

Sexual selection for low male voice pitch among Amazonian forager-horticulturists

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ABSTRACT

Pitch is the most perceptually salient feature of the voice, yet it is approximately five standard deviations lower in men than in women, a degree of sexual dimorphism exceeding that of all extant nonhuman apes. Evidence from Western samples suggests that low-frequency vocalizations may have augmented male mating success ancestrally by intimidating competitors and/or attracting mates. However, data are lacking from small-scale societies. We therefore investigated sexual selection on male pitch (measured by fundamental frequency, f_0) in a population of Bolivian forager-horticulturists, the Tsimané. We found that experimentally lowering f_0 in audio clips of men speaking increased perceptions of fighting ability but did not affect perceptions of prestige and decreased their attractiveness to women. Further, men with lower speaking f_0 reported higher numbers of offspring, and this was mediated by the reproductive rates of men's wives, suggesting that men with lower f_0 achieved higher reproductive success by having access to more fertile mates. These results thus provide new evidence that men's f_0 has been shaped by intrasexual competition.

1. Introduction

The acoustic properties of the human voice convey information about speakers' physiological stress (Patil, Nayak, & Saxena, 2013), developmental instability (Hughes, Harrison, & Gallup, 2002), and emotional state (Bachorowski & Owren, 1995; Banse & Scherer, 1996; Goudbeek, Goldman, & Scherer, 2009; Scherer, 2003), as well as dominance-related characteristics, such as levels of aggressive intent in competitive scenarios (Zhang, 2013). Many of these acoustic features are sexually dimorphic, including fundamental frequency (f_0), the acoustic property that we perceive as pitch. Fundamental frequency corresponds to the rate of vocal fold vibration during phonation, and is approximately twice as high in women as in men on average (Titze, 1989). This sex difference is not a byproduct of larger male body size; f_0 dimorphism greatly exceeds sexual size dimorphism as a consequence of rapid, testosterone-induced vocal fold growth at puberty in males (Fitch & Giedd, 1999; Pedersen, Møller, Krabbe, & Bennett, 1986).

Sexual dimorphism in f_0 and other acoustic parameters has been observed in several non-human primate species (Ey, Pfefferle, & Fischer, 2007; Mitani & Gros-Louis, 1995; Rendall, Owren, Weerts, & Hienz, 2004), and phylogenetic reconstruction indicates a monotonic

increase in f_0 dimorphism from the common ancestor of Hominoidea to modern *Homo sapiens*, culminating in humans exhibiting the greatest f_0 dimorphism of the extant apes (Puts et al., 2016). It is possible that f_0 dimorphism has continued to increase as recently as the divergence of our lineage from those of Neanderthals and Denisovans, as the largest observed changes in gene regulation via DNA methylation during this period influence laryngeal development (Gokhman et al., 2017). Reconstructed evolutionary transitions toward increased male mating competition are also associated with increases in sexual dimorphism in f_0 across anthropoids, suggesting an important role of intermale competition in engendering these sex differences (Puts et al., 2016).

Supporting this interpretation, in modern populations, men with deeper voices report higher annual salaries (Mayew, Parsons, & Venkatachalam, 2013), more sexual partners (Hill et al., 2013; Puts, 2005), and higher reproductive success (Apicella, Feinberg, & Marlowe, 2007; Smith, Olkhov, Puts, & Apicella, 2017; but see Atkinson et al., 2012). While the latter results are correlational and therefore cannot confirm a causal role for vocal masculinity, the robustness of results from experimental perception studies support vocal masculinity as an independent driver of characteristics related to reproductive success. For example, a number of experimental studies have found that men

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with lower f_0 are perceived by other men to be more socially and physically dominant, and by women to be more attractive (Feinberg, Jones, Little, Burt, & Perrett, 2005; Puts, Apicella, & Cárdenas, 2012; Puts et al., 2016; Puts, Gaulin, & Verdolini, 2006; Puts, Hodges, Cárdenas, & Gaulin, 2007; Saxton, Mackey, McCarty, & Neave, 2016; Simmons, Peters, & Rhodes, 2011). Men with more masculine voices, including lower f_0 and formant frequencies, were also rated as being more physically formidable by familiar male peers. It seems clear that such sexually dimorphic features of men's voices exert social influences that could affect the acquisition and retention of mates and resources, and hence, reproductive success.

Given its high degree of sexual dimorphism and apparent importance in male-male competition, it has been suggested that f_0 and other acoustic parameters of the human voice have been the targets of intrasexual selection as signals of competitive ability (Puts et al., 2012). Such signals, can serve as deterrents to potential challengers for dominance and prevent minor conflicts from escalating to physical violence, benefitting subordinates and dominants alike. Some evidence suggests that f_0 is associated with physical formidability. For example, Evans, Neave, and Wakelin (2006) found that body weight, shoulder and chest circumference, and shoulder-to-hip ratio were negatively related to mean f_0 among a sample of British men. A meta-analysis by Pisanski et al. (2014) found that f_0 explained < 2% of the variation in height but was not significantly related to body weight in men.

The modest associations and mixed results of tests relating f_0 to body size have called into question whether f_0 honestly signals formidability or competitive ability (Feinberg, Jones, & Armstrong, 2018). Following others (Puts et al., 2016; Rendall, Vokey, & Nemeth, 2007), Feinberg et al. suggest that an evolutionarily ancient perceptual mechanism causes listeners to attribute large size to objects that produce low-pitched sounds. However, in contrast to previous authors, Feinberg et al. argue that the available evidence does not support f_0 as an honest signal of formidability. Under this perceptual exploitation model, men with low voice pitch are favored because they *sound* formidable, but there need not be any true relationship between the trait (i.e. formidability) and its putative signal (i.e. voice pitch).

