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Acoustic variation and group level convergence of gelada, *Theropithecus gelada*, contact calls

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The acoustic structure of nonhuman primate vocalizations can vary substantially within a call type and may converge between social partners. Examining which social partners share call structure can inform our understanding of the function of vocal learning and communication in nonhuman animals. We assessed vocal convergence of female gelada contact grunts within multiple levels of gelada society: small female-philopatric reproductive units that maintain close proximity and larger bands of units that preferentially associate while foraging. We also measured the extent to which grunt acoustic structure varied by caller identity and behavioural state at the time of the call, as well as genetic relatedness, when assessing acoustic similarity between females' grunts. The acoustic structure of female gelada grunts differed between individuals as well as between foraging, travelling and socializing behavioural states. Female gelada grunts were more similar between pairs living in the same band than between pairs living in different bands. This effect was not found for pairs living in the same unit compared to pairs living in different units within the same band. As genetic relatedness did not predict similarity in grunt acoustic structure, we propose that vocal convergence within bands is the result of vocal learning. Vocal convergence at the higher level of gelada society suggests this vocal learning is selective and not simply the result of auditory exposure to conspecific calls. Vocal convergence in geladas may function to maintain spatial cohesion, which is a more critical challenge for bands than for units.

A remarkable ability to produce vocalizations based on auditory input enables human to learn speech and language. Vocal learning is not unique to humans, most notably occurring in songbirds, but it is rare among mammals (Jarvis, 2019). This discrepancy has prompted researchers to look for simpler forms of experienced-based vocal flexibility, both as a way to identify potential evolutionary pathways to vocal learning and to gain a broader understanding of how vocal flexibility functions (Bergman et al., 2019). Simple forms of vocal production learning, e.g. modifying existing vocalizations based on experience, appears to be relatively common in group-living mammals and often appears to have a social function (Janik & Knörnschild, 2021; Ruch et al., 2018). Notably, vocal accommodation, the modification of existing vocalizations to acoustically converge with (or diverge from) those produced by other individuals, is a particularly relevant form of vocal flexibility, as it is both widespread and integral to speech (Ruch et al., 2018).

Vocal accommodation is a common phenomenon in human speech, often occurring as adjustments to accents, pitch or speech rates during interpersonal or intergroup interactions and possibly functioning to increase feelings of social closeness or perception of shared social identity (Bernhold & Giles, 2020; Gregory & Webster, 1996; Pardo et al., 2012). Nonhuman primates and other mammals are also capable of adjusting both acoustic and temporal aspects of

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vocalizations in response to social experience (Janik & Knörnschild, 2021). When controlling for genetic relatedness among individuals (which may lead to similarity due to inherited similarities in the vocal apparatus), meerkat, *Suricata suricatta*, 'close calls' and mandrill, *Mandrillus sphinx*, contact calls show group signatures indicative of social accommodation to those individuals most frequently encountered (Levréro et al., 2015; Townsend et al., 2010). Exposure to vocalizations from individuals in other social groups, and even from other closely related species, can also influence the acoustic structure of an individual's vocalizations (Crockford et al., 2004; Kitchen et al., 2019; Panova & Agafonov, 2017; Zürcher et al., 2019). However, such vocal convergence is not ubiquitous or uniform in social mammals. Bottlenose dolphins (*Tursiops truncatus*), for example, do not exhibit signature whistle convergence among cooperative partners (King et al., 2018), and vocal divergence in social calls increases among female Diana monkeys, *Cercopithecus diana*, when visibility is hampered and neighbours are nearby (Candiotti et al., 2012).

Patterns of vocal accommodation may reflect social closeness or group membership and thus vary depending on species' social structures (De Marco et al., 2019). Like in humans, vocal accommodation appears to signal social closeness or group membership in nonhuman primates (Ruch et al., 2018). However, a simple correlation between degree of association and acoustic similarity could result from different processes. For example, the interactive alignment model of vocal learning posits a direct relationship between exposure to a sound and convergence to that sound, while the communication accommodation theory posits that vocal accommodation has an explicit social function and individuals may therefore converge preferentially with others (Ruch et al., 2018). These can be difficult to tease apart in species with a single level social structure, where there is little substructure within social groups, because the callers to whom individuals are exposed more often are also the callers with whom they are bonded or share a group. In multilevel societies, however, there is more variation both in physical proximity and in levels of social bonding between individuals, allowing these factors to be distinguished. Multilevel societies therefore provide an opportunity to test a key question: does vocal accommodation occur selectively in certain contexts or with certain social partners, regardless of how often they are likely to hear those individuals call (i.e. relative auditory exposure)?

Geladas, *Theropithecus gelada*, provide an excellent system to study the contexts in which vocal accommodation occurs because they have a multilevel social structure and vocalize at relatively high rates (mean ± SD: 16.95 ± 8.51 calls/h for geladas compared to 8.84 ± 4.49 calls/h for closely related chacma baboons, *Papio ursinus*; Gustison et al., 2012). Small, female-philopatric family 'units' preferentially associate with certain other units, forming 'bands', and multiple bands form 'communities' of units that join together occasionally, but significantly less often than do units within bands (Snyder-Mackler et al., 2012). As the unit is the core reproductive group and the band generally sleeps and forages together, geladas have a need to maintain cohesion within units and among units within bands (Snyder-Mackler et al., 2012). In addition, geladas are known for their social use of vocalizations (Gustison et al., 2012). One vocalization, the contact grunt (Aich et al., 1990; Richman, 1987) is both highly variable acoustically (e.g. between sexes: Gustison & Bergman, 2017) and appears to be used to maintain social bonds and cohesion, as females exchange these calls with close social partners and males utter them in long sequences during travel (Gustison et al., 2019; Tinsley Johnson, 2018). The present study aims to examine patterns of vocal accommodation in female gelada contact calls across different levels of social overlap while also accounting for potential correlates of vocal variation, including caller behavioural state and genetic relatedness.

Specifically, we had two goals. First, to better understand overall variation in grunts so that we could then control for them in subsequent analyses, we measured differences in acoustic structure across behavioural states and between individuals. Contact calls have been shown to differ across these variables in other nonhuman primates and mammals (Crockford et al., 2018; Taylor & Reby, 2010). Second, we tested hypotheses about when and why vocal accommodation occurs. This work builds on a recent study in Guinea baboons, *Papio papio*, a species with a comparable social structure, that found more similar contact grunt structure within 'gangs' (their equivalent of bands) and 'parties' (a social level intermediate to gelada units and Guinea baboon gangs) than between gangs and parties (Fischer et al., 2020). However, these findings were unable to differentiate passive convergence based on the amount of social contact (i.e. vocal learning consistent with the interactive alignment model) from more selective learning that might adaptively signal group membership (i.e. vocal learning consistent with the communication accommodation theory). If female gelada grunts are learned to any extent and call similarity is not simply the result of inherited similarities in vocal apparatus physiology, we expected the acoustic structure of contact calls to be more similar within groups than between groups after controlling for any effect of genetic similarity within groups. Then, if vocal convergence is strictly linked to call exposure rates, we expected to see stronger convergence at the unit level than at the band level, as members of the same unit are consistently in vocal contact. If, however, vocal accommodation is selective and not purely driven by call exposure rates, we expected to see stronger convergence at the band level than at the unit level. The challenge of maintaining spatial cohesion is greater in these larger bands that fission and fuse than in smaller units that are always found together. Furthermore, within units, there may be a benefit to individual recognition favouring distinctiveness and possibly counteracting any benefit of convergence at this level. Therefore, signalling group membership at the band level might be particularly beneficial for geladas. To compare these predictions, we assessed the effects of group membership on pairwise vocal similarity within behavioural states, controlling for the effects of individual caller identity and genetic relatedness.

