

Inter-sexual multimodal communication during mating in wild geladas: the leading role of females

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Abstract

Female primates can emit vocalizations associated with mating that can function as honest signals of fertility. Here, we investigated the role of mating calls and visual signals in female geladas (*Theropithecus gelada*). Because females have a central role in the gelada society and seem to solicit sexual interactions, we answered whether they emit vocalizations in conjunction with gazing to increase mating success probability. Before and during copulations, females can emit pre-copulation calls and copulation calls. For the first time, we identified a new female vocalization emitted at the final stage of copulations (end-copulation call), possibly marking the occurrence of ejaculation. We found that longer pre-copulation call sequences were followed by both prolonged copulations and the presence of end-copulation calls, thus suggesting that females use pre-copulation calls to ensure successful copula completion. Moreover, we found that different combinations of female vocal types and gazing had different effects on male vocal behavior and motivation to complete the copula. The analysis of the vocal and visual signals revealed a complex inter-sexual multimodal chattering with the leading role of females in the signal exchange. Such chattering, led by females, modulates male sexual arousal, thus increasing the probability of the copula success.

Keywords: copulation calls, female end-copulation call, inter-sexual coordination, mating success, multimodal communication, *Theropithecus gelada*

Communication is a crucial requirement for sociality and has developed with the evolution of social systems (Freeberg et al. 2012). Usually, animal communicative signals are beneficial to both sender and receiver, as they provide reliable information about senders' intrinsic characteristics (e.g., body size; Hebets and Papaj 2005) and/or circumstances under which they are acting (e.g., motivation, *sensu* Tinbergen 2020). Because individual fitness depends on mating opportunities, the reproductive context requires effective communication via different sensory modalities (Moreira et al. 2013). Due to sexual competition, males and females have evolved a wide variety of signals, including visual and vocal ones (Partan and Marler 2005). Considering the visual channel, Eye-to-Eye Contact (EEC) is an essential element of visual communication (Kret et al. 2015; Schino and Sciarretta 2016). In many primate species, females during copulation usually turn to look back and engage EEC with males (Dixson 2015). According to previous reports, EEC helps the male's pelvic thrusting and prolongs sexual contact, thus improving the chances of ejaculation (Dixson 2015; Palagi et al. 2020; Zanolì et al. 2021). As concerns the acoustic channel, several animal species, in particular primates, can emit rhythmic vocalizations before, during, or after copulations, the so-called “copulation calls” (e.g.,

insects: *Drosophila* sp., Kerwin and von Philipsborn 2020; amphibians: *Rana blythii*, Emerson 1992; Emerson and Boyd 1999; rodents: *Rattus norvegicus*, Thomas and Barfield 1985; mammals: *Loxodonta africana*, Poole et al. 1988; *Mirounga angustirostris*, Cox and LeBoeuf 1977; New-World monkeys: *Cebus apella*, Carosi and Visalberghi 2002; *Brachyteles arachnoides*, Milton 1985; Old-World monkeys: *Macaca sylvanus*, Pfefferle et al. 2008b; *Papio* sp., Maestripieri and Rooney 2005; *Miopithecus talapoin*, Dixson et al. 1975; great apes: *Pan paniscus*, Clay et al. 2011; *Pan troglodytes*, Townsend et al. 2011; *Gorilla gorilla*, Salmi et al. 2013; see also Pradhan et al. 2006; Dixson 2015; Pfefferle 2016 for reviews; humans: *Homo sapiens*, Dixson 2015; Hamilton and Arrowood 1978). Although both sexes can separately or concurrently call during mating (Doyle et al. 1967; Hamilton and Arrowood 1978; Townsend et al. 2008; Salmi et al. 2013), females are the sex that most likely emits copulation calls (e.g., *C. apella*, Carosi and Visalberghi 2002; *B. arachnoides*, Milton 1985; *M. sylvanus*, Pfefferle et al. 2008b; *Papio* sp., Maestripieri and Rooney 2005; *M. talapoin*, Dixson et al. 1975; *P. paniscus*, Clay et al. 2011; *P. troglodytes*, Townsend et al. 2011; *H. sapiens*, Dixson 2015; Hamilton and Arrowood 1978). The investigation of the role of copulation calls needs to consider the

