TOTAL SEXUAL SELECTION ON MEN’S VOICES

A Thesis in

Anthropology

by

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Abstract

The human voice is particularly well suited for the study of sexual selection in humans. Vocal traits exhibit some of the largest human sex differences, these differences emerge during sexual maturation, and sexually differentiated vocal traits are linked to men’s mating and reproductive success. Men’s voices differ from women’s in pitch, timbre, and pitch variation. Prior experimental research has examined the influence of pitch and timbre on perceptions relevant to sexual selection, such as dominance and attractiveness, but the effects of pitch variation are unclear. Correlational research is also necessary to determine the relative importance of these different acoustic parameters in naturally varying speech, but prior correlational research is sparse and generally limited to estimating directional selection. We conducted two studies to fill these gaps in knowledge. In the first study, we manipulated pitch variation to observe its influence on perceptions of attractiveness, dominance, and prestige. In the second study, we examined linear, quadratic and interaction effects of all three parameters on perceptions of dominance and attractiveness. Experimentally manipulated pitch variation negatively, quadratically affected perceptions of attractiveness to women and dominance and prestige to other men. In regression models using naturally varying speech, mean pitch and timbre, but not pitch variation, predicted perceptions of dominance and attractiveness. Pitch negatively, linearly predicted dominance and attractiveness, and timbre negatively quadratically predicted attractiveness and negatively linearly predicted dominance. These results suggest that men’s vocal pitch and timbre signal dominance and mate quality, and that both inter- and intrasexual selection shaped men’s voices over human evolution.
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1. Introduction

Acoustic signals comprise the class of traits most frequently demonstrated to be sexually selected (Andersson, 1994). Songs, calls, and other acoustic signals have been shown to play a role in intersexual mate choice (typically female mate choice) and/or intrasexual competition and aggression (typically male-male competition) across diverse taxa. These taxa include insects, anurans, and birds; as well as mammals including primates such as gibbons, howler monkeys, and orangutans (Andersson, 1994). Research also suggests that acoustic signals once believed to have no sexual function (e.g. some alarm calls) may in fact play a role in sexual selection (e.g. as male displays) (Greig & Pruett-Jones, 2009).

Understanding the components of signals, including their variability and correlates is crucial to determining the role of the signal in sexual communication (Rivero, Alatalo, Kotiaho, Mappes, & Parri, 2000). For instance, if vocal signals vary in attractiveness, it is important to understand what influences the attractiveness of the signal (Zuckerman & Miyake, 1993). According to the source-filter theory of acoustic speech production, vibration of the vocal folds in the larynx serve as an acoustic signal generator, or source (Fant, 1960). This signal is then modified (filtered) as it travels through the supralaryngeal vocal tract, a tube-like structure that selectively amplifies certain frequencies (Reby & McComb, 2003). The filtering of the signal determines the spectral envelope of the sound which can be characterized by predominant peaks known as formants (Fant, 1960). Vocal parameters that arise from the source can vary independently from those parameters that arise from the filter; either or both may provide information about the sender (Fitch & Hauser, 2002). Speech is thus a complex signal made of multiple components perceived within the same sensory modality (i.e. hearing) (Hebets & Papaj, 2004; Rowe, 1999). Acoustic signals can indicate the sender’s species, group affiliation, age, sex, dominance status, physical condition, or individual identity simultaneously (see Gerhardt, 1992).

To establish relationships between a vocal signal and its function requires identifying the properties that provide information and demonstrating that this information is perceived and acted upon
(Gerhardt, 1992). Research on the use of multiple cues in mate choice shows that each component may contain its own information and can potentially be evaluated together to indicate the general quality of the sender, alternatively different receivers may pay attention to different components and thus different aspects of sender quality (Candolin, 2003). Sexual selection theory predicts that intersexual mate choice favors the evolution of charms and ornaments while same-sex contests favor size, strength, weapons, and aggression (Andersson, 1994; Darwin, 1871). Males and females have likely evolved to respond to different components of a complex signal. To understand the total sexual selection operating on a signal, it is important to determine the relative contributions of intrasexual competition and intersexual mate choice to each component (Hunt, Breuker, Sadowski, & Moore, 2009).

Human voices show large sex differences in multiple acoustic parameters, including pitch (measured by mean fundamental frequency, $F_0$) and timbre (measured from formant frequencies) (Fitch, 1997; Puts, Apicella, & Cárdenas, 2012). Vocal pitch and timbre sexually differentiate during puberty (Titze, 2000). These two vocal traits also predict men’s attractiveness (Feinberg, Jones, Little, Burt, & Perrett, 2005) and dominance (Puts, Hodges-Simeon, Cárdenas, & Gaulin, 2007), as well as mating success (Hodges-Simeon et al., 2011; Puts, 2005), and reproductive success (Apicella, Feinberg, & Marlowe, 2007)(See also Puts, Jones, & DeBruine, 2012 for a review). These results suggest an evolutionary history of sexual selection on the pitch and timbre of men’s voices.

