



Masculine voice is associated with better mucosal immune defense in adolescent and adult males

Carolyn R. Hodges-Simeon^{a,*}, Graham Albert^a, Timothy McHale^{b,c}, Steven J.C. Gaulin^d, Michael Gurven^d, Nick Landry^e, Jessica K. Hlay^a, Nicole Merullo^a, David A. Puts^f, Steven A. Arnocky^e

^a Department of Anthropology, Boston University, Boston, MA, United States of America

^b Department of Anthropology, California State University, Dominguez Hills, United States of America

^c Department of Anthropology, California Polytechnic State University, San Luis Obispo, United States of America

^d Department of Anthropology, University of California Santa Barbara, Santa Barbara, CA, United States of America

^e Department of Psychology, Nipissing University, North Bay, ON, Canada

^f Department of Anthropology, Pennsylvania State University, State College, PA, United States of America

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ABSTRACT

The immunocompetence handicap hypothesis (ICHH) contends that testosterone-dependent, masculine traits are honest signals of the bearer's ability to withstand immunosuppression, yet empirical studies testing the ICHH have produced mixed results. The present research addressed the relationship between masculine vocal parameters and immunity in two samples: young adult men from the US and Canada ($N = 267$) and adolescent males from Bolivia ($N = 44$). All participants provided saliva samples, assayed for a biomarker of mucosal immunity associated with respiratory disease resistance: secretory immunoglobulin-A (sIgA). Participants also contributed speech samples, analyzed for two sexually dimorphic aspects of the human voice: 1) fundamental frequency (f_0 ; perceived as pitch) and vocal tract length (VTL; estimated using formant frequencies). Multiple regression models were used to assess the association between masculine vocal parameters and sIgA. Results indicated that lower f_0 and longer VTL were associated with higher sIgA levels. That is, both adult and adolescent males with more masculine voices showed better mucosal immunity (and therefore disease resistance) than those with less masculine voices. Although this accords with several previous studies on voice and sIgA, it contrasts with standard ICHH-derived predictions. We suggest that life-history theory provides a better conceptual framework for understanding the association between testosterone-dependent secondary sexual characteristics and immunity as it shifts the focus from immunosuppression to efficient immunoredistribution.

1. Introduction

Human male vocal frequencies become dramatically lower in comparison to females as a result of increasing levels of testosterone (T) at puberty (Butler et al., 1989; Harries, Hawkins, Hacking, & Hughes, 1998; Harries, Walker, Williams, Hawkins, & Hughes, 1997; Hodges-Simeon, Gurven, Cárdenas, & Gaulin, 2013; Hodges-Simeon, Gurven, & Gaulin, 2015; Hollien, Green, & Massey, 1994). Adult males' "lower" voice is the psychoacoustic product of changes along two main anatomical dimensions. First, via laryngeal androgen receptors (Newman, Butler, Hammond, & Gray, 2000; Voelter et al., 2008), pubertal T causes male vocal folds to lengthen by 60%, lowering fundamental

frequency (f_0 ; perceived as pitch) (Dabbs & Mallinger, 1999; Puts, Apicella, & Cardenas, 2011; Titze, 2000). Second, vocal tract length (VTL; the space from the vocal folds to the lips or teeth), increases by 15% compared to women (Fitch & Giedd, 1999; Titze, 2000), lowering formant frequencies by a similar degree (Hodges-Simeon et al., 2015; Pedersen, Møller, Krabbe, & Bennett, 1986; Puts et al., 2011). These changes make the voice one of the most sexually dimorphic human traits (Puts, Jones, & Debruine, 2012; Rendall, Kollias, Ney, & Lloyd, 2005), more sexually dimorphic than in any other living ape (Aung et al., 2023; Puts et al., 2016).

Dimorphism of the human vocal tract has spawned evolutionary explanations since Darwin (1871), yet considerable debate remains

* Corresponding author at: Department of Anthropology, Boston University, 232 Bay Stated Rd., Room 102-B, Boston, MA, 02215, United States of America.
E-mail address: crhodes@bu.edu (C.R. Hodges-Simeon).

across two fronts: 1) the type of fitness-relevant information low vocal frequencies convey to potential mates and/or competitors (e.g., immunocompetence, phenotypic quality, hunting/foraging ability, hormonal status, strength, size, physical and social dominance; Albert, Arnocky, Puts, & Hodges-Simeon, 2021; Arnocky, Hodges-Simeon, Ouellette, & Albert, 2018; Aung et al., 2024; Aung & Puts, 2020; Feinberg, 2008; Feinberg, Jones, & Armstrong, 2018; Puts et al., 2016; Puts & Aung, 2019; Rosenfield, Sorokowska, Sorokowski, & Puts, 2020; Smith, Olkhov, Puts, & Apicella, 2017); and 2) how this information remains honest and reliable over time (Aung, Rosenfield, & Puts, 2021; Hodges-Simeon et al., 2015; Zhang et al., 2021; Zhang, Hodges-Simeon, Gaulin, & Reid, 2021). These explanatory gaps in knowledge have generated several competing hypotheses. For example, attention to low voices may be a by-product of sensory exploitation (Feinberg et al., 2018) or perceptual bias (Armstrong, Lee, & Feinberg, 2019; Rendall, Vokey, & Nemeth, 2007), rather than a result of sexual selection pressures (see Aung & Puts, 2020, for a response to Feinberg et al., 2018).

A key theoretical and empirical piece of this debate is the extent to which masculine vocal parameters vary with the somatic condition or genetic quality of the speaker (Arnocky et al., 2018; Atkinson et al., 2012; Aung et al., 2021; Hill et al., 2017; Pisanski et al., 2014, 2016; Puts et al., 2012, 2016; Schild et al., 2020). Evolutionary theory predicts that potential mates and competitors attend to more exaggerated secondary sexual characteristics because they indicate some less observable, but fitness-enhancing, quality about the signaler (Andersson, 1994; Hamilton & Zuk, 1982; Krebs & Dawkins, 1984). The link between signal and underlying quality supports the evolution of the signal itself, as well as attention to signal strength by mates and/or competitors (Dawkins & Krebs, 1978; Guilford & Dawkins, 1991). Inspired by Zahavi's handicap principle (Zahavi, 1975, 1977), Folstad and Karter (1992) asserted that this less observable quality is immunocompetence, or the ability to successfully mount an immune response to prevailing pathogen threats, which they called the Immunocompetence Handicap Hypothesis (ICHH). A key assumption of the ICHH is that T links immunocompetence to the expression of sexually dimorphic traits. According to the ICHH, T suppresses immunity, which would make T-dependent sexual signals, such as low vocal frequencies in humans, an observable metric of the degree to which the signaler can bear the costs of immunosuppression (Folstad & Karter, 1992). In spite of the initial coherence of this idea, the ICHH has come under criticism because of inconsistent, contradictory, and null associations between various measures of immunity and T-dependent secondary sexual characteristics (e.g., Alonso-Alvarez, Bertrand, & Sorci, 2007; Casagrande & Groothuis, 2011; Cox & John-Alder, 2007; Deviche & Cortez, 2005; Edler, Goymann, Schwabl, & Friedl, 2011; Evans, Goldsmith, & Norris, 2000; Fuxjager, Fofopoulos, Diaz-Uriarte, & Marler, 2011; Lindström, Krakower, Lundström, & Silverin, 2001; Owen-Ashley, Hasselquist, & Wingfield, 2004; Zaidi et al., 2019), including the voice (Arnocky et al., 2018; Skrinda et al., 2014).