We are skeptical of the hypothesis that humans cede resources and reproductive opportunities to rivals based on an unreliable signal, such that f_0 has become one of the most robust predictors of perceived formidability despite having no relationship with actual formidability. Natural selection, as well as learning mechanisms, would presumably favor inattention to f_0 as a signal of formidability if it were purely deceptive.

Moreover, several additional lines of evidence suggest that f_0 signals aspects of condition relevant to competitive ability (Puts & Aung, 2018). For example, some studies have found negative associations between f_0 and men's testosterone concentrations (Dabbs & Mallinger, 1999; Evans et al., 2006; Puts et al., 2012). In humans, testosterone has been linked to aggression, status, and status-seeking behaviors (Archer, 2006; Dekkers et al., 2019). In two samples, Puts et al. (2016) found that testosterone negatively interacted with cortisol, such that f_0 was lower specifically in men with both high testosterone and low cortisol levels. Although the relationships are likely to be complex, cortisol has been linked to infection and other physiological stressors (Sapolsky, Romero, & Munck, 2000) and may inhibit testosterone action on target tissues (Chen, Wang, Yu, Liu, & Pearce, 1997; Smith, Syms, Nag, Lerner, & Norris, 1985). The negative interaction of cortisol and testosterone has also been linked to status-seeking behaviors in humans (albeit weakly, see Dekkers et al., 2019), as well as immune function in both humans (Rantala et al., 2012) and nonhuman vertebrates (Evans, Goldsmith, & Norris, 2000; Møller, 1995). Hodges-Simeon, Gurven, and Gaulin (2015) more directly tested the relationship between f_0 and immune function in peri-pubertal male forager-horticulturists, finding a non-significant correlation between f_0 and salivary immunoglobulin-A (a marker of mucosal immunity) in the predicted (negative) direction, and a significant negative relationship between f_0 and energetic condition

(indexed by age-adjusted body-mass index) that was mediated by testosterone levels. In addition, Arnocky, Hodges-Simeon, Ouellette, and Albert (2018) found that low f_0 predicted higher salivary immunoglobulin-A as well as lower self-reported infection risk in 107 men, but another study found no significant relationship between f_0 and immune response to a hepatitis B vaccination in 60 men (Skrinda et al., 2014).

Nevertheless, we agree that the evidence that voice pitch honestly signals formidability is not as compelling as the evidence that low voice pitch is intimidating to rivals. Because the present research does not rest on the outcome of this debate, we leave its further exploration for subsequent work.

Unlike in many animals species, rank in human social hierarchies is determined not only by dominance (coerced social status; Gil-White & Henrich, 2001), but also through prestige (freely-conferred social status; Gil-White & Henrich, 2001; von Rueden, Gurven, & Kaplan, 2011). Individuals become prestigious or dominant via mechanisms that do not always overlap. For example, von Rueden, Gurven, and Kaplan (2008) found that perceived fighting ability, a proxy for dominance, was more closely related to male body size than to various proxies for men's ability to confer benefits on their peers. In contrast, men's prestige, as measured by respectability and influence within their community, showed stronger associations with traits such as the amount of social support they received, acculturation, and skill in food production. Thus, dominance and prestige do not rely equally on previously-observed correlates of f_0 , most notably body size. This finding suggests that associations between men's f_0 and social status may vary in strength based upon the relative contributions of prestige and dominance to maintaining that status, with dominance being more closely related to f_0 .

Despite accumulating evidence supporting a role for sexual selection in the evolution of low f_0 in men, key data are missing. First, cross-cultural perception data are vitally needed, particularly from small-scale societies. While evidence has accumulated to suggest that f_0 is involved in intrasexual competition among men, much of this evidence comes from Western populations. In many of these studies, low f_0 has been found to strongly increase men's apparent physical formidability and, to a lesser extent, their attractiveness to women (Feinberg et al., 2005; Jones, Feinberg, DeBruine, Little, & Vukovic, 2010; Puts et al., 2007). However, perceptions of masculine traits vary cross-culturally; for example, women tend to prefer masculine male faces in some populations and feminine male faces in others (Scott et al., 2014). The scanty available data suggest that the effects of f_0 are also culturally variable. For instance, women showed no overall preference for male f_0 among the Hadza of Tanzania (Apicella & Feinberg, 2009). Filipino women tended to prefer a feminine f_0 (Shirazi, Puts, & Escasa-Dorne, 2018), and the effects of f_0 on men's perceptions of formidability are untested in both of these populations. Second, it is unknown whether low f_0 may augment reproductive success by increasing access to high quality or to a high quantity of mates (Apicella et al., 2007).

To clarify the role of sexual selection in the evolution of low f_0 in men, it is necessary to address these questions cross-culturally, particularly in small-scale societies. The Tsimané of Bolivia (Huanca & T., 2008; Ringhofer, 2010) represent one such society, comprising approximately 15,000 individuals living in over 90 villages along the Maniqui River and surrounding areas in lowland Beni in the Bolivian Amazon. The Tsimané are forager-horticulturists who subsist by hunting, fishing, and cultivating plantains, rice, corn and manioc, with < 10% of calories obtained from purchased foods (Martin et al., 2012). Several long-term field studies of the Tsimané have been carried out, including The Tsimané Amazonian Panel Study (Leonard et al., 2015) and The Tsimané Health and Life History project (Gurven et al., 2017). The wealth of information related to reproduction and competition in this population, including several studies focused on the voice (Hodges-Simeon et al., 2015; Sell et al., 2010), make the Tsimané an especially well-described group that is ideal for addressing the above

questions.

