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## Research



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Electronic supplementary material is available online at [rs.figshare.com](https://rs.figshare.com).

# Predicting strength from aggressive vocalizations versus speech in African bushland and urban communities

Q1

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The human voice carries information about a vocalizer's physical strength that listeners can perceive and that may influence mate choice and intrasexual competition. Yet, reliable acoustic correlates of strength in human speech remain unclear. Compared to speech, aggressive nonverbal vocalizations (roars) may function to maximize perceived strength, suggesting that their acoustic structure has been selected to communicate formidability, similar to the vocal threat displays of other animals. Here, we test this prediction in two non-WEIRD African samples: an urban community of Cameroonians and rural nomadic Hadza hunter-gatherers in the Tanzanian bushlands. Participants produced standardized speech and volitional roars and provided handgrip strength measures. Using acoustic analysis and information-theoretic multi-model inference and averaging techniques, we show that strength can be measured from both speech and roars, and as predicted, strength is more reliably gauged from roars than vowels, words or greetings. The acoustic structure of roars explains 40–70% of the variance in actual strength within adults of either sex. However, strength is predicted by multiple acoustic parameters whose combinations vary by sex, sample and vocal type. Thus, while roars may maximally signal strength, more research is needed to uncover consistent and likely interacting acoustic correlates of strength in the human voice.

This article is part of the theme issue 'Voice modulation: from origin and mechanism to social impact (Part I)'.

## 1. Introduction

Vocalization is among the most powerful communication and signalling channels in all major vertebrate clades [1,2]. Mammalian males of various taxa can produce mighty roars that have a functional role within intrasexual competition and mating contexts, such as the roars of red deer stags that putatively function to exaggerate size and communicate dominance [3]. Humans are no exception as roar-like vocalizations appear within various social interactions such as competition between rivals, combatants and conflicts between larger groups (e.g. sports and warfare [4–7]), as well as in deceptive mimicry of animal calls used for hunting [8]. Multiple converging lines of evidence indicate that

64 nonverbal acoustic features in speech, particularly voice  
65 pitch, and more recently the acoustic structure of nonverbal  
66 vocalizations such as roars, screams and grunts can influence  
67 listeners' judgements of speaker traits and can predict repro-  
68 ductive outcomes particularly in mate choice and intrasexual  
69 competition (see [9] and [10] for review).

70 Research on the communicative function of agonistic  
71 vocalizations in animals has focused largely on the inverse  
72 relationship between vocal frequencies, namely fundamental  
73 frequency ( $f_0$ , perceived as voice pitch) or formant frequen-  
74 cies (resonances of the vocal tract) and body size [11–14].  
75 Indeed, in many mammals including humans, longer vocal  
76 tracts result in lower and more closely spaced formants that  
77 provide a reliable index of body size [14–17]. While larger  
78 individuals with bigger larynges also produce lower  $f_0$ ,  
79 than do smaller individuals [13,18],  $f_0$  is not a reliable predic-  
80 tor of body size in many mammals when age and sex are  
81 controlled [19], including in humans [17].

82 A small number of studies have also investigated the vocal  
83 correlates of physical strength in the human voice, with mixed  
84 and often null results [20–24]. Surprisingly, while human lis-  
85 teners appear capable of assessing the strength of vocalizers  
86 from their speech [20,25,26] and from their nonverbal vocaliza-  
87 tions, namely roar-like vocalizations (hereafter, 'roars')  
88 [25,26], studies have largely failed to find robust and consist-  
89 ent acoustic indices of strength in the human voice. While  
90 there is some limited evidence that  $f_0$  may predict strength  
91 in young peri-pubertal Bolivian Tsimane males after control-  
92 ling for body size [22], this result has not been consistently  
93 replicated in adult men in various other cultures [20,23,26].  
94 Indeed, a recent meta-analysis of eight published studies  
95 showed a significant but very weak inverse relationship  
96 between adult men's mean  $f_0$  and their upper body strength  
97 ( $r = -0.07$ ) [24]. Some investigations further suggest a potential  
98 link among strength, fighting ability and sexually dimorphic  
99 vocal characteristics, but here too the evidence is equivocal  
100 for various measures of fighting success [27], hunting  
101 reputation [28] and strength [23].

102 In addition to focusing on a relatively small set of vocal  
103 parameters, the vast majority of past research investigating  
104 form and function in the human voice has focused almost  
105 exclusively on *speech* signals. Importantly, recent research  
106 suggests that human roars (compared to speech) may maxi-  
107 mize the perceived strength of the vocalizer. Indeed, the  
108 acoustic structure of aggressive vocalizations in humans may  
109 have been selected to communicate, and to some degree exagger-  
110 ate, functional cues to physical formidability [25,26],  
111 similar to the vocal threat displays of other animals [18,29].  
112 Human roars serve to intimidate the enemy and to motivate  
113 an individual or whole group of individuals, as seen in mili-  
114 tary contexts—in armies as distinctive as the fourteenth  
115 century Japanese fighters [4], World War II Soviet soldiers  
116 [5] and Ancient Greek troops [6]—and in the context of  
117 modern-day sport competitions [7]. Battle cries, and their  
118 derivatives in collective sports, are often combined with war  
119 dances and intimidating bodily expressions, thus being part  
120 of human behavioural patterns of aggression that can lead to  
121 the immediate escalation of physical confrontation preceding  
122 an attack, or otherwise function to overt it.