Recent developments in life-history theory have reframed the role of T away from an immune-suppressing handicap to a coordinating molecule tasked with efficiently allocating limited energetic resources across competing investments in reproduction and immunity in response to available energy and the relative costs and benefits in the prevailing social and ecological context (Getty, 2006; McDade, 2003; McDade, Georgiev, & Kuzawa, 2016; Muehlenbein & Bribiescas, 2005; Muehlenbein, Prall, & Nagao Peck, 2017). For example, investment in T-dependent signals should increase when available energy is higher and when the slope of fitness on investments in reproductive competition is steep (Pérez-Rodríguez, Blas, Viñuela, Marchant, & Bortolotti, 2006). According to this view, no special "handicapping" function is necessary to understand the relationship between T-dependent traits and immunity because the same environmental factor(s) would be regulating both T and immunity in parallel (Getty, 2006).

To maximize energetic efficiency, T may suppress or enhance different measures of immunity depending on the prevailing costs and benefits. However, a coherent, organizing theory for understanding and

predicting when, why, and how T affects immunity is still missing. Braude and colleague's (1999; see also Martin II, Weil, & Nelson, 2006) "immunoredistribution hypothesis" suggests that T may temporarily redistribute immune resources to sites of potential injury given the association between T, mating competition, and physical altercations (Anestis, 2006; Beehner, Bergman, Cheney, Seyfarth, & Whitten, 2006; Butovskaya et al., 2018; Christiansen & Winkler, 1992; Fales, Gildersleeve, & Haselton, 2014; Roney, Lukaszewski, & Simmons, 2007; van der Meij, Buunk, Vandesande, & Salvador, 2008). Others have suggested that T may enhance "first-line" immune defenses (e.g., innate immunity) over "second-line" defenses like adaptive immunity (Ezenwa, Ekernas, & Creel, 2012; Lee, 2006; McDade et al., 2016). Trumble et al. (2016) suggest that T selectively downregulates more costly T-cell mediated function over less costly B-cell mediated immunity. Yet others propose that the T-immunity relationship is partially or entirely mediated by corticosteroids and therefore better understood as a by-product (Buchanan, 2000; Setchell, Smith, Wickings, & Knapp, 2010; Vágási et al., 2018).

Developing a cohesive theory of the relationship between immunity and the expression of secondary sexual characteristics requires attention to consistent patterns of association. One biomarker of mucosal immunity, secretory immunoglobulin-A (sIgA), has shown reliable, positive associations with T (Arnocky et al., 2018; Fornieles et al., 2014; Gettler, McDade, Agustin, Feranil, & Kuzawa, 2014; Hodges-Simeon et al., 2015, 2020; Hodges-Simeon, Prall, Blackwell, Gurven, & Gaulin, 2017; Koçar et al., 2000; Peñailillo, Maya, Niño, Torres, & Zbinden-Foncea, 2015; Sullivan & Allansmith, 1987), as well as links with a lower, more masculine voice (Arnocky et al., 2018; Hodges-Simeon et al., 2015). sIgA is an initial line of defense in the upper respiratory system, gastrointestinal tract, and genitourinary tract that prevents pathogens' entry to the epithelium and past mucosal surfaces (Brandtzaeg, 2009; Macpherson, McCoy, Johansen, & Brandtzaeg, 2008).

Low sIgA has been associated with depressed immunity and infection risk (Fahlman & Engels, 2005; Gleeson, 1999, 2002; Gleeson, Bishop, Oliveira, McCauley, & Tauler, 2011; Neville, Gleeson, & Folland, 2008). For example, Mortatti et al. (2012) demonstrated a significant relationship between decreases in sIgA and increases in upper respiratory tract infections in players across a 20-day soccer tournament. Other studies show similar associations between lower concentrations of sIgA and increased risk of upper respiratory tract infections or cold/flu symptoms among children and adults (Fahlman & Engels, 2005; Gettler et al., 2014; Gleeson, 1999, 2002; Gleeson et al., 2011; Neville et al., 2008). Additionally, a 19-year longitudinal study found significantly higher mortality (from cancer and respiratory diseases in particular) among those with low sIgA (Phillips, Carroll, Drayson, & Der, 2015). Evidence is also mounting that sIgA levels may play an important role in SARS-Cov-2 (i.e., COVID-19 disease) severity, vaccine failure, and prolonged viral shedding (Chao, Röttschke, & Tan, 2020; Naito, Takagi, Yamamoto, & Watanabe, 2020; Wang et al., 2020). Thus, sIgA concentrations represent one component of immune function (i.e., mucosal immunity; Brandtzaeg, 2009) functionally related to disease resistance.

Two previous studies have examined relationships between masculine vocal parameters and sIgA. Among Canadian adult males, Arnocky et al. (2018) showed that lower, more masculine vocal frequencies were associated with higher sIgA; however, the effect has not yet been replicated. Therefore, Study 1 targets the relationship between masculine voice measures and sIgA in two new samples of North American young-adult males ($N = 119$ from the US and $N = 162$ from Canada). In addition, Hodges-Simeon et al. (2015) previously examined vocal frequencies and sIgA among Bolivian Tsimane aged 8–22 (Hodges-Simeon et al., 2015). Like Arnocky et al. (2018), results indicated that the link between masculine frequencies and sIgA was positive; however, the findings were not statistically significant when age and BMI were controlled. Study 2 offers a reanalysis of these data, but limits the sample to adolescents only (i.e., excluding pre-pubescent juveniles), defined as those who have observable signs of puberty (Petersen, Crockett,

Richards, & Boxer, 1988). Study 2 also uses updated voice analyses to parallel procedures from Arnocky et al. (2018) and Study 1.

