

Acoustic and Temporal Variation in Gelada (*Theropithecus gelada*) Loud Calls Advertise Male Quality

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Abstract Many animals rely on information from vocal signals to assess potential competitors and mates. For example, in primates, males use loud calls to assess rivals when the acoustic properties of the calls reliably indicate the condition or quality of the sender. Here, we investigate whether the loud calls of male geladas (*Theropithecus gelada*) function as a quality signal. Gelada males produce loud calls during ritualistic chases with rival males. Given the physically taxing nature of these displays, we hypothesize that variation in the acoustic properties of loud calls reliably signal male stamina or competitive ability. To test this hypothesis, we examined whether the acoustic properties of the gelada loud call varied in relation to individual, age, status, and exhaustion. Specifically, we examined 12 call parameters (*e.g.*, fundamental frequency) and 3 bout parameters (*e.g.*, number of calls per bout), that have been previously shown to vary across condition in male primates. We found that several acoustic features varied consistently across age and status such that males deemed

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higher quality in gelada society (e.g., high status) produced more calls per bout, produced calls that were lower in overall frequency measures, and exhibited a greater vocal range. In addition, we found that similar acoustic features varied with exhaustion; after a long chase event, males produced both fewer calls per bout and calls with higher spectral measures. Results from this study are consistent with the hypothesis that gelada loud calls are quality signals, contributing to the growing evidence that primates may use acoustic information to assess the quality of a rival or a potential mate.

Keywords Acoustic analysis · Mate choice · Quality signal · Rival assessment · Sexual selection · *Theropithecus*

Introduction

In many species of birds, amphibians, and mammals, individuals make reproductive decisions based on information gleaned from vocalizations (e.g., red deer, *Cervus elaphus*: Reby *et al.* 2005; gray tree frog, *Hyla chrysoscelis*: Gerhardt *et al.* 2000; red grouse, *Lagopus lagopus scoticus*: Mougeot *et al.* 2004). Vocalizations can function as quality signals (Vehrencamp 2000; Zahavi 1975) if there is an associated cost or constraint on vocal production that prevents low-quality individuals from producing a strong acoustic signal (e.g., nightingales, *Luscinia megarhynchos*: Thomas 2002; canary, *Serinus canaria*: Ward *et al.* 2003; bottlenose dolphin, *Tursiops truncatus*: Holt *et al.* 2015). Acoustic signals can function in sexual selection (Darwin 1871) by signaling individual quality to females for mate choice (e.g., red deer, *Cervus elaphus*: McComb 1991; gray treefrog, *Hyla versicolor*: Gerhardt *et al.* 2000; red grouse, *Lagopus lagopus scoticus*: Mougeot *et al.* 2004) or by signaling competitive ability to rivals in male–male competition (e.g., Blanchard’s cricket frog, *Acris crepitans blanchardi*: Wagner 1992; red deer (Reby *et al.* 2005). For example, in primates, adult males produce long-distance vocalizations (i.e., “loud calls”) that may be used in both contexts (Delgado 2006; Fischer *et al.* 2004; Kitchen *et al.* 2003). Potential rivals or mates likely attend to loud calls because, in addition to providing information about caller identity (Barelli *et al.* 2013; Bouchet *et al.* 2012; Erb *et al.* 2013; Fischer *et al.* 2002; Neumann *et al.* 2010; Spillmann *et al.* 2010; Wich *et al.* 2003) and context (Fischer *et al.* 2002; Wich *et al.* 2003), acoustic properties of the call often correlate with a caller’s body size (e.g., Japanese macaques, *Macaca fuscata*: Inoue 1988; rhesus macaques, *Macaca mulatta*: Fitch 1997; hamadrayas baboons, *Papio hamadryas*: Pfefferle and Fischer 2006; chacma baboons, *Papio ursinus*: Kitchen *et al.* 2003), age (e.g., chacma baboons, Fischer *et al.* 2002, 2004; Kitchen *et al.* 2003; pig-tailed langur, *Simias concolor*: Erb *et al.* 2013; Thomas langurs, *Presbytis thomasi*: Wich *et al.* 2003; gibbons, *Hylobates lar*: Barelli *et al.* 2013), current condition (e.g., chacma baboons, Fischer *et al.* 2004; simakobus, Erb *et al.* 2013), and dominance rank (e.g., chimpanzees, *Pan troglodytes*: Riede *et al.* 2007; Thomas langurs, Wich *et al.* 2003; crested macaques (*Macaca nigra*, Neumann *et al.* 2010; chacma baboons, Fischer *et al.* 2004; Kitchen *et al.* 2003).

Despite a long history of research on sexually selected vocalizations in primates, several questions remain. First, although many primate species are known to emit loud

calls, it is not clear how many of these actually function in mate selection or rival assessment. Unlike avian and amphibian taxa that depend heavily on vocal signals, the vast majority of primate species rely on individual recognition and social knowledge when making reproductive choices (Bergman and Sheehan 2013; Tomasello and Call 1997). Thus, for primates that live in relatively small, stable, social groups, loud calls may function as a means to obtain information about caller identity rather than caller condition or fighting ability. However, individual recognition likely has a reduced role in large primate groups where recognition of every group member may not be possible (*e.g.*, geladas, *Theropithecus gelada*: Bergman 2010). Moreover, large primate societies (where individual recognition is expected to be low) are exactly the situations in which we expect selection to favor the evolution of loud calls to function as quality signals. In the absence of individual recognition, loud calls can allow conspecifics to quickly assess the relative condition of an unknown rival or the quality of a potential mate.