123 Nonverbal vocalizations are also special in human vocal  
124 communication because of their acoustic structure: they often  
125 occupy a part of acoustic space that corresponds to perceptual  
126 roughness and that is separated from other vocal signals,

including speech [26,30]. Indeed, unlike speech, human  
nonverbal vocalizations are often characterized by a high pro-  
portion of nonlinear phenomena (NLPs) caused by aperiodic  
vibration of the vocal folds that can give the voice a rough or  
harsh quality. Nonlinearities are also found in animal distress  
cries and vocal threat displays [29,31–33], and a wide range  
of vertebrate species are sensitive to nonlinearities [2,34]. In  
humans too, they can increase the perceived aversiveness of  
vocalizations [33]. It has been hypothesized that the nonlinear  
acoustic parameters that uniquely characterize nonverbal voca-  
lizations may function to communicate physical traits and  
states, such as physical strength [25,26]. However, given that  
research on human vocal communication has focused largely  
on speech, the functional role of nonlinearities in the human  
voice remains unclear.

Research on the human voice is also largely culturally  
restricted. While there is relatively rich evidence on the form  
and function of the human voice (focusing on speech) in  
'WEIRD' human populations [35], namely European, North  
American and Asian cultures, less is known about indigenous  
populations for whom access to media portrayals is limited  
and, in the case of nomadic tribes, traditional modes of  
living more closely resemble those of our ancestors. To our  
knowledge, research on African populations is limited to  
Namibian Himba and Nama, Cameroonians of Bantu origin,  
and Tanzanian Hadza [21,28,36–40], and has, with a few  
exceptions (see [36,40,41]), again focused almost exclusively  
on speech. In Hadza, males who produce lower pitched  
speech have been reported to have more children and, there-  
fore, higher reproductive success [38]. Hunting reputation,  
a trait associated with reproductive success [42,43] and  
strength [44], also correlates with lower voice pitch in men  
and appears to explain much of the variance in reproductive  
success [28]. Similarly, women whose voices were manipu-  
lated to be higher pitched were regarded as better gatherers  
[39]. Though the relationship between reproductive success  
and voice pitch appears negligible when controlling for hunt-  
ing reputation, hunting reputation remains a reliable predictor  
of reproductive success when controlling for voice pitch [28].  
Both fundamental frequency and handgrip strength (HGS)  
are positively associated with reproductive success in  
indigenous Himba women [37].

HGS measured by a dynamometer has been repeatedly  
shown to predict upper body strength [45,46] and recently,  
also shown to predict the outcomes of male–male competi-  
tion in Hadza men [44]. HGS has been used in a series of  
studies reporting its positive association with men's facial  
masculinity [47,48], other male sex-specific characteristics  
and fitness indicators [49–52], and clinical traits associated  
with health, ageing and mortality (see, e.g. [53–55]). HGS  
data from rural African and Western populations have  
revealed comparable relationships with ageing and mortality  
across populations and thus may represent a cross-culturally  
robust measure [56]. Although both HGS and sexually  
dimorphic vocal characteristics are positively correlated  
with testosterone levels [21,24,57–59], the evidence that indi-  
viduals with more masculine voices are physically stronger  
than other individuals of the same sex with less masculine  
voices remains equivocal [20–24].

Uncovering the vocal correlates of physical strength has  
emerged as a key question within the evolutionary voice  
sciences. Previous research assessing physical strength from  
*speech* has tested both 'WEIRD' vocalizers (namely students

127 from the UK, America or China) and ‘non-WEIRD’ vocalizers  
 128 (e.g. Hadza, Bolivian Tsiname) [20–23]. However, only one  
 129 previous study has tested for acoustic correlates of strength  
 130 in human nonverbal vocalizations (roars) in a sample of  
 131 British drama students, but did not examine the potential  
 132 role of nonlinear acoustic phenomena [26]. In the present  
 133 study, we take a new approach to this scientific challenge  
 134 by directly comparing indices of strength in roars to speech  
 135 in two African non-WEIRD samples and specifically cultures  
 136 in which strength is important for evolutionary fitness. We  
 137 examine the vocalizations of an urban sample of Cameroo-  
 138 nian men and women, mainly of Bantu origin, and a rural  
 139 sample of nomadic Hadza hunter–gatherers living in the  
 140 Tanzanian bushlands, where access to Western culture  
 141 including media portrayals of emotional expression is extre-  
 142 mely limited and physical strength is important for survival  
 143 [44,60]. Voice recordings of standardized speech sentences  
 144 and volitional aggressive vocalizations in response to  
 145 hypothetical agonistic contexts were collected for each indi-  
 146 vidual together with measures of HGS assessed. Testing not  
 147 only speech, but also nonverbal vocalizations (herein,  
 148 ‘roars’), allows us to test the prediction that roars will maxi-  
 149 mize signals of strength relative to speech, which is far  
 150 more constrained by the rules of language.

151 We employ a state-of-the-art information-theoretic  
 152 approach based on multi-model inference and averaging  
 153 [61], which we predict may be more powerful than the  
 154 traditional linear regression models used in previous studies  
 155 examining vocal indices of strength in the human voice  
 156 [20–23,26]. Given the exploratory nature of this study, a large  
 157 number of potential acoustic predictors of strength, and the  
 158 discrepancies and null results of previous studies [20–23],  
 159 this technique may provide important advantages, as it  
 160 allows the evaluation of multiple models to make inferences  
 161 without *a priori* selecting one single model as the best approxi-  
 162 mation to a phenomenon [61], and thus allows us to evaluate  
 163 the relative importance of numerous nonverbal acoustic  
 164 parameters in predicting the actual strength of African men  
 165 and women.