We focus on two masculine vocal parameters: estimated VTL from formant frequencies and f_0 . Following Arnocky et al. (2018) and Hodges-Simeon et al. (2015), we predict that longer estimated VTL and lower f_0 will be associated with higher sIgA. Further, as in Arnocky et al. (2018), we expect the association between f_0 and sIgA to be stronger than the association between VTL and sIgA due to the purported regulatory role of T. That is, T appears to affect f_0 more strongly than VTL. For example, during puberty, T explains 54% of the variation in f_0 , yet only 26% of the variation in VTL (Markova et al., 2016). Among adults, numerous studies show associations between f_0 and T (Aung & Puts, 2020; Dabbs & Mallinger, 1999; Evans, Neave, Wakelin, & Hamilton, 2008; Puts et al., 2011; Schild et al., 2020; Titze, 2000), yet few studies have found associations between adult formants and T (e.g., Puts et al., 2011). Finally, exogenous T therapy has a stronger effect on f_0 than VTL (Hodges-Simeon et al., 2021).

For similar reasons, we also expect the association between masculine vocal traits and sIgA to be stronger for adolescents than adult males. This is due to the rapid change in both T and secondary sexual traits that occur from the beginning of puberty to the end of adolescence (Hodges-Simeon et al., 2016). T increases by nearly an order of magnitude from Stage 1 to Stage 5 of puberty (Butler et al., 1989) and f_0 plummets by nearly half in some males. As such, if T plays any regulatory role in voice change and/or sIgA, the association between them should be greater in adolescence than adulthood.

2. Methods

All data were collected in accordance with procedures approved by the Institutional Review Boards at each university, including informed written consent (North American participants) and verbal assent (for Tsimane participants). The North American sample was collected in two university locations in the US and Canada. The demographics and data-collection details for the two samples are described separately below. We specifically targeted adolescents and younger men for the current study because the ICHH was proposed to describe the appearance of costly secondary sexual characteristics for mammalian males who are at the peak of reproductive competition (Folstad & Karter, 1992).

2.1. Participants

2.1.1. US University sample

119 male participants between 18 and 30 years of age from a university in Boston, MA ($M_{\text{age}} = 21.2$, $SD = 3.1$) contributed voice samples and saliva (further described in Hodges-Simeon et al., 2021). The ethnic composition of the sample was as follows: Caucasian (41%), Asian (19%), South Asian (14.9%), Latin American (11%), Black (7%), Arab West Asian (4%), Southeast Asian (2%).

2.1.2. Canadian University sample

162 male participants between 18 and 39 years of age were recruited from a university in Ontario, Canada ($M_{\text{age}} = 22.7$, $SD = 4.7$; 91.4% were students). This sample was part of a larger study on physiological development, immunology, and social behavior. The ethnic composition of the sample was Caucasian (90%), Black (4%), East Asian (3%), South Asian (2%), and Indigenous / First peoples (1%) (for further detail see Landry, Desrochers, Hodges-Simeon, & Arnocky, 2019).

2.1.3. Tsimane adolescent sample

44 Tsimane males ($M_{\text{age}} = 15.3$, $SD = 3.1$) were drawn from a larger study that investigated voice pitch, energetics, testosterone, and health among males and females aged 8 to 22 (see Hodges-Simeon et al., 2015; Hodges-Simeon, Asif, Gurven, Blackwell, & Gaulin, 2019). This study reanalyzes data from Hodges-Simeon et al. (2015), but eliminates pre-pubertal individuals, whose LH and FSH are too low to trigger

gonadal T production (Albertsson-Wikland et al., 1997). If T affects both voice parameters and sIgA, then pre-pubertal boys are also unlikely to show voice change and increases in sIgA. Consistent with Hodges-Simeon et al. (2019), only males who had reported any physical signs of puberty were included (i.e., score of 2 or higher on the Pubertal Development Scale (PDS), a self-report measure of physical development; Petersen et al., 1988). Age was also obtained from each participant and cross-checked with the Tsimane Health and Life History Project census (see Hodges-Simeon et al., 2015 for more detail on age-estimation methods).

The Tsimane are Amazonian forager-horticulturalists who live in central Bolivia. This population is characterized by high rates of parasitic infection and gastrointestinal and respiratory disease due to living in a tropical, immunologically challenging environment (Gurven, Kaplan, Winking, Finch, & Crimmins, 2008; Vasunilashorn et al., 2010). As a result, half of all Tsimane deaths are due to infection, the majority of which are categorized as respiratory infections (Gurven, Kaplan, & Supa, 2007). Given the empirical links between low sIgA and risk of respiratory illness (Fahlman & Engels, 2005; Gettler et al., 2014; Gleeson, 1999, 2002; Gleeson et al., 2011; Neville et al., 2008), sIgA levels likely have implications for morbidity and mortality in this population.

2.2. Saliva collection

For all three samples, participants provided saliva samples via passive drool and avoided eating at least one hour prior to saliva collection. Saliva flow rate affects sIgA; therefore, sample collection time was recorded during saliva collection sessions, which was used to calculate flow rate (Eliasson, Birkhed, Österberg, & Carlén, 2006; Kugler, Hess, & Haake, 1992). In all analyses, "sIgA" refers to sIgA secretion rate ($\mu\text{g}/\text{min}$).

2.2.1. US University sample

Participants were provided with a package containing written instructions and a 2 mL polypropylene barcoded cryogenic vial (Globe Scientific) labeled with the day and time they were to be filled by the participant. Participants provided three saliva samples (see Hodges-Simeon et al., 2021); we utilized the first of these, provided the following morning upon waking, which was contiguous to the voice recording session for this study. At the time of collection, participants recorded both the start and end time (mean start time was 8:44 AM, $SD = 119$ min), and then immediately refrigerated the sample until they transported it to the lab. Saliva samples were then stored at -80°C until shipped on dry ice for assay. Samples were assayed using commercially available enzyme immunoassay kits (DRG International, NJ, USA) in the same laboratory, using the same procedures and kits as the Canadian University sample described below. Average intra- and inter-assay coefficients of variation (CVs) were as follows: 4.85% and 20.67% for sIgA.

2.2.2. Canadian University sample

Directly prior to the voice recording, saliva samples were collected into a 5 mL polystyrene culture tube and stored at -60°C until assayed via enzyme immunoassay kits (DRG International, NJ, USA). Saliva sample provision time recorded and ranged between 8:30 AM and 5:00 PM. Intra- and inter-assay CVs were below 6% for sIgA.