METHODS

Study Subjects

Data for this study come from 25 units across four bands in a community of approximately 1200 wild geladas living in the Sankaber area of the Simien Mountains National Park, Ethiopia. Geladas in this area inhabit high-elevation open grasslands and adjacent cliffsides. Units comprised one leader male, 0–3 follower males and 1–11 females and their young offspring (Snyder-Mackler et al., 2012). Subjects for this study included 87 female geladas from 24 units across four bands. As the Simien Mountains Gelada Research Project has studied this community since 2005, subjects were habituated to human presence within 3–5 m and individuals were identifiable by unique body markings and coloration.

Ethical Note

This work was conducted under the Institutional Animal Care and Use Committee of the University of Michigan protocol IACUC 0008871 and was made possible through a memorandum of understanding (MOU) with the Ethiopian Wildlife Authority. The data were collected through noninvasive research with wild animals. Long-term project presence at the site ensured the animals' habituation to human presence to minimize impact on our subjects.

Data Sets

Vocalization recordings for this study come from three separate data sets collected between March 2008 and May 2008 and between November 2013 and June 2014. All vocalizations were recorded using a Sennheiser ME66 directional microphone connected to a Marantz PMD 660 or 661 Digital Recorder. In 2008, vocalizations were recorded opportunistically from female callers, and both the identity of the caller and the caller's behavioural state (rest, travel, forage or socialize) at the time of the call were noted (Gustison et al., 2012). From November 2013 to June 2014, vocalizations from focal females were recorded continuously for 2 min every half hour during day-long follows (Gustison et al., 2019). This data set includes female's behavioural state (rest, travel, forage, socialize or infant-focused) at the time of the call. Calls uttered while looking at or touching an infant were classified as occurring in an infant-focused state in this 2013–2014 data set, while other data sets classified such calls as occurring in a socializing state. In the last data set, from January 2014 to June 2014, vocalizations were recorded continuously during 15 min focal follows of male geladas (Gustison et al., 2019). Females' calls were opportunistically captured in these recordings but without behavioural state information.

Exhaled affiliative grunt vocalizations (characterized in Gustison et al., 2012) were identified by ear in the field and confirmed by visual inspection of spectrograms (Fig. 1). We confined our data analyses to high-quality recordings, which included grunts that did not overlap with other vocalizations or environmental noise. Our final data set included 545 female grunts (227 calls from 36 females in the November 2013 to June 2014 data set, 252 calls from 56 females from the 2008 data set and 66 calls from 25 females in the January to June 2014 data set). Caller behavioural state was known for 360 grunts (see Appendix, Table A1 for additional details on sample sizes across behavioural states).

Estimates of genetic relatedness between females were available from previous work with this population (Snyder-Mackler et al., 2014). Subjects, methods and results for complementary analyses of male gelada grunts across behavioural states and individual callers are detailed in the Appendix.

Acoustic Data Processing

For each recorded grunt vocalization, we used Avisoft SAS-Lab Pro (version 5.2.12) to generate a spectrogram with a 1024-point fast Fourier transformation. Spectrograms had a frequency range of 22 kHz and a time resolution of 2.903 ms and were viewed with a Hamming window with a 100% frame. We applied a 50 Hz high-pass infinite impulse response filter to all spectrograms to reduce background noise at low frequencies. For a small proportion of grunts, we used the fading tool in Avisoft to diminish steep amplitude transitions at the start and/or end of grunts to reduce the likelihood of errors in automated acoustic measures.

We measured nine temporal and acoustic parameters using automatic functions in two software programs designed to extract such measures from spectrograms: LMA version 2012 (Fischer et al., 2013) and Praat version 6.0.43 (Boersma & Weenink, 2013). The selected parameters align with those measured in previous analyses of comparable gelada and baboon vocalizations (Fischer et al., 2001; Gustison & Bergman, 2017; Gustison et al., 2012; Meise et al., 2011). We log-transformed seven of the nine parameters to approximate a Gaussian distribution. We kept two variables (fundamental frequency and location of maximum peak frequency) as raw scores, as their original distributions best approximated a Gaussian distribution. Pearson correlations between parameters (Table 1) were all below 0.60.

Statistical Analyses

To characterize the behavioural and social correlates of gelada grunt structure, we assessed grunt acoustic variation across behavioural states, among individuals and across social groups. To assess vocal convergence within units and bands, we tested whether sharing a unit or a band predicted grunt similarity between pairs of individuals beyond the effect of genetic relatedness.

We carried out all analyses in R (version 3.5.2), centering and scaling parameters prior to discriminant function analyses and principal component analyses. We used a two-tailed alpha level of 0.05 to reject null hypotheses.

Grunt variation across behavioural states

First, we asked whether grunt acoustic structure differed across the behavioural states in which they occurred. We conducted a linear discriminant function analysis (hereafter referred to as discriminant analysis) and a multivariate analysis of variance (MANOVA) to assess acoustic variation across grunts from three behavioural states: foraging, socializing and travelling.

Discriminant analyses identify functions along which cases can reliably be separated into classes. They perform best with balanced data sets that reduce differences in variables other than the variable of interest. As such, we represented individuals equally across behavioural state classes for these analyses to the extent possible. We averaged temporal and acoustic parameters for each

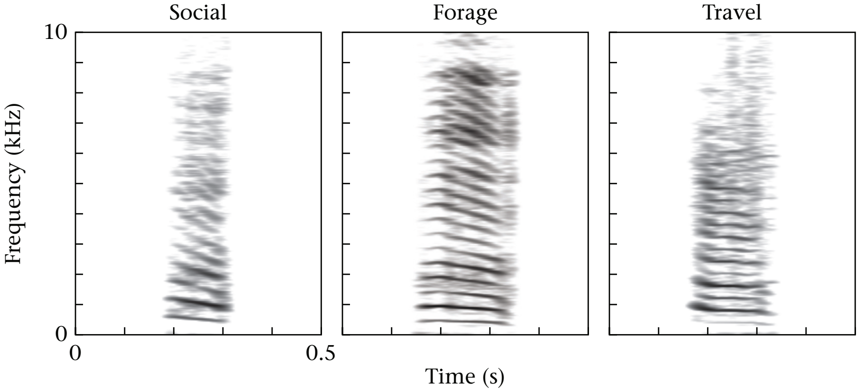

Figure 1. Representative spectrograms of female gelada grunts in social, foraging and travel contexts. These grunts were produced by adult females from different reproductive units. Spectrograms were made in Praat (version 6.0.23) with a Gaussian window of 50 ms. Audio files are available for these spectrograms in the Supplementary Materials (Audio S1–S3).