## 168 2. Methods

### 169 (a) Participants

170 We collected voice recordings from 141 men and women of  
 171 African origin, with an even sex ratio, from two distinct samples:  
 172 urban-dwelling Cameroonians ( $N = 101$ , 51 women and 50 men)  
 173 and bush-living Hadza hunter–gatherers ( $N = 40$ , 20 women and  
 174 20 men). The Cameroonians included in this sample were mainly  
 175 university students of Bantu origin, residing at the time of  
 176 sampling in the English-speaking Southwest Region. Data were  
 177 collected at the University of Buea in the regional capital town  
 178 of Buea. The Hadza are a small nomadic group of hunters and  
 179 gatherers made up of approximately 1000 individuals residing  
 180 in small camps in the bushlands of Tanzania [60]. The Hadza  
 181 share ancestry with Khoisan populations in southern Africa  
 182 [62]. The distributions of all measured variables (e.g. strength,  
 183 age and body size) for both men and women are summarized  
 184 in electronic supplementary material, figure S1, and additional  
 185 sample descriptive are given in electronic supplementary  
 186 material, table S1 [63]. All participants provided informed con-  
 187 sent to take part in the research and were monetarily  
 188 compensated for their participation (Cameroonians: 5000 CFA;  
 189 Hadza: 5000 TZS).

### (b) Voice recording

We recorded three types of voice stimuli from each sample of  
 vocalizers—a sentence-long greeting (herein, greeting speech), a  
 series of mono-syllabic vocal sounds or words (vowels or count-  
 ing, herein, short speech) and volitional nonverbal vocalizations  
 (herein, roars). Cameroonian voice recordings were collected in  
 the Anglophone region of Cameroon (SouthWest) where English  
 is among the official languages and were taken under standar-  
 dized conditions at the campus of the University of Buea.  
 Vocalizers were recorded individually in a quiet room. Record-  
 ings were made using a SONY PCM D50 recorder equipped  
 with a windscreen and saved as WAV files. Each recording ses-  
 sion included a short greeting in English: ‘Hello, how are you’,  
 counting from ten to one (short speech), and three aggressive  
 nonverbal vocalizations (roars). To elicit volitional vocalizations,  
 participants were instructed to imagine themselves in a combat  
 situation in which they are facing the risk of being attacked by  
 an enemy. They were asked to vocally impress the enemy to pre-  
 vent confrontation or increase their chances of winning a fight,  
 without words, three times in a continuous sequence.

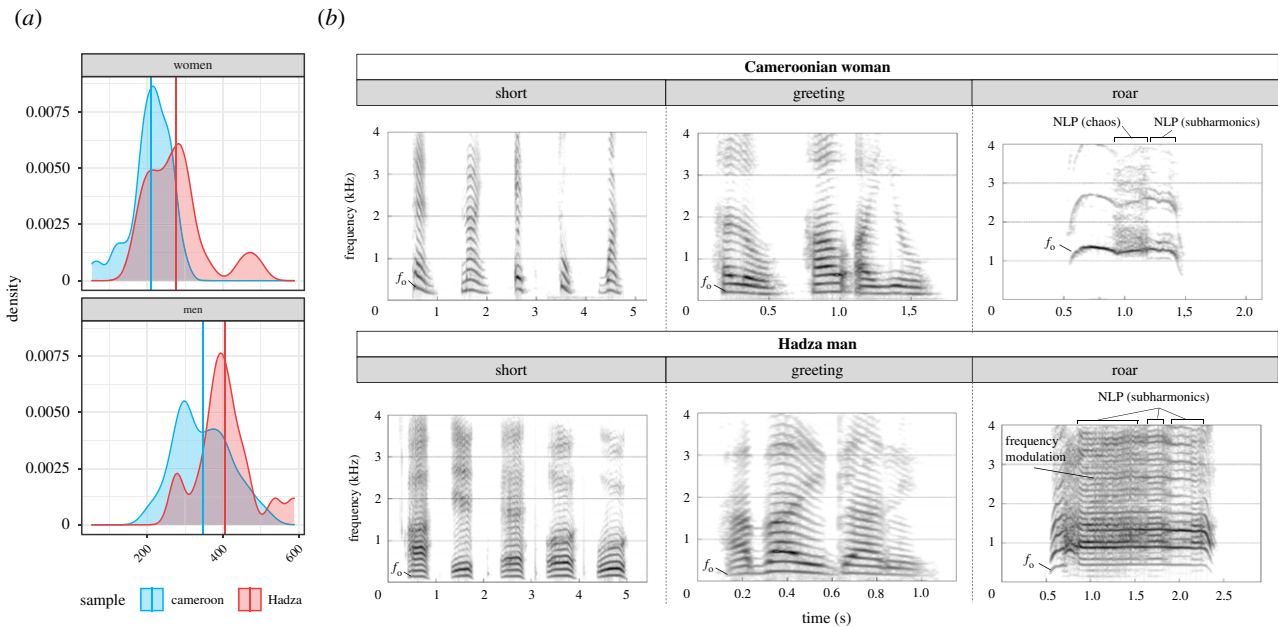
Hadza voice recordings were taken in the Savannah bushland  
 habitat in the Lake Eyasi region of Tanzania. Hadza participants  
 were recorded in individual sessions at 11 different campsites,  
 located with the aid of a local guide and translator who  
 accompanied the field research team on all expeditions. Record-  
 ings were taken in a quiet area at an inaudible distance from the  
 campsite to ensure privacy, using a Tascam DR05 recorder  
 equipped by a windscreen and saved as WAV files. Recording ses-  
 sions followed a standardized procedure in which each participant  
 was instructed to produce a short greeting in Swahili ‘Habari gani’  
 (equivalent to ‘how are you’), the five vowel sounds /a i e o u/  
 (short speech) and an aggressive nonverbal vocalization (roar).  
 To elicit volitional vocalizations, participants were instructed to  
 imagine themselves in a combat situation in which they are  
 facing the risk of being attacked by an enemy, and to produce a  
 single nonverbal vocalization, without words, to express threat  
 toward the enemy. They were shown an image of an aggressive  
 war vocalization to aid their interpretation of the task.