Growing evidence suggests that pitch variation or monotonicity (measured by standard deviation in fundamental frequency, $F_0$-SD) has also been a target of sexual selection in men. Pitch variation is highly sexually differentiated (Hodges-Simeon et al., 2011; Puts, Apicella, et al., 2012). Some research indicates negative correlations between pitch variation and men’s attractiveness and dominance (Hodges-Simeon, Gaulin, & Puts, 2010), physical aggression (Puts, Apicella, et al., 2012), and mating success (Hodges-Simeon et al., 2011). Whereas much experimental research has explored the effects (and moderators) of pitch and timbre on perceptions of attractiveness and dominance, only one study has explored the effects of pitch variation, perhaps because of the technical difficulty of doing so.
systematically. Although Riding et al. (2006) found no effect of manipulating men’s pitch variation on attractiveness to women, they did not explore the effects of pitch variation on perceptions of dominance among men.

In order to understand how sexual selection shaped men’s voices and what they advertise to competitors and potential mates, it is necessary to establish the relative importance of different acoustic parameters to success under intra- and intersexual selection. What are the relative contributions of mean pitch, pitch variation, and formant structure to attracting mates, for example? What are their contributions to perceptions of dominance?

Hodges-Simeon et al. (2010) attempted to resolve such questions by analyzing relationships between acoustic parameters and perceptions of attractiveness and dominance using naturally varying, unscripted speech. However, although only ratings of unmanipulated stimuli were analyzed, raters also heard recordings experimentally manipulated in both fundamental frequency and formant structure. This may have diminished the effects of fundamental frequency and formant structure on ratings of unmanipulated stimuli (Hodges-Simeon et al., 2010). Moreover, the measure of formant structure utilized (average distance between consecutive formant frequencies) has been shown to be less sexually dimorphic and less strongly related to measures of men’s physical prowess than the mean standardized formant frequency (“formant position”) (Puts, Apicella, et al., 2012). Finally, although some evidence suggests stabilizing selection on male vocal parameters (reviewed in Puts, Jones, et al., 2012), previous studies have explored only linear (e.g., Collins, 2000) or linear and interaction (Hodges-Simeon et al., 2010) terms, but not quadratic terms, in predicting men’s attractiveness and dominance.

The present research attempted to fill these gaps. In study 1, we experimentally manipulated pitch variation to determine its effects on fitness under sexual selection. We used multivariate analyses to evaluate sexual selection via mate choice (indicated by attractiveness to females) and contest competition (indicated by dominance and prestige among men) in the evolution of masculine pitch variation (i.e. monotonicity). Multivariate analysis also indicates the form of selection (e.g. directional
vs. stabilizing). In study 2, we examined total sexual selection on men’s voices, using multivariate analysis to determine the relative linear, quadratic, and interactive contributions of pitch, pitch variation, and formant structure to perceptions of attractiveness and dominance.
2. Study 1

2.1 Methods

2.1.1. Voice Recording, Analysis, and Manipulation

Six male undergraduates from a large Midwestern U.S. university read the first sentence of the “Rainbow Passage” (Fairbanks, 1960) in an anechoic recording booth into a Shure SM58 vocal cardioid microphone. A curved wire projection from the microphone stand kept each participant’s mouth approximately 9.5 cm from the microphone. Recordings were made in mono at a sampling rate of 44,100 Hz and 16-bit quantization using Goldwave software. All files were saved as uncompressed “.wav” files.

Each recording was analyzed using Praat software (version 5.2.27). Praat determines fundamental frequency (pitch) using acoustic periodicity detection on the basis of autocorrelation, the correlating of a time-domain signal with itself (Boersma & Weenik, 2011). This technique is more accurate, noise-resistant, and robust, than alternative methods such as cepstrum or comb techniques (Boersma & Weenik, 2011). A pitch floor of 75 Hz and a pitch ceiling of 300 Hz were used in accordance with the programmers’ recommendations for male voices (Boersma & Weenik, 2011). All fundamental frequency ($F_0$) and frequency variation (F0SD) values were converted from Hz (cycles per second) to ERB (equivalent rectangular bandwidth). The greater linearity between ERB and psychosocial auditory perception allows for more perceptually uniform manipulation across voice recordings from different speakers.

Using a Praat script, fundamental frequency variation ($F_0$ variation) was manipulated to create the experimental stimuli. Fundamental frequency ($F_0$, pitch) was manipulated according to the following formula:

$$\text{new } F_0(x) = \text{mean } F_0 + ((x - \text{mean } F_0) * w)$$

(1)
The fundamental frequency of each point \((x)\) in the accompanying pitch tier was increased or decreased by an intonation factor \((w)\). The intonation factor is the amount of manipulation applied to fundamental frequency variation across the utterance. Intonation factors greater than one result in more dynamic/less monotone voices (greater pitch variation), and those between 0 and 1 produce less dynamic/more monotone voices (lower pitch variation). Using Praat, we increased and decreased the \(F_0\) variation of each voice stimulus by both one and two within-sex standard deviations for a total of five levels: -2SD, -1SD, unmanipulated, +1SD, +2SD corresponding to the most monotone, more monotone, unmanipulated, less monotone, and least monotone treatments respectively.