Second, we have yet to establish if there are universal indicators of strength or high quality in vocal signals across primates. Some acoustic features, particularly those relating to body size, should be similar across primate species. Yet, we lack the comparative data to assess if there are any similarities in how loud calls convey information about identity, condition, or dominance rank across closely related species. Currently, we have detailed acoustic analyses (*e.g.*, spectral analysis) for only a handful of primate species-specific loud calls (langurs: Erb *et al.* 2013; sportive lemurs, *Lepilemur* spp.: Méndez-Cárdenas *et al.* 2008; titi monkeys, *Callicebus nigrifrons*: Caselli *et al.*, 2014), and we have even fewer from species in which loud calls may function in direct assessment (chacma baboons: Fischer *et al.* 2004; Kitchen *et al.* 2003; Thomas langurs, Wich *et al.*, 2003). There are some similarities in properties of vocal signals across species; for example, temporal features are known to decline as a male fatigues (Erb *et al.* 2013; Fischer *et al.* 2004). Yet, for the most part, vocal features show variation across species. For example, high-ranking chacma baboons produce calls with higher frequency measures (Fischer *et al.* 2004) while high-ranking crested macaques produce lower-frequency calls (Neumann *et al.* 2010). Whether these differences are species specific or context specific remain unknown.

Geladas are well suited for studies of quality signals in primates for two reasons. First, the gelada social system may have favored the evolution of signals for direct assessment due to the sheer size and fluidity of their groups (Bergman 2010; Bergman and Sheehan 2013). Geladas live in extremely large, multilevel societies comprising dozens of reproductive units. Each unit consists of one dominant “leader male,” several adult females, their offspring, and occasionally one or more subordinate “follower males” (Dunbar 1983; Dunbar and Dunbar 1975; Kawai *et al.* 1983; Mori 1979a). These units are nested together within a foraging unit known as a band and several bands may come together to form herds as large as 1200 individuals (Dunbar 1983; Kawai *et al.* 1983; Snyder-Mackler *et al.* 2014). In the largest aggregations of gelada society, individual recognition has a reduced role compared to most other primate groups (Bergman 2010; le Roux and Bergman 2012). Second, reproductive competition between gelada males consists of extremely costly, winner-take-all contests between leader males and prereproductive “bachelor males” (Dunbar and Dunbar 1975). Selection should favor the bachelors that challenge leader males that are in poor condition or of low quality; and that, presumably, are unable to advertise high quality.

One avenue for advertising quality is for a leader male to engage in a highly ritualized loud-call display that allows bachelor males to assess his strength (Dunbar 1984). A display begins when the leader male approaches, threatens, and solicits a chase from a group of bachelor males (Dunbar 1984). During these displays, males run, throw rocks, climb trees, and shake branches while simultaneously uttering a series of high-pitched, two-phase loud calls (“ee-yow” calls; Dunbar and Dunbar 1975). For geladas, loud calls are always given within about (two to eight calls per bout), and a male can give multiple bouts during the same display (Fig. 1a). Loud calls appear “contagious” with multiple males sequentially engaging the bachelors in a chase prior to calling. Although bachelors also vocalize during these displays (*i.e.*, “how bark”), leader males (and sometimes subordinate follower males) predominantly produce the two-syllable loud calls during these chases. Loud call displays occur on a daily basis when bachelors are present and multiple display events per day are common (Benítez, *unpubl. data*).

Here, we seek to broaden our understanding of the features and function of primate loud calls by examining the loud calls of male geladas. Previous research on this

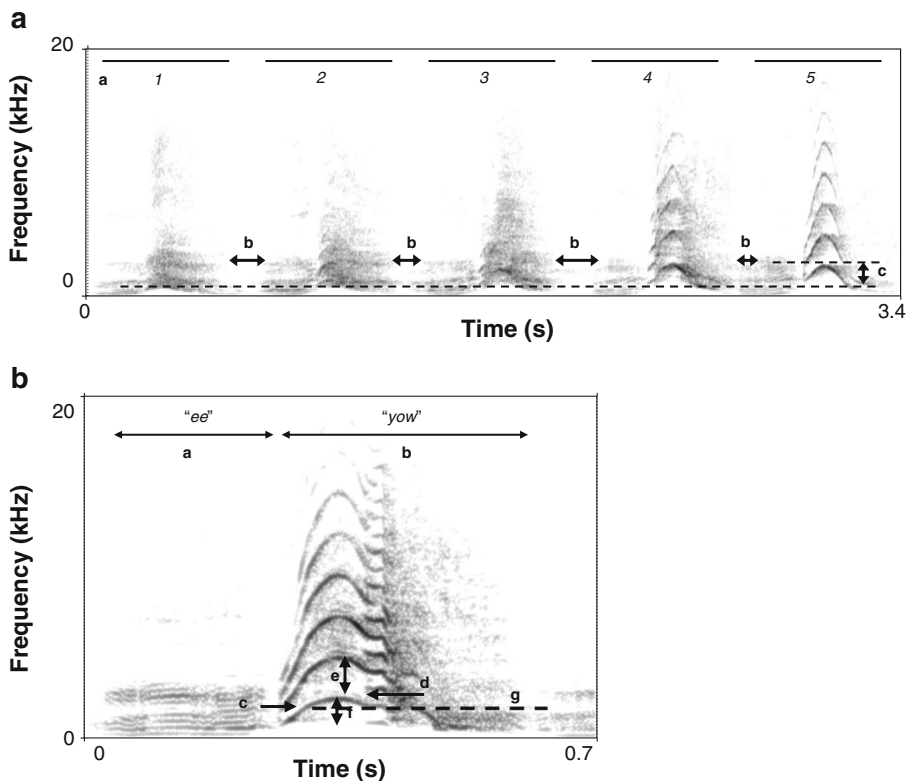


Fig. 1 Spectrograms of gelada loud calls recorded at the Simien Mountain National Park from April 2008 to December 2013. **a** A bout containing five calls indicating the bout parameters measured in the acoustic analysis: *a*, number of calls per bout; *b*, call interval (averaged in analysis), and *c*, range in pitch. **b** A gelada loud call indicating the call parameters measured in the acoustic analysis: *a*, “ee” duration; *b*, “yow” duration; *c*, fundamental frequency and dominant frequency band (same for this call); *d*, peak frequency; *e*, distance between frequency bands, *f*, frequency range; and *g*, first quartile frequency.

population of geladas has shown that bachelor males pay attention to loud calls significantly more often than other salient vocal cues (*i.e.*, copulation calls) suggesting that bachelors may extract information about the condition of the sender from the acoustic properties of these calls (le Roux and Bergman 2012). To test this hypothesis, we examined whether variation in acoustic and temporal measures of loud calls functioned as a reliable indicator of male quality. We cannot adequately distinguish true quality (*i.e.*, genetic quality) from condition (*e.g.*, current energetic/health condition), and thus we use the term quality loosely to encompass both possibilities.