2.2.3. Tsimane adolescent sample

Saliva samples were collected in a 2 mL polystyrene cryotube. The average time of saliva collection was at 1:22 PM ($SD = 169$ min, range = 8:39 AM – 6:09 PM; see Hodges-Simeon et al., 2015 for additional detail). Samples were stored in liquid nitrogen (LN_2) 20–40 min after collection and kept frozen in LN_2 until transported on dry ice to the University of California, Santa Barbara, where they remained frozen at -80°C until shipment on dry ice to Salimetrics LLC, State College, Pennsylvania, for assay. For sIgA, the average intra-assay and inter-assay coefficients of variation were 5.6% and 8.8%. The lower limit of

sensitivity was 2.5 µg/mL.

2.3. Acoustic recordings

All acoustic samples were recorded in mono with a sampling rate of 44.1 kHz and 16-bit quantization and saved as high-quality uncompressed wav files.

2.3.1. US University sample

Participants recited phrases into an Audio-Technica AT4041 Cardioid Condenser Microphone, positioned ~20 cm from the participants' lips, which was connected to a Focusrite Scarlett 2i2 audio interface. Recordings were made using Goldwave version 6. The phrases included the following: vowel sounds from the International Phonetic Alphabet (/ε/ /i/ /a/ /õ/ /u/), the first sentence of the Rainbow Passage, and counting from 1 to 10.

2.3.2. Canadian University sample

Participants recited the same vowels, numbers, and phrase as described for the US University sample into an Audio-Technica ATR-1200 microphone, positioned ~20 cm from the participants' lips. Voices were recorded using Goldwave version 6.10 software.

2.3.3. Tsimane adolescent sample

Voice samples of Tsimane participants were recorded as they named objects from five photographs. The words were selected if they had a terminal vowel that sounded similar to the vowels in the US sample (mishi [cat]: "ee", aɕuj [dog]: "oo", pe're [plantain]: "ā", perota [ball]: "ah", and ococo [frog]: "oh"); however, we cannot ensure that these vowels were exactly the same to those produced in English. This makes direct comparisons of the formants between the Tsimane and the North American samples inappropriate. Samples were recorded on a Sony PCM-M10 digital audio recorder, with an Audio-Technica lavalier head-mounted microphone that was positioned approximately 5 cm away from participants' mouths. For more details refer to Hodges-Simeon et al. (2015).

2.4. Acoustic analysis

All three samples were analyzed using Praat voice analysis software version 5.4.22 (Boersma & Weenick, 2010) in the same way as Arnocky et al. (2018) to maintain analytical consistency across studies. Therefore, formant frequencies for the Tsimane sample were reanalyzed due to slight variations in method across the prior studies.

2.4.1. Fundamental frequency

Praat was used to determine mean f_0 , which was measured in Hertz (Hz; Boersma & Weenick, 2010) by means of the autocorrelation method (pitch floor: 75 Hz, pitch ceiling: 300 Hz, otherwise default settings).

2.4.2. Vocal tract length

Only the vowel voice samples were used to estimate VTL. Before analyzing formant frequencies, we first extracted vowel sounds by means of the Vocal Toolkit Extract Vowels plug-in (Corrette, 2012) to eliminate sporadic background noise, microphone pops, and accidental fricatives. Praat's Burg linear predictive coding algorithm was then used (maximum formant value: 5 kHz, time step between analysis frames: 0.01 s, window length: 0.025 s). Formant frequencies were obtained automatically for the first four formants of the five vowels. In Arnocky et al. (2018), we also calculated P_f (Puts et al., 2012), which averages across standardized formants and is therefore best understood in relation to the group mean. Because VTL estimates vocal tract length in centimeters (average adult VTL is 16 cm for men and 10 cm for women; Titze, 2000), it has advantages in being intuitive and better facilitating comparisons across studies and samples. VTL estimation is based on an algorithm provided by Stevens (2000) that is derived from modeling the

vocal tract as a uniform tube that is closed at one end (i.e., the vocal folds) and open at the other (i.e., the mouth).

Arnocky et al. (2018) did not examine the associations between the individual formants (F1-F4) and sIgA; however, later, unpublished analyses showed that the association between VTL and sIgA was driven by F4 (zero-order correlations with F1-F4 were 0.08, 0.06, 0.01, and -0.17, respectively). Pisanski et al. (2014), finding that the higher formants (F3 and F4) best predicted body size, suggested that F1 and F2 vary more with speech while the third and fourth formants provide more reliable and consistent information about the vocal tract. Other researchers have also cautioned against using F1 and F2 because they tend to be more unstable and produce worse estimates of VTL (Wakita, 1977). In keeping with this evidence, we used only F3 and F4 to calculate VTL, which was used in the models below. We also present models that include F1-F4 in the Supplementary Material (see Table S2), which shows that F3 is driving the associations between VTL and sIgA in both the North American and Tsimane samples. Finally, we include VTL-ΔF (Reby & McComb, 2003), which was calculated using the *soundgen* R package (Anikin, 2019; Anikin, Barreda, & Reby, 2023; v4.3.1, R Core Team, 2023). The estimateVTL function was used with F1-F4 for each participant using the regression method. For a closed-open tube, the equation used is $(2 * \text{formant_number} - 1) * \text{speedSound} / (4 * \text{formant_frequency})$ (Anikin, 2019). These results, also found in the Supplement (Table S3), indicate that VTL-ΔF did not significantly predict sIgA.

2.5. Anthropometrics

Height and weight were collected directly from participants in all three samples in accordance with standard anthropometric protocols (Lohman, Roche, & Martorell, 1988). BMI was calculated as weight (kg) over height (m) squared. Because the Tsimane have a high rate of stunting, age-and-sex-standardized z-scores were then calculated for body mass index using Tsimane-specific BMI-for-age curves (TBAZ; Blackwell et al., 2017).

2.6. Statistical analyses

2.6.1. Data transformation

sIgA was assayed in duplicate and the average of the two values was used for all statistical analyses. Descriptive statistics for all study variables (raw, un-transformed values) are presented in Table 1. For analysis, age, sIgA, BMI, f_0 , and VTL were log-transformed to reduce skew (based on the Shapiro-Wilk test) and approach normality.

2.6.2. A priori power analysis

Arnocky et al. (2018) demonstrated that sIgA levels correlated negatively with f_0 among adult participants [$r(104) = -0.21, p = 0.01$, one-tailed]. Because our aim was to replicate these results in a similar population, an a priori power analysis was conducted to assess the number of participants needed to detect a small association ($0.10 < r < 0.30$) between sIgA and f_0 . With an alpha = 0.05 and power = 0.90, the projected sample size needed with this effect size (G*Power 3.1.97; Faul,

Table 1
Descriptive statistics for study variables (Mean ± standard deviation).