Table 1
Definitions and transformations of measured spectrogram parameters

Parameter	Definition	Transformation	Software source
Bandwidth	Mean frequency range (Hz)	ln	LMA
Fundamental frequency	Mean lowest frequency (Hz)	Not transformed	Praat
Starting quartile frequency	Frequency under which 25% of the amplitude distribution occurs, measured at the start of the call (Hz)	ln	LMA
Ending quartile frequency	Frequency under which 25% of the amplitude distribution occurs, measured at the end of the call (Hz)	ln	LMA
Frequency band difference	Difference between the mean frequencies of the first (i.e. lowest) and second (i.e. high amplitude) dominant frequency bands (Hz)	ln	LMA
Peak frequency	Mean frequency with the highest amplitude (Hz)	ln	LMA
Duration	Length of call (ms)	ln	LMA
Location of maximum peak frequency	Relative location within a call's duration of the maximum peak frequency ((1/duration in ms) × time location in ms)	Not transformed	LMA

individual's grunts within each behavioural state. All averaged calls from the state with the smallest sample size (travelling, $N = 11$) were included. Subsets of averaged calls from the other two behavioural states were included to balance data points across states (see Appendix, Table A2 for individuals represented in each state). A leave-one-out cross-validation determined the probability of the discriminant functions correctly classifying an averaged call by behavioural state.

We then conducted a MANOVA to assess whether the behavioural state in which a grunt occurred significantly predicted the averaged calls' scores on the first and second discriminant functions. Using a linear mixed model and pairwise post hoc Tukey tests, we tested which states' calls significantly differed on these discriminant scores. In these models, behavioural state served as a fixed effect and caller identity served as a random effect.

Grunt variation across individuals

Next, we asked whether grunt acoustic structure differed based on the caller's individual identity. We conducted a discriminant analysis and a MANOVA to assess acoustic variation across grunts from different individuals. For each of 12 females, we selected 14 calls at random (the number of calls available for the individual with the fewest calls qualifying for the analysis) to be included in the discriminant analysis (168 grunts). We did not consider behavioural state in this analysis (see Appendix, Table A3 for the number of calls available and randomly selected within each state for each individual). A leave-one-out cross-validation procedure determined the probability of the discriminant functions correctly classifying a call by individual caller.

We then conducted a MANOVA to assess whether caller identity significantly predicted grunts' scores on the first and second discriminant functions. We followed these with pairwise post hoc Tukey tests for scores on each of the first two discriminant functions to assess which individuals' grunts differed from one another.

Pairwise grunt similarity across social groups

Next, we asked whether living in the same band or unit predicted greater similarity in grunt structure between pairs of individuals. We controlled for pairwise genetic similarity in these analyses. We also analysed grunts separately for each of two behavioural states with the largest number of recordings, foraging and socializing, which limited the sample to females from three bands.

For grunts in each behavioural state, we conducted a principal component analysis, weighting the contribution of each female's grunts equally. To estimate vocal similarity between two individuals, we first calculated each female's average scores on each of the first three components from the principal component analysis, as scree plots indicated these accounted for the majority of the variance. We calculated averages for 51 females' foraging grunts and 36 females' socializing grunts. Using component score averages as an individual's coordinate location in a three-dimensional space, we then measured the Euclidean distance between all pairs of females within a given behavioural state. We weighted each component score's contribution to these distance measurements by its proportion of variance accounted for in the principal component analysis. These distances served as a measure of vocal dissimilarity for a given pair; the smaller the distance score, the greater the acoustic similarity between those two individuals' average grunts. We calculated foraging state grunt distances (1275 pairs) and socializing state grunt distances (630 pairs) for all pairs for whom we had genetic relatedness estimates.

Estimates of genetic relatedness between females were available from previous work with this population (Snyder-Mackler et al., 2014). We generated the Wang pairwise relatedness estimates based on shared alleles at 23 microsatellite locations in the gelada genome. Wang estimates range between -1 and 1, with positive scores representing higher relatedness than average and negative scores representing lower relatedness than average.

We conducted linear mixed models to assess the relationship between shared group membership (at the band level and separately at the unit level) and vocal dissimilarity, accounting for genetic similarity. For tests assessing vocal dissimilarity between individuals in different units, we restricted comparisons to pairs from units in the same band (418 pairs in foraging state; 187 pairs in socializing state). Fixed effects in these models were shared group membership (yes or no) and Wang relatedness estimates, and random effects were the individuals in each pair. To assess whether vocal dissimilarity was greater across certain groups, we conducted linear mixed models with the composition of the pair (e.g. same band, Band 1 and Band 2, Band 1 and Band 3, Band 2 and Band 3) and Wang relatedness estimates as fixed effects and the individuals in each pair as random effects.

Descriptive comparison of variables contributing to grunt variation

We conducted a final descriptive analysis to illustrate the relative importance of each of the previously examined variables in explaining grunt structure variation. To do so, we calculated vocal distances between pairs of individual calls that shared a certain characteristic (e.g. two calls from the same behavioural state; two calls from members of the same band) and those that did not (e.g. two calls from two different behavioural states; two calls from members of two different bands). Variables showing a greater difference in vocal distance between calls that shared the characteristic and those that did not were interpreted descriptively as accounting for greater variation in grunt structure.

Within each variable, we limited comparisons to subsets of call pairs that would not introduce variation from other variables. For behavioural state, we compared vocal distances between pairs of calls from the same individual in different behavioural states to vocal distances between pairs of calls from the same individual in the same behavioural state. The difference between the mean of these distances was then used as an estimate of behavioural state's influence on grunt variation. For individual callers, we compared vocal distances between pairs of calls from the same individual (occurring in the same behavioural state) to vocal distances between pairs of calls from different individuals (in the same unit and occurring in the same behavioural state). For caller unit membership, we compared vocal distances between pairs of calls from different individuals in the same unit (occurring in the same behavioural state) to vocal distances between pairs of calls from different units (in the same band and occurring in the same behavioural state). Finally, for caller band membership, we compared vocal distances between pairs of calls from different individuals in the same band (occurring in the same behavioural state) to vocal distances between pairs of calls from different individuals in different bands (occurring in the same behavioural state).