Specifically, we examined 12 call parameters and 3 bout parameters (Table I) that have been previously shown to vary due to individual or condition (*e.g.*, age, status, and stamina) in chacma baboons (Fischer *et al.* 2004). There are remarkable similarities between the loud calls of geladas and baboons (*i.e.*, “wahoos”) in both delivery and context. Loud calls in both species consist of several bouts of two-syllable calls predominately given by males during chases with rivals (Aich *et al.* 1990; Dunbar

Table I Spectral (of “yow” element) and temporal parameters analyzed in this study

Bout parameter	Definition
Number of calls per bout	Number of calls given per bout
Call interval <i>mean</i>	Mean duration (s) of intervals between calls within a bout
Range in pitch	Range in pitch (Hz), measured by the difference in mean fundamental frequency between the call with the lowest F0 (<i>e.g.</i> , first call) and the call with the highest F0 (<i>e.g.</i> , last call) during a bout
Call parameters	Definition
Duration: “ee”	Duration (s) of the “ee” element of the call
Duration: “yow”	Duration (s) of the “yow” element of the call
Fundamental frequency <i>mean</i>	Mean frequency (Hz) of the first frequency band
Dominant frequency band <i>mean</i>	Mean frequency (Hz) of the dominant frequency band
Dominant frequency band <i>maximum</i>	Maximum frequency (Hz) of the dominant frequency band
Peak frequency <i>mean</i>	Mean peak frequency (Hz)
Peak frequency <i>maximum</i>	Maximum peak frequency (Hz)
Distance between frequency bands <i>mean</i>	Mean distance (Hz) between the first and second dominant frequency bands
Distance between frequency bands <i>maximum</i>	Maximum distance (Hz) between the first and second dominant frequency bands
Frequency range <i>mean</i>	Mean frequency range (Hz) within the call
First quartile frequency <i>mean</i>	Mean frequency (Hz) under which 25 % of the energy for each call is located
First quartile frequency <i>maximum</i>	Maximum frequency (Hz) under which 25 % of the energy for each call is located

1984; Fischer *et al.* 2002; Hall and DeVore 1965). Similar to the contest wahoos of baboons, gelada loud calls are produced only during aggressive encounters with adult males (Dunbar 1984). We predicted that, similar to the loud calls of baboons, several acoustic features of gelada loud calls would be linked to a male's condition.

If loud calls are honest signals of a male's competitive ability in geladas, we predicted that acoustic features would vary among individual, age, status, and exhaustion. First, we investigated which acoustic parameters varied between individuals. We predicted significant individual differences in one or more acoustic measures, mainly fundamental frequency and peak frequency because these two were found to differ within chacma baboons (Fischer *et al.* 2002) and simakobu colobines (Erb *et al.* 2013). Second, we examined acoustic differences in calls in relation to age (immature, prime, late-prime males). Owing to differences in overall body size between immature and prime-aged males (Ey *et al.* 2007), we predicted calls to vary with (and thus potentially convey information about) the relative age of the caller. Specifically, we predicted that prime-aged males would produce calls with lower frequency measures than immature males owing to differences in the length or development of the vocal tract (Fitch and Hauser 1995). In addition, because temporal features of calls can vary with lung capacity, and the size of the lungs is closely related to body size (Fitch and Hauser 1995), we predicted prime-aged males would produce longer calls and/or more calls per bout than immature males (*cf.* Kitchen *et al.* 2003). Third, we examined acoustic differences in relation to status (dominant leaders *vs.* subordinate followers) to assess if the best males in gelada society produced acoustically distinct calls. Fourth, we tested whether call features changed during chase displays, presumably due to exhaustion, *i.e.*, by comparing calls from the beginning of a chase display to calls from the end of a chase display from the same male. Based on the assumption that loud calls are energetically costly to produce, we predicted that only males in the best physical condition would have the stamina and strength to produce certain acoustic properties. Thus, we predicted that the calls of leader males would differ in both acoustic and temporal measures from those of follower males and that similar acoustic features would degrade across a long chase event, presumably as a male fatigues.

Methods

Study Site and Subjects

We collected data from a population of wild geladas living in the Simien Mountains National Park, Ethiopia. The University of Michigan Gelada Research project has been collecting long-term behavioral, demographic, and hormonal data on this population since January 2006. For this study, we collected vocalizations opportunistically from 79 males (29 immatures, 50 adults) from April 2008 to December 2013. All males were individually recognized and habituated to observers on foot.

Age and Status

For all males in the study, we estimated age to the nearest half year based on secondary sexual characteristics such as canine eruption, physical size, pelage coloration, and cape

length (Beehner *et al.* 2015; Dunbar and Dunbar 1975). We classified males as immature (5–8 years), prime (8–12 years), or late-prime (>12 years) (Beehner *et al.* 2015). Immature males consisted of both older juvenile males (5–6 years) and subadult males (6–8 years) (Beehner *et al.* 2015). Adult males were all males >8 years of age. For unit males, status categories (leader or follower) were determined by behavioral observations of group membership and dyadic dominance interactions. Leader males included all males with unlimited reproductive access to the females in the unit. Follower males included additional adult males in a unit that were subordinate to the leader male. Follower males were typically former unit leaders but could be young males that submissively joined and remained with a unit (Mori 1979b).