In the present study, we therefore investigated sexual selection on male f_0 among the Tsimané by testing the relative contributions of f_0 to attractiveness to women vs. perceptions of social status and dominance among male competitors (Study 1). We also investigated whether low f_0 positively predicts components of men's mating success, and in this way augments men's reproductive success (Study 2). All procedures were approved by the Ethics Review Board at the University of Wrocław Institute of Psychology and the Great Tsimané Council (the governing body of the Tsimané), and are in accordance with the Helsinki Declaration of 1975, as revised in 2000.

2. Study 1

2.1. Materials and methods

2.1.1. Participants

We approached prospective participants at their homes or public locations in five villages (Campo Bello, Maracas, Puerto Yucumo, Catumare, and Anachere) in the Tsimané region. The rate of refusal was low (10%–15%) in each village. Thirty-nine women (mean age = 29.7y, range = 17–50) and 45 men (mean age = 33.4y, range = 18–50) provided voice perception data. All participants provided informed oral consent, documented via audio recording, and received a gift of household items worth ~6 USD.

2.1.2. Stimulus creation

We selected four voice clips of men reading part of the first sentence of the Rainbow Passage (“They act as a prism and form a rainbow;” Fairbanks, 1960) from a larger sample of US university students (Puts et al., 2012). The starting mean f_0 of these clips was within 1 SD (14.2 Hz) of the mean (111.4 Hz) of the larger sample. Each clip was manipulated to the mean f_0 of the larger sample, and to 2 SD below and above the mean pitch using Pratt software (v. 4.4.11). However, differences in f_0 are more easily detected by the human auditory system at lower frequencies (i.e. a 10-Hz increase from 50 to 60 Hz is easier to perceive than an increase from 100 to 110 Hz, although the absolute increase is the same). We therefore manipulated in units of equivalent rectangular bandwidth (ERB). ERB is a psychophysical measure of pitch perception related to f_0 according to

$$ERB = 21.4 \times \log_{10}(0.00437f + 1) \quad (1)$$

where f is the fundamental frequency in Hz. Shifts of a given number of ERB units are perceptually equivalent no matter how high or low the starting frequency (Smith & Abel, 1999). We shifted fundamental frequency by 0.559 ERB (2 SD) above and below the mean pitch (3.687 ERB), resulting in mean fundamental frequencies of 139.59 and 91.56 Hz for feminized and masculinized stimuli, respectively.

Clips manipulated to mean f_0 were paired with both the corresponding feminized (+2 SD; $N = 4$) and masculinized (−2 SD; $N = 4$) clips. Voice pairs were distributed in two iTunes playlists so that each list was comprised of each of the eight possible voice pairings: four voice identities with mean f_0 paired with feminized f_0 , and four paired with masculinized f_0 . Order within each pair was counterbalanced across the two playlists, and both playlists contained two pairs of each possible order: mean-feminized, feminized-mean, mean-masculinized, masculinized-mean. Voice pairs were presented using an iPod Touch and Sennheiser HD280 Pro headphones. The order in which different pairs were presented was randomized using the iPod shuffle function. Henceforth, we will use the term “masculine stimulus” to refer to the *more masculine* stimulus in a pair. In feminized vs. mean pairs, this will refer to the stimulus manipulated to the mean. In mean vs. masculinized pairs, this will refer to the masculinized stimulus.

2.1.3. Voice perception

Male participants ($N = 45$) judged which voice clip in each pair

sounded more respected, admired, talented and successful (“Prestige”; see Gil-White & Henrich, 2001), and which voice in each pair sounded more likely to win a physical fight (“Fighting”). Female participants ($N = 39$) judged which voice in each pair sounded as if it came from the man with the more attractive body (“Attractiveness”), and which voice was more attractive for marriage (“Marriage”). The order of task presentation (Prestige vs. Fighting for men, Attractiveness vs. Marriage for women) was counterbalanced across participants.

Participants listened to all eight pairs on one dimension, and then all eight pairs again on the other dimension, for a total of 16 total responses. After listening to a pair of stimuli, subjects verbally indicated which one they thought was, e.g., more masculine, by saying ‘first/second’ or ‘earlier/later,’ and we recorded their answer on a response sheet. We measured preference for f_0 on a given task (i.e. characteristic rated) as the number of masculine stimuli chosen out of two (one mean vs. feminized f_0 pair and mean vs. masculinized f_0 pair). Thus, four preference measures (2 tasks \times 2 manipulation pairs per task) were produced for each participant, each ranging from 0 to 4 masculine stimuli chosen.

We did not assess menstrual cycle phase in female raters. Although early studies (Feinberg et al., 2006; Puts, 2005, 2006) suggested that women's preferences for masculine voices change over the ovulatory cycle, two recent large, well-powered within-subjects studies failed to replicate this effect (Jünger et al., 2018). Hence, if there is an effect of cycle phase on women's preferences for male f_0 , the effect is likely to be undetectable in a between-subjects analysis of a sample of the present size.

2.1.4. Data treatment and analysis

All data manipulations and analyses were performed in R 3.5.0 (R Core Team, 2018) using RStudio 1.0.153 (RStudio Team, 2016). For a list of all non-base R packages used in data treatment and analyses, and their references, see Supplementary Table 1. Scripts are available in the supplement.