RESULTS

Grunt Variation across Behavioural States

The acoustic structure of female grunts differed across behavioural states. The first discriminant function accounted for 30.03% of the averaged grunt variance across behavioural states, and the second discriminant function accounted for 27.29% of this variance. Leave-one-out cross validations correctly classified 47.92% of averaged grunts by behavioural state (expected by random classification: 33.33%). Location of maximum peak frequency (negative coefficient) and duration (positive coefficient) contributed most to the first discriminant function, while peak frequency (negative coefficient) and duration (positive coefficient) contributed most to the second discriminant function (see Appendix, Table A4 for coefficients). Based on scores on these two discriminant functions, female averaged grunts differed across states ($F_{2,45} = 8.84$, $P < 0.001$, Wilks $\lambda = 0.51$). Travelling grunts scored lower on the first discriminant function than did foraging grunts (mean difference = 1.01, $t_{36.7} = 2.81$, $P = 0.021$) and socializing grunts (mean difference = 1.53, $t_{36.7} = 4.24$, $P < 0.001$; Fig. 2). On the second discriminant function, foraging grunts scored higher than travelling grunts (mean difference = 1.10, $t_{36.7} = 3.05$, $P = 0.011$) and socializing grunts (mean difference = 1.37, $t_{36.7} = 3.81$, $P = 0.002$). Full results of post hoc Tukey comparisons based on a linear mixed model including behavioural state as a fixed effect and caller identity as a random effect are available in the Appendix, Table A5. Overall, travelling grunts were shorter with maximum peak frequency located later in the calls compared to grunts in the other two contexts. Foraging grunts were longer with lower peak frequencies compared to grunts in the other two contexts.

Grunt Variation across Individuals

The acoustic structure of female grunts differed across individuals. The first discriminant function accounted for 56.66% of the call variance across individuals, and the second discriminant function accounted for 38.94% of this variance. Leave-one-out cross validations correctly classified 34.52% of grunts by individual (expected by random classification: 8.33%). Peak frequency (positive coefficient) and frequency band difference (positive coefficient) contributed most to the first discriminant function, while fundamental frequency (positive coefficient) and frequency band difference (negative coefficient) contributed most to the second discriminant function (see Appendix, Table A4 for coefficients). Based on scores on the first two discriminant functions (Fig. 3), female grunts differed by caller ($F_{11,156} = 13.30$, $P < 0.001$, Wilks $\lambda = 0.26$). Each female's grunts differed from those of at least four other individuals (post hoc Tukey tests: $P < 0.05$; see Appendix, Fig. A3).

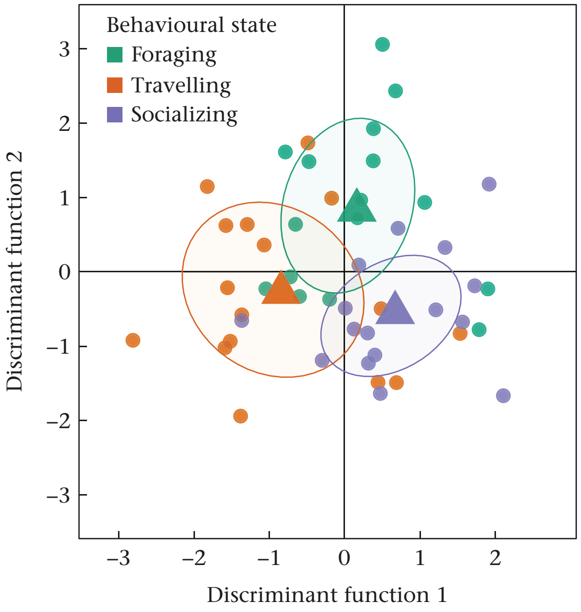

Figure 2. Acoustic properties of female grunts across behavioural states. Each data point represents an individual's average grunt occurring within a given behavioural state. Triangles represent centroids for each behavioural state; ellipses represent 50% confidence intervals for each behavioural state. High scores on discriminant function 1 indicate long duration and maximum peak frequency located early in the call. High scores on discriminant function 2 indicate long duration and low peak frequency.

Pairwise Grunt Similarity across Social Groups

For grunts uttered in both foraging and socializing states, pairs living in the same band were more vocally similar than pairs living

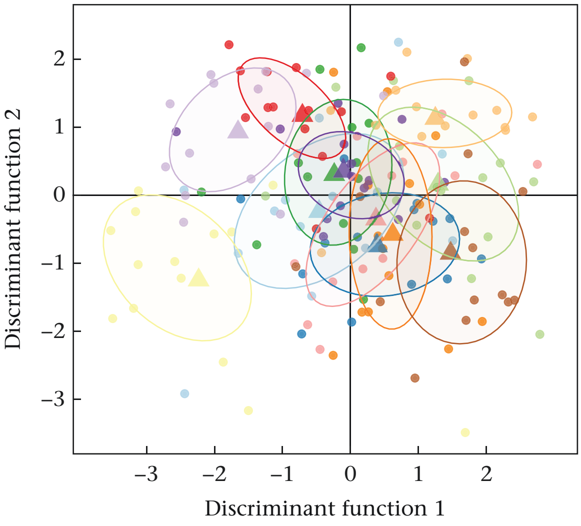

Figure 3. Acoustic properties of female grunts across individuals. Each data point represents a single grunt uttered by a given individual. Each colour represents one individual; triangles represent centroids for each individual; ellipses represent 50% confidence intervals for each individual. High scores on discriminant function 1 indicate high peak frequency and large frequency band difference. High scores on discriminant function 2 indicate high fundamental frequency and small frequency band difference.

in different bands (foraging grunt model: $b = -0.12$, $P = 0.001$; socializing grunt model: $b = -0.16$, $P < 0.001$; Fig. 4, see Table 2 for full linear mixed model results). Vocal similarity was no greater between pairs living in the same unit than between pairs living in different units within the same band. Genetic similarity did not significantly predict vocal similarity in any model.

For foraging grunts, the first three components from the principal component analysis accounted for 61.11% of variance in acoustic and temporal structure (see Appendix, Table A6 for coefficients from both foraging and socializing grunt principal component analyses). Foraging grunts were more dissimilar for pairs across Band 1 and Band 3 ($b = 0.13$, $P = 0.002$) and pairs across Band 2 and Band 3 ($b = 0.17$, $P < 0.001$) than for pairs within the same band. Grunts were no more dissimilar for pairs across Band 1 and Band 2 than they were for pairs within the same band ($b = -0.03$, $P > 0.05$).

For socializing grunts, the first three components from the principal component analysis accounted for 64.05% of variance in acoustic structure. Socializing grunts were more dissimilar for pairs across Band 1 and Band 2 ($b = 0.26$, $P < 0.001$) and across Band 1 and Band 3 ($b = 0.34$, $P < 0.001$) than for pairs within the same band. Grunts were no more dissimilar for pairs across Band 2 and Band 3 than they were for pairs within the same band ($b = -0.02$, $P > 0.05$). Overall, band membership predicted vocal similarity between individual pairs but not unit membership or genetic similarity. Pairs living in the same band had more acoustically similar grunts, and some specific bands' grunts were more dissimilar to one another.

Descriptive Comparison of Variables Contributing to Grunt Variation

Individual caller identity seemed to account for the greatest variation in grunt structure, as the average vocal distance between pairs of calls from individuals in the same unit and behavioural state was 25% larger (mean ± SD = 1.25 ± 0.63, $N = 1642$) than the average between pairs of calls from the same individual in the same behavioural state (mean ± SD = 1.00 ± 0.57, $N = 720$). The average vocal distance between calls from the same individual in different behavioural states was 10% larger (mean ± SD = 1.10 ± 0.52, $N = 597$) than the average between calls from the same individual in the same behavioural state (mean ± SD = 1.00 ± 0.57, $N = 753$). The average vocal distance between calls from individuals in different bands in the same behavioural state was 6.3% larger (mean ± SD = 1.34 ± 0.67, $N = 15\,260$) than the average between calls from individuals in the same band in the same behavioural state (mean ± SD = 1.26 ± 0.64, $N = 7297$). Caller unit membership seemed to account for the least variation in grunt structure, as the average vocal distance between calls from different individuals in different units within the same band and behavioural state was only 1.6% larger (mean ± SD = 1.27 ± 0.64, $N = 5655$) than the average between calls from different individuals in the same unit and behavioural state (mean ± SD = 1.25 ± 0.63, $N = 1642$). These results reflect the same pattern from the previous analysis in which shared band membership was predictive of vocal similarity, while shared unit membership was not.