Acoustic Analyses

We opportunistically recorded loud calls from all males across the study period. We recorded loud calls using a Sennheiser ME-66 directional microphone and a Marantz PMD 660 digital recorder. At the time of the recording, we noted (1) the identity of the caller, (2) the activity of the male while calling (*e.g.*, approach, chase, or fight), (3) the position of the bout within the chase event (*e.g.*, first, second, *etc.*), and (4) the position of the call within the bout. Before analyses, we audibly and visually inspected calls using Avisoft SASLab Pro (Avisoft Bioacoustics, Berlin, Germany) acoustic software. We generated spectrograms in Avisoft with a fast Fourier transformation size of 1024 points (frequency range = 22 kHz; frequency resolution = 43 Hz; temporal resolution = 2.903 ms; 100 % frame). We selected only complete recordings that were devoid of background noise (*e.g.*, bird song), and interruptions (*e.g.*, calls from other individuals). We accumulated 785 loud call recordings (across 272 bouts) of sufficient quality from 79 males for acoustic analysis.

We conducted acoustic analyses at the level of the bout (*bout analysis*) and at the level of the individual call (*call analysis*). For the bout analysis, we measured three bout parameters: the number of calls per bout, the call interval, and the range in pitch (Table I; Fig. 1a). For the call analysis, we submitted the frequency time spectra of the “yow” element (*i.e.*, the predominant component of the call) of each call to a custom software program (LMA) that extracts acoustic parameters from vocal signals (Fischer *et al.* 2013) (Fig. 1b). In addition, we manually extracted the mean fundamental frequency (*i.e.*, lowest frequency of a harmonic series) of each call by visually inspecting pitch contour using PRAAT v. 5.0.29. The minimum and maximum values for the fundamental frequency were set according to the pitch contour as observed on the spectrogram. In total, we examined 12 call parameters (Table I) related to duration, frequency, energy, and pitch.

Data Analyses

Factor Analysis Before all analyses, we checked the distribution of each parameter and, where necessary, we transformed the data to approximate a normal distribution. Next, to remove redundancy between the acoustic parameters (*i.e.*, many of the acoustic properties were highly correlated), we ran a factor analysis (FA) using all 12 call parameters. The FA was run in SPSS using a varimax rotation. The two factors that emerged from this analysis (factor scores) are listed in Table II.

Table II Results of the factor analysis

Call parameters	Factor 1 Spectral measures	Factor 2 Temporal measures
Duration: "ee"	-0.06	0.77
Duration: "yow"	0.05	0.78
Fundamental frequency	0.59	-0.15
Dominant frequency band <i>mean</i>	0.96	0.00
Dominant frequency band <i>maximum</i>	0.94	0.04
Peak frequency <i>mean</i>	0.96	-0.01
Peak frequency <i>maximum</i>	0.90	0.04
Distance between frequency bands <i>mean</i>	0.87	0.02
Distance between frequency bands <i>maximum</i>	0.79	0.05
Frequency range <i>mean</i>	0.67	-0.12
First quartile frequency <i>mean</i>	0.96	0.00
First quartile frequency <i>maximum</i>	0.96	0.52
<i>Eigenvalues</i>	7.59	1.25
<i>Variance explained (%)</i>	63.20	10.40

Individual Differences To test for differences between calls due to individual identity, we used discriminant function analysis (DFA). DFA is commonly used in behavioral and bioacoustics research to determine whether calls differ between subjects, groups, and context (Mundry and Sommer 2007). The benefit of DFA is that it addresses how reliably groups can be distinguished and which acoustic parameters are important in those classifications. However, DFA can be inaccurate when using nonindependent data (*i.e.*, multiple calls from the same individual to test group differences)(Mundry and Sommer 2007). To account for nonindependence, we subsequently ran a permuted discriminant function analysis (pDFA) controlling for bout number using an R algorithm written by Roger Mundry (Mundry and Sommer 2007). *P*-values of the pDFA were based on cross-validated calls and determined using 1000 permutations into which the original data were included as one permutation. To balance the variance in the number of calls from each individual in the dataset, we used a subset of our data for each DFA analysis. In the DFA data sets, we used only the first three calls per bout per male to balance any acoustic changes due to the position of the call within the bout. For individual differences, we conducted a DFA on calls collected from adult males from which ≥ 13 calls were recorded, *i.e.* at least one more than the number of acoustic parameters examined in the DFA. For the seven males that fit this criterion, all had at least 18 calls of sufficient acoustic quality

for analysis. For males with >18 calls, we randomly selected 18 calls to balance individual contribution ($N = 7$, $n = 126$ calls).

Age and Status To investigate whether call and bout parameters varied in relation to age and status, we constructed a series of linear mixed models (LMMs). First, we compared calls of immature males ($N = 29$, $n = 84$ calls), prime males ($N = 39$, $n = 531$ calls), and late-prime males ($N = 11$, $n = 170$ calls) to assess if age influenced the acoustic properties of these calls. For call parameters, we used the factor scores from the FA as the dependent variables, age and call position as fixed effects, and caller as a random effect. We included call position as a continuous predictor to control for variation in acoustic changes within a single bout.

We further examined the differences in bout parameters between immature and adult males by constructing three additional models with call interval, range in pitch, or number of calls as dependent variables, age as a fixed effect, and bout id and caller as random effects (immature, $n = 36$ bouts; prime, $n = 188$ bouts; late prime, $n = 48$ bouts). For range in pitch, we included only bouts from males in which all calls within the bout were of sufficient quality to be analyzed (Table 1; $N = 57$, $n = 218$ bouts). For number of calls per bout, we conducted a general linear mixed model with a negative binomial distribution.