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social organization typical of the species and the timing of calls' emission (i.e., before, during, or after copulas; Pfefferle 2016). Indeed, due to the differences across species in these 2 aspects, the function of copulation calls is still under debate (Maestripieri and Roney 2005; Pradhan et al. 2006; Pfefferle 2016). Several non-mutually exclusive hypotheses were proposed to explain the role of copulation calls (reviewed in Maestripieri and Roney 2005), including vocalizations caused by phylogenetic inertia, nonadaptive byproducts of other behaviors (Henzi 1996), and vocalizations that play a role in synchronizing the orgasms of mating partners (Hamilton and Arrowood 1978). Despite their diversity, all hypotheses converge in suggesting that copulation calls are signals selected to increase female reproductive success (Pradhan et al. 2006). The most common way female primates seem to have selected to benefit their reproductive success is to use “*Copulation calls as signals to the mating partner*” (reviewed in Pfefferle 2016). According to this view, copulation calls seem to affect timing and occurrence of the partner orgasm (e.g., Pfefferle et al. 2008a), to induce mate guarding and strengthen pair-bonding (Hamilton and Arrowood 1978). Visual and acoustic mating signals can also be conveyed simultaneously as complex multimodal signals (e.g., Narins et al. 2005; Bretman et al. 2011; Ullrich et al. 2016), particularly in primates, in which females can establish EEC with males in conjunction with copulation calls (Dixon, 1975; Saayman 1971; reviewed in Dixon 2015). However, methodological and theoretical reasons often made it possible to investigate the functions of these signals only once at a time (Halfwerk et al. 2019; Liebal et al. 2014).

Here, we investigated the vocal and visual mating behavior in a derived species of Papionini, the gelada (*Theropithecus gelada*, Jablonski 1993). Owing to its complex social and communication features, this species represents a suitable model for studying vocal communication and its function in the reproductive context. This highly dimorphic species lives in a multilevel social system that is composed of reproductive one-male units (OMUs; Dunbar 1993; Kawai et al. 1983) and all-male units often roaming in the neighborhood (Snyder-Mackler et al. 2012). In this scenario, males do not compete directly for oestrus females, but they must compete for long-term hegemony over OMUs (Dunbar and Dunbar 1975). Females are the philopatric sex (Dunbar 1993; Grueter et al. 2012; Johnson et al. 2014) and represent the unit's core, thanks to their relatedness and social affiliation (Dunbar 2014). The social relationship between females allows them to choose their leading male and make their strategic decisions, which lead to critical reproductive consequences (Roberts et al. 2012; Dunbar 2014). For example, contrary to other Papionini species, female geladas tend to initiate sexual interactions (Dunbar 1978). Geladas also possess a complex facial (Palagi et al. 2009; Palagi and Mancini 2011; Leone et al. 2014; Lazow and Bergman 2020; Gallo et al. 2021a) and vocal (Gustison and Bergman 2016; Gustison et al. 2016; Bergman et al. 2019) communicative repertoire. The typical long-term bond between male and female geladas probably played a key role in the evolution of their visual and vocal repertoire with the emergence of facial expressions and calls unique to this species (Bergman and Beehner 2013; Gustison et al. 2012).