### (c) Hand grip strength measurement

Using a hand dynamometer, we measured the HGS of each par-  
 ticipants’ left and right hands three times each. Participants  
 were asked to hold the dynamometer in a vertical position,  
 while standing, with their arm bent at the elbow such that the fore-  
 arm takes the position perpendicular to the body axis. Participants  
 were further instructed to press the grip of the device with as  
 much force as possible in three rounds for each hand, alternating  
 the right and left hand in each round. Analysis of video-recorded  
 footage of tool use has previously revealed that the Hadza are  
 strikingly lateralized using the right hand in 96% of all tool-use  
 tasks [64]. Nevertheless, the HGS measures were highly correlated  
 between hands (Hadza:  $r = 0.77$ ; Cameroon:  $r = 0.87$ ) and across  
 three rounds (Hadza:  $r = 0.96$ ;  $r = 0.97$ ;  $r = 0.95$ ; Cameroonian:  
 $r = 0.93$ ;  $r = 0.93$ ;  $r = 0.95$  correlation between first and second,  
 first and third, and second and third HGS measurement, respec-  
 tively), and thus HGS measures were averaged across all three  
 attempts and for both hands for the purpose of further analysis.  
 We additionally measured participants’ weight using metric  
 scales, and height using a portable anthropometer (Hadza) or  
 metric tape affixed to a wall (Cameroon). See figure 1a for a  
 graphical representation of HGS distribution and electronic sup-  
 plementary material, table S1 for HGS descriptive statistics [63].

### (d) Acoustic editing and analysis

To standardize recordings between Cameroonian and Hadza  
 samples for acoustic analysis, the greeting vocalizations contained



**Figure 1.** (a) Distribution of HGS by sex and sample; coloured vertical lines represent mean HGS. (b) Spectrograms of example vocalizations for a Cameroonian woman (top) and a Hadza man (bottom); fundamental frequency ( $f_0$ ) is labelled in all spectrograms; NLPs, including subharmonics and deterministic chaos, as well as frequency modulations (inflex), are common in roars but are largely absent in speech. (Online version in colour.)

five syllables in all cases (i.e. ‘He-llo, how-are-you’ and ‘Ha-ba-ri ga-ni’, respectively), and short speech samples were a string of five single-syllable utterances: five vowels in the case of Hadza and five numbers in the case of Cameroonian participants. To account for prosodic changes that mark the beginning and end of a string of utterances, we selected the first three and the last two numbers for Cameroonians (i.e. ‘10, 9, 8, 2, 1’), and all five vowels for the Hadza (/a i e o u/). For the Cameroonian sample, one of the three roars was selected at random for acoustic analysis. In all cases, recordings were checked for background noise and instances of clipping that could affect acoustic analysis, and we selected recordings with an adequate signal-to-noise ratio. Silence gaps of 0.5 s were inserted at the beginning and end of each recording, and between utterances, for analysis. Voice stimuli thus included ‘141’ greetings, ‘141’ short speech and ‘135’ roars for a total of 417 stimuli used for acoustic analysis. Figure 1b provides spectrograms of example vocalizations for each vocal type.

Acoustic analysis was performed in Praat v. 6.1.08 and 6.1.35 [65]. We measured a range of voice parameters (see electronic supplementary material, table S2) predicted to communicate biologically and socially relevant information about a vocalizer, including potentially indicating physical strength [20,25–27]; see also [9,12] for reviews. These measures included fundamental frequency ( $f_0$ ) parameters linked to the perception of voice pitch and its variability:  $f_0$  mean (figure 1b),  $f_0$  minimum, and  $f_0$  coefficient of variation ( $f_0$  CV), mean absolute slope (MAS), and modulation wherein smoothing algorithms were applied to the pitch contour to measure major  $f_0$  modulations (inflex2) and minor vibrato-like inflections (inflex25). Fundamental frequency parameters were measured with a search range of 60–2000 Hz, 0.05 s window length and 0.01 time step. Extracted  $f_0$  contours were systematically verified and corrected, including where nonlinearities in roar stimuli impeded pitch tracking, following previous work (e.g. [25,66]). We additionally measured vocal perturbation and noise parameters including harmonics-to-noise ratio (HNR, ratio of harmonic to chaotic spectral energy), jitter (minor fluctuations in periodicity) and shimmer (minor fluctuations in amplitude). Finally, we computed the proportion of each roar stimulus containing nonlinear phenomena (%NLP), identified and annotated manually from spectrograms (0–5 kHz; window length 0.05) and amplitude waveforms of voice recordings in Praat (note

that only roars contained NLPs, our speech sample did not). Proportions of nonlinear vocal phenomena included in %NLP were sidebands (amplitude modulation), subharmonics (vocal fold vibration at an integer multiple of  $f_0$ ), and deterministic chaos (aperiodic, irregular vocal fold vibration; see [31,33]; see figure 1b for examples). With the exception of manually measured nonlinearities, all-acoustic measures were performed using an established custom Praat script (see e.g. [25,26,66]).

See electronic supplementary material, figure S2 for a graphical summary of all-acoustic variables and their distributions. Descriptive statistics of the acoustical parameters of Cameroonian and Hadza participants are summarized in the electronic supplementary material, tables S2 and S3, for female and male participants, respectively [63].

### (e) Statistical analysis

To analyse the relationship between strength and nonverbal vocal parameters, we employed an information-theoretic approach [61,67,68]. Because this is an exploratory study, by using this technique, we were able to evaluate all possible candidate models derived as subsets of predictors from a global model. In addition, because several candidate models could be equally robust, with no strong reason to prefer one over the others (e.g. candidate models with  $\Delta AICc < 2$ ), we used model averaging techniques to produce both parameter and error estimates derived from weighted averages, and thus not restricted to one model [61].