Second, to investigate whether the acoustic properties of calls differed due to status, we constructed five additional LMMs on a subset of the data that included only calls from adult males (leaders, $N = 33$, $n = 552$ calls; followers, $N = 17$, $n = 114$ calls). For call parameters, we constructed two LMMs, one for each factor score from the FA analysis as the dependent variable and status (leader or follower) as a predictor variable. We controlled for age (prime or late-prime), call position (fixed effect), and caller id (random effect). To examine the effect of status on bout parameters, we constructed three additional models with each bout parameter as the dependent variable, status and age as a fixed effects, and bout id and caller as random effects (leaders, $n = 204$ bouts; followers, $n = 32$ bouts). For each model, we determined the statistical significance of the full model by comparing its fit using likelihood test with that of a null model including only the intercept and the random effect. We conducted all model analyses in R v.3.2.0 using the lmer function in the lme4 packages v.1.1–11 (Bates *et al.* 2015). We visually inspected each model using a Q–Q plot, histogram of residuals, and scatterplot of fitted *versus* residual values. Residual values for all models were normally distributed.

Exhaustion To evaluate differences in loud calls due to exhaustion, we conducted a pairwise comparison on all males from which we had recorded at least three consecutive bouts during an observed chase event ($N = 10$). For each male, we compared the first call given during the first bout to the first call given during the last bout of a display ($n = 20$ calls). Because of our small sample size, we used a paired Wilcoxon signed rank test with exact *P*-values (Mundry and Fischer 1998). We expected that acoustic and/or temporal features of calls would degrade as a male fatigued during a chase event. For each male and for each chase event, we compared the factor scores of calls given during the first bout with the factor scores of calls given during the last bout. Note that these calls are from the same male for the same chase event. We limited our analysis to the first call within the bout to control for call position. In addition, we compared between the first and last bout of a chase event the number of calls given per bout, the range in pitch, and the call interval.

Results

Factor Analysis

The factor analysis resulted in two factors with eigenvalues >1 together explaining 73.6 % of the total variance. All spectral parameters measured showed high loadings on factor 1, which explained 63.2 % of the variance. Factor 2 showed high loadings on “ee” and “yow” duration only and explained an additional 10.4 % of the variance (Table II). Based on the loadings of these parameters on the rotated components, we characterized and labeled factor 1 as *spectral measures* and factor 2 as *temporal measures*. In other words, a high score along factor 1/spectral measures indicates that calls have higher dominant frequency bands, greater distance between the first and second dominant frequency bands, higher fundamental frequency, higher peak frequency, a greater range in pitch, and energy concentrated at higher frequencies. A high score in factor 2/temporal measures signifies longer “ee” and “yow” elements resulting in overall longer calls.

Individual Differences

The DFA revealed one factor with eigenvalues >1 . This first function accounted for 54 % of the variance and exhibited a high positive loading (>0.4) on four parameters (mean fundamental frequency, mean peak frequency, mean distribution of the first dominant frequency band, and mean first quartile energy). The second function (eigenvalue = 0.7) accounted for 27.1 % of the variance and exhibited a high absolute loading only on the duration of the “yow” element. The results from the pDFA indicated that calls were significantly different between individuals, with 38.1 % of cross-classified calls assigned correctly ($P = 0.001$).

Age and Status

The first set of LMMs revealed that both the position of the call within the bout and age influenced the acoustic properties of the calls (spectral measures, R^2 full model = 0.29, full vs. null model, $\chi^2 = 509.17$, $P < 0.001$; temporal measures, R^2 full model = 0.03, full vs. null model, $\chi^2 = 13.56$, $P = 0.001$). Specifically, we found that spectral measures increased throughout a bout ($\beta = 0.38$, $SE = 0.02$, $t = 26.23$, $P < 0.001$; Fig. 2). However, we found no effect of call position on temporal measures ($\beta = 0.04$, $SE = 0.04$, $t = 1.16$, $P = 0.248$; Table III).

Immature males produced calls with higher spectral measures (Fig. 3a) and shorter temporal measures (Fig. 3b) than both prime (spectral measures, $\beta = -1.12$, $SE = 0.18$, $t = -6.49$, $P < 0.001$; temporal measures, $\beta = 0.51$, $SE = 0.18$, $t = 2.891$, $P = 0.005$; Table III) and late prime (spectral measures, $\beta = -1.53$, $SE = 0.20$, $t = -7.58$, $P < 0.001$; temporal measures, $\beta = 0.82$, $SE = 0.22$, $t = 3.81$, $P < 0.001$) males (Table III). We found no difference between the full model including age and the null model for any of the three bout parameters (number of calls, R^2 full model = 0.007, full vs. null model, $\chi^2 = 1.45$, $P = 0.485$; range in pitch, R^2 full model = 0.009, full vs. null model, $\chi^2 = 1.06$, $P = 0.587$; interval, R^2 full model = 0.003, full vs. null model, $\chi^2 = 0.07$, $P = 0.966$).

Within adult males, we found that both age (prime and late-prime) and status influenced loud call production (spectral measures, R^2 full model = 0.28, full vs. null

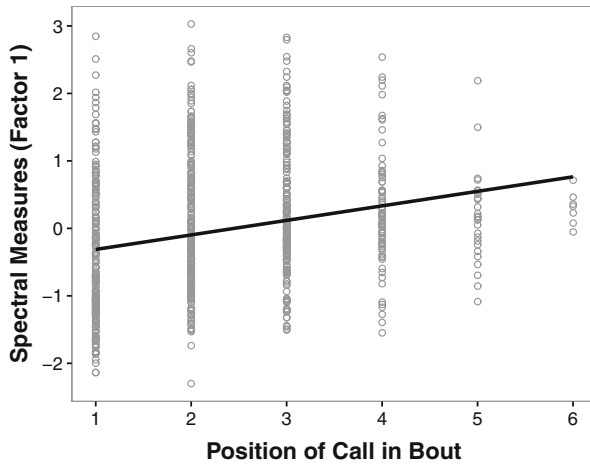


Fig. 2 Variation in spectral measures (factor 1) due to the position of the call within a bout of gelada loud calls recorded at the Simien Mountain National Park from April 2008 to December 2013. Spectral measures significantly increased throughout a bout.