2.1.2. Raters

One hundred sixty-five undergraduates (122 women) from a large, northeastern U.S. university participated as raters in this Institutional Review Board- approved study (mean age ± SD=20.38 ± 1.26 years, range=18-26). Raters identified as 72.7 percent White, 9.7 percent Black or African American, 8.5 percent Asian, 4.8 percent Hispanic or Latino, 3.6 percent other, and 0.6 percent (one rater) American Indian or Alaska Native. Participants were asked about their present sexual fantasies and present sexual feelings while taking a demographic survey. 93.3 percent of raters self-identified as heterosexual.

Female raters completed a menstrual cycle survey. We assessed menstrual status (whether or not a participant was currently having menstrual periods), menstrual cessation (for any reason other than pregnancy), first day of bleeding of the last menstrual period, expected first day of bleeding for the next menstrual period, average cycle length, menstrual cycle regularity, contraceptive use, and pregnancy status. We used menstrual cycle information to estimate the rater’s risk of conception at the time of the trial because previous research has found that women's preferences for masculine voices vary over the course of the cycle (Feinberg, Jones, & Smith, 2006; Puts, 2005, 2006).

2.1.3 Procedure

Raters sat at an isolated computer station and wore headphones (Sony MDR-V250 or Sennheiser HD 280, 64 ohm headphones) during the experiment. Each rater listened to the complete set of 30
stimuli (four manipulations and one original sample from six different voices). Stimuli were presented one at a time, in random order via SuperLab stimulus presentation software. After each stimulus was played, an on-screen prompt instructed the rater to evaluate the voice on a ten-button scale with only the ends labeled. Men rated each stimulus for physical dominance on a scale from “not dominant at all” to “extremely dominant” and for prestige on a scale from “no prestige” to “extremely high prestige”. Women rated each stimulus for attractiveness in a short-term mating context and for long-term mating desirability on scales from “not attractive at all” to “extremely attractive”. Each participant listened to each voice and rated it on one perception and then repeated the trial, rating voice samples for the second perception rated by that sex. The order of rating tasks was assigned randomly across raters but was held constant within raters.

A definition of each dependent variable was presented with each rating task. We defined short-term attractiveness as “desirability for a short-term, purely sexual relationship such as a one-night stand.” We defined long-term attractiveness as “desirability for a long-term, committed relationship such as steady dating or marriage.” We defined physical dominance as “capability of winning physical contests, such as sports and physical fights.” We defined prestige by explaining that someone high in prestige “is respected, admired, and held in high esteem. People consider him an expert, talented and likely to be successful in some areas, value his opinion and want to be like him.” Henrich & Gil-White (2001) argue that in contrast to dominance, prestige is a “second avenue to human status and status competition” based on freely conferred deference.

2.1.4 Data analysis

We examined the effect of the manipulations within voices while controlling for between-voice variability by calculating the difference in ratings between the unmanipulated stimulus and the manipulated stimulus for each participant’s assessment of each voice.

We conducted a multivariate analysis of variance (MANOVA) to test for significant effects of pitch variation on mean differences in physical dominance and prestige for male raters to account for
experiment-wise error. We performed a separate MANOVA to test for significant effects of pitch variation on mean differences in the attributes short-term attractiveness and long-term attractiveness for female raters. In the presence of a significant variance, we conducted post-hoc tests to examine differences between manipulation levels using a Bonferroni correction at the $\alpha=0.05$ significance level. To further characterize the influence of pitch variation on selection, we performed curve estimations. All data analyses were performed in IBM SPSS version 20.

2.2 Results

In a MANOVA in which conception risk was treated as a covariate with manipulation while controlling for the influence headphone type, conception risk was not a significant predictor of differences in rating from the unmanipulated stimuli ($Pillai’s Trace(2,3263)=0.000, F=0.283, p=0.754$). In an additional multivariate analysis treating headphone type as a covariate with manipulation, conception risk, and the interaction between manipulation and headphones, neither headphone type ($Pillai’s Trace(2,3258)=0.001, F=1.955, p=0.142$) nor the interaction between headphone type and manipulation ($Pillai’s Trace(8,6518)=0.002, F=.739, p=0.657$) was a significant predictor of differences in rating from the unmanipulated stimuli. Consequently, neither headphone type nor conception risk was used in subsequent analysis.

Multivariate analysis of variance (MANOVA) revealed a significant effect of pitch variation (i.e. manipulation) on mean difference in perceptions related to male-male competition (i.e. physical dominance and prestige) ($Pillai’s Trace(8,2570)=0.031, F=5.058, p=<0.0001$). Levene’s test suggested unequal variances for physical dominance ($F(4,1285)=79.445, p=<0.0001$) and prestige ($F(4,1285)=84.667, p=<0.0001$). However, analysis of variance (ANOVA) is robust against unequal variances considering the equality of sample sizes, so ANOVAs are reported with an $\alpha=0.025$. Tests of between-subjects effects reveal a significant effect of pitch variation (i.e. manipulation) on both physical dominance ($F(4)=5.097, p=<0.001$) and prestige ($F(4)=4.940, p=<0.001$). Correction for multiple comparisons using the Bonferroni method can be found in Appendix A1.
An independent MANOVA revealed a significant effect of pitch variation on mean difference in perceptions related to female mate choice (i.e. short-term and long-term attractiveness) (*Pillai’s Trace*\(_{8,7310}=0.028, F=12.750, p=<0.0001\)). Levene’s test suggested unequal variances for short-term attractiveness (*F*\(_{4,3655}=214.926, p=<0.0001\)) and long-term attractiveness (*F*\(_{4,3655}=198.341, p=<0.0001\)). ANOVAs are reported with an *α*=0.025. Tests of between-subjects effects reveal a significant effect of pitch variation (i.e. manipulation) on both short-term attractiveness (*F*\(_{4}=13.431, p=<0.0001\)) and long-term attractiveness (*F*\(_{4}=13.584, p=<0.0001\)). Correction for multiple comparisons using the Bonferroni method can be found in Appendix A2.