The first three components from this principal component analysis accounted for 60.16% of variance in grunt structure (see Appendix, Table A7 for coefficients from principal component analysis).

DISCUSSION

The acoustic structure of female gelada grunts was more similar between individuals living in the same higher-level social group (the band) than between individuals living in different bands. This pattern did not hold at the level of the immediate social group, the unit. Genetic similarity did not predict vocal similarity, which indicates that vocal similarity at the band level is likely to be the result of experience-based vocal convergence. While individuals from different units are often in close spatial proximity, individuals spend more time in close proximity to other members of their own unit, meaning that geladas are most often exposed to grunts from others in their unit (Snyder-Mackler et al., 2012). This result, that convergence occurs at the band level and not at the unit level, does not support the interactive alignment model of vocal learning. Rather, these findings suggest that selective vocal accommodation serves a social function , which has been posited by the communication accommodation theory. Similar to the finding that gelada copulation calls can be selectively suppressed (le Roux et al., 2013), geladas may also have some volitional control over grunt production.

This finding of vocal convergence at a higher-level social structure in female geladas mirrors findings in male Guinea baboons (Fischer et al., 2020). Effect sizes of vocal similarity within

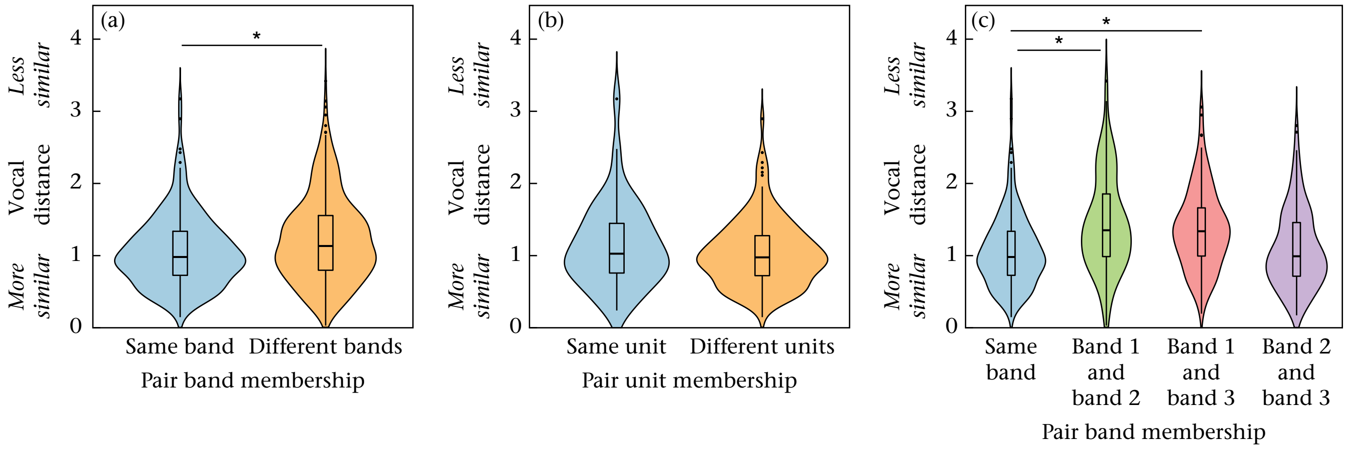

Figure 4. Vocal distance of female gelada grunts (a) for pairs living in the same band (but not in the same unit) and for pairs living in different bands, (b) for pairs living in the same unit and for pairs living in different units (within the same band) and (c) for pairs by specific band membership. Lower vocal distance scores indicate greater vocal similarity within pairs of individuals. Raw scores for socializing grunts are plotted. The width of the violin plot indicates the relative kernel probability density of the data at each *Y* value. Inlaid box plots include a centre line indicating the median, a box capturing the interquartile range, whiskers extending to the most extreme data point no more than 1.5 times the interquartile range past the box and points indicating extreme values. Asterisks indicate a significant difference at an alpha level of 0.05.

Table 2
Results of linear mixed models testing differences in pairwise vocal dissimilarity based on social group membership

Effect	Foraging grunts				Socializing grunts			
	Estimate	SE	*t*	*P*	Estimate	SE	*t*	*P*
Model 1a: vocal dissimilarity within bands								
Intercept	1.07	0.04	25.79	<0.001	1.22	0.07	17.04	<0.001
Wang relatedness	<0.01	0.07	0.01	0.992	0.09	0.13	0.72	0.469
Pair in same band	−0.12	0.03	−4.74	<0.001	−0.16	0.05	−3.41	0.001
Model 1b: vocal dissimilarity across specific bands								
Intercept	0.95	0.04	21.86	<0.001	1.06	0.07	14.20	<0.001
Wang relatedness	−0.04	0.07	−0.50	0.620	0.11	0.13	0.84	0.401
Pair in Bands 1 and 2	−0.03	0.04	−0.82	0.415	0.26	0.07	3.80	<0.001
Pair in Bands 1 and 3	0.13	0.04	3.11	0.002	0.34	0.06	5.62	<0.001
Pair in Bands 2 and 3	0.17	0.03	6.00	<0.001	−0.02	0.06	−0.27	0.786
Model 2: vocal dissimilarity within units								
Intercept	0.97	0.05	19.09	<0.001	1.04	0.09	12.28	<0.001
Wang relatedness	0.02	0.12	0.19	0.853	0.05	0.19	0.26	0.794
Pair in same unit	−0.05	0.06	−0.84	0.404	0.07	0.10	0.73	0.726

For Model 1a, the intercept represents vocal dissimilarity for pairs in which each individual lives in a different band. For Model 1b, the intercept represents vocal dissimilarity for pairs in which both individuals live in the same band. For Model 2, the intercept represents vocal dissimilarity for pairs in which each individual lives in a different unit within the same band.

versus between gelada bands/Guinea baboon gangs are both small. However, male Guinea baboons affiliate frequently across units within a gang, while female geladas do not groom across units within a band (Patzelt et al., 2014; Tinsley Johnson et al., 2014). Female geladas therefore seem to have less intimate social interactions within bands than Guinea baboons do within gangs, yet the extent of vocal convergence within bands and gangs that maintain spatial proximity is similar. These results support the hypothesis that vocal convergence broadly functions to maintain spatial cohesion at the band level in gelada fission–fusion societies, rather than to support close social bonds at the unit level. This hypothesis stands in contrast to other primates that show correlations between social bond strength and vocal similarity (Lemasson et al., 2011; Snowdon & Elowson, 1999), or where vocal similarity between social partners emerges during vocal exchanges (Candiotti et al., 2012; Mitani & Gros-Louis, 1998). Whether gelada grunts converge during vocal exchanges remains to be tested; this question was not assessed in the present study. In summary, there are many potential functions of vocal accommodation in primates.