We first tested whether subjects' selections were influenced by either manipulation type (i.e. mean vs. feminized or masculinized) or characteristic assessed (i.e. body or marriage attractiveness for women, dominance or prestige for men) using a repeated-measures ANOVA with subject ID entered as a random factor, characteristic and manipulation as independent variables, and number chosen as the dependent variable.

Women did not differ in their number of masculine stimuli selected as a function of manipulation type (mean vs. masculinized: mean \pm SEM masculine chosen = 1.62 ± 0.133 ; mean vs. feminized: 1.53 ± 0.134 ; $F_{1,114} = 0.253$, $p = .616$); i.e., women chose the lower- f_0 or higher- f_0 stimulus as often when listening to mean vs. feminized pairs as when listening to mean vs. masculinized pairs. Women also did not differ in their number of masculine stimuli selected as a function of character assessed (body attractiveness: 1.59 ± 0.142 ; marriage attractiveness: 1.55 ± 0.125 ; $F_{1,114} = 0.046$, $p = .83$), or the interaction between manipulation type and character assessed ($F_{1,114} = 0.624$, $p = .431$; Fig. 1). Likewise, men's responses did not differ as a function of manipulation type (mean vs. masculinized: 2.43 ± 0.147 ; mean vs. feminized: 2.41 ± 0.143 ; $F_{1,132} = 0.019$, $p = .891$) or manipulation \times characteristic interaction ($F_{1,132} = 1.197$, $p = .276$); however, men selected more masculine stimuli when assessing dominance than when assessing prestige (dominance: 2.72 ± 0.132 ; prestige: 2.12 ± 0.151 ; $F_{1,132} = 13.63$, $p < .001$; Fig. 1).

Because women did not differ in their responses across manipulation type or characteristic assessed, we averaged each female participant's responses across all four conditions. Because men's responses differed according to characteristic assessed, for each male participant, we averaged the number of masculine stimuli chosen for dominance and prestige separately (for each characteristic, maximum possible number of masculine stimuli chosen = 4). We then performed one-sample t -tests to determine whether participants tended to choose more

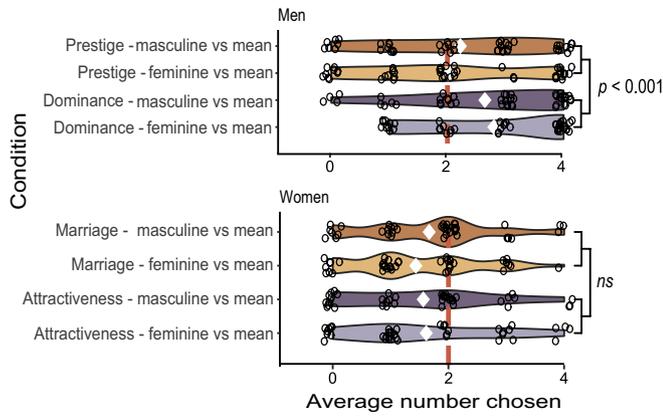


Fig. 1. Violin plots depicting numbers of more masculine stimuli chosen, grouped by condition. Open circles indicate how many masculine stimuli the subject chose in the given condition, out of 4. Red dotted lines indicate the chance line, representing 2 out of 4 masculine stimuli chosen. White diamonds indicate the condition-mean. Vertical and horizontal jitter applied for ease of viewing. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

masculine or more feminine stimuli in each task (against a test value of 2 = no preference). To assess robustness, we repeated all analyses with women's data averaged separately for body and marriage attractiveness and with men's data averaged across all four conditions. These tests produced results consistent with the main analyses (see Supplementary Table 2). Finally, to test for confounding effects of stimulus manipulation, we checked whether men or women tended to choose more or fewer stimuli manipulated away from the mean than would be predicted by chance. To do so, we ran one-sample *t*-tests (assuming chance = 2) on men's and women's within-subject average (across all four conditions) numbers of ± 2 SD manipulated stimuli chosen. Neither men nor women tended to choose more or fewer manipulated stimuli than would be predicted by chance (mean \pm SEM manipulated chosen: men: 2.01 ± 0.056 , $t_{44} = 0.20$, $p = .842$; women: 2.04 ± 0.072 , $t_{38} = -0.62$, $p = .538$; similar results of Wilcoxon tests; see both in Supplementary Table 3).

2.2. Results

When all four conditions were averaged, women chose more feminine male stimuli than expected by chance (mean \pm SEM masculine chosen 1.57 ± 0.11 , $t_{38} = -3.91$, $p < .001$). Men did not show a preference for masculine or feminine stimuli when evaluating other men on prestige (2.12 ± 0.2 , $t_{44} = 0.63$, $p = .534$); however, men tended to choose more masculine stimuli when evaluating fighting ability (2.72 ± 0.17 , $t_{44} = 4.34$, $p < .001$; Fig. 2). As noted above, we assessed the robustness of our results by repeating all analyses with women's data averaged separately for body and marriage attractiveness