Overall, manipulations generally made the voices sound less attractive, dominant, and prestigious. The less monotone manipulation was more prestigious than the unmanipulated, and the less monotone manipulation was only slightly less attractive than the unmanipulated voice for raters rating for long-term attractiveness although these trends were non-significant. This tendency creates a convex, parabolic relationship between pitch variation and all four attributes. (Fig. A.)
Figure 1: The level of manipulation in increments of one within-sex SD (x-axis) affects the mean difference in rating from the unmanipulated stimuli (y-axis) for each perception (with interpolation lines).

According to curve estimation, pitch variation affected short-term attractiveness to women significantly and quadratically ($R^2=0.013$, $F_{(2,3657)}=23.382$, $p<0.0001$). Although pitch variation linearly affected long-term attractiveness to women ($R^2=0.002$, $F_{(1,3658)}=5.910$, $p=0.015$), the quadratic effect was stronger ($R^2=0.014$, $F_{(2,3657)}=26.795$, $p<0.0001$). Pitch variation also quadratically affected perceptions of physical dominance ($R^2=0.014$, $F_{(2,1287)}=8.861$, $p<0.001$). Although pitch variation linearly affected variance in men’s prestige ratings ($R^2=0.003$, $F_{(1,1288)}=4.172$, $p=0.041$), again the quadratic effect was stronger ($R^2=0.014$, $F_{(2,1287)}=9.333$, $p<0.0001$).
3. Study 2

3.1 Methods

3.1.1 Participants

One hundred seventy-five self-identified heterosexual male undergraduate students (mean age ± SD=20.9±1.7 years) participated in this IRB-approved study at a large Midwestern U.S. university. Participants self-identified as 90.3 percent White, 3.4 percent Asian, 2.3 percent Black or African American, 2.3 percent Hispanic or Latino, 0.6 percent American Indian or Alaska Native, and 1.1 percent other.

3.1.2 Voice recording and measurements

Participants scheduled two laboratory sessions, approximately 1 week apart. Voice recordings were made at each session, and participants were recorded using the same protocol described in study 1.

Each recording (duration Mean± SD = 5.33±0.69 seconds) was analyzed using Praat for pitch or fundamental frequency \((F_0)\) (Mean± SD = 112.5±14.6 Hz), fundamental frequency variation or monotonicity \((F_0\) variation) (Mean± SD =15.9±4.5 Hz), and four formant frequencies \((F_1 - F_4)\) (Mean± SD = 444.2±30.1 Hz for F1, 1512.6±64.5 Hz for F2, 2397.5±83.0 Hz for F3, & 3388.6±113.7 Hz for F4). We used a pitch floor of 75 Hz and a pitch ceiling of 300 Hz, in accordance with the programmer's recommendation for male voices (Boersma & Weenik, 2011) and default settings for all other program parameters.

Formants \(F_1\) through \(F_4\) were measured at each glottal pulse (automatically detected by Praat) and averaged across measurements. This procedure calculated formant measurements for the entire utterance, sampling a greater range of vocal tract configurations when compared with only measuring individual vowels. This method measures only voiced speech, avoiding fricatives, which artificially lower apparent vocal tract length because the fricative originates in oral turbulence, not vocal fold vibration (Baken, 1987)
Praat sometimes shifts formants (e.g. calculating F2 as F1). Because of this tendency, formant measurements from glottal pulses for which any value exceeded a predetermined threshold (less than 2% of pulses) were omitted. Published data were used to determine thresholds for formant measurements (Rendall, Koliias, Ney, & Lloyd, 2005), which were 1000, 2850, 2750 and 4500 Hz for F1-F4.

All measurements were converted from cycles per second (Hz) to equivalent-rectangular bandwidths (ERB). The greater linearity between ERB measurements and auditory perception allows for a more meaningful interpretation of data throughout the range of human vocal parameters. To convert from frequency in Hz ($F_c$) to ERB we used the formula described by Glasberg and Moore (1990):

$$ERB = 21.4 \times \log(0.00437 \times F_c + 1)$$  

We then calculated formant position ($P_f$). Formant position is the standardized between session mean of standardized formant values for the first $n$ formants, where formants are standardized using between-sex means and standard deviations.

$$P_f = \frac{\sum_{i=1}^{n} F'_i}{n}$$  

In this equation the standardized $i^{th}$ formant, and $n$ is the number of formants measured. Essentially, this method assigned each standardized formant a unit weight, rather than a beta weight obtained via regressing formants on sex or height. This approach follows Cohen (1990) who suggested that “unit weights have better predictive power than beta weights derived from moderate-sized samples”. (Puts, Apicella, et al., 2012)

Pitch ($F_0$) and pitch variation ($F_0SD$) were also averaged together for both sessions to create composite measures of pitch and pitch variation. Data from one session were used in lieu of means for
participants who only had one session of data. Twenty-three participants had only first session ratings. One of these participants does have second session measurements averaged into pitch and variation only. Three participants had only second session voice measurements and ratings. One participant had only first session ratings but was not rated for dominance. There is one less mean dominance score \((n=174)\).