We built linear models using the *lm* function from base R version 4.0.4 [69]. We fitted separate models for each vocalization type (greeting, short, roar), and for both sexes for a total of six models. We fitted equivalent global models in each case, including Sample, Mean  $f_0$ , Minimum  $f_0$ ,  $f_0$  CV, Inflex25, Inflex2, MAS, HNR, Jitter, Shimmer and NLP proportion (NLP only for models from roar vocalizations where NLPs were present). Individuals with missing data on any model variables were excluded to maintain equal  $n$ 's, regardless of predictor variables. This step was necessary to ensure models from different vocalization types were comparable (by second-order Akaike Information Criterion -  $AICc$ ) within each sample/sex combination. Thus, all models had an equivalent structure, sample size, and were in all cases (with each sample/sex combination), based on

**Table 1.** Information criteria for the best-supported models for each vocal type by sex and sample. *Note:* for a detailed description of values, see the lctab function documentation.

	Cameroon				Hadza				
	<i>AICc</i>	$\Delta AICc$	<i>d.f.</i>	$w_i(AICc)$	<i>AICc</i>	$\Delta AICc$	<i>d.f.</i>	$w_i(AICc)$	
<b>women</b>									
<i>roar</i>	465.51	0.00	7	0.95	<i>greeting</i>	230.25	0.00	7	0.90
<i>greeting</i>	472.15	6.64	6	0.03	<i>roar</i>	235.48	5.23	8	0.07
<i>short</i>	474.31	8.80	3	0.01	<i>short</i>	237.15	6.90	4	0.03
<b>men</b>									
<i>roar</i>	486.21	0.00	7	0.91	<i>short</i>	209.04	0.00	4	0.50
<i>short</i>	491.70	5.49	5	0.06	<i>roar</i>	209.99	0.95	7	0.31
<i>greeting</i>	492.97	6.76	3	0.03	<i>greeting</i>	211.04	2.00	3	0.19

vocalizations from the same participants, with the same data as the dependent predicted variable (strength, HGS).

These highly parametrized global models were subsequently reduced by multi-model inference techniques, using the *dredge* and *model.avg* functions from the R package MuMIn (Multi-Model Inference) [70]. First, the *dredge* function was used to fit all possible combinations (subsets) of predictor terms (both main effects and interactions) from the global model and to rank the generated models based on their *AICc* and Akaike weights ( $w_i(AICc)$ ) [71]. Based on these criteria, we empirically selected the best-supported models (i.e. those with  $\Delta AICc \leq 2$  units from the best-supported model) and averaged them using the *model.avg* function. Coefficients were weighted in all averaged models.

To determine which vocalization type best predicts HGS, models for each type of vocalization by sex were then compared in two ways. First, by comparing the top best-supported models using *AICc*,  $\Delta AICc$  and Akaike weights  $w_i(AICc)$ , and second, by plotting and fitting a linear regression between actual (measured) HGS and the HGS predicted by each averaged model on the basis of vocal parameters. See electronic supplementary material for detailed information on model parameterization, selection, averaging and the related R code.

Given the difference in HGS between the samples (Hadza were significantly stronger than Cameroonian participants, see figure 1a and electronic supplementary material, table S1), the sample emerged as a strong predictor in most models, particularly for Greeting speech (see electronic supplementary material, figure S11). Thus, to prevent resultant reductions in the predictive power of acoustic variables, we repeated exactly the same modelling, selection and averaging process separately for each combination of sample and sex (thus excluding sample as a predictor in all models). For models of Hadza participants, given the smaller sample size, we limited the number of predictor terms in the subset models produced by *dredge* to between one and 10 (excluding intercept) as recommended by Austin and Steyerberg [72].