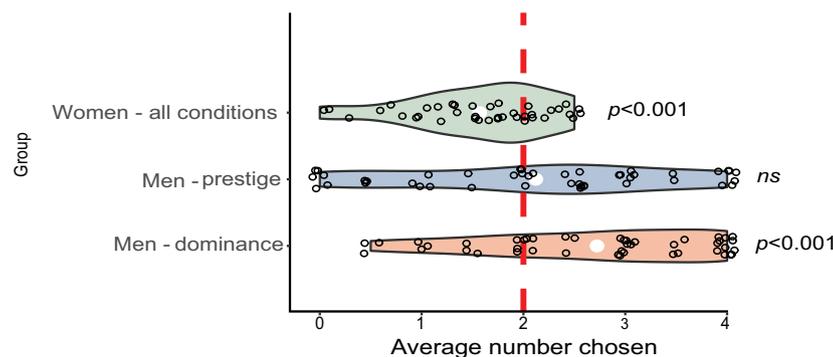


Fig. 2. Violin plots depicting numbers of more masculine stimuli chosen. Reflecting main analyses, all 4 conditions are averaged for women, and men's dominance and prestige conditions are averaged separately. Open circles indicate how many masculine stimuli the subject chose in the given condition set, out of 4. Red dotted lines indicate the chance line, representing 2 out of 4 masculine stimuli chosen. White circles indicate the condition set mean. Vertical and horizontal jitter applied for ease of viewing. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

and with men's data averaged across all four conditions, and came to conclusions that were consistent with those of the main analyses (see Supplementary Table 2). Because the proportion of masculine stimuli selected behaves more like a discrete than a continuous variable, our data are unlikely to conform to the assumptions of a normal distribution; we thus repeated these analyses using non-parametric, one-sample Wilcoxon tests to check the robustness of our results, and came to similar conclusions in all cases (see Supplementary Table 2).

3. Study 2

3.1. Materials and methods

3.1.1. Participants

Subjects who participated in Study 2 (women: $N = 59$, mean age = 30.8y, range = 17- ~50; men: $N = 70$, mean age = 33.4y, range = 18- ~50) included those who participated in Study 1, plus some who did not wish to participate in the perception study. Study 2 subjects provided demographic and anthropometric data, and in addition, men provided voice recordings.

3.1.2. Procedure

Voice recordings, interviews and measurements were collected from participants in private in the Tsimané language with the help of a local Tsimané interpreter (see Supplementary Fig. 1). Participants were instructed to state where they live and count from 1 to 10. Voices were recorded using a Zoom H4n recorder and either the built-in microphone or an attached Sennheiser MKH-80 condenser microphone. If background noise was high, a recording was not made. Recordings were saved as '.wav' files and analyzed using Praat software, with pitch floor and ceiling set to 75 Hz and 300 Hz, respectively. Otherwise, default settings were used.

Height was measured with an anthropometer, weight with a Tanita BF679W scale, and flexed biceps circumference with tailor's tape. We asked participants their age, age at birth of first child, total number of children, number of children who died before reaching age 16 (from which we calculated % offspring mortality), identity of any current spouses, and about their possession of certain valuable objects found in all Tsimané communities. Not all participants knew their exact age, and thus some ages are estimates (i.e. for 13 subjects who estimated that they were around 50 years old, we recorded their ages as 50). Wealth was calculated as the value, in bolivianos, of the objects possessed by a family.

3.1.3. Data treatment and analysis

For two subjects, their mean f_0 was outside the normal male range (both $f_0 > 240$ Hz). We attribute these values to background noise during the recordings. We therefore excluded these men from all analyses.

We performed a principal components analysis with Oblimin rotation and Kaiser normalization (IBM SPSS Statistics 25) for dimension

reduction of the control variables for men: height, weight, flexed biceps circumference, and wealth. Two factors with eigenvalues > 1.0 emerged: Height, weight, and biceps circumference loaded heavily (loadings 0.68, 0.93, and 0.84, respectively) onto the first component (“Size”, $EV = 2.0$, 50.9% of variance explained), and wealth loaded heavily (loading 0.99) onto the second component (“Wealth”, $EV = 1.0$, 25.2% of variance explained), which did not significantly correlate with Size ($r = 0.03$, $p = .816$). We used each subjects' factor loadings for Wealth and Size as control variables in later analyses. The three variables that comprised the Size component were all positively and significantly correlated (Height and Biceps: $r = 0.26$, $p = .041$; Height and Weight: $r = 0.47$, $p \leq .001$; Weight and Biceps: $r = 0.71$, $p \leq .001$).

All subsequent data manipulations and analyses were performed in R 3.5.0 (R Core Team, 2018) using RStudio 1.0.153 (RStudio Team, 2016). For a list of all non-base R packages used in data treatment and analyses, and their references, see Supplementary Table 1. Scripts are available in the supplement.

Because men's and wives' total number of offspring and age at first reproduction were positively skewed (skew = 1.09 and 1.04, respectively), we natural log-transformed these variables for analysis. To account for effects of age on reproductive success, we regressed wives' log-transformed number of offspring on age and age², resulting in a new variable, which we refer to as ‘reproductive rate.’ Three men were married to pairs of sisters, and all other married men were married monogamously. For each man with multiple wives, we averaged his wives' reproductive rates and ages at first reproduction.

Before conducting the main analyses, we checked for between-village differences in mean f_o , components of reproductive success (i.e. men's current and total number of wives, men's and wives' ages at first reproduction, offspring mortality and men's and wives log-transformed total number of offspring), or either control variable (i.e. Size and Wealth) using a multivariate ANOVA with village as the independent variable and the above-mentioned variables as dependents. This analysis revealed no general between-village differences ($F_{50,200} = 1.26$, $p = .14$); however, post-hoc one-way ANOVAs demonstrated significant differences between villages in men's offspring mortality rate ($F_{5,45} = 4.14$, $p < .001$), and f_o ($F_{5,45} = 3.67$, $p = .007$; see all results in Supplementary Table 4). Because the sample sizes for most villages were very small, we decided against a mixed-effects model with village entered as a random effect in favor of multiple linear regressions with mean f_o as the predictor and proxies for subjects' reproductive success as dependent variables. To account for possible confounds, we entered subjects' age and age², and their PC scores for both Size and Wealth as additional predictors.