Band level vocal convergence occurred alongside unit level differences in female grunt structure. Interestingly, band membership was nearly as strong a predictor of grunt similarity as behavioural state. These results make sense when taking the gelada social system into account; individual recognition may be important only for the small subset of individuals that are encountered most regularly (Zürcher et al., 2021). This interpretation is supported by experimental evidence that gelada males do not recognize vocalizations from extra-unit males within their band (Bergman, 2010). Band level vocal convergence may support cohesion beyond the unit, for which individual recognition is not needed. Conversely, the lack of a relationship between genetic relatedness and vocal similarity suggests that vocal divergence among close relatives (who often live in the same unit) facilitates recognition. A similar dissociation was found in Guinea baboons (Fischer et al., 2020), but not in other Asian and African primates such as mandrills (Levréro et al., 2015). Overall, a broader understanding of how and why some mammals are vocally similar is needed.

Gelada grunt acoustic structure varied with co-occurring behavioural states, which is a pattern found in a number of other social mammals, including bats (e.g. Egyptian fruit bats, *Rousettus aegyptiacus*: Prat et al., 2016), meerkats (Townsend et al., 2011) and other primates (Crockford et al., 2018; Lemasson et al., 2004; Meise et al., 2011; Owren et al., 1997). We tested for acoustic variation between three contexts: foraging, travelling and socializing. Geladas have somewhat discrete times of day for these activities (Mamo & Wube, 2019; Woldegeorgis & Bekele, 2015). It is plausible that differences in grunt structure across contexts may help to indicate behavioural transitions or coordinate group behaviour, and our findings pave the way for future exploration of how this variation functions in gelada society.

Sample sizes only allowed us to assess vocal similarity within foraging and socializing states. However, if vocal convergence facilitates spatial cohesion within bands, we would expect to find grunt similarity within bands during travelling states, which is when herds fission and bands move in different directions. Future work is needed to test the hypothesis that vocal accommodation in contact calls supports spatial cohesion in fission–fusion primate societies. This future work should focus on calls uttered during travel and other times of transition. In this gelada population, assessing bands' ranging and movement patterns will help us understand why vocal dissimilarity was greater between some bands than others. It is possible that bands with greater spatial overlap may not only vocally converge within bands, but also diverge between bands, as chimpanzee, *Pan troglodytes*, groups seem to have done with loud calls coordinating group travel (Crockford et al., 2004). Finally, playback experiments will be required to determine whether variation in grunt structure leads to geladas differentiating between grunts at each of these levels and whether this variation leads listeners to adjust behaviour in a functionally relevant way (e.g. Bergman, 2010; Rendall et al., 1999).

Vocal convergence is thought to play a role in social bonding between pairs and within groups in many gregarious species, including humans (Tyack, 2008). Stronger vocal convergence at higher levels of gelada and Guinea baboon societies (Fischer et al., 2020) suggests this limited form of vocal learning may also play a role in mitigating the uncertainty inherent in fluid social dynamics and the resulting pressures to maintain cohesion. Vocal divergence between chimpanzee groups, which use loud calls to coordinate parties reuniting within their fission–fusion groups, further suggests this role for vocal learning (Crockford et al., 2004). Given that these nonhuman primates' fluid social structures share similarities with human societies, it is also possible that vocal accommodation helped our hominin ancestors navigate their fluid social groups.

Author Contributions

M. C. Painter: Conceptualization, Data curation, Formal analysis, Methodology, Visualization, Writing - Original draft. **M. L. Gustison**: Conceptualization, Data curation, Funding acquisition, Investigation, Methodology, Visualization, Writing - Review & editing. **N. Snyder-Mackler**: Data curation, Funding acquisition, Investigation, Writing - Reviewing & editing. **E. Tinsley Johnson**: Data curation, Funding acquisition, Investigation, Writing - Reviewing & editing. **A. le Roux**: Data curation, Investigation, Writing - Reviewing & editing. **T. J. Bergman**: Conceptualization, Funding acquisition, Methodology, Project administration, Resources, Supervision, Writing - Review & editing.

Data Availability

Data and R code for this study are available as Supplementary material.

Declaration of Interest

None.

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Supplementary Material

Supplementary material associated with this article is available, in the online version, at https://doi.org/10.1016/j.anbehav.2023.10.002.

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Appendix

Complementary Methods

Differences between female and male grunts were previously described (Gustison & Bergman, 2017). We therefore examined female and male grunts separately for all analyses.

Study subjects and data set

A total of 357 grunts, from 18 males across 13 units in three bands, were available for these analyses. These male grunt recordings were available from the 2014 data set (Gustison et al., 2019). The observer noted the focal male's behavioural state (resting, travelling, foraging or socializing) continuously during sampling, allowing focal individuals' calls to be matched with their behavioural state at the time of the call. Behavioural state was known for 348 of the calls.

Statistical analyses

To assess grunt variation across behavioural states and individuals, we conducted analyses equivalent to those for females using equivalent data subsets.

Table A1
Number of female and male grunt recordings available by behavioural state

Behavioural state	Number of grunts	Number of individuals	Number of grunts per individual (range)
Females			
Resting	8	4	1–5
Travelling	22	16	1–2
Foraging	194	59	1–15
Socializing	110	37	1–11
Infant-focused	26	4	2–11
Unknown	185	43	1–18
Total sample	545	87	1–23
Males			
Resting	50	14	1–5
Travelling	37	11	1–14
Foraging	130	15	1–32
Socializing	131	16	1–29
Unknown	9	3	1–5
Total sample	357	18	1–80

Table A2
Individuals represented in each behavioural state for discriminant analyses by behavioural state

Individual ID	Travelling	Foraging	Socializing
Females			
Bom	–	X	–
Bre	–	X	–
Col	–	X	–
Coo	–	–	X
Cor	–	–	X
Del	X	X	X
Des	–	–	X
Dia	X	–	–
Dot	X	–	–
Gin	X	X	–
Had	–	–	X
Gyp	X	–	–
Hel	X	X	X
Hic	X	–	–
Him	–	X	X
Kee	X	–	–
Kyl	X	X	X
Mab	X	X	X
Mar	X	X	–
Maz	X	–	–
Mee	X	–	X
Moo	–	–	X
Pia	X	–	–
Roo	–	X	–
Tea	–	X	X
Tri	–	–	X
Val	–	–	X
Vie	–	X	–
Vio	X	–	X
Zam	–	X	–
Zay	–	X	–
Zoo	X	X	X
Males			
Dev	X	X	X
Die	X	X	X
Dik	X	X	X
Dja	X	X	X
Gap	X	X	X
Hoo	X	–	X
Imp	–	X	X
Qho	X	X	X
Saw	X	X	X
Sol	X	X	–
Tal	X	X	X
Wal	X	X	X