In managing mating interactions, females can use visual communication to engage in EEC with males and enhance their arousal, copulatory activity, and ejaculation chances

(Zanoli et al. 2021). At the end of such interactions, females can prolong the time spent with the male and strengthen their social bonds by post-mating affiliation (Zanoli et al. 2021). Concerning acoustic communication, a peculiarity of this species is that males and not just females emit copulation calls during mating (Aich et al. 1990; Gustison et al. 2012). Additionally, while approaching the leader male, females can utter the so-called “pre-copulation call”, not reported in other Papionini species (Gustison et al. 2012). Previous research obtained mixed results on the emission of this call in a specific reproductive stage (exclusively during estrus versus throughout the year but primarily during estrus; Dunbar 2014; Moos-Heilen and Sossinka 1990; Roberts et al. 2017). However, the literature tends to agree on the role of pre-copulation calls as a reliable proxy of estrus (Dunbar 2014; Moos-Heilen and Sossinka 1990; Roberts et al. 2017). This vocalization draws the attention of the male, which usually engages in a copulatory event after inspecting the female's genital area (Dunbar 1978). During the copula, typically from the beginning to the end, males emit sequences of “copulation calls” (Aich et al. 1990). Although less frequently, females can concurrently emit with males “copulation-calls” sequences of variable length (Aich et al. 1990). Then, after the copula, both sexes can emit “post-copulation calls” (Aich et al. 1990), vocal sequences composed of different affiliative “close calls” (Gustison and Bergman 2017; Gustison et al. 2019). Previous studies on geladas reported empirical and anecdotal evidence on how vocal sequences are used in many social contexts to solicit and prolong male–female affiliative interactions (Gustison and Bergman 2016, 2017; Gustison et al. 2019). What remains to be clarified is whether geladas use vocal sequences to solicit and prolong mating in the reproductive context as well.

To fill this gap, we aimed at investigating whether females use vocal signals, in conjunction with EEC, to improve inter-sexual communication. Our preliminary spectrogram analyses revealed that, during the final stage of the copulation event, females often stopped emitting copulation calls and continued to overlap male's calls with a different type of vocalization, which we called “end-copulation call” (Figure 1A; see Supplementary Video S1), described here for the first time. During our field expeditions in which we collected data also in other social contexts (affiliative interactions: Gallo et al. 2021a; Caselli et al. 2021b; aggressions: Caselli et al. 2021a; play sessions: Gallo et al. 2021b), we never recorded this vocalization outside the copulatory context. Therefore, we preliminarily validated the end-copulation call as a new vocalization with acoustic measurements. Then, we formulated the following predictions.

Prediction 1—Female pre-copulation calls are consistent indicators of estrus and can unveil female intrinsic motivation to engage in successful sexual contacts, namely those in which ejaculation occurs and, consequently, the likelihood of conception increases (Dunbar 1978; Moos-Heilen and Sossinka 1990; Roberts et al. 2017). Copula duration may be related to the likelihood of ejaculation and, therefore it can be a proxy of mating success probability (spider monkeys, *B. arachnoides*: Milton 1985; Dixon 2015). Females from different non primate (*Drosophila* sp.: Kerwin and von Philipsborn 2020; *R. blythii*: Emerson 1992, Emerson and Boyd 1999) and primate species can emit vocalizations during male ejaculation (e.g., Old-World monkeys: *Macaca fascicularis*: Deputte and Goustard