To test the robustness of the relationships between men's f_o , their number of offspring, and their wives' reproductive rate, we reran multiple regressions with univariate reproductive rate outlier cases excluded ($N = 1$ man who had zero offspring at age 23, and his wife, and 1 additional subjects' wife, who had only two offspring at age 43), and additionally with men of unknown ages ($N = 13$) and the aforementioned outliers excluded. For all outliers identified, values were > 3 standard deviations from the mean in their univariate distributions, and the residuals of a regression of these variables on mean f_o and covariates were > 3 standard deviations from the mean residual score; Fig. 3). Finally, we ran the same analyses using negative binomial rather than ordinary least-squares regression (for number of offspring data only, as they conform to the assumptions of a negative binomial distribution).

3.2. Results

Descriptive statistics and correlations between men's f_o and all dependent and control variables are presented in Tables 1 and 2, respectively. Of the dependent variables, only men's log-transformed number of offspring and wives' reproductive rate were significantly (negatively) correlated with men's f_o . In addition, neither control

variable (i.e., the Wealth and Size PC scores) was correlated with men's f_o . There was no effect of microphone type (Zoom H4n built-in vs. Sennheiser MKH-80) on f_o ($t_{63} = 0.28$, $p = .779$).

With covariates statistically controlled and outliers removed, men's f_o continued to negatively predict both men's log-transformed number of offspring and their wives' reproductive rate (Table 3). This was also the case when men whose exact ages are unknown were excluded from analysis (see Supplementary Table 5). However, when covariates were statistically controlled and outliers were included, subjects' mean f_o did not significantly predict proxies for reproductive success (Fig. 3). Assuming negative binomial distributions for men's and wives' reproductive success also produced non-significant relationships between these variables and f_o (see Supplementary table 5).

We conducted a mediation analysis (Preacher & Hayes, 2004, 2008) to determine whether wives' reproductive rate mediated the relationship between men's f_o and number of offspring. In other words, did men with lower f_o achieve higher reproductive success by marrying women who produced offspring at a higher rate? With outliers removed, the relationship between mean f_o and men's reproductive success was mediated by their wives' reproductive rate (Fig. 4). While the total effect of mean f_o and men's reproductive success was negative and statistically significant ($\beta = -0.18$, 95% CI $[-0.32, -0.05]$, $p = .01$), when divided into average causal mediation effects (ACME) and average direct effects (ADE), only the ACME remained statistically significant ($\beta = -0.13$, 95% CI $[-0.24, -0.04]$, $p = .006$; ADE: $\beta = -0.05$, 95% CI $[-0.16, 0.06]$, $p = .342$), indicating at least partial mediation. As the direct effect of mean f_o on men's reproductive success is not significant in the mediation model, we cannot reject the hypothesis of full mediation by wives' reproductive rates.

4. Discussion

Results from Study 1 show that lower f_o strongly increased men's perceptions of physical formidability, perhaps because a low f_o is indicative of male condition or competitive ability. However, f_o did not influence men's perceptions of prestige, and lower f_o decreased women's perceptions of men's attractiveness and desirability for marriage. A deep male voice appears to function more effectively and consistently in augmenting men's apparent formidability than in attracting mates (Puts et al., 2007; Puts et al., 2016; Saxton et al., 2016). In this regard, men's voices resemble other secondary sexual characteristics, such as facial hair and a masculine facial structure (Dixson & Vasey, 2012; Hill et al., 2017; Puts, 2010; Puts et al., 2016; Saxton et al., 2016; Scott et al., 2014).

Because signals used in intrasexual competition tend to be costly to produce and maintain and are constantly tested by competitors, they should also provide information about mate quality (Berglund & Pilastro, 1996). Tsimané women's preferences for the more feminine among male voice pairs may thus be the result of a mate choice strategy that prioritizes other characteristics (e.g. trustworthiness, prestige, high quality paternal care) over traits that convey dominance to competitors. Mean pitch was lower in U.S. compared to Tsimané men (111.4 vs. 126.0 Hz in our sample), and perhaps Tsimané women would prefer voices that are low for Tsimané men, but not as low as the mean f_o stimuli (111.4 Hz). However, this seems unlikely, as feminized stimuli (139.6 Hz) were nearly 14 Hz above the Tsimané male mean and were still preferred by Tsimané women.

Alternatively, under some circumstances, women may avoid masculine partners because of attending costs. A masculine voice suggests the increased capacity for physical violence, as the present research illustrates, whereas feminine male voices have been perceived as generous and investing toward romantic partners (O'Connor, Fraccaro, & Feinberg, 2012). Despite the potential benefits of mating with men with low voice pitch, Tsimané women may avoid such men because they appear uninvesting and potentially coercive. Indeed, 85% of Tsimané women reported spousal abuse, and wives' jealousy over husbands'