Table III Results of the age and status models for *spectral* (factor 1) and *temporal* (factor 2) measures

Spectral measures (factor 1)

Predictors	Age				Status			
	β	SE	<i>t</i>	<i>P</i>	β	SE	<i>t</i>	<i>P</i>
Intercept	0.63	0.15	4.13	<0.001	-1.32	0.24	-5.60	<0.001
Call position	0.38	0.02	26.23	<0.001	0.36	0.02	19.34	<0.001
Prime	-1.12	0.18	-6.49	<0.001 ^a	1.25	0.17	7.14	<0.001 ^b
Late-prime	-1.53	0.20	-7.58	<0.001				
Status (leader)					-0.61	0.21	-2.87	0.005

Temporal measures (factor 2)

Predictors	Age				Status			
	β	SE	<i>t</i>	<i>P</i>	β	SE	<i>t</i>	<i>P</i>
Intercept	-0.54	0.16	-3.46	0.001	-0.47	0.27	1.75	0.084
Call position	0.04	0.04	1.16	0.248	0.01	0.04	0.29	0.772
Prime	0.51	0.18	2.89	0.005 ^a	0.05	0.25	0.20	0.842 ^b
Late-prime	0.82	0.22	3.81	<0.001				
Status (leader)					-0.64	0.18	-3.50	0.001

^a For the age model, calls from prime and late-prime males were compared to calls from immature males

^b For status, only calls from adult males were included in the model, so calls from prime males were compared to calls from late-prime

model, $\chi^2 = 431.79$, $P < 0.001$; temporal measures, R^2 full model = 0.06, full vs. null model, $\chi^2 = 12.46$, $P = 0.014$). Late-prime males had calls with the lowest spectral measures (prime, $\beta = 1.25$, $SE = 0.17$, $t = 7.14$, $P < 0.001$; Fig. 3a) but did not differ significantly in temporal measures (prime, $\beta = 0.05$, $SE = 0.25$, $t = 0.20$, $P = 0.842$; Fig. 3b). Regardless of age, leader males produced calls that were lower in spectral measures ($\beta = -0.61$, $SE = 0.21$, $t = -2.87$, $P = 0.005$; Fig. 4a) and shorter in temporal measures ($\beta = -0.64$, $SE = 0.18$, $t = -3.50$, $P = 0.001$; Fig. 4b) than follower males (Table III). Call position within a bout was again a significant predictor of spectral ($\beta = 0.36$, $SE = 0.02$, $t = 19.34$, $P < 0.001$) but not temporal measures in the status models ($\beta = 0.01$, $SE = 0.04$, $t = 0.29$, $P = 0.772$).

In addition to these acoustic changes, leader males produced loud calls bouts that differed along several bout parameters (number of calls, R^2 full model = 0.09, full vs. null model, $\chi^2 = 10.65$, $P = 0.005$; range in pitch, R^2 full model = 0.07, full vs. null model, $\chi^2 = 11.23$, $P = 0.004$; call interval, R^2 full model = 0.001, full vs. null model, $\chi^2 = 0.20$, $P = 0.907$). Leader males gave more calls per bout ($\beta = 0.28$, $SE = 0.12$, $t = 2.33$, $P = 0.020$; Fig. 4c) and exhibited a greater range in pitch throughout a bout ($\beta = 0.35$, $SE = 0.10$, $t = 3.38$, $P = 0.001$; Fig. 4d) than follower males.

Exhaustion

We found significant differences between the first and last bout of a chase event with respect to spectral measures, temporal measures, number of calls per bout, and mean call interval. Specifically, we found that as a male fatigued across the chase event, he produced calls with higher spectral measures (Wilcoxon signed rank test; $T = 55$, $N = 10$, ties = 0, $P < 0.01$; Fig. 5a) and longer temporal measures ($T = 50$, $N = 10$, ties = 0, $P = 0.02$; Fig. 5b). In addition, males gave fewer calls per bout ($T = 28$, $N = 7$, ties = 3, $P = 0.02$; Fig. 5c) and had a longer interval between calls ($T = 47.5$, $N = 10$, ties = 0, $P = 0.04$; Fig. 5d) during the last rather than the first bout of the display. We found no difference in range in pitch ($T = -1.27$, $N = 10$, ties = 0, $P = 0.2$).

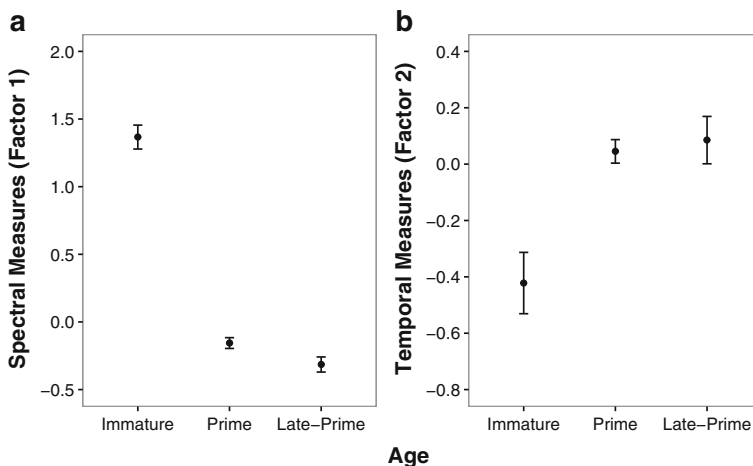


Fig. 3 Age-based difference in spectral (a) and temporal (b) parameters expressed as mean (\pm SEM) factor scores of gelada loud calls recorded at the Simien Mountain National Park from April 2008 to December 2013.