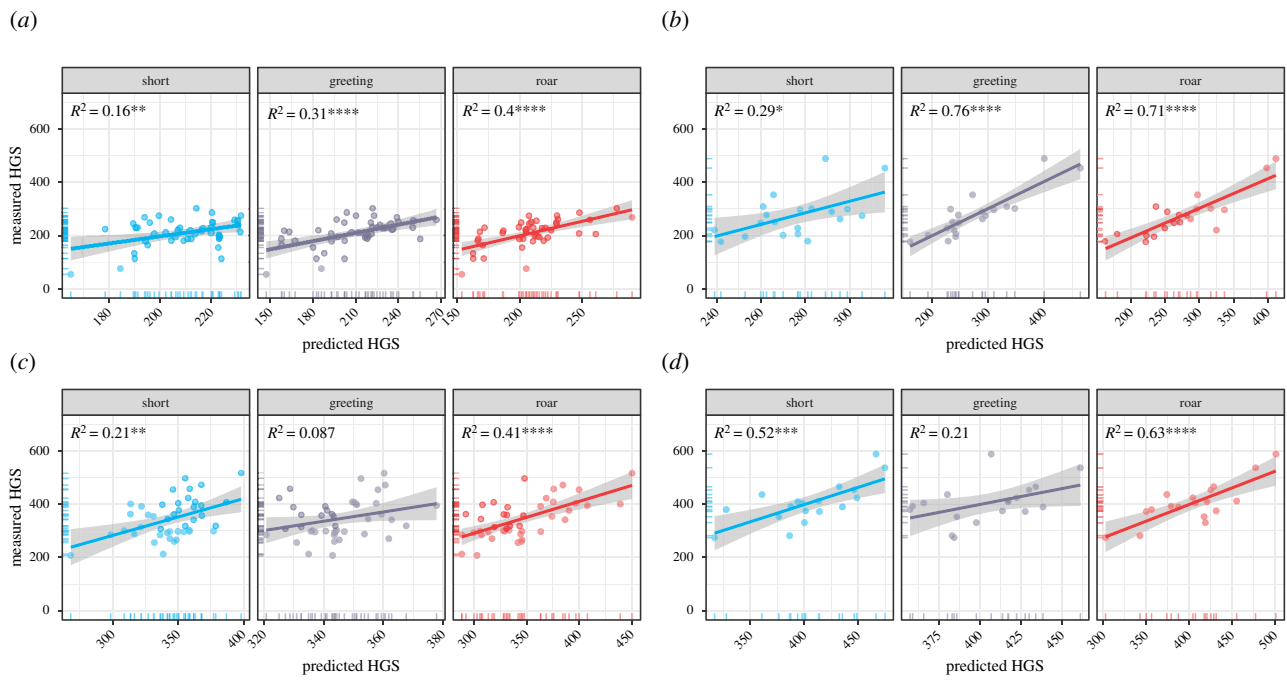
### 3. Results

Multi-model inference procedures first reduced the products of linear modelling, and the best-supported models were subsequently selected. table 1 presents the information criteria for the top best-supported models for each grouping. The comparison of the best-supported models for predicting strength from each type of vocal stimulus (i.e. single best

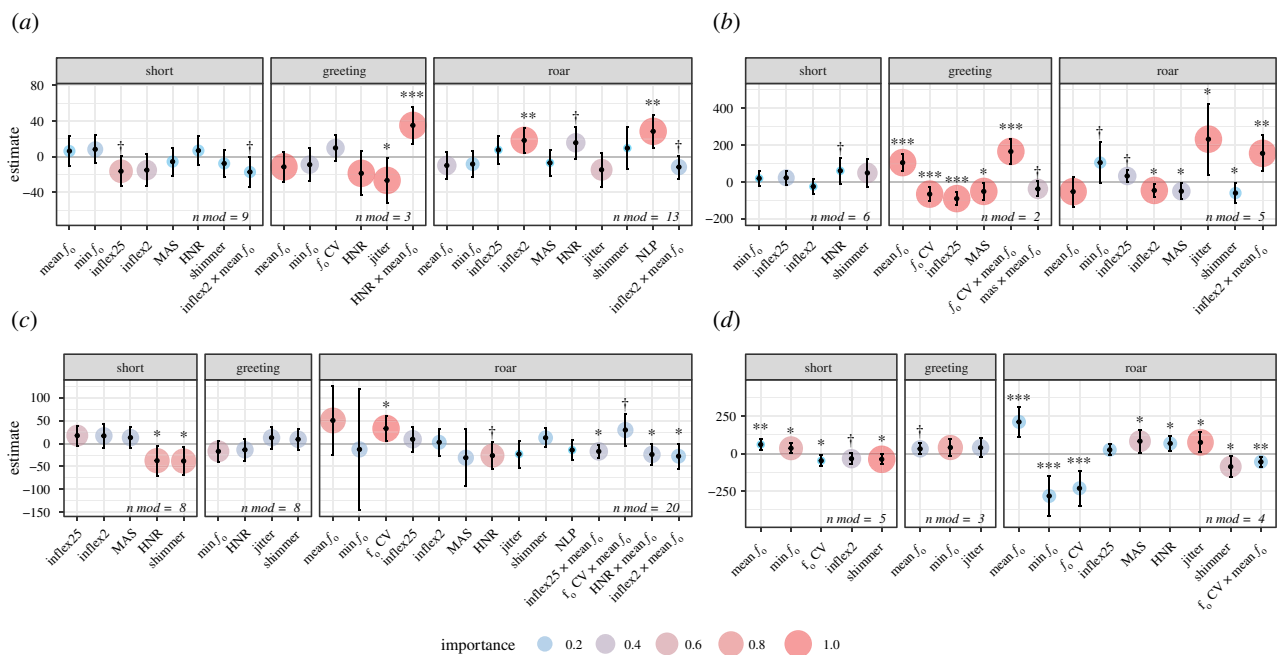
model per vocal type) revealed a relatively stable pattern for Cameroonians, while the results appeared less consistent among the Hadza (table 1).

Model averaging conveyed clearer results. Figure 2 shows scatterplots resulting from the regression of the actual (measured) strength (HGS) and the strength predicted by each average model, providing a comparison of the predictive power of each voice stimulus type. Roar vocalizations showed the highest predictive power in all examined groups, with the exception of Hadza women. Indeed, the acoustic parameters measured from roars explained the most variance in actual strength for Cameroonian women (40% variance explained), Cameroonian men (41% variance explained) and Hadza men (63% variance explained) (figure 2). In the Cameroonian sample, roars explained more than twice the variance in actual strength than that explained by a short speech, and three to four times more variance than that explained by greeting speech in Cameroonian and Hadza men (figure 2c,d). Among Hadza women, while roars still explained a high amount of variance in actual strength (71%), models based on roars and greetings had similar predictive power (the difference between coefficients of determination was negligible,  $\Delta R^2 = 0.05$ , figure 3b). In general, the results for Cameroonian participants (both men and women) corroborated the patterns found by the comparisons of the top best-predicted models (table 1), while for Hadza participants, we found only partial congruence between comparisons based on top best-predicted and weighted average models. While this may be due to differences in the vocal expression of strength between Cameroonian and Hadza participants, we cannot rule out the possibility that sample-level differences are due to the smaller sample size for Hadza and thus model instability.

Figure 3 provides coefficient estimates from final average models (models where  $\Delta AICc < 2$  were averaged), and thus a detailed summary of the relative consistency and therefore the importance of various acoustic parameters in together predicting the physical strength of vocalizers for each sample of African men and women and for all voice stimulus types. Models for roar vocalizations consistently involved a higher number of acoustic parameters than did models for speech (short or greeting). The most consistently observed predictors of strength across sexes, samples and voice types



**Figure 2.** Comparison of the predictive power of the average vocalization models, by vocalization type (*short*, *greeting* and *roar*). (a) Cameroonian women, (b) Hadza women, (c) Cameroonian men and (d) Hadza men. Regression lines represent the association between actual hand grip strength (measured HGS, averaged between right and left hand), and the predicted HGS from the final average model from each type of vocalization. \*\*\*\* $p < 0.0001$ , \*\*\* $p < 0.001$ , \*\* $p < 0.01$ , \* $p < 0.05$ . (Online version in colour.)