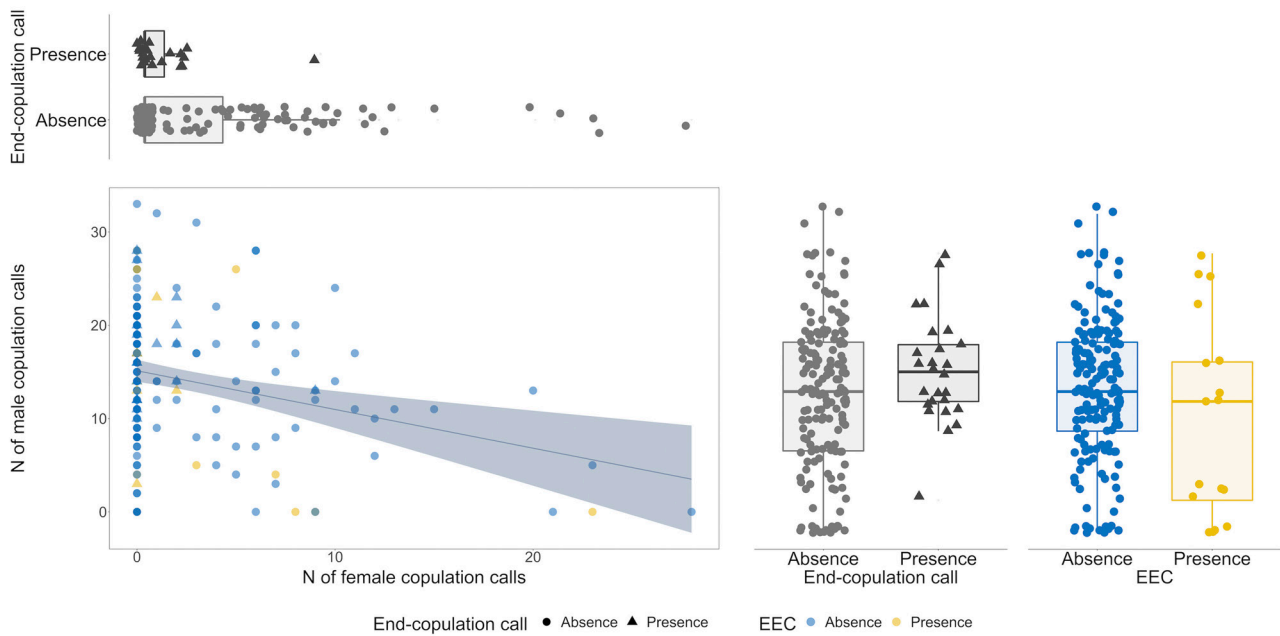


Figure 1. (A) Spectrogram of gelada copulation with a schematic representation of the fundamental frequency of female pre-copulation calls (pink), female copulation calls (orange), male copulation calls (blue), female end-copulation call (green), female post-copulation close call sequence (yellow), and male post-copulation close call sequence (violet). Red dashed lines indicate the copulatory event's start (S) and the end (E). The spectrogram was generated in Praat with the following parameters: window length: 0.05 s; dynamic range: 70 dB; frequency range: 0–8,000 Hz. (B) Flow diagram representing the sequential analysis output. *** $P = 0.001$; * $P < 0.05$. The dashed arrow indicates the nonsignificant transition between pre-copulation call and female copulation call (P -value=1).

1980; *M. talapoin*: Dixon et al. 1975; *Papio cynocephalus*: O'Connell and Cowlshaw 1994; *M. sylvanus*: Todt et al. 1995; African great apes: *P. troglodytes*: van Lawick-Goodall 1968; *P. paniscus*: Thompson-Handler et al. 1984; reviewed in Maestriperi and Roney 2005; Dixon 2015; *H. sapiens*: Prokop 2021; Brewer and Hendrie 2011). Hence, the gelada end-copulation call may be a marker of completed copulation. Therefore, both copula duration and end-copulation call may inform mating success. Here, we aim at exploring whether females emit pre-copulation calls to increase mating success probability (i.e., the occurrence of ejaculation). Specifically, we predicted that the longer the sequence of pre-copulation calls, the longer the copulation and the higher the probability of emission of the end-copulation call.

Prediction 2—In primates, both sexes can express sexual arousal by vocalizations (Dixon 2015), and female calls and gazing can influence the copulation outcome (Pfefferle et al. 2008a, 2008b; Palagi et al. 2020; Zanolini et al. 2021). In geladas, females tend to initiate sexual contact (Dunbar 1978) and use visual communication (EEC) to favor male's copulatory activity and possibly influence the mating outcome (Zanolini et al. 2021). In this perspective, we hypothesized that females emit calls, in conjunction with visual signals, to maintain the male motivation to complete the copula and increase the probability of inter-sexual audio-visual coordination. If so, we predicted that the multimodal combination of female vocalizations (copulation calls and end-copulation calls) and gazing (EEC; Zanolini et al. 2021), rather than unimodal signal transmission, can increase the number of copulation calls in males thus unveiling their sexual arousal.

