevant in contexts of sexual selection.

One limitation with our study is that we tested only hypotheses associated with receiver-independent costs and did not consider receiver-dependent costs associated with attention to male \( f_o \). Some have suggested that additional mechanisms that incorporate receiver-dependent costs are required to ensure signal honesty. For example, under a mating-motive priming condition, male voices with low \( f_o \) enhanced recognition for men with high threat potential and elicited aggressive cognitions and intent in men who perceived themselves to be more dominant and stronger. Future studies should investigate the extent to which receiver-dependent and independent costs are needed in ensuring the signal honesty of low \( f_o \) in cross-cultural contexts.

Following suggestions by Lakens, we used one-sided significance tests for preregistered directional hypotheses. The only result influenced by this decision is the relation between \( f_o \) and height, which would be non-significant using a two-sided test. However, we note that meta-analytic findings suggest a robust link between \( f_o \) and height, and the lack of a significant relation in this particular study is likely due to a lack of statistical power. Thus, also our conclusions remain highly similar when two-sided tests are used.

**Conclusion**

Vocal parameters were linked to hormone levels, as well as body morphology and physical strength, and appear to be used for judgements relevant to intrasexual competition and intersexual mate choice. The present study thus provides evidence that natural interindividual variation in men’s vocal parameters influences judgements of attractiveness and dominance because these parameters provide valid information about speakers’ underlying condition.
Appendix A

Demographic Questions for Raters

What is your sex? (Female/Male)
How old are you? (text box)
Relationship status: (Single, Dating, Cohabiting/Married)
Which best describes your sexual attractions?
“I am attracted…”
(only to females mostly to females equally to males and mostly to males only to males)

How well do you understand German? (7-point Likert Scale: 0 Not at All - 6 Fluent)

Voice Rating Questions

1. **Short-term attractiveness:** How attractive does the speaker sound for a short-term, uncommitted romantic relationship?
   a. 7-point Likert Scale (-3 very unattractive - 3+ very attractive)

2. **Long-term attractiveness:** How attractive does the speaker sound for a long-term, committed romantic relationship?
   a. 7-point Likert Scale (-3 very unattractive - 3+ very attractive)

3. **Social dominance:** How respected does the speaker sound?
   a. 7-point Likert Scale (-3 very unrespected - 3+ very respected)

4. **Physical dominance:** How likely would the speaker win a physical fight against an average college student?
   a. 7-point Likert Scale (-3 very unlikely - 3+ very likely)

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**Author contributions**

C.S., L.P., and D.A.P. conceived of the presented idea. C.S., L.P., and D.A.P. designed and planned the experiments. C.S., T.L.K., and D.A.P. planned the data collection and collected the data. R.A.C. programmed the rating study. C.S. and T.A. analyzed the data. C.S. took the lead in writing the manuscript. All authors provided critical feedback and helped shape the research, analysis, and manuscript.

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