**Figure 3.** Coefficient estimates of the averaged best models (where  $\Delta AIC_c < 2$ ) by vocalization type (*short*, *greeting* and *roar*). (a) Cameroonian women, (b) Hadza women, (c) Cameroonian men and (d) Hadza men. Points and error bars represent average unstandardized weighted  $B$  estimates and 95% confidence intervals. The colour and size of the bubbles (Importance) represents the proportion of the averaged models in which a term is included, and hence how robust each term is across averaged models.  $n_{mod}$  is the number of averaged models for each group. HNR = harmonic-to-noise ratio. MAS = mean absolute slope. NLP = nonlinear phenomena. All predictors were centred and scaled. For term significance, \*\*\*\* $p < 0.001$ , \*\*\* $p < 0.01$ , \*\* $p < 0.01$ , \* $p < 0.05$ ,  $\dagger p < 0.10$ . (Online version in colour.)

(speech and roars) were mean  $f_0$  (voice pitch) and various indices of its variability or instability ( $f_0$  CV, jitter, inflex2 and inflex25). However, the direction of these relationships was inconsistent. Indeed, the model averaging results clearly show that vocal indices of strength depend on the combination of multiple acoustic parameters and cannot be predicted as a function of a single acoustic variable, and

moreover, that these combinations vary to some extent across voice stimulus type, sex and sample. For example, while nonlinear acoustic phenomena (NLPs) appear to play a critical role in predicting strength from the roars of Cameroonian women, along with major modulations in voice pitch (inflex2; figure 3a), the contribution of nonlinearities was negligible in the roars produced by men.

379 Thus, while our results show that human vocal parameters  
380 holistically encode information about physical strength and  
381 that roars predict strength more effectively than does speech  
382 (figure 2), our acoustic modelling techniques (figure 3), like  
383 the acoustic analyses of most previous studies ([20,23,26], see  
384 also [22]) have failed to identify consistent individual markers  
385 of physical strength in the human voice.

#### 388 4. Discussion

389 Our results support the prediction that vocal signals to phys-  
390 ical strength in humans are maximized in aggressive  
391 nonverbal vocalizations (roars) compared to speech. While  
392 this prediction has been supported in a Western population  
393 (UK drama students: [25,26]), here we extend this research  
394 to two African samples, one from the relatively urbanized  
395 municipality of Buea (students at the local university) and  
396 the other from a rural and nomadic small-scale population  
397 of Hadza hunter-gatherers. Applying a bottom-up infor-  
398 mation-theoretic modelling approach, we show that the  
399 nonverbal acoustic structure of roars best predicts physical  
400 strength. Indeed, predicted strength based on vocal param-  
401 eters in roars explained the most variance in actual  
402 strength for Cameroonian men and women (explaining 40%  
403 of the variance in measured hand grip strength) and for  
404 Hadza men (explaining 63% of the variance), and explained  
405 generally two to four times more variance in strength than  
406 did speech (vowels, words or phrases). While roars relative  
407 to greetings predicted strength better in men than in  
408 women, roars produced by Hadza women explained an  
409 impressive 71% of the variance in their actual physical  
410 strength, though this was comparable to the predictive  
411 power of their greeting speech (77%). Thus, in contrast with  
412 speech, nonverbal roars appear to most effectively encode  
413 functional cues to physical strength, as also observed in  
414 non-human mammals [29].

415 However, despite our finding that roars and, to a lesser  
416 extent, speech, encode information about physical strength  
417 in non-WEIRD samples of men and women of African  
418 origin, our analyses did not identify a single vocal parameter  
419 nor a consistent combination of vocal parameters that pre-  
420 dicted strength in both sexes and in both speech and roars.  
421 The complex combinations of acoustic predictors revealed  
422 by our models, and their high variability across sex, sample  
423 and vocal stimulus type, corroborate the discrepancies of  
424 past studies conducted in Western samples [20,22–24,26].

425 In an attempt to overcome the mixed and null results of  
426 this past work, we (i) employed an information-theoretic  
427 approach [61,67,68] in order to more extensively explore  
428 potential acoustic predictors of strength; (ii) examined these  
429 predictors in both speech and roars, wherein the latter was  
430 predicted to carry more information about physical formid-  
431 ability [25,26] and (iii) tested for acoustic indices of strength  
432 in two non-WEIRD African samples. In both samples, but  
433 particularly among the Hadza, physical strength may signifi-  
434 cantly contribute to the biological fitness of an individual  
435 given that it positively affects hunting outcomes [44]. There-  
436 fore, acoustic communication may be an optimal way to  
437 mediate social dominance hierarchies and maintain  
438 resource-control without engaging in a risky physical con-  
439 frontation. Indeed, we found that Hadza men and women  
440 were physically stronger than our more urban sample of  
441

Cameroonian men and women (on average by 16–31%) and  
that roars predicted strength better in Hadza men and  
women than in Cameroonian men and women. However,  
we also found that acoustic predictors of actual strength  
were more difficult to identify and less stable in the Hadza  
sample. The reasons for this could be ecological. For instance,  
Hadza are bush-living people who often communicate at  
long distances using loud vocalizations or speech, whereas  
our Cameroonian sample is urbanized, and more often  
communicate at shorter distances and at a lower volume.  
The two samples also speak different languages. While  
Cameroonians from Southwest and Northwest regions  
speak fluent English, alongside a variety of local native  
languages, the Hadza speak Swahili and/or Hadzane, a  
click language consisting of three types of click consonants  
that may be produced in voiceless oral, voiced nasal, or voi-  
celess nasal, and glottalised variant [60]. Despite these  
differences, we cannot rule out the possibility that sample-  
level differences emerged due to small sample size in the  
Hadza. Indeed the small sample size of the Hadza is a key  
limitation of this study. While data from extreme non-  
WEIRD samples are rare and difficult to obtain, the small  
sample size may have contributed to inconsistencies in the  
predictive power of vocal parameters and these results thus  
should be interpreted with caution.