Materials and Methods

Study subjects and site

We studied a herd of wild geladas (Caselli et al. 2021a; Gallo et al. 2021b) living on the Kundi highland (Amhara Region, Ethiopia, N9°40.402' E39°45.060'). We collected data in the field from January to May 2019 (4 observers) and from December 2019 to February 2020 (2 observers), every day from 09:30 to 17:00, for a total of 94 full days (658h). Individual recognition of animals was possible by using natural physical markers (size, permanent scars, alopecia, abnormal swelling of body parts, and shapes of the red chest area; as per Caselli et al., 2021a). By using the all-occurrences sampling method (Altmann 1974), the observers audio- and video-recorded the copulas performed by the visible animals. Audio and video recording started each time an adult female began to approach a leader male. This procedure allowed the observers to anticipate impending copulations and record them well before they began. Audio recordings were made via Zoom H5, OLYMPUS-LS100, and Marantz PMD661 solid-state digital audio recorders built up with Sennheiser ME64 and Sennheiser ME66 microphones with a sampling rate of 96kHz (16-bit depth). Videos were recorded via Panasonic HDV180 Full HD video cameras (optical zoom 50×; resolution 1,920 × 1,080 pixels; 2cs accuracy). A total of 443 mating events were recorded. After discarding from the analyses the copulations for which we did not have good quality audio and video recordings, we obtained a subset of 187 copulations performed by 56 dyads from 19 OMUs (19 alpha males and 55 adult females; mean copula per OMU: $\bar{x} \pm \text{standard deviation [SD]} = 9.84 \pm 9.56$; mean copula per dyad: $\bar{x} \pm \text{SD} = 3.33 \pm 2.99$).

Data processing

We edited segments containing the copulation events using Praat version 6.1.40 (Boersma and Weenink 2021) and saved the sounds corresponding to each mating event in a single audio file (Waveform Audio File format). Then, following the spectrograms published by Gustison et al. (2012) and Aich et al. (1990), 2 coders classified the vocalizations by visual inspection of the copula spectrograms. As vocalizations around copulas are usually emitted in sequences, we did not just record their occurrence for each copula, but we counted the number of female pre-copulation calls, female copulation calls, and male copulation calls. In addition, because the female end-copulation call was emitted as a single call, we recorded its presence/absence. We cross-checked the actual emission of the end-copulation call by verifying whether the occurrence of the call as indicated in the spectrogram coincided at video with the mouth opening of the copulating female (see [Supplementary Video S1](#); for the classification of presence/absence of the end-copulation call, the Cohen's κ between 2 blind coders was 0.90).

For each copula, we calculated the duration by matching the audio and the video. Each copulatory event started when the genital areas of the male and the female entered in contact and ended when one of them moved away. Because pre-copulation calls and post-copulation close calls were emitted when the genitals of the subject were not in contact, we excluded them when calculating the duration of each copula ([Figure 1A](#)). We assessed the identity of each OMU and mating dyad, and we recorded the presence/absence of EEC through the video analysis. Following Zanoli et al. (2021), we recorded the presence of EEC when the male directed its gaze toward the female by lowering its head and when the female directed its gaze toward the male by turning its head back. In this condition, the look-at was reciprocated, and males and females established EEC by looking into each other's eyes.