Table A3
Number of grunts selected from those available in each behavioural state for discriminant analyses by caller

Individual ID	Resting	Travelling	Foraging	Socializing	Infant-focused	Unknown
Females						
Cas	–	–	3	6	–	5 of 6
Cey	–	–	2 of 3	–	5	7 of 12
Coc	–	–	2 of 5	1 of 2	1 of 2	10 of 11
Del	–	1	2 of 9	4 of 5	–	7 of 11
Har	–	–	14 of 15	–	–	–
Him	–	–	10	4	–	–
Kee	–	1 of 2	4	–	–	9
Kyl	–	2	1	2 of 3	–	9 of 12
Mar	5	1	6	–	–	2
Mon	1	–	2 of 3	4	7 of 8	–
Val	–	–	1 of 2	1 of 3	–	12 of 18
Vio	–	1 of 2	–	4 of 8	7 of 11	2
Males						
Dev	0 of 5	1 of 14	4 of 32	9 of 29	–	–
Die	3	2 of 3	4 of 6	5 of 8	–	–
Dik	1	2	3	5	–	3
Dja	1 of 5	4 of 9	4 of 17	5 of 13	–	–
Gap	5	0 of 1	6 of 7	3 of 4	–	–
Imp	1	–	1 of 2	10 of 20	–	2 of 5
Len	4 of 5	–	–	10 of 14	–	–
Mhe	2 of 4	–	5	6 of 14	–	1
Noh	5	–	7 of 11	2 of 4	–	–
Saw	0 of 3	1 of 2	10 of 13	3 of 5	–	–
Tal	–	1	10 of 12	3 of 4	–	–
Wal	2 of 4	0 of 1	9 of 13	3 of 4	–	–

Complementary Results

Grunt variation across behavioural states

Male grunts differed significantly across behavioural states. The first discriminant function accounted for 37.95% of the call variance across behavioural states, and the second discriminant function accounted for 19.26% of this variance. Leave-one-out cross validations correctly classified 42.42% of averaged grunts by behavioural state (expected by random classification: 33.33%). Starting quartile frequency (negative coefficient) and duration (positive coefficient) contributed most to the first discriminant function, while duration (negative coefficient) and bandwidth (positive coefficient) contributed most to the second discriminant function. Based on scores on the first two discriminant functions, male averaged grunts differed across states ($F_{2,30} = 5.99$, $P < 0.001$, Wilks $\lambda = 0.50$). Socializing grunts scored higher on the first discriminant function than did foraging grunts (mean difference = 1.76, $t_{20.6} = 4.11$, $P = 0.001$) and travelling grunts (mean difference = 1.29, $t_{20.6} = 3.01$, $P = 0.018$; Fig. A1). On the second discriminant function, foraging grunts scored higher than travelling grunts (mean difference = 1.10, $t_{20.6} = 2.57$, $P = 0.046$). Full results of post hoc Tukey comparisons based on a linear mixed model including behavioural state as a fixed effect and caller identity as a random effect are available in Table A5. Overall, socializing grunts were longer with lower starting quartile frequencies compared to grunts in the other two contexts. Foraging grunts were shorter with a larger bandwidth compared to travelling grunts.

Table A4
Linear discriminant function (DF) coefficients from classifications by behavioural state and individual caller

Parameter	Averaged grunt classification by behavioural state				Grunt classification by individual caller			
	Females		Males		Females		Males	
	DF1 (30.03%)[a]	DF2 (27.29%)[a]	DF1 (37.95%)[a]	DF2 (19.26%)[a]	DF1 (31.06%)[a]	DF2 (18.89%)[a]	DF1 (15.80%)[a]	DF2 (7.75%)[a]
Bandwidth (log)	0.110	0.135	−0.720	0.747	0.378	0.072	0.040	0.368
Fundamental frequency	0.238	0.160	0.139	−0.452	0.487	1.013	1.485	0.227
Starting quartile frequency (log)	−0.295	0.376	−1.038	−0.307	0.074	0.339	−0.143	0.967
Ending quartile frequency (log)	0.120	−0.116	0.350	−0.470	0.372	0.234	0.076	0.012
Frequency band difference (log)	−0.240	0.216	−0.115	0.494	0.543	−0.990	−0.006	0.316
Peak frequency (log)	0.007	−1.175	0.419	−0.203	0.682	−0.133	−0.061	0.019
Duration (log)	0.652	0.625	1.021	0.255	0.341	−0.074	−0.228	0.248
Location of maximum peak frequency	−0.930	0.491	0.957	−0.886	−0.050	0.351	−0.366	−0.042

[a] Percentage of variation in grunt parameters accounted for by the discriminant function is provided in parentheses.

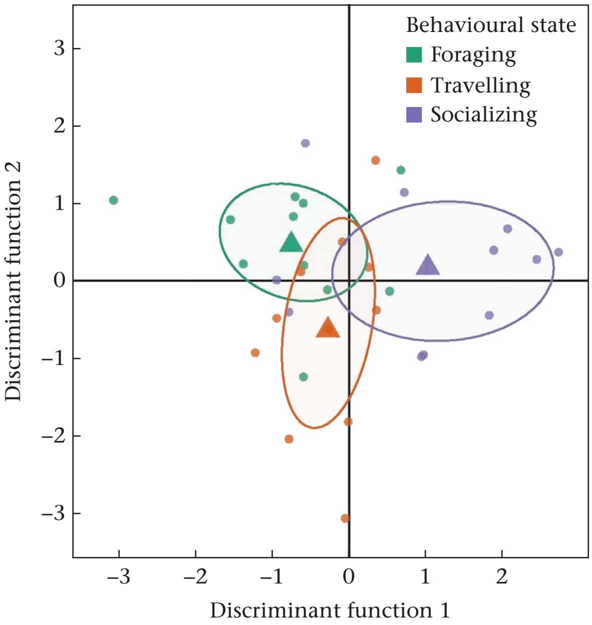

Figure A1. Acoustic properties of male grunts across behavioural states. Each data point represents an individual's average grunt occurring within a given behavioural state. Triangles represent centroids for each behavioural state; ellipses represent 50% confidence intervals for each behavioural state. High scores on discriminant function 1 indicate long duration and low starting quartile frequency. High scores on discriminant function 2 indicate short duration and large bandwidth.

Table A5
Post hoc Tukey comparisons of discriminant function (DF) scores across behavioural states

Comparison	Mean difference	*t*	*P*
Females (SE = 0.36, *df* = 36.7)			
DF1			
Foraging – Travelling	1.01	2.81	0.021
Foraging – Socializing	−0.51	−1.42	0.340
Travelling – Socializing	−1.53	−4.24	<0.001
DF2			
Foraging – Travelling	1.10	3.05	0.011
Foraging – Socializing	1.37	3.81	0.002
Travelling – Socializing	0.27	0.75	0.735
Males (SE = 0.43, *df* = 20.6)			
DF1			
Foraging – Travelling	−0.47	−1.10	0.523
Foraging – Socializing	−1.76	−4.11	0.001
Travelling – Socializing	−1.29	−3.01	0.018
DF2			
Foraging – Travelling	1.10	2.57	0.046
Foraging – Socializing	0.30	0.69	0.773
Travelling – Socializing	−0.81	−1.88	0.170

Linear mixed models included behavioural state as a fixed effect and caller identity as a random effect. Random effect estimates for each model were as follows: females: DF1 (<0.01, SD = 0.02); DF2 (<0.01, SD = <0.01); males: DF1 (<0.01, SD = <0.01); DF2 (<0.01, SD = <0.01).