Regarding specific acoustic parameters, it is difficult to  
derive a clear generalization of their independent contri-  
butions due to the lack of consistency in the pattern of  
acoustic predictors included in each final average model.  
However, unlike in studies based on assessments of formid-  
ability in voice perception (e.g. [73]), and evidence that  
relatively low  $f_0$  can predict strength in the speech of  
peri-pubertal Bolivian Tsiname males (but not females;  
[22]), we did not find a consistent relationship between low  
male fundamental frequency ( $f_0$ ) and strength across samples  
and different vocal types. In fact, in several cases, for example  
in the short speech and roars of Hadza men, *higher* mean  $f_0$   
signalled strength. As increased subglottal pressure will  
cause an increase in voice pitch [74], this result could be  
due to greater lung capacity and/or louder vocalizations  
produced by stronger men, a prediction that can be directly  
tested in future work. Notably, a recent meta-analysis  
showed, using data from eight studies and 845 adult men,  
that mean  $f_0$  explains a mere 0.005% of the variance  
( $r = -0.07$ ) in men's upper body strength [24]. The present  
study is, to our knowledge, the first to examine whether  
nonlinear acoustic phenomena (NLPs) predict strength in  
human roars. While we find preliminary evidence to support  
this, the positive relationship between NLPs and strength was  
most evident in Cameroonian women's roars. In order  
to reduce the number of terms in our statistical models, we  
computed a single cumulative proportion (%NLP) combining  
sidebands, subharmonics and deterministic chaos. This  
cumulative proportion has previously been shown to reliably  
index ostensible pain levels in volitional human pain vocali-  
zations [75]. However, we cannot rule out the possibility  
that specific NLP sub-types (e.g. deterministic chaos, which  
is typically the most strongly associated with affective inten-  
sity [33]) may predict strength more effectively than others.  
This possibility can be tested in future studies that employ  
larger samples of vocalizers to ensure adequate sampling of  
various sub-types of NLP in nonverbal vocalizations, and  
adequate statistical power to test their relative roles.



## 5. Conclusion

Altogether our findings offer four key conclusions. First, we replicate the finding that both speech and roars can predict strength, and critically, that roars tend to predict strength better than does speech. Moreover, we show that this is true across three extremely different human cultures (UK students, Congolese urban-dwellers and Hadza hunter-gatherers). Second, we show that roars consistently predict HGS with a relatively high level of accuracy than does speech, explaining 40–80% of the variance in strength within adults of either sex (association between actual and predicted HGS,  $R^2 > 0.4$  in all cases; see figure 2). Third, our acoustic analyses show that strength cannot be predicted solely by one acoustic variable, such as voice pitch or NLP alone; rather it seems that vocal indices of strength are likely to depend on combinations of multiple acoustic parameters. Thus, to uncover the clearly complex vocal predictors of physical strength, our results suggest that researchers may need to employ likewise complex models with multiple predictors and interaction terms. In addition, having larger sample sizes and a broader range of samples from different cultural and linguistic backgrounds (at least five) will allow researchers to include those samples as levels in a random factor, with random intercepts as well as random slopes for specific acoustic characteristics. This may provide a clearer picture of the effect of individual voice parameters in communicating strength across diverse human cultures and could produce more generalizable results. Fourth, our results show that volitionally produced human roars retain honest information about a vocalizer's actual physical strength. This research thus adds to a growing body of literature examining form and function in human vocalizations in light of the special capacity of humans to volitionally modulate our vocal output or to produce vocalizations entirely on demand [76–78]. Such a capacity for volitional voice modulation in humans is not observed to the same extent in other mammals including other primates [76]. In addition to being a precursor to articulated speech [78,79], the capacity to modulate our voices could be

beneficial for our fitness, for instance in the context of deceptive signalling of body size [80], and strength [25,26], an important avenue for continued research.

**Ethics.** Experiment protocols involving humans were in accordance with the guidelines of the Declaration of Helsinki and followed all national/international/institutional guidelines. Procedures were approved by the Institutional Review Board of the Faculty of Science of the Charles University (protocol ref. no. 06/2017) and by the Scientific Council of the Institute of Ethnology, Russian Academy of Sciences, protocol N 1., issued on 19th February 2015. Research on the Hadza population was approved by the Tanzania Commission for Science and Technology (2016-176-ER-2009-151).

**Data accessibility.** Electronic supplementary material, including code and data, are available online at: <https://doi.org/10.17605/OSF.IO/JU6M8>.

The data are provided in the electronic supplementary material [81].

**Authors' contributions.** K.K., K.P., J.D.L., D.R. and V.F. conceived and designed the research studies; K.K., K.P., J.D.L. and V.R. conceived the analytical approach and drafted the manuscript; J.D.L., K.P. and C.C. performed acoustic analyses; J.D.L. performed statistical analyses, wrote the code and created supplementary materials; J.D.L. and C.C. designed the figures; K.K. and R.M.A. collected field data on the Cameroonian population; K.P., A.G.B., M.B. and P.S. collected field data on the Hadza population; all authors critically reviewed and commented on the manuscript. All authors gave final approval for publication and agree to be held accountable for the work performed therein.

**Competing interests.** The authors declare no competing interests.

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