Acoustic and classification analyses

We performed an acoustic analysis to classify the different vocal types emitted by females around copulas. We extracted high-quality female vocalizations from our recordings, saving them into single files ($n = 1330$). We then labeled the calls according to 4 putative vocal types identified in previous studies (Aich et al. 1990; Gustison et al. 2012) and the end-copulation call identified here for the first time. In total, we obtained: pre-copulation calls ($n = 437$), female copulation calls ($n = 266$), female inhaled grunts ($n = 202$), female post-copulation calls ($n = 369$), and end-copulation calls ($n = 56$). It is worth noting that female inhaled grunts are vocalizations comprised in the post-copulation call sequences (Aich et al. 1990). However, only inhaled grunts have been defined so far among the vocalizations emitted by females in the post-copulation call sequences (Gustison et al. 2012). Thus, following the information present in the existing literature (Aich et al. 1990; Gustison et al. 2012), we separated inhaled grunts from post copulation calls, and used them as 2 different vocal types emitted after copulas. We extracted information from the calls by focusing on the fundamental frequency (f_0 = the lowest frequency produced by the vibration of the vocal folds, Torti et al. 2017) to quantify the relative variation between and within the putative call types. We processed the calls to extract the f_0 contour in Praat, discarding other individuals' vocalizations and the background noise. For each call, we extracted 18 temporal and spectral parameters from the f_0 contour ([Supplementary Table S2](#)).

By using the R-function “*princomp*” (R Core Team 2020), we implemented a principal component analysis (PCA) on the original set of acoustic measurements to reduce the number of variables before performing the classification analysis. Then, we used the principal components (PCs) showing eigenvalues >1 to classify vocalizations with a Random Forest (RF) algorithm (Breiman 2001). An RF is a robust supervised classifier that constructs many decision trees (weak learners) during the training phase (we used a ratio of 70:30 training/testing for our dataset). We built each tree using a bootstrapped version of the original dataset (i.e., replacing the original data and resampling). We obtained the first output using majority voting from all trees in the forest. Next, each tree cast a vote for the query sample (in this case, a female vocalization for which we would like to determine the membership in one of the 5 classes). By using the R-function “*randomForest*” (Liaw and Wiener 2002), we ran 2 RF procedures (one by testing the 30% of the dataset and one by testing the whole dataset as a testing set) by setting the number of trees to 300 and the minimum number of observations at each split to 2, as in standard classification settings (Liaw and Wiener 2002). Next, we estimated the classification error rate (i.e., out-of-bag [OOB]) from the training observations not used in each bootstrapped iteration (OOB data). We then aggregated call classification based on the OOB data and calculated an OOB error rate. Finally, we plotted OOB against the number of trees in the model to confirm that error had stabilized (Hastie et al. 2009).

Statistical analysis

By using the “*glmmTMB*” R-package (Brooks et al. 2017), we ran 4 general linear mixed models (GLMMs) by using our complete dataset ($n = 187$ copulas). We used Model 1 to investigate whether the number of female pre-copulation calls could influence the copula duration, a proxy of the probability of success of a copulatory event (i.e., ejaculation; Milton 1985; Dixson 2015). In this model, the logarithm of the copula duration was the response variable. We log-transformed the copula duration to reach a normal distribution after verifying the distribution and homogeneity of the residuals by looking at the Q-Q plot and plotting the residuals against the fitted values (Estienne et al. 2017). We set the number of female pre-copulation calls as fixed factor. We also included the number of female copulation calls and male copulation calls and the presence/absence of the end-copulation call as control fixed factors. In addition, the OMU ID and dyad ID were included as nested random factors. To investigate whether female pre-copulation calls could influence the copula outcome, we also used the end-copulation call as a marker of completed copulation (i.e., ejaculation), based on previous literature (Dixson 2015). To reach this goal, we ran Model 2, including the female end-copulation call (presence/absence) as response variable and the number of female pre-copulation calls as fixed factor. The OMU ID and dyad ID were the nested random factors.

Finally, to test our second prediction, we ran 2 Poisson GLMMs. In Model 3a, we included the number of copulation calls emitted by females as response variable; the number of pre-copulation calls and male copulation calls, the end-copulation call (Presence/Absence), and EEC (Presence/Absence) were the fixed factors. The OMU ID and dyad ID were the nested random factors. Model 3b included the number of copulation calls emitted by males as response variable. The number of pre-copulation calls and female copulation

calls, the end-copulation call (Presence/Absence), and EEC (Presence/Absence) were included as fixed factors. The OMU ID and dyad ID were the nested random factors.