Grunt variation across individuals

Male grunts differed significantly across individuals. The first discriminant function accounted for 60.63% of the call variance across individuals, and the second discriminant function accounted for 36.90% of this variance. Leave-one-out cross validations correctly classified 30.36% of male grunts by individual (expected by random classification: 8.33%). Fundamental frequency (positive coefficient) and location of maximum peak frequency (negative coefficient) contributed most to the first discriminant function, while starting quartile frequency (positive coefficient) and bandwidth (positive coefficient) contributed most to the second discriminant function (see Table A4 for coefficients). Grunts' scores on the first two discriminant functions are plotted by individual caller in Fig. A2. Based on scores on the first two discriminants, a MANOVA determined that male grunts differed by caller ($F_{11,156} = 14.18$, $P < 0.001$, Wilks $\lambda = 0.25$). Each male's grunts differed from those of at least three other individuals (post hoc Tukey tests: $P < 0.05$; see Fig. A3).

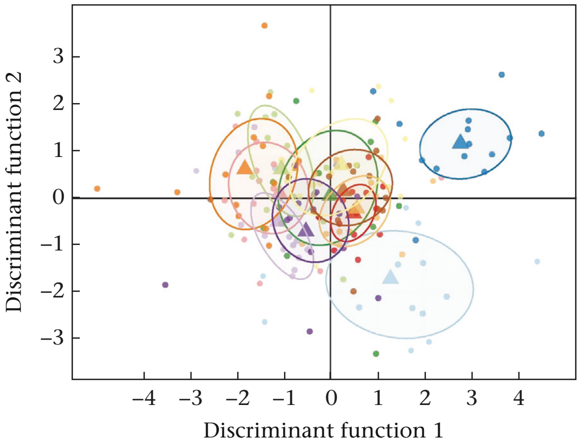

Figure A2. Acoustic properties of male grunts across individuals. Each data point represents a single grunt uttered by a given individual. Each colour represents one individual; triangles represent centroids for each individual; ellipses represent 50% confidence intervals for each individual. High scores on discriminant function 1 indicate high fundamental frequency and maximum peak frequency located early in the call. High scores on discriminant function 2 indicate high starting quartile frequency and large bandwidth.

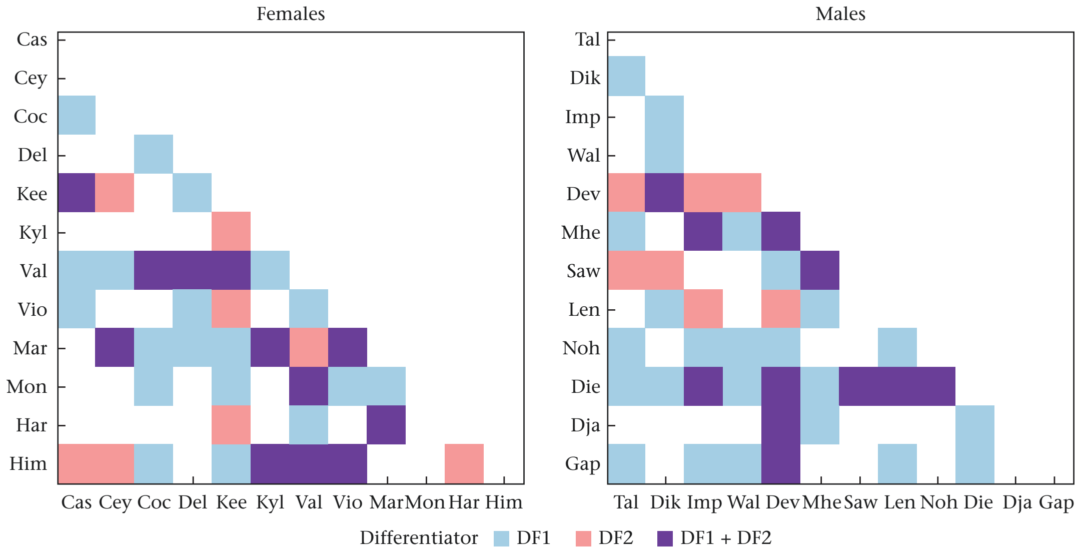

Figure A3. Discriminant function (DF) scores of individuals' grunts for each sex. Post hoc Tukey comparisons were conducted on ANOVAs that tested whether grunts' DF scores differed across individual callers (ANOVA: females: DF1: $F_{11,156} = 18.54$, $P < 0.001$; DF2: $F_{11,156} = 9.04$, $P < 0.001$; males: DF1: $F_{11,156} = 21.84$, $P < 0.001$; DF2: $F_{11,156} = 8.29$, $P < 0.001$). Two individuals' grunts were found to be significantly different if post hoc Tukey comparisons had a P value of <0.05.

Table A6

Coefficients from principal component (PC) analyses for vocal dissimilarity analysis across social groups

Parameter	Foraging grunts			Socializing grunts		
	PC1 (29.68%)[a]	PC2 (16.89%)[a]	PC3 (14.54%)[a]	PC1 (33.15%)[a]	PC2 (17.27%)[a]	PC3 (13.63%)[a]
Bandwidth (log)	0.699	−0.160	−0.056	0.651	0.470	−0.302
Fundamental frequency	−0.213	−0.723	0.324	−0.236	0.351	0.574
Starting quartile frequency (log)	0.762	−0.168	−0.082	0.848	0.097	0.023
Ending quartile frequency (log)	0.730	0.206	0.371	0.734	−0.165	0.182
Frequency band difference (log)	0.099	0.140	0.907	0.620	−0.417	0.321
Peak frequency (log)	0.818	−0.180	−0.168	0.641	0.518	0.023
Duration (log)	0.130	0.801	−0.084	0.331	−0.709	0.114
Location of maximum peak frequency	−0.182	0.196	0.229	−0.101	0.237	0.721

[a] Percentage of variation in grunt parameters accounted for by the component is provided in parentheses.

Table A7

Coefficients from principal component (PC) analyses for vocal dissimilarity comparison of grunt variation predictors

Parameter	PC1 (30.47%)[a]	PC2 (16.03%)[a]	PC3 (13.65%)[a]
Bandwidth (log)	0.651	−0.348	−0.064
Fundamental frequency	−0.193	−0.388	0.664
Starting quartile frequency (log)	0.814	−0.107	−0.045
Ending quartile frequency (log)	0.741	0.210	0.174
Frequency band difference (log)	0.325	0.542	0.623
Peak frequency (log)	0.776	−0.326	−0.048
Duration (log)	0.200	0.739	−0.158
Location of maximum peak frequency	−0.128	−0.095	0.448

[a] Percentage of variation in grunt parameters accounted for by the component is provided in parentheses.