	Combined Canada & US	Canada	US	Tsimane
f_0 (Hz)	115.6 ± 15.3	117.3 ± 14.3	113.0 ± 16.4	155.2 ± 48.3
VTL (cm)	17.1 ± 0.8	17.2 ± 0.7	17.0 ± 0.8	15.2 ± 1.1
Age (years)	22.1 ± 4.1	22.7 ± 4.7*	21.2 ± 2.9*	15.3 ± 2.9
BMI (kg/m ²)	24.9 ± 5.8	25.7 ± 7.0*	23.7 ± 3.0*	20.3 ± 2.4
sIgA (µg)	111.3 ± 101.0	111.3 ± 84.7*	112.9 ± 122*	129.8 ± 87.4

Note. All variables represent untransformed values. sIgA is not corrected for secretion rate in this table. *Significant differences between Canadian and US means, $p < 0.05$.

Erdfelder, Buchner, & Lang, 2009) is approximately $N = 234$ (two-tailed). Therefore, we combined the US and CAN sample ($N = 267$) to minimize the chance of a type I error. Both the voice analysis and immunoassays were conducted in the same laboratories using the same methodologies, participants were sampled from geographically and culturally similar locations, and variable means were similar (see Table 1); nevertheless, we also controlled for sample location in all analyses presented below. Because the Tsimane participants differ widely in age, ecology, disease risk, and language from the North American participants, direct comparisons between the populations on acoustic parameters and sIgA is not appropriate. Instead, we analyze the association between voice and sIgA separately for the two groups. Furthermore, we did not conduct a priori power analysis for the Tsimane sample because there were no similar studies (i.e., studies on the sIgA of adolescent and/or Tsimane or any other energy-limited population) on which to base one.

2.6.3. Analytic strategy

Previous studies indicate a relationship between age and vocal parameters. This relationship is strongest among individuals going through the pubertal transition (Harries et al., 1997; Hodges-Simeon et al., 2013,

2015; Hollien et al., 1994) and among those over 40 (Harnsberger, Shrivastav, Brown, Rothman, & Hollien, 2008), but it has also been shown in young adult samples as well, including the current North American sample ($r = 0.12$, $p < 0.05$). Studies also show that body weight may impact vocal frequencies (Barsties, Verfaillie, Roy, & Maryn, 2013; de Souza & dos Santos, 2018). BMI is also used as a measure of energy balance, and is therefore used as a rough control for phenotypic correlation (Hodges-Simeon et al., 2015; Roff & Fairbairn, 2007). For these reasons, and to maintain methodological and analytical consistencies across the samples, we control for age and BMI in all analyses using multiple regression. Removing those who were obese (i.e., BMI above 30; $N = 20$) did not substantially change the results, so they were included in the final model. All variables are continuous (aside from population), but showed some skew; therefore, variables were natural log transformed to approach a normal distribution. Listwise deletion was used for missing data. See Fig. 1 for zero-order associations between vocal parameters and sIgA in each sample.

Both sIgA (Hodges-Simeon et al., 2021) and voice (Evans et al., 2008) show diurnal fluctuations in the expected direction for an association with T, which also has a diurnal pattern. That is, both sIgA and T decrease from morning to evening (Hodges-Simeon et al., 2021) and

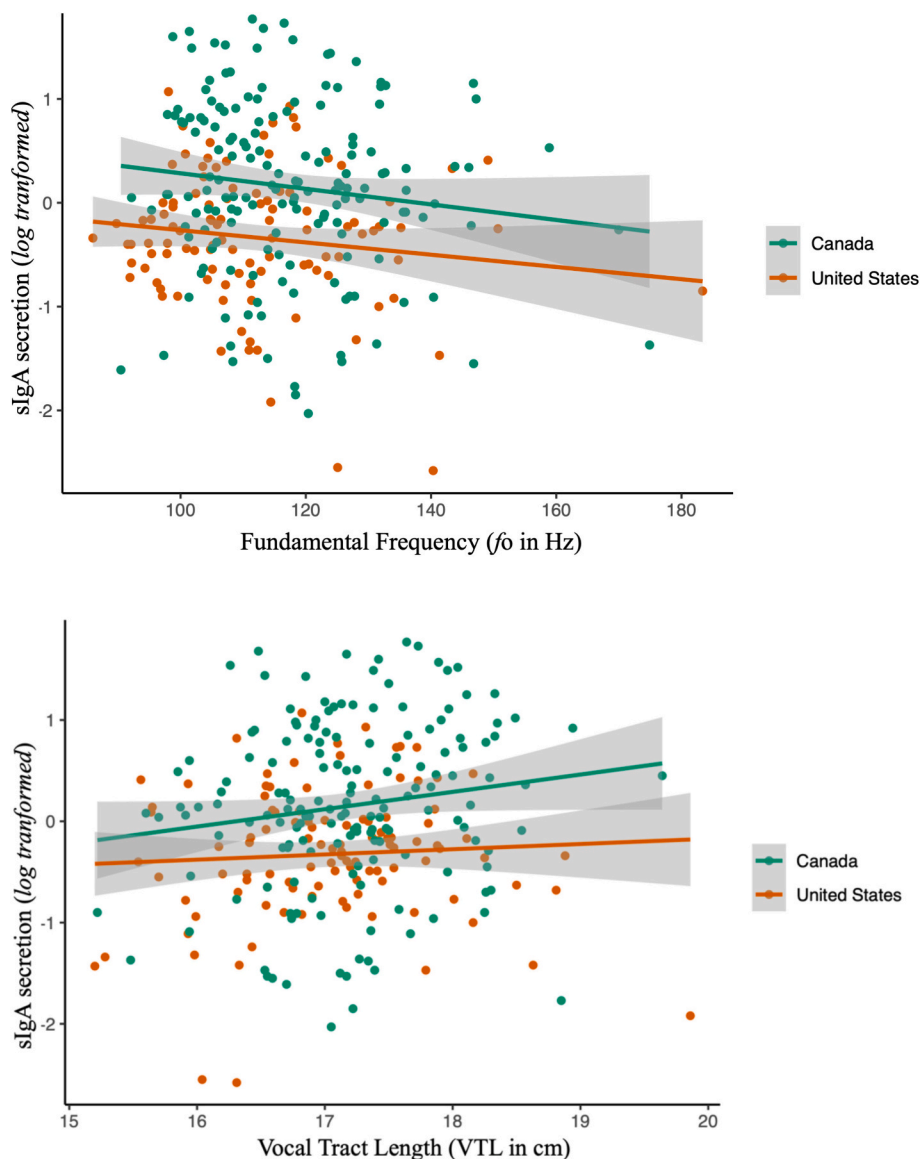


Fig. 1. Associations between masculine vocal parameters and sIgA secretion rate in US and Canadian adult samples.

fundamental frequency is lower in the morning, when T is higher (Evans et al., 2008). Because of these associations, sIgA and voice should be associated whether it is morning or evening. Nevertheless, time of day was included in an initial analysis. As it had no effect on the models, it was then removed.

