



Original Article

The low male voice is a costly signal of phenotypic quality among Bolivian adolescents



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ABSTRACT

The human voice is one of the most conspicuous and dimorphic human secondary sexual characteristics; males' low fundamental and formant frequencies barely overlap with females'. Researchers often assert that low male voices are costly signals of phenotypic quality; however, no evidence currently exists linking low voices with indicators of quality (i.e., health or physical condition) during the ages where the larynx develops to adult proportions. In the present study, we examine the relationships between condition, testosterone, and vocal parameters in 91 Bolivian peri-pubertal adolescent males. Condition is operationalized as immune function (based on secretory IgA) and energetic reserves (BMI-for-age residuals from Tsimane-specific growth curves, and body fat percentage), and "masculine" vocal parameters is operationalized as having low fundamental frequency, narrow formant position, and low fundamental-frequency variation. We target peri-pubertal individuals to capture variation in vocal parameters during the canalization period for vocal fold and vocal tract growth. Results indicate that males in better energetic condition have higher testosterone levels and lower voices, controlling for age. Further, testosterone mediates the relationship between condition and a lower voice (i.e., lower fundamental and formant frequencies). We suggest that testosterone plays a key mediating role in the causal pathway linking phenotypic condition to a "masculine" voice. Our results provide support for a costly-signal model of low men's voices.

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1. Introduction

Secondary sexual characteristics facilitate male competitive and courtship interactions in a wide variety of vertebrates (Andersson, 1994). Among humans, one of the most conspicuous and dimorphic secondary sexual characteristics is the voice. Males have substantially lower fundamental and formant frequencies than women (Baken, 1987; Puts, 2005; Titze, 1994) due to testosterone-driven vocal fold enlargement and vocal tract lengthening during male puberty (Fitch & Giedd, 1999; Kahane, 1978; Harries, Hawkins, Hacking, & Hughes, 1998; Vuorenkoski, Lenko, Tjernlund, & Vuorenkoski, 1978). Lower male voices are perceived as belonging to men who are older (Collins, 2000; Feinberg, Jones, Little, Burt, & Perrett, 2005), larger (Collins, 2000; Feinberg et al., 2005), more physically and socially dominant (Puts, Gaulin, & Verdolini, 2006; Puts, Hodges, Cárdenas, & Gaulin, 2007; Sell et al., 2010; Wolff & Puts, 2010), and more attractive to women (Collins, 2000; Feinberg et al., 2005; Puts, 2005). These perceptions carry important reproductive, social, economic, and political consequences (Apicella, Feinberg, & Marlowe, 2007; Hodges-Simeon, Gaulin, & Puts, 2010; Klofstad, Anderson, & Peters, 2012; Tigue, Borak, O'Connor, Schandl, & Feinberg, 2012).

According to Hamilton and Zuk (1982), observers attend to conspicuous sexually dimorphic traits like the voice because they provide important information about the condition or quality of the speaker. In this model, quality- or condition-dependent characteristics provide conspecifics with honest signals of the bearer's genetic resistance to parasites due to the costs involved in building and maintaining the display trait (Zahavi, 1975). Folstad and Karter (1992) later proposed a proximate mechanism for this model; according to their 'immunocompetence handicap hypothesis' only males who are highly immunocompetent can tolerate the high testosterone (T) levels required to fully express their conspicuous characters. Experimental manipulation of T in animal models shows that high levels of T down-regulate humoral and cell mediated immune function (Duffy, Bentley, Drazen, & Ball, 2000) further supporting the idea that T imposes an immunosuppressant burden that only can be sustained by high quality individuals. Amendments to this view highlight the role of T as immunomodulatory rather than -suppressive (Braude, Tang-Martinez, & Taylor, 1999; Da Silva, 1999; McDade, 2003), upregulating investment in secondary sex characteristics like the voice only in response to surplus immune and energetic capacity (Bribiescas, 2001; Ellison, 2001; Muehlenbein & Bribiescas, 2005). In this way, T—and the signal traits developmentally influenced by T—can serve as costly indicators of quality-dependent condition to potential mates and competitors.

Among adults (Dabbs & Maling, 1999; Evans, Neave, Wakelin, & Hamilton, 2008; Hamdan et al., 2012; Puts, Apicella, & Cárdenas,

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2012) and adolescents (Harries, Walker, Williams, Hawkins, & Hughes, 1997; Pedersen, Moller, Krabbe, & Bennett, 1986), lower fundamental and formant frequencies are associated with higher T; however, no evidence currently links lower vocal frequencies with any indicators of phenotypic quality such as health or physical condition. Demonstration of relationships between circulating T, phenotypic quality, and vocal masculinization has been conspicuously missing, especially given the large evolutionary literature on vocal attractiveness and dominance judgments (e.g. Collins, 2000; Feinberg et al., 2005, 2006; Hodges-Simeon et al., 2010; Hodges-Simeon, Gaulin, & Puts, 2011; Puts et al., 2006, 2007; Wolff & Puts, 2010).