For all models, we checked for the absence of the collinearity among predictors with the variance inflation factors (VIFs; Fox and Weisberg 2019) with the function *check_collinearity* (R-package “performance,” Lüdecke et al. 2020). No collinearity was found between fixed factors (range $VIF_{min} = 1.01$; $VIF_{max} = 1.33$). We tested the significance of the full model (Forstmeier and Schielzeth 2011) by comparing it against a null model comprising only the random factor using the Likelihood Ratio Test (ANOVA with argument test “Chisq”; Dobson 2002). Then, we calculated the *P*-values for the individual predictors based on likelihood ratio tests using the R-function ANOVA (R-package “car,” Fox and Weisberg 2019).

We performed a sequential analysis evaluating the temporal association of the visual and acoustic patterns expressed during copulas to explore the audio–visual coordination between mates. For each copula, we generated a behavioral string including each audio and visual pattern performed by mates. As a result, we obtained a list of strings representing the ordered concatenation of patterns as they occurred during copulations. We submitted the strings to the software Behatrix version 0.9.13 (Friard and Gamba 2021) to generate a flowchart diagram picturing the separate steps of copulation in sequential order, with the percentage values of occurrence. To test the significance of each transition, we ran a permutation test based on the observed behavioral transitions counts (*Run random permutation test* Behatrix function). We obtained *P*-values for each behavioral transition by permuting the strings 10,000 times (to obtain a 0.001 accuracy of the *P*-values).

Results

The female end-copulation call is a new vocal type

We performed a PCA to summarize the information contained in the original set of end-copulation calls 18 *f0*-related parameters. We found that the procedure summarized the data into 5 PCs showing eigenvalues >1, which accounted for 85% of the total variance (PC1 = 38%, PC2 = 17%, PC3 = 12%, PC4 = 10%, PC5 = 8%). To validate the presence of the end-copulation call as a different call

type, we used the 5 PCs scores to classify female vocal types through an RF. We obtained a plot of OOB error against the number of trees showing that the error stabilized when the model used 300 or more trees (see Supplementary Figure S3). The forest decision trees classified female vocalizations with an OOB error rate of 38.71%. The confusion matrix in Table 1 shows the number of misclassified calls using the training dataset in the RF model. The model typically well classified end-copulation calls (error rate 2.7%), although other female vocalizations had relatively high classification error rates. The confusion matrix shows that the highest misclassification rate was for inhaled grunt (62.2%) and copulation calls (44.1%). These rates were higher than for post-copulation calls (36.3%) and pre-copulation calls (30.4%), with most confusion occurring between inhaled grunts and post-copulation calls.

Overall, RF followed the rule of thumb of 25% of correct classification, and it correctly classified 97.3% of end-copulation calls. We validated the predictions of the RF model by using 30% of the original dataset, which had not been used to train the model, and the entire dataset. Table 2 and 3 show the prediction matrices and prediction error output from the RF model obtained by using the validation dataset and the entire dataset. The classifications of end-copulation calls performed better for the validation data than for the training data with 100% correct classification in both validations.

Females signal their motivation to initiate a successful copulation

Concerning the strategical use of female pre-copulation calls to initiate copulations, we found a significant difference between Model 1 and the null model ($df=8$, $X^2=26.119$, $P < 0.001$; Table 4). As the number of female pre-copulation calls increased, the copula was more likely to last longer (Figure 2), whereas none of the other vocalizations had a significant effect.

Model 2, built to investigate whether the number of pre-copulation calls affected the presence of the end-copulation call, significantly differed from the null model ($df = 4$, $X^2 = 13.279$, $P < 0.001$; Table 5). We found that an increased number of female pre-copulation calls was associated with an increased likelihood of the presence of end-copulation calls (Figure 2).