3. Results

3.1. Combined North American sample

Multiple regression was used to test a model in which f_0 , age, BMI, and population (US vs. Canada) were simultaneously entered as predictors of sIgA (Table 2; Model 1). Zero-order correlations between the predictor and outcome variables can be found in Tables 2 and 3. In the multiple regression model, f_0 was a significant inverse predictor of sIgA, as predicted; that is, lower pitched voices were associated with higher levels of sIgA. Age and BMI did not explain any additional variance in sIgA; however, population did. The sample size of 267 was used for post-hoc statistical power analysis and a four-predictor variable equation was used as a baseline. The post-hoc analysis revealed the statistical power ($1 - \beta$) for this study of 0.99 was more than adequate for detecting the small effect of 0.14.

In a second multiple regression model predicting sIgA, VTL, age, BMI, and population were simultaneously entered as predictors (Table 3; Model 3). As predicted, VTL was a significant positive predictor of sIgA; that is, a longer vocal tract (and lower formant frequencies) was associated with higher levels of sIgA. Age and BMI did not explain additional variance in sIgA; however, population did.

To address population differences between the two North American samples, we conducted independent samples *t*-tests for each of the variables. Although means were similar across the two samples, variance differed noticeably, contributing to significant differences in age, BMI, and sIgA (see Table 1). We conducted multiple regression models separately for each sample, which indicate that relationships between sIgA and f_0 and between sIgA and VTL were similar across the two samples and in the same, predicted, direction (see Supplementary Tables). There were five low values for sIgA in the US sample (sIgA, untransformed, of 8 $\mu\text{g}/\text{mL}$ or less); however, eliminating these individuals did not substantially alter the results.

3.2. Tsimane adolescent sample

Secretory IgA showed a significant zero-order correlation with age ($r = 0.35$, $p = 0.009$), f_0 ($r = -0.45$, $p = 0.001$), and VTL ($r = 0.29$, $p = 0.03$). A multiple regression model was then run to determine the unique effects of f_0 on sIgA levels, controlling for age and BMI (Table 2; Model 2). f_0 significantly predicted sIgA. Age and BMI did not significantly predict sIgA. The sample size of 44 was used for post-hoc statistical

Table 2
Multiple regression models predicting sIgA from voice pitch (f_0).

	Unstandardized β	Std. Error	Standardized β	t statistic	Zero-order correlation
Model 1: North America (N = 267)					
f_0	-0.89	0.39	-0.14	-2.23*	-0.08
Age	0.02	0.29	0.01	0.05	0.05
BMI	0.37	0.33	0.07	1.12	0.12*
Population	0.50	0.10	0.31	5.00***	0.29***
Model 2: Tsimane (N = 44)					
f_0	-2.03	0.96	-0.40	-2.10*	-0.45***
Age	0.56	1.36	0.08	0.41	0.35**
BMI	-0.06	0.10	-0.08	-0.56	-0.07

Note. sIgA: secretory IgA corrected for flow rate. * $p \leq 0.05$; ** $p \leq 0.01$; *** $p \leq 0.001$, $\dagger p \leq 0.10$.

Table 3
Multiple regression models predicting sIgA from VTL.

	Unstandardized β	Std. Error	Standardized β	t statistic	Zero-order correlation
Model 3: North America (N = 267)					
VTL	2.07	1.07	0.11	1.94*	0.15*
Age	-0.09	0.29	-0.02	-0.30	0.05
BMI	0.33	0.33	0.06	1.00	0.11 [†]
Population	0.43	0.10	0.27	4.38***	0.29***
Model 4: Tsimane (N = 44)					
VTL	1.52	1.26	0.20	1.21	0.29*
Age	1.93	1.14	0.27	1.70 [†]	0.35**
BMI	-0.05	0.11	-0.07	-0.48	-0.07

Note. sIgA: secretory IgA corrected for flow rate. * $p \leq 0.05$; ** $p \leq 0.01$; *** $p \leq 0.001$, $\dagger p \leq 0.10$.

power analysis and a three-predictor variable equation was used as a baseline. The post-hoc analysis revealed the statistical power ($1 - \beta$) for this study of 0.79 was adequate for detecting the moderate effect of 0.27. In a second model, VTL, age, and BMI were simultaneously entered to predict sIgA levels (Table 3; Model 4). In this multivariate analysis, none of the predictors explained significant variance in sIgA; however, age approached conventional levels of significance.

4. Discussion

A key assumption of immunocompetence models for sexually selected signals is that the strength of these signals is proportional to the immunocompetence of the signaler (Folstad & Karter, 1992; Zahavi, 1975). Yet, clear evidence for this assumption has been lacking (e.g., Alonso-Alvarez et al., 2007; Arnocky et al., 2018; Casagrande & Groothuis, 2011; Cox & John-Alder, 2007; Deviche & Cortez, 2005; Edler et al., 2011; Evans et al., 2000; Fuxjager et al., 2011; Owen-Ashley et al., 2004; Roberts, Buchanan, Hasselquist, & Evans, 2007; Skrinda et al., 2014; Zaidi et al., 2019). Controlling for age, BMI, and population, we show that a more masculine voice, specifically a lower f_0 , predicts one measure of disease resistance (i.e., salivary sIgA) in both industrialized and indigenous rural males, as well as among adolescents and young adults. More masculine VTL predicted higher sIgA in the adult North American sample and was in the predicted direction in the Tsimane sample. Together, these results provide support for the idea that lower vocal frequencies convey fitness-relevant information about a male's immune status to potential mates and competitors. In doing so, these findings support evolutionary models for the co-evolution of sexually dimorphic traits with preference for the trait in mating contexts and deference in competitive contexts (Apicella, Little, & Marlowe, 2007; Feinberg et al., 2012; Han et al., 2017, 2017; Hodges-Simeon, Gaulin, & Puts, 2010, 2011; Pisanski, Mishra, & Rendall, 2012; Puts, 2005; Puts, Hodges, Cárdenas, & Gaulin, 2007).