3.1.3 Rating procedures

Five hundred sixty-eight men (mean age: 19.4±1.8 years) and 558 women (mean age: 19.1±2.4 years) from a large northeastern U.S. university rated voices in this study. Each rater assessed one of 30 stimulus sets. Each stimulus set contained 25 voice recordings. Recordings were randomly allocated to a set with only one recording per participant in each set. Each rater assessed an average of 24.9±2.6 voice recordings. Raters listened to the voices in this sample as well as the voices of male siblings and female participants not included in this sample. No rater assessed a voice more than once. Using 7-point Likert-type scales, women rated voices for short-term and long-term attractiveness, and men rated voices for physical dominance. The order of rating tasks (i.e. short- or long-term first) and the order of stimulus presentation were randomized. On average, 18.9 raters assessed each recording, and the first 15 ratings obtained for each voice and each type of rating were averaged to produce mean short-term attractiveness, long-term attractiveness, and physical dominance ratings. Additional ratings were discarded.

3.1.4 Data analysis

We used Pearson’s correlation to examine the relationship between short-term attractiveness and long-term attractiveness to determine the feasibility of creating a composite measure, attractiveness. Pearson’s correlation indicates a near-perfect correlation between long-term and short-term attractiveness \((r(173)=0.96, p<0.0001)\). A new variable, attractiveness (i.e. mean attractiveness), was used in further analysis.
We used regression techniques to quantify the strength and form of sexu
al selection, following
Hunt et al. (2009). First, we standardized trait values for mean pitch (mean \(F_0\)), pitch variation (\(F_0-SD\)),
and formant position (\(P_f\)) using the following formula:

\[
 z = \frac{(x - \mu)}{\sigma}
\]  

(4)

In this equation the mean of all data points (\(x\)) is subtracted from each individual value (\(\mu\)) and the
difference is divided by the standard deviation of the sample (\(\sigma\)) generating a standardized value for
each data point (\(z_i\)).

Then fitness (i.e. attractiveness and dominance) was converted to relative fitness (\(\omega\)) by dividing individual fitness (\(W\)) by mean fitness for the sample (\(\bar{W}\)).

\[
 \omega = \frac{W}{\bar{W}}
\]  

(5)

We examined zero-order correlations among all pair-wise combinations of the pooled set of
predictor and response variables (i.e. acoustic measurements [standardized trait values] and relative
sexual selection [relative attractiveness and relative dominance]) using Pearson’s \(r\).

Multiple regressions were used to calculate linear selection gradients:

\[
 \omega = \alpha + \beta_1 z_1 + \beta_2 z_2 + \beta_3 z_3 + \epsilon
\]  

(6)

In this equation, alpha (\(\alpha\)) is the regression intercept, Betas (\(\beta\))s are the partial regression
coefficients, and epsilon (\(\epsilon\)) is the random error component. The partial regression coefficients are the
standardized linear selection gradients. These coefficients estimate the contribution of a particular trait to fitness while holding the effects of the other traits constant. Beta represents the direction of the greatest incline from the population average on that particular fitness surface (Hunt et al., 2009; Lande & Arnold, 1983)

Nonlinear forms of selection are then estimated by running separate regressions that include quadratic \((z_i^2)\) and cross-product \((z_iz_j)\) terms:

\[
\omega = \alpha + \beta_1z_1 + \beta_2z_2 + \beta_3z_3 + \gamma_1z_1^2 + \gamma_2z_2^2 + \gamma_3z_3^2 + \rho_1z_1z_2 + \rho_2z_1z_3 + \rho_3z_2z_3 + \epsilon
\] (7)

The linear terms \((\beta)\) are not interpreted from this equation. Instead, the equation is used with higher order terms to indicate how selection influences the variance and covariance of traits when the effects of linear selection are removed (Hunt et al., 2009; Lande & Arnold, 1983). The \(\gamma\)-coefficients associated with the squared terms of each standardized variable reflect the direct effects of nonlinear selection on the trait variance. These coefficients characterize the curvature of the fitness surface along the individual traits axes \((z_1-3z_3)\) (Hunt et al., 2009; Lande & Arnold, 1983). A negative \(\gamma\) indicates convex (i.e. downwardly curved) selection while a positive \(\gamma\) indicates concave (i.e. upwardly curved) selection. The \(\rho\) coefficients for cross-products represent the direct effects of correlational selection for traits to become positively (positive \(\rho\)) or negatively (negative \(\rho\)) correlated (Hunt et al., 2009).

Hunt cautions that interpretation of nonlinear selection can be troublesome as the number of individual traits being examined increases (2009). When only a few traits show nonlinear forms of selection, the multiple-regression approach provides an adequate description and quantification (Hunt, Wolf, & Moore, 2007). Since the current analysis only involves three traits, canonical analysis was not employed.