Table 1. Confusion matrix and classification error output from the RF model used to classify female vocalizations using the training dataset

	Predicted					Classification error (%)
	PRECALL	COPCALL	ENDCALL	POSTCALL	INGR	
Observed						
PRECALL	215	41	0	44	9	30.4
COPCALL	62	104	0	16	4	44.1
ENDCALL	0	0	35	1	0	2.8
POSTCALL	52	16	1	160	22	36.3
INGR	29	12	0	51	56	62.2

PRECALL, pre-copulation calls; COPCALL, female copulation calls; ENDCALL, end-copulation calls; POSTCALL, female post-copulation calls; INGR, female inhaled grunts. Bold numbers show the number of calls correctly classified. Nonbold numbers represent the misclassified calls. The classification error shows the total percentage of vocalizations that were misclassified for each call type.

Table 2. Prediction matrix and prediction error output from the RF model using the validation dataset. The prediction matrix shows the number of correctly classified calls (bold numbers) and misclassified (nonbold numbers). The prediction error shows the total percentage of vocalizations that were misclassified for each call type.

	PREDICTED					Prediction error (%)
	PRECALL	COPCALL	ENDCALL	POSTCALL	INGR	
Observed						
PRECALL	84	19	0	20	5	0.34
COPCALL	34	38	0	8	0	0.53
ENDCALL	0	0	20	0	0	0
POSTCALL	22	10	0	71	15	0.4
INGR	11	4	0	20	19	0.34

Table 3. Prediction matrix and prediction error output from the RF model using the whole dataset

	PREDICTED					Prediction error (%)
	PRECALL	COPCALL	ENDCALL	POSTCALL	INGR	
OBSERVED						
PRECALL	391	20	0	20	6	0.11
COPCALL	34	225	0	7	0	0.15
ENDCALL	0	0	56	0	0	0
POSTCALL	22	9	0	322	16	0.13
INGR	10	3	0	22	167	0.17

The prediction matrix shows the number of correctly classified calls (bold numbers) and misclassified (nonbold numbers). The prediction error shows the total percentage of vocalizations that were misclassified for each call type.

Table 4. Results of Model 1 showing the effect of female pre-copulation calls, male and female copulation calls, and female end-copulation calls on the copula duration

Fixed effect	Estimate	SE	df	z value	P-value
(Intercept)	2.090	0.064	a	32.650	a
No. of pre-copulation calls	0.010	0.002	1	4.860	0.000
No. of male copulation calls	0.003	0.003	1	0.800	0.425
No. of female copulation calls	0.006	0.005	1	1.040	0.298
End-copulation call (Presence) ^{b,c}	0.027	0.071	1	0.380	0.705

Significant *P*-values are shown in bold.

^aNot shown as not having a meaningful interpretation.

^bEstimate ± SE refers to the response difference between the reported level of this categorical predictor and the reference category of the same predictor.

^cThis predictor was dummy coded, with the “End-copulation call (Absence)” being the reference category.

Females emit signals to coordinate with males during the copulation

We used Model 3a and Model 3b to investigate if females emit vocalizations to maintain the male motivation to complete the copula. In both cases the full model differed from the respective null model ($df = 7$, $X^2 = 71.794$, $P < 0.001$; Table 6, female copulation calls; $df = 7$, $X^2 = 65.089$, $P < 0.001$; Table 6, males copulation calls). We found that signals are not randomly distributed. There is a female sequential organization of vocal emission and inter-sex coordination between partners. As the number of female copulation calls increased, the number of male copulation calls decreased and vice versa (Figure 3).

Furthermore, the presence of the end-copulation calls negatively affected the number of female copulation calls, whereas it positively affected the number of male copulation calls (Figure 3). In addition, the presence of EEC had a positive effect on the number of male copulation calls, whereas it had no significant effect on the number of female copulation calls (Figure 3).

The sequential analysis on visual and acoustic signals revealed that the most occurring concatenation of signals emitted by mates during a copula was (Figure 1B): female pre-copulation calls → male copulation calls → female copulation calls → EEC → end-copulation call ($P < 0.001$ for all the transitions). In addition, when EEC was present, it was