Replicating Arnocky et al. (2018), we found an inverse association between mucosal immunity as measured by sIgA and more masculine voice pitch. In other words, young-adult, North American men with lower, more masculine f_0 had higher levels of sIgA, and therefore likely greater resistance to respiratory disease-causing pathogens. Also in line with Arnocky et al. (2018), we found a positive association between mucosal immunity and estimated VTL; that is, men with a longer (more masculine) VTL (estimated using formant frequencies) had higher sIgA.

In the present research, as in Arnocky et al. (2018), sIgA was more strongly associated with f_0 than VTL (based on standardized β s). This finding, along with numerous studies linking sIgA and T (Arnocky et al., 2018; Fornieles et al., 2014; Gettler et al., 2014; Hodges-Simeon et al., 2015, 2017, 2020; Koçar et al., 2000; Peñailillo et al., 2015; Sullivan & Allansmith, 1987) suggest that the mechanism linking voice and immunity may be hormonal. In the case of f_0 , T drives voice change during

puberty (Butler et al., 1989; Harries et al., 1997, 1998; Hodges-Simeon et al., 2013, 2015; Hollien et al., 1994; Markova et al., 2016), and continued to predict f_0 in adulthood (Aung & Puts, 2020; Dabbs & Mallinger, 1999; S. Evans et al., 2008; Puts et al., 2011; Titze, 2000), particularly in males with lower cortisol levels (Schild et al., 2020). The relationship between VTL and T, however, is more tenuous. While T appears to affect the pubertal descent of the larynx (Fitch & Giedd, 1999), explaining 26% of the variance in VTL among adolescent males (Markova et al., 2016), few studies have found associations between adult formants and T (e.g., Puts et al., 2011). VTL instead may more strongly index earlier development events that influence overall body size (Pisanski et al., 2014), as well as the descent of the larynx resulting from pubertal T (Hodges-Simeon et al., 2021).

In addition to the North American sample of well-nourished, young adult males, we also examined the association between masculine vocal parameters and sIgA among indigenous adolescents in rural Bolivia. This is a reanalysis of the data presented by Hodges-Simeon et al. (2015) with updated acoustic analyses and a narrower developmental range (i.e., only those boys with measurable signs of puberty and therefore rising T levels). Previously, Hodges-Simeon et al. (2015) found that masculine frequencies and sIgA were correlated, but the association was not statistically significant when age and BMI were controlled. Our updated analyses suggest that the link between masculine vocal parameters and mucosal immunity emerges during puberty with rising steroid hormones and development of secondary sexual characteristics. As in the North American sample, sIgA was more strongly associated with f_0 than VTL, which supports T as the physiological mechanism linking voice and sIgA.

Pubertal males provide an interesting avenue to approach this question; that is, if voice and sIgA vary together, then they should vary in concert during the rapid changes that occur during ontogeny. The Tsimane sample presented here spans from 11 to 23 years old, a period marked by dramatic changes in male phenotypes. Any traits influenced by sexual selection and affected by hormones like T undergo large transformations during this age range. Further, the wide differences in average T levels between energy-abundant populations and energy-limited populations (e.g., AM T levels: $M = 589$ for Boston males and $M = 192$ for Ache males; Bribiescas, 2001) suggests that “baseline” T levels for adult males may be calibrated during ontogeny. The size of the vocal folds and the dimensions of the vocal tract reach adult dimensions during this time as well. In a separate analysis of the Tsimane adolescent data presented here, well-nourished boys’ f_0 plummeted at a faster rate than poorly nourished boys (Hodges-Simeon et al., 2013). This introduces the possibility that voice may vary with T (and other hormones like DHEA-S and DHT) and immunity primarily in adolescence and any association between them during adulthood may be a byproduct of this developmental association (see “developmental-stress hypothesis”; Buchanan, 2011). Future studies may test this idea by following boys from juvenility to adulthood.

The ICHH contends that T acts as a Zahavian handicap by suppressing the immune system, making the degree of T-dependent trait expression an honest signal of the extent to which the signaler can bear the costs of immunosuppression (Folstad & Karter, 1992). However, Braude, Tang-Martinez, and Taylor (1999) and others have noted that this theoretical model provides a poor guide to making predictions in real data and that positive, negative, and null associations between immunity and T (or T-regulated traits) could all be justified from Folstad and Karter’s writing. The most common ICHH-derived prediction, however, is that high-T males should exhibit lower immunity because if T is suppressive, it should drive immunity measures lower. Therefore, the present study stands in contrast to this prediction.

After several decades of experimental and correlational research, consistent support for any of these predictions is lacking in both human and non-human species (Nowak, Pawlowski, Borkowska, Augustyniak, & Drulis-Kawa, 2018; see reviews by Boonekamp, Ros, & Verhulst, 2008; Foo, Nakagawa, Rhodes, & Simmons, 2017; Muehlenbein et al., 2017; Prall & Muehlenbein, 2014; Roberts et al., 2007). Cumulatively,

this suggests that the ICHH does not have the kind of theoretical or empirical predictive utility offered by life-history theory (Getty, 2006). That is, Folstad and Karter (1992) conceptualized T solely as a handicap and exclusively suppressive. In contrast, a life-history theory approach conceptualizes T as a coordinator of energy allocation, shaped by the relative costs and benefits of investments in immunity and reproductive competition (Alvarado et al., 2015; Gettler et al., 2014, 2017; Gettler, McDade, Agustin, & Kuzawa, 2011; Gettler, McDade, Feranil, & Kuzawa, 2011; Trumble, Brindle, Kupsik, & O’Connor, 2010; McDade et al., 2016; Lee, 2006), and predicts that T should orchestrate efficient energy allocation (Lee, 2006; McDade et al., 2016; Muehlenbein et al., 2017) to maximize reproductive success. Further, what is efficient depends on the social and ecological context for each species (McDade, 2003; McDade et al., 2016). Depending on the context, T may up- or downregulate different parts of immunity.

Several versions of this reasoning have been adopted. First, Braude et al. (1999) suggest that immunity should be designed to adjust to the dangers of reproductive competition—namely increased cuts, bites, and other wounds—for species that engage in physical altercations. Saliva has various components that increase wound healing and decrease bacterial and fungal infection (Vila, Rizk, Sultan, & Jabra-Rizk, 2019). Therefore, sIgA’s ability to bind to substances to prohibit pathogen invasion (i.e., immune exclusion; Corthesy, 2013; Mantis, Rol, & Corthesy, 2011) may be adaptive when wound risk is higher. Second, T may enhance cheaper, “first-line” immune defenses (e.g., innate immunity) over more expensive “second-line” defenses like adaptive immunity (Ezenwa et al., 2012; Lee, 2006; McDade et al., 2016). While sIgA is an antibody synthesized by B cells (part of adaptive immunity), it has been suggested that it may also be characterized as innate immunity given its additional, non-specific roles in immune exclusion and as a competitive inhibitor (i.e., “decoy”) protecting the epithelium (Corthesy, 2013; Mantis et al., 2011). Third, Trumble et al. (2016) (see also Miller & Mcconnell, 2014) suggest that T selectively downregulates more costly T-cell mediated function over less costly B-cell mediated immunity. Finally, given that T increases rapidly in response to cues of mating (reviewed by Geniole & Carré, 2018), greater mucosal defense at sites of intromission may mitigate the infection risks of sexual contact (Hodges-Simeon et al., 2019; Lorenz, Heiman, & Demas, 2017).