Mitchell-Olds & Shaw (1987) caution that violation of distributional assumptions can make interpreting significance from this type of analysis problematic. We employed a resampling procedure to
evaluate the significance of both linear and nonlinear selection gradients. We randomly shuffled the response variable in each analysis (i.e. relative attractiveness and relative dominance) across individuals in the dataset. Through this procedure we obtained a null distribution for each gradient (i.e. no relationship between the standardized trait values and response variables. Therefore, we report all significant p-values following 10,000 randomizations of the response variable in each case (i.e. relative attractiveness and relative dominance). Reported probabilities represent the number of times out of 10,000 permutations of the data in which the pseudo-estimated gradient was less than or equal to the original estimated gradient. Separate permutation tests were run for the linear selection models and the full quadratic models (which included linear, quadratic, and interaction terms).

We performed all data analyses in IBM SPSS Statistics version 20.

3.2 Results

Zero-order Pearson correlations for ratings and acoustic measures are reported in Table 1.

<table>
<thead>
<tr>
<th></th>
<th>F₀-SD (N=175)</th>
<th>F₀ (N=175)</th>
<th>Attractiveness (N=174)</th>
<th>Dominance (N=174)</th>
</tr>
</thead>
<tbody>
<tr>
<td>F₀-SD (N=175)</td>
<td>0.157*</td>
<td>0.039</td>
<td>-0.131</td>
<td>-0.361****</td>
</tr>
<tr>
<td>F₀ (N=175)</td>
<td>0.541****</td>
<td>-0.187*</td>
<td>-0.321****</td>
<td></td>
</tr>
<tr>
<td>Attractiveness (N=175)</td>
<td>-0.324****</td>
<td></td>
<td></td>
<td>-0.427****</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>0.644****</td>
<td></td>
</tr>
</tbody>
</table>

*p<.05, **p<.01, ***p<0.001, ****p<0.0001

A linear regression revealed that formants, variation, and pitch predict a significant proportion of the variance in attractiveness (R²=0.12, F(3,171)=7.69, p<0.001). However, only pitch significantly linearly predicted attractiveness (β=-0.32, p<0.001; Fig 2.). A second linear regression including quadratic and interaction terms (R²=0.17, F(9,165)=3.85, p<0.001) indicated that (formant position)² significantly negatively predicted relative attractiveness (β=-0.18, p=0.036; Fig. 3).
A linear regression revealed that formants, variation, and pitch significantly predicted relative dominance ($R^2=0.30$, $F_{(3,170)}=24.74$, $p<0.0001$). Both pitch ($\beta=-0.38$, $p=0.0001$; Fig. 4) and formant position ($\beta=-0.34$, $p=0.0001$; Fig. 5) significantly and linearly predicted dominance. A second linear regression including quadratic and interaction terms ($R^2=0.34$, $F_{(9,164)}=9.41$, $p<0.0001$) indicated that (mean pitch)$^2$ significantly negatively predicted relative dominance ($\beta=0.18$, $p=0.047$). Curve estimation revealed that although pitch was quadratically related to dominance ($R^2=0.19$, $F_{(2,171)}=20.09$, $p<0.0001$), dominance is more accurately described as a linear function of pitch ($R^2=0.18$, $F_{(1,172)}=38.38$, $p<0.0001$).

\[\text{Figure 2: The relationship between standardized pitch (x-axis) and relative attractiveness (y-axis)}\]
Figure 3: The relationship between standardized formant position (x-axis) and relative attractiveness (y-axis)
Figure 4: The relationship between standardized pitch (x-axis) and relative dominance (y-axis)
Figure 5: The relationship between standardized formant position (x-axis) and relative dominance (y-axis)
4. Discussion

The lack of menstrual cycle effect supports the idea that fundamental frequency variation may provide state-dependent information in social settings where relationship dynamics are circumstantial. Previous research has shown that women’s preferences for masculine traits such as voices, facial structure, and facial skin color vary across the menstrual cycle (Puts, 2006). Several evolutionary explanations have been offered to account for these facultative fluctuations including adaptations for timing the recruitment of good genes from males of high genetic quality, adaptations for increasing the probability of conception, and a by-product of a hormone-response pattern favored during pregnancy (Puts, 2006). Traits that demonstrate these fluctuations are typically sexually dimorphic and sexually differentiate during the process of sexual maturity due to the influence of masculinizing androgens (Puts, 2006). Fundamental frequency variation (i.e. vocal monotonicity) is sexually dimorphic (Puts, Apicella, et al., 2012) and pitch variation is significantly correlated with voice pitch - a trait which sexually differentiates during puberty and is associated with an increased preference for masculine values (i.e. low pitch) as conception risk increases over the course of the cycle, an important pattern among traits for which female preference varies over the course of the cycle (Puts, 2006). Together, this led us to suspect that we might find a pattern of cyclic variation in preference for pitch variation.