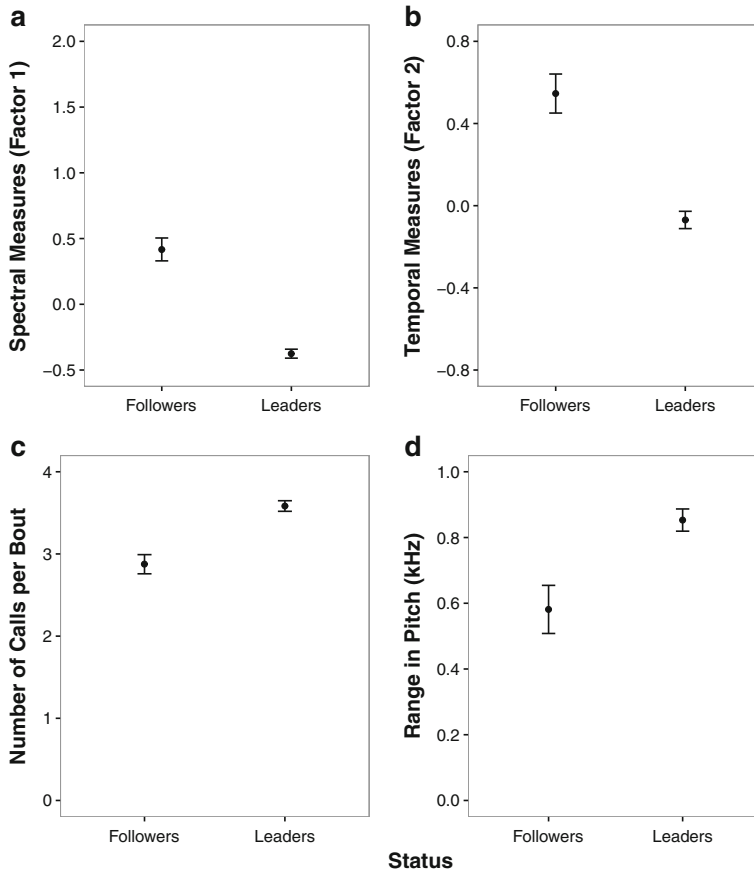


Fig. 4 Status-based differences in spectral measures (a) and temporal measures (b) expressed as mean factor scores (\pm SEM), the number of calls per bout (\pm SEM) (c), and the range of pitch throughout the bout (\pm SEM) (d) of gelada loud calls recorded at the Simien Mountain National Park from April 2008 to December 2013.

Discussion

Our results are consistent with the hypothesis that loud calls serve as quality signals in male geladas. Gelada loud calls can reliably signal the sender's competitive ability because the highest quality males produced the strongest vocal signal. Specifically, dominant leader males—the only males with reproductive access to females—produced significantly more calls per bout, produced acoustically different calls that were lower in several frequency measures and exhibited a greater vocal range across the entire bout as compared to subordinate follower males (see Electronic Supplementary Material Figs. S1 and S2 for sample calls). Similar acoustic “decay” was observed from prime-aged to immature males and from “fresh” to “fatigued” adult males, suggesting that these acoustic features can reliably indicate male condition due to either physical constraints (*e.g.*, body size) and/or energetic costs (*e.g.*, stamina).

In birds, amphibians, and some mammalian species, several acoustic features, such as fundamental frequency, have been linked to variation in body size. As fundamental

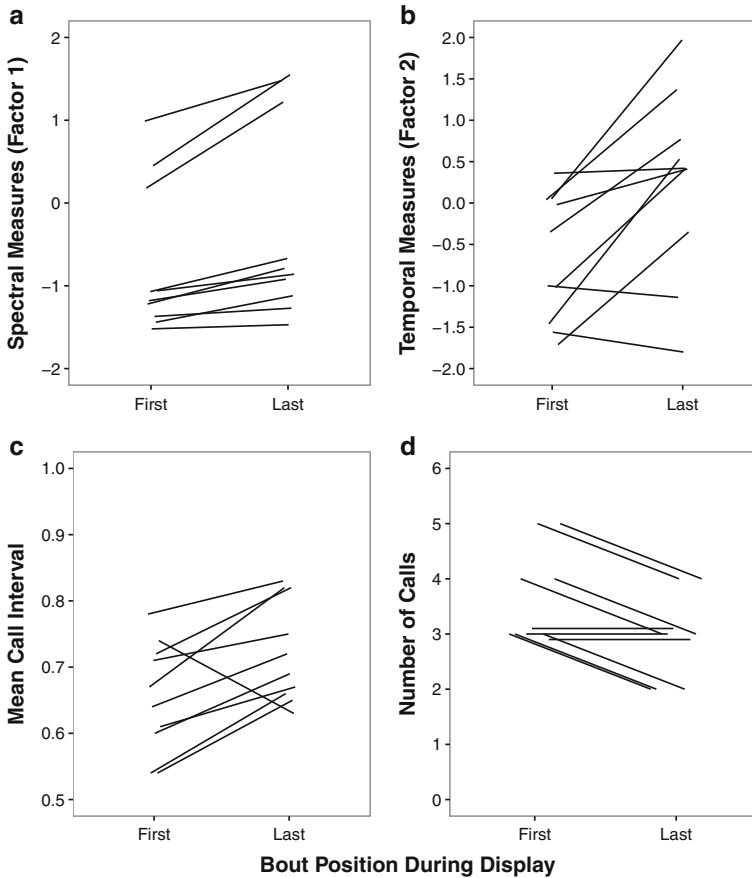


Fig. 5 Intramale differences in spectral measures (a), temporal measures (b), number of calls given per bout (c), and the mean call interval (d) between gelada loud calls given during the first bout and the last bout of an observed chase display. Calls were recorded at the Simien Mountain National Park from April 2008 to December 2013. Lines are jittered to reduce overlapping points.

frequency depends on the length and tension of the vocal folds, the longer the larynx, the lower the fundamental frequency of the caller (Fitch and Hauser 1995). Similar to results from chacma baboons and other primates, in geladas the differences in body size across males also influenced acoustic features; immature males, with smaller body sizes, produced higher frequency calls than prime-aged males. However, among a sample entirely of adults, body size alone did not account for the differences in acoustic properties that were related to exhaustion: our analysis of exhaustion was within the same male across a single chase event. Thus, although we do not discount the effects of body size entirely, we are also confident that additional factors contribute to variance in the quality of loud calls.