To explore these relationships, the present study assessed the degree to which vocal masculinization is influenced by immunological and energetic condition during adolescence, and evaluated the role of T as a possible mediator of this hypothesized developmental relationship. We target adolescence because sexual differentiation and, ultimately, final adult dimensions of the vocal tract develop during this time. Adolescence is also an important period for negotiation of status hierarchies (Ellis, Shirtcliff, Boyce, Dearnorff, & Essex, 2011), especially in small-scale societies where individuals often remain with the same peers through life. We predict that those in better energetic and immune condition will have lower fundamental and formant frequencies after controlling for age in our cross-sectional sample. With structural equation modeling we also test whether T mediates the relationship between condition and masculine voice characteristics. Among adults, energetic deficits (Friedl et al., 2000; Trumble, Brindle, Kupsik, & O'Connor, 2010) and immunological load (Simmons & Roney, 2009) are associated with lower T levels, and lower T levels impact vocal frequencies (Dabbs & Malinger, 1999; Evans et al., 2008; Hamdan et al., 2012). Chronic energy shortages due to high workloads, high pathogen load or other insults during the period of vocal tract development may result in less masculine age-adjusted adolescent (and, ultimately, adult) voices (Hodges-Simeon, Gurven, Cardenas, & Gaulin, 2013). Evidence of these relationships between stressors, hormone levels and voice parameters during the canalization period for sexual differentiation of the vocal tract would provide support for the costly-signaling model of male voice.

In this study vocal masculinization is indexed using three vocal parameters associated with greater dominance and attractiveness ratings in previous studies: low fundamental frequency (F_0 ; Feinberg et al., 2006; Puts et al., 2007), lower and more closely spaced formants (i.e., formant position, P_i ; Puts et al., 2012), and lower F_0 variation (F_0 -SD; Hodges-Simeon et al., 2010, 2011; Puts et al., 2012). F_0 is the primary determinant of perceived pitch, and formants provide a resonant quality or timbre to a voice.

We assess condition in two ways: energetic availability and immune function. Energetic budget is assessed using measures of adiposity; individuals with greater fat stores have greater available energy to allocate to biological demands. Immune functioning is measured using a biomarker of adaptive mucosal immunity, secretory IgA (sIgA). sIgA is the dominant immunoglobulin on mucosal surfaces (e.g., saliva, tears, breast milk), acting as the initial defence against invading pathogens in the oral and nasal cavities, respiratory system, gastrointestinal tract, and genito-urinary tract (Brandtzaeg, 2009). Low sIgA is indicative of depressed immunity and is associated with an increased risk of infections, particularly those of the upper respiratory tract (Drummond & Hewson-Bower, 1997; Fahlman & Engels, 2005; Nakamura, Akimoto, Suzuki, & Kono, 2006).

2. Methods

2.1. Population

The Tsimane are a small-scale, kin-based society of forager-horticulturalists in the lowland Amazonian forests of central Bolivia (Godoy et al., 2006; Gurven, Kaplan, & Supa, 2007; Gurven, Kaplan, Winking, Finch, & Crimmins, 2008). The Tsimane obtain the majority

of calories from non-market sources (Martin et al., 2012), and experience more energetically demanding conditions than in the developed world, including calorically demanding workloads, limited food supply and medical access, and no sanitation or water treatment infrastructure. These factors contribute to an immunologically challenging environment, one characterized by high rates of parasite infection (Vasunilashorn et al., 2010), respiratory and gastrointestinal disease (Gurven et al., 2008), and anemia (Vasunilashorn et al., 2010). Measures of phenotypic quality were specifically selected for this energetic- and immune-challenged population. Our measures of fat stores (Tsimane-specific BMI-for-age and body fat percentage) capture variation in adipose stores relative to peers, reflecting the sum of energetic (including immunological) demands to the phenotype. The high rates of periodontal and respiratory infections in the Tsimane in particular are targeted using sIgA levels.

2.2. Participants

Ninety-one males, aged 8 to 22 ($M \pm SD = 13.6 \pm 3.3$), participated in the present study. Ages were estimated by integrating multiple sources of information. Participants were asked their age and date of birth during testing sessions. Then, stated age was checked against the Tsimane Health and Life History Project (THLHP) census. Censuses have been collected and updated annually since 2002, in conjunction with demographic interviews on most adults. The demographic interviews employ a combination of methods (e.g., relative age list anchored by people of known age, photo comparisons with individuals of known ages, reconciling multiple sources of information on several generations), for aging adults and children (Gurven et al., 2007). Census ages are most accurate for children and adolescents because parents were interviewed when their child was young. Parents of the current participants are also more likely to keep documentation of their child's birth than earlier generations. For these reasons, census age was used when in conflict with stated age or when participants were unsure of their exact date of birth. Eight participants who did not know their birth date also could not be found in the census. These individuals were assigned their stated whole number age plus 0.5. Omitting these eight did not change the reported results, and therefore they are included in the sample.

2.3. Anthropometrics

Height and weight were measured in accordance with standard protocols (Lohman, Roche, & Martorell, 1988). To provide data on relative energetic status, age-standardized residuals were calculated for body mass index using Tsimane-specific BMI-for-age curves (BMI-R; Blackwell, Snodgrass, Madimenos, & Sugiyama, 2010). A second measure of energetic status—body fat percentage—was used in parallel with BMI-R in all analyses. This second measure uses the Slaughter algorithm, which is designed to accurately calculate body-fat percentage for adolescents using tricep and subscapular skinfolds (Slaughter et al., 1988).

2.4. Saliva collection and analysis

Participants discharged 1 mL of relatively bubble-free saliva via passive drool into a polystyrene cryotube. In order to mitigate contamination, participants rinsed their mouths with clean water prior to saliva collection. Because secretory IgA is affected by saliva flow rate, (Kugler, Hess, & Haake, 1992; Miletic, Schiffman, Miletic, & Sattely-Miller, 1996), start and end times of saliva collection were recorded and secretion rate was multiplied by the total concentration. Therefore, sIgA is expressed as a flow rate in $\mu\text{g}/\text{min}$. Cryotubes were then stored in liquid nitrogen while in Bolivia and transported on dry ice to University of California Santa Barbara where they remained frozen (at -80°C) until analysis, at which time they were shipped on dry ice to Salimetrics LLC (State College, PA).

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