These explanations are not mutually exclusive and align with the idea that subtypes of immunity may not be unidirectionally related to T and T-dependent secondary sexual characteristics. Future research should aim to test these hypotheses by examining multiple measures of immunity, T, and secondary sexual characteristics. For instance, to test Braude et al. (1999), the relationship between secondary sexual characteristics and sIgA may be compared between species where males compete aggressively versus those that perform non-contact mating displays. To our knowledge, no such systematic comparisons exist.

Future studies should also better account for phenotypic correlation, which, in life history theory, is the idea that individuals with larger energy budgets will be able to invest more across all systems than an individual with a lower energy budget, trade-offs between systems notwithstanding. Controlling for energy balance (via BMI, as we have done here) is a rather crude way to control for phenotypic correlations. One way to circumvent this issue is through experimental design. One option would be to experimentally manipulate T levels and assess the impact on sIgA and vocal parameters. Several previous longitudinal studies have shown parallel changes in T and sIgA over time (Fornieles et al., 2014; Gettler et al., 2014; Hodges-Simeon et al., 2020; Peñailillo et al., 2015); however, experimental work would provide more compelling support. Finally, BMI may affect T differently in rural, developing environments (such as Bolivia) versus industrialized, obeseogenic environments (such as the US) where obesity is associated with lower T (Gates et al., 2013). Among the Tsimane, higher BMI is the result of better nutrition and lower infection, obesity is non-existent, and greater fat is associated with higher T (Hodges-Simeon et al., 2013). In contrast, the highest BMIs in the North American sample were obese.

Removing those who were obese (i.e., BMI above 30; $N = 20$), however, did not substantially change the results.

A potential limitation of this research is the use of relatively brief read or rote voice samples, which may have lower ecological validity than longer vocal samples and/or samples recorded in other contexts, such as during mating competition (Hodges-Simeon et al., 2010) or in situations where speakers are authorities (e.g., Sorokowski et al., 2019). Nevertheless, previous research has found good correspondence in both vocal acoustic parameters and social perceptions of voices across different types of speech segments collected from the same speakers (Groyecka-Bernard et al., 2022; Pisanski, Groyecka-Bernard, & Sorokowski, 2021).

In addition, the Tsimane language differs dramatically from the English language, and Canadian and American English exhibit vowel differences, as well, although steps were taken to match vowel sounds across groups. Therefore, the data presented here do not facilitate comparisons of variables of interest across groups, nor do they represent comprehensive formant profiles for these different groups, but rather they provide evidence of relationships between f_0 and VTL and sIgA within speakers of a given language.

Although these data should not be used as a guide to the laryngeal dimensions of Tsimane, Canadian, and American men, they conform to expectations, indicating their validity. First, Tsimane VTL is smaller and f_0 higher than NA participants because most of these individuals are not yet fully developed – the average age is 15 and some are as young as 12. Given the energy limitations of their environment, Tsimane develop later than NA populations (Hodges-Simeon et al., 2013) and have shorter adult height (Blackwell et al., 2017). The Tsimane may also have higher f_0 because they have lower T than men in industrialized populations (Trumble et al., 2012). Finally, Tsimane have higher levels of sIgA. Hodges-Simeon et al. (2019) suggested that this may be due to the Tsimane's high rate of dental caries, which are associated with higher sIgA (Thaweboon, Thaweboon, Nakornchai, & Jitmaitree, 2008).

5. Conclusions

Folstad and Karter (1992) immunocompetence handicap hypothesis (ICHH) has been an influential theoretical framework in evolutionary biology for the last 30 years. Because they conceptualized T as an immune-suppressing hormone, predictions generated by the ICHH usually take the form of an inverse correlation between secondary sexual characteristics and immunity; that is, the “bigger” the trait, the more immunity must be suppressed. Yet three decades of research have produced a mixed set of inconsistent findings on the ICHH. In that time, life history theory has emerged as meta-explanatory frameworks. Life history theory begins with the assumption that immunity (as a subset of maintenance effort) is inherently costly (Abrams & Miller, 2011; Lassek & Gaulin, 2009; Lochmiller & Deerenberg, 2000; Muehlenbein & Bribiescas, 2005; Prall & Muehlenbein, 2014; Sheldon & Verhulst, 1996), and therefore selection will favor efficient allocation of energy to different demands. This also includes specific energetic trade-offs between different branches of the immune system.

In the present study, both adult and adolescent males with more masculine voices showed better mucosal immunity (and therefore better disease resistance) than those with less masculine voices. Although this accords with several previous studies on voice and sIgA, it stands in contrast with standard ICHH-derived predictions. We suggest that life-history theory provides a more parsimonious conceptual framework for understanding the association between testosterone-dependent secondary sexual characteristics and immunity across the life course.

CRedit authorship contribution statement

Carolyn R. Hodges-Simeon: Conceptualization, Data curation, Formal analysis, Funding acquisition, Methodology, Project administration, Supervision, Writing – original draft, Writing – review & editing.

Graham Albert: Data curation, Methodology, Writing – review & editing. **Timothy McHale:** Resources, Writing – original draft, Writing – review & editing. **Steven J.C. Gaulin:** Conceptualization, Project administration, Resources, Writing – review & editing. **Michael Gurven:** Conceptualization, Funding acquisition, Methodology, Project administration, Resources, Supervision, Writing – review & editing. **Nick Landry:** Formal analysis, Methodology, Writing – review & editing. **Jessica K. Hlay:** Data curation, Formal analysis, Visualization, Writing – review & editing. **Nicole Merullo:** Formal analysis, Writing – review & editing. **David A. Puts:** Resources, Supervision, Writing – review & editing. **Steven A. Arnocky:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Methodology, Project administration, Resources, Supervision, Writing – original draft, Writing – review & editing.

Declaration of competing interest

None.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.evolhumbehav.2024.05.004>.

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