Alternatively, preference for masculine pitch variation may primarily provide information that is not directly related to heritable genetic quality, male fertility, or a hormone associated response pattern. Pitch variation may indicate neuropsychological differences that impact physical control of the voice. In this case feminine pitch variation (i.e. high fundamental frequency variability, less vocal monotonicity) may be analogous to smiling, indicating both deference and affiliation (Hodges-Simeon et al., 2010). By contrast, masculine pitch variation may be associated confidence, status, and dominance. Previous research has demonstrated that masculine pitch variation is more strongly related to perceptions of dominance than attractiveness, and that modulation of pitch reflects relative dominance and submissiveness across animal species (see Puts, Apicella, et al., 2012 for a review).
The fact that we did not find a significant effect of conception risk suggests that pitch variation may reflect neuropsychological differences as we did not find evidence of cyclic fluctuation in preference for masculine pitch variation. However, this may also be related to the distribution of conception risk within our sample, as over 90% of our participants had a conception risk of zero. Future research should be conducted explicitly for the purpose of testing this relationship. It will be important in those studies to recruit women not using hormonal birth control, perhaps implementing a within-subjects design.

Importantly, we demonstrated that a moderate increase in pitch variation increased perceptions of prestige (although the mean is significantly different from only the least monotone manipulation). This result supports previous research associating moderate to high pitch variation with increased social attractiveness. In accordance with the discussion above, this result is consistent with idea of greater pitch variation being associated with deference and affiliation. In contrast, lower pitch variation may be an indicator of greater threat potential. Prior research has associated masculine pitch variation with physical measures of men’s threat potential, self-assessments of physical aggression, and perceptions of vocal dominance (Hodges-Simeon et al., 2010; Puts, Apicella, et al., 2012). However, our results did not support this prediction. Future research should evaluate the relationship between vocal monotonicity and additional correlates of competitive ability such as past success in fights and peer ranking of physical formidability (Puts, Apicella, et al., 2012).

Multivariate analysis of variance indicated that pitch variation has a significant effect on perceptions relevant to both mate choice and contest competition modes of sexual selection. Curve estimation indicated that a convex quadratic function significantly describes the relationship between experimentally manipulated pitch variation and short-term attractiveness as well as experimentally manipulated pitch variation and physical dominance. A convex quadratic function more significantly described the relationships between experimentally manipulated pitch variation and both long-term attractiveness and prestige than a linear function. Although this suggests stabilizing selection, it is
possible that the observed result reflects the effect of experimental manipulation. Future research on both experimental and naturally occurring stimuli is needed to determine if indeed intermediate phenotypes are the most fit under both intra- and inter-sexual forms of sexual selection. Importantly, we also demonstrate significant linear and non-linear forms of selection on masculine pitch variation under both forms of sexual selection. Future research will be designed to explicitly test the relative contributions of linear and non-linear forms of selection when both are significant (e.g. the relationship between pitch variation and long-term attractiveness).

According to our correlational research in naturally occurring speech, pitch negatively, linearly predicted relative attractiveness; however, formant position and pitch variation did not. This result supports current research suggesting that women use pitch to a greater degree than pitch variation or formants in assessing mate quality, and judge men with lower pitched voices to be more attractive. In naturally occurring speech formants are negatively, quadratically related to relative attractiveness (convex selection). This may suggest that men’s voices reflect a natural history of stabilizing selection for timbre, such that voices near the within-sex mean in formant position are the most attractive. Voices ‘too masculine’ in formant structure may sound harsh, unhealthy, or intimidating, while voices near the other end of the formant spectrum sound ‘too effeminate’. More work is needed to clarify the perceptual correlates of male timbre at these extremes. In contrast to our experimental results, in naturally occurring speech pitch variation is not significantly related to attractiveness, when controlling for the influence of pitch and formant structure. More research is needed to explicitly test the relative contributions of both pitch and timbre to linear and non-linear forms of selection in naturally occurring and experimental stimuli on perceptions of both short-term and long-term attractiveness.

Pitch and formant position linearly predicted relative dominance; however pitch variation did not, again contrasting the results from the experimental manipulation and the analysis of naturally occurring speech. Our results support research correlating masculine voice pitch with other measures of physical dominance such as height, weight, arm strength, and testosterone levels. Our results also support
research that correlates timbre with other measures of physical dominance such as height, weight, physical aggressiveness, and arm strength. Pitch also positively, quadratically predicts relative dominance (concave selection), but the relationship is predominately linear in nature. Together these results suggest that vocal masculinity serves as an indicator of threat potential. Future research should ascertain the relative contributions of both pitch and timbre to linear and non-linear forms of selection in naturally occurring and experimental stimuli on perceptions of both physical dominance and prestige.

It is important to note the contrast between our experimental and correlational results. Previous correlational research suggested the salience of masculine pitch variation in sexual selection on men’s voices. Previous experimental research was limited (i.e. only examined attractiveness and linear relationships). We used experimental manipulation to address previous limitations. Interestingly, our experimental manipulation allowed us to detect non-linear selection under both mate choice and contest competition. However this effect was found while holding all other variables constant. The effect determined in an experimental setting also depends on the size of manipulation. Once we found an effect experimentally, we could not be sure that naturally occurring pitch variation contributes meaningfully to perceptions of attractiveness and dominance. Indeed, when naturally occurring stimuli were considered, and the influence of all three traits accounted for; pitch variation was no longer a significant predictor of total sexual selection on men’s voices.