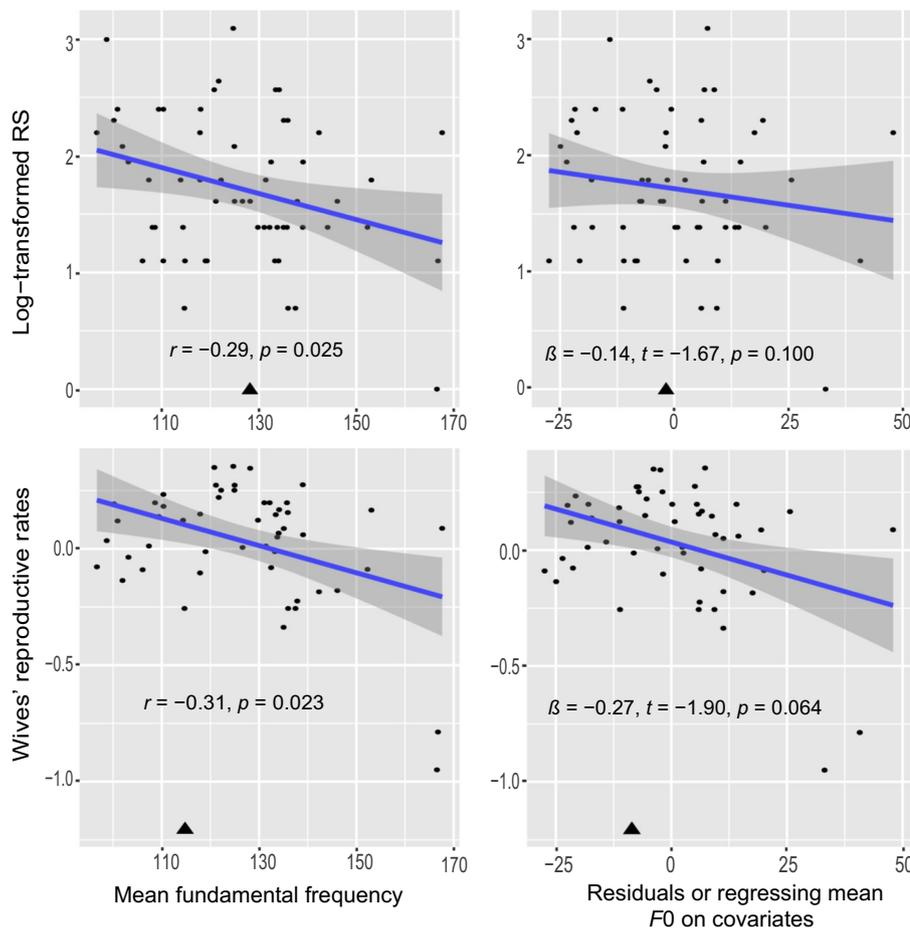


Fig. 3. Subjects' mean f_0 plotted against own and wives' reproductive rate. Male subjects' log transformed reproductive success (top panels) and their wives' reproductive rate (bottom panels) plotted against subjects' mean f_0 (left panels) and the residuals of a linear model regressing mean f_0 on model covariates (age, age², Wealth PC score, and Size PC score). Results of Pearson correlation reported for simple bivariate (left panel) plots. Results of linear models including covariates reported on adjusted mean f_0 (right panel) plots. Points are individuals, blue line is line of best fit, and dark gray shaded area is 95% confidence interval of the line. Triangles are outliers on univariate reproductive success distributions and have outlier residuals from line of best fit. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1
Study 2 descriptive statistics.

Variable	Men (N = 67)		Women (N = 59)	
	Mean	SD	Mean	SD
Age	33.32	11.21	30.80	10.36
f_0 (Hz)	125.61	16.38		
Height (cm)	64.20	6.83		
Weight (kg)	166.34	5.55		
Biceps (cm)	30.80	2.07		
Wealth (Bs.)	2577.57	1420.67		
Current wives	0.94	0.38		
Total wives	1.16	0.41		
Total children	5.58	4.18	5.42	3.54
Offspring mortality ^a	14.70%	17.30%	16.80%	14.86%
Age at birth 1st child	21.24	4.29	17.50	3.10

^a Proportion of offspring who died before age 16.

extramarital affairs was the most likely subject of arguments that led to such abuse (Stieglitz, Gurven, Kaplan, & Winking, 2012; Stieglitz, Kaplan, Gurven, Winking, & Tayo, 2011). U.S. women primed with images of male-on-female aggression prefer less masculine faces and voices compared to women exposed to other primes (Li et al., 2014), and among Colombian women, those living under conditions of greater violence tended to prefer less masculine male faces (Borras-Guevara, Batres, & Perrett, 2017).

In Study 2, men with a lower mean f_0 had more offspring, and their wives had higher reproductive rates (Table 1). When covariates (i.e., age, wealth, size) were included as predictors along with f_0 in multiple regression models, these relationships remained statistically significant upon excluding outliers or men whose exact ages were unknown, but

Table 2
Zero-order correlations between f_0 and dependent variables (all Ns = 62).

Dependent	Pearson's r	p-value
Current wives	0.05	0.709
Total wives	-0.20	0.127
Offspring mortality ^a	0.02	0.901
Age	-0.02	0.130
Wealth ^b	-0.19	0.153
Size ^b	-0.12	0.377
Age at 1st reproduction	-0.14	0.321
Wives' age at 1st reproduction	-0.10	0.449
Log number of offspring	-0.29	0.025*
Wives' reproductive rate	-0.31	0.023*

p-values between 0.05 and 0.10

^a Proportion of offspring who died before age 16.

^b Scores on PC1 (Size) and PC2 (Wealth).