Similar to previous research conducted on the loud calls of chacma baboons (Fischer *et al.* 2004), gelada loud calls were energetically costly to produce with calls exhibiting significant spectral and temporal changes as a male fatigued. However, unlike chacma baboons where fundamental frequency declined during a loud call display (Fischer *et al.* 2004), gelada calls produced at the end of a chase event (during the last bout)

were significantly higher in frequency measures (including fundamental frequency) than calls produced during the beginning of a chase event (during the first bout). As was found in chacma baboons, we found significant differences between the calls of high- and low-status males. But, in contrast to high-ranking male baboons, high-status male geladas produced calls that were lower in frequency measures. Moreover, gelada males with the longest tenures, late-prime leaders, produced the lowest acoustic measures. Taken together, these results suggest that while frequency measures may be important indicators of stamina and competitive ability in primate loud calls, exactly *how* these acoustic features change in response to caller condition may differ, even among closely related species.

Notably, the loud calls of male geladas exhibit a large and rapid increase in frequency measures (86 % mean F0 change throughout a bout) such that call position had a significant effect on the acoustic properties measured. Previous studies have shown slight decreases in frequency measures over multiple seconds of repeated calling in other primates (chacma baboons: Fischer *et al.* 2004; langurs: Erb *et al.* 2013), presumably due to lung deflation. However, in geladas frequency measures increased throughout a bout, with significant changes occurring between successive calls in a period as short as 0.7 s. These results suggest that vocal range may be a key factor for distinguishing quality in gelada vocal displays. Recent work on the larynx and vocal tract of cervids (*e.g.*, red deer) has shown that for the same larynx to produce calls with high and low fundamental frequencies requires an enormous amount of muscular effort to stiffen the vocal ligaments and a large lung capacity to overcome phonation threshold pressure (Titze and Riede 2010). In other words, showcasing vocal range may accurately represent an increase in lung capacity, laryngeal control, and/or vocal muscular strength. We found that leader males produced the smallest range in fundamental frequency *within* each call, but the largest range in fundamental frequency *between* calls across the same bout. We suggest that, for geladas, a key feature of a high quality loud call may be the ability to maintain a controlled, even, tone for a single call while simultaneously displaying a large range in fundamental frequency across the bout. Thus, for geladas, the entire bout, and not just the individual calls that comprise the bout, may function as a quality signal. Similar findings have been documented in chimpanzees, where the highest ranking males are those that can drive their voices to a higher maximum fundamental frequency during a pant hoot vocalization (Riede *et al.* 2007). An interesting avenue of future research might be to assess why showcasing vocal range may be important in some primates but not others.

In terms of temporal features, the number of calls given per bout appears to be a better indicator of male stamina than the duration of the calls within a bout. As males fatigued during a chase event, the number of calls per bout decreased, resulting in an overall shorter bout even though call duration increased. Furthermore, follower males had calls with longer temporal measures, but ultimately gave fewer calls per bout than the higher-status leader males. Given that these temporal features are likely constrained by lung capacity, there may be a tradeoff between how many calls an individual can produce and the duration of each of those calls. For geladas, producing more calls per bout may be more energetically taxing than investing in a longer call.

We also found differences in acoustic measures across individual males. Similar to other primate studies, fundamental frequency (*e.g.*, Fischer *et al.* 2002; Erb *et al.* 2013; Barelli *et al.* 2013), peak frequency (Neumann *et al.* 2010), the position of the first

dominant frequency band, (Fischer *et al.* 2002; Neumann *et al.* 2010), and first quartile energy (Fischer *et al.* 2002) all contributed to the discrimination of individuals. Individual acoustic differences may allow bachelors to identify and monitor how often specific males engage in signaling displays. If males that signal less often are challenged more often (Dunbar 1984), then individual identification may be a necessary piece of information contained within each call. However, given that individual recognition is limited in this species (Bergman 2010), bachelors may be attending to the acoustic cues related to call quality rather than individual identity. In other words, males that call more frequently may avoid getting replaced (Dunbar 1984) simply because they have higher quality calls.

One limitation of this study (which holds true for much of the research on primate loud calls) is that it is correlational. To test the hypothesis that a loud call is indeed a sexually selected signal, a relationship between the quality of the caller and the quality of the call is *necessary* (otherwise listeners would not benefit from attending to such calls), but it is not *sufficient*. A relationship might be spurious or it might not be attended to by potential receivers. However, the consistency of acoustic changes across age, fatigue, and status are evidence that the patterns vary in a predictable way. For the future, playback experiments are necessary to demonstrate that geladas attend to these differences in loud calls. Nevertheless, two lines of evidence suggest that loud calls in geladas likely function as signals in rival assessment. First, bachelor males pay close attention to signaling bouts between rival males (le Roux and Bergman 2012), suggesting that bachelors may be extracting information about male condition from these calls. Second, the males that were able to maintain their units the longest (arguably the highest quality males), produced the strongest acoustic signals, suggesting that males with high-quality calls are the most successful at deterring challenges from rivals. If this is the case, we then expect bachelor males to distinguish between high- and low-quality males based on the acoustic and temporal patterns described here.

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