4.1 Conclusions

Study 1 suggests that pitch variation affects dominance and attractiveness perceptions in a curvilinear fashion. This result indicates that pitch variation has played a role in the perception of vocal masculinity for both men and women.

Study 2 suggests that pitch variation is not an important contributor to total sexual selection in male voices, relative to pitch and formant position in naturally-varying speech. Pitch is important to perceptions of attractiveness and dominance, but the ordering of magnitude suggests it is more important to dominance. This result indicates that selection for low-pitched voices is both intrasexual (related to
contest competition) and intersexual (related to mate choice). It also suggests a predominance (even if marginally) of contests competition in the evolution of masculine voice pitch, comparable to the predominance of contest competition in the evolution of other secondary masculine traits.

Study 2 also suggests that formant position negatively predicts attractiveness to women in a curvilinear fashion. Formant position negatively and linearly predicts physical dominance attributions by men. This result supports research correlating sexually dimorphic formant measurements (i.e. masculine vocal timbre) with attractiveness to women and indicators of physical dominance. That a linear relationship describes the association between formant position and dominance while a quadratic relationship describes the relationship between formant position and attractiveness may suggest that masculine vocal timbre plays a role in assessing the life history and health status of conspecifics. This may help explain why masculine vocal timbre is correlated with physical dominance attributions by men, and the perception of age in women. In comparison, formant structure has a more significant influence on dominance, again suggesting the primacy of contest competition in the evolution of vocal masculinity.

Importantly we demonstrate that vocal masculinity is salient to total sexual selection—demonstrating an effect on both contest competition and mate choice. This suggests that masculine voices may serve both as an indicator of threat potential to other males and as a sexual display to females.

The current study demonstrates that experimental results need to be interpreted in the context of related traits in naturally occurring stimuli. In general, we also present evidence of stronger selection on men's voices through male contests than female choice. More research is needed, designed explicitly to answer this question. Finally, future research should also determine if selection via contests in other traits is directional while selection via female mate choice on other, associated traits or trait components demonstrates stabilizing selection. This is one of the first studies to examine quadratic relationships between sexually dimorphic anthropometrics (i.e. vocal parameters) and sexual selection. Importantly,
we examined both linear and non-linear forms of selection under both contest competition and mate choice. This total sexual selection approach may prove to be highly useful in studying the natural history of sexually dimorphic traits in species with significant intra- and inter- sexual components of fitness.
### Appendix A: Multiple Comparisons - Intrasexual Selection

<table>
<thead>
<tr>
<th>Dependent Variable</th>
<th>Means Comparison</th>
<th>Mean Difference (I-J)</th>
<th>Std. Error</th>
<th>Sig. 95% Confidence Interval Lower Bound</th>
<th>Upper Bound</th>
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</thead>
<tbody>
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<td>Physical Dominance</td>
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<td>0.137</td>
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</tr>
<tr>
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<td>least monotone</td>
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<td>1.000</td>
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</tr>
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<td>0.146</td>
<td>1.000</td>
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</tr>
<tr>
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<td>less monotone</td>
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<td>0.146</td>
<td>1.000</td>
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<td>0.468</td>
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</tr>
<tr>
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<td>0.001</td>
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<tr>
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</tr>
<tr>
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<td>0.146</td>
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<td>0.011</td>
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</table>

Based on observed means. The error term is Mean Square(Error)=2.754

*The mean difference is significant at the .05 level.
### Appendix B: Multiple Comparisons- Intersexual Selection

**Bonferroni**

<table>
<thead>
<tr>
<th>Dependent Variable</th>
<th>Most Monotone</th>
<th>More Monotone</th>
<th>Unmanipulated</th>
<th>Less Monotone</th>
<th>Least Monotone</th>
<th>Std. Error</th>
<th>Sig.</th>
<th>95% Confidence Interval</th>
<th>Lower Bound</th>
<th>Upper Bound</th>
</tr>
</thead>
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<td>-0.35</td>
<td>-0.22</td>
<td>-0.41</td>
<td>-0.19</td>
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<td>0.094</td>
<td>-0.68 to -0.15</td>
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<td></td>
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<td></td>
<td>-0.66</td>
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<td>-0.22</td>
<td>-0.36</td>
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<td>-0.93 to -0.40</td>
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<tr>
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<td>-0.35</td>
<td>-0.36</td>
<td>-0.37</td>
<td>0.094</td>
<td>0.094</td>
<td>-0.62 to -0.09</td>
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<tr>
<td></td>
<td>-0.22</td>
<td>0.06</td>
<td>-0.22</td>
<td>-0.36</td>
<td>-0.37</td>
<td>0.094</td>
<td>0.094</td>
<td>-0.49 to 0.04</td>
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<td></td>
</tr>
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<td></td>
<td></td>
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<td>-0.19</td>
<td>-0.36</td>
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<td>0.094</td>
<td>-0.80 to 0.45</td>
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<td>Long-term</td>
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<td>-0.62 to -0.10</td>
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<td>-0.17</td>
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<td>0.092</td>
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</tr>
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</table>

Based on observed means. The error term is Mean Square(Error) = 3.092

*The mean difference is significant at the .05 level.*
References

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