* significant at $\alpha = .05$.

not with both outliers and men of unknown age included. Fundamental frequency did not predict men's number of current or total wives, offspring mortality rate, or own or wives' age at first birth in either zero-order correlations or any main analysis or robustness check model. These results are consistent with a prior finding that perceptions of Tsimané men's fighting ability (linked to low f_0 in the present research) are associated with intra-marital fertility but not offspring mortality when controlling for age (von Rueden et al., 2011), although this study did not control for male wealth or size. Low male f_0 also predicted greater numbers of sexual partners in U.S. undergraduate students (Puts, 2005), as well as higher reproductive success among Hadza foragers of Tanzania (Apicella et al., 2007), and a non-significant but negative relationship between f_0 and reproductive success was reported

Table 3
Summary of linear regression model results, controlling for age, age², Wealth, and Size, and with outliers removed; each row is a unique model.

Dependent	β	<i>t</i> -statistic	<i>p</i> -value
Current wives	0.02	0.17	0.867
Total wives	-0.12	-0.94	0.357
Offspring mortality ^a	0.05	0.33	0.745
Age at 1st reproduction	-0.06	-0.43	0.666
Wives' age at 1st reproduction	-0.13	-0.93	0.356
Log number of offspring	-0.14	-1.67	0.039*
Wives' reproductive rate	-0.27	-1.90	0.008*

^a Proportion of offspring who died before age 16.

* $p \leq .05$.

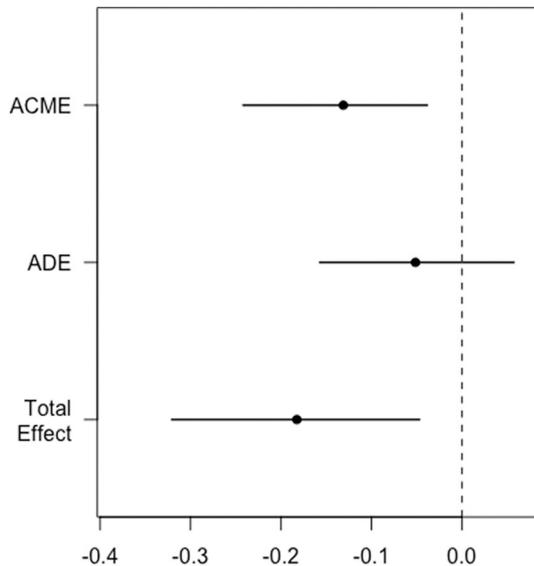


Fig. 4. The mediating effect of wives' reproductive rate on the relationship between subjects' mean f_0 and their reproductive success. Total effect is the standardized total effect of mean f_0 on men's reproductive success. Average causal mediation effects (ACME) represents the effect of wives' reproductive rate on men's reproductive success, while average direct effects (ADE) represents the direct effect of mean f_0 on men's reproductive success, excluding the effects of wives' reproductive rate. Filled circles are point estimates, and horizontal lines represent 95% confidence intervals. The vertical line is zero; if a point estimate's 95% CI crosses this line, the relationship is not significant at $\alpha = 0.05$.

among the Himba of Namibia (Atkinson et al., 2012). Our results provide evidence that Tsimané men with lower f_0 produce more offspring, and that this is due to their having wives with higher reproductive rates (Fig. 4; Supplementary Table 5). These associations were robust across many, but not all, statistical approaches and analytical decisions.

4.1. Limitations

We recognize several limitations to this research. First, we could not measure every avenue by which men's f_0 might influence their mating or reproductive success. For example, a low f_0 could increase men's extra-pair copulations. Indeed, prior work found that Tsimané men who were perceived as being better fighters had more extra-marital affairs (von Rueden et al., 2011). Low f_0 might also help men guard against their wives' infidelity by intimidating potential interlopers. Additionally, men with low f_0 may be more fertile themselves (Puts, 2006), although f_0 did not predict semen quality in an Australian university sample (Simmons et al., 2011). Moreover, f_0 may correlate with traits that influence fitness but for which we did not statistically control. The independent contribution of f_0 to men's fitness may be

correspondingly smaller than our estimate ($\beta = -0.14$). Indeed, Atkinson et al. (2012) found the relationship between men's f_0 and their reproductive success to be substantially weaker, albeit in the same direction ($\beta = -0.04$) in a sample of men from Namibia. However, Apicella et al. (2007) obtained a stronger estimate of this relationship among the Hadza ($\beta = -0.32$). In addition, we did not control for village membership in our statistical analyses as the small number of villages and small number of subjects per village make within- and between- village analyses impractical, and adding an additional covariate to an already crowded model would decrease our ability to detect true effects. The modest size of the present sample also decreases the precision of effect size estimates, and some analyses were sensitive to the exclusion outliers and other analytical decisions.

5. Conclusions

Among anthropoid primates, male mating competition favors low male f_0 relative to female f_0 (Puts et al., 2016), and humans appear to be no exception. Men's voice pitch drops a full octave at puberty, when traits important in mating competition tend to develop across species (Hill et al., 2017). In diverse samples, a lower voice pitch in men increases perceptions of intrasexual competitiveness and predicts mating success and reproductive success. By examining the influence of f_0 on men's success under inter- and intrasexual competition for mates in a small-scale society, the present work provides evidence that men's f_0 was – and in some populations, continues to be – shaped by intrasexual competition for fertile mates.

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Data availability

The data associated with this research are available at <https://osf.io/en8bs/>.

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Open practices

The experiment in this article earned Open Materials and Open Data badges for transparent practices. Materials and data for the experiment are available at (URL will appear here).

Declarations of interest

None.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.evolhumbehav.2019.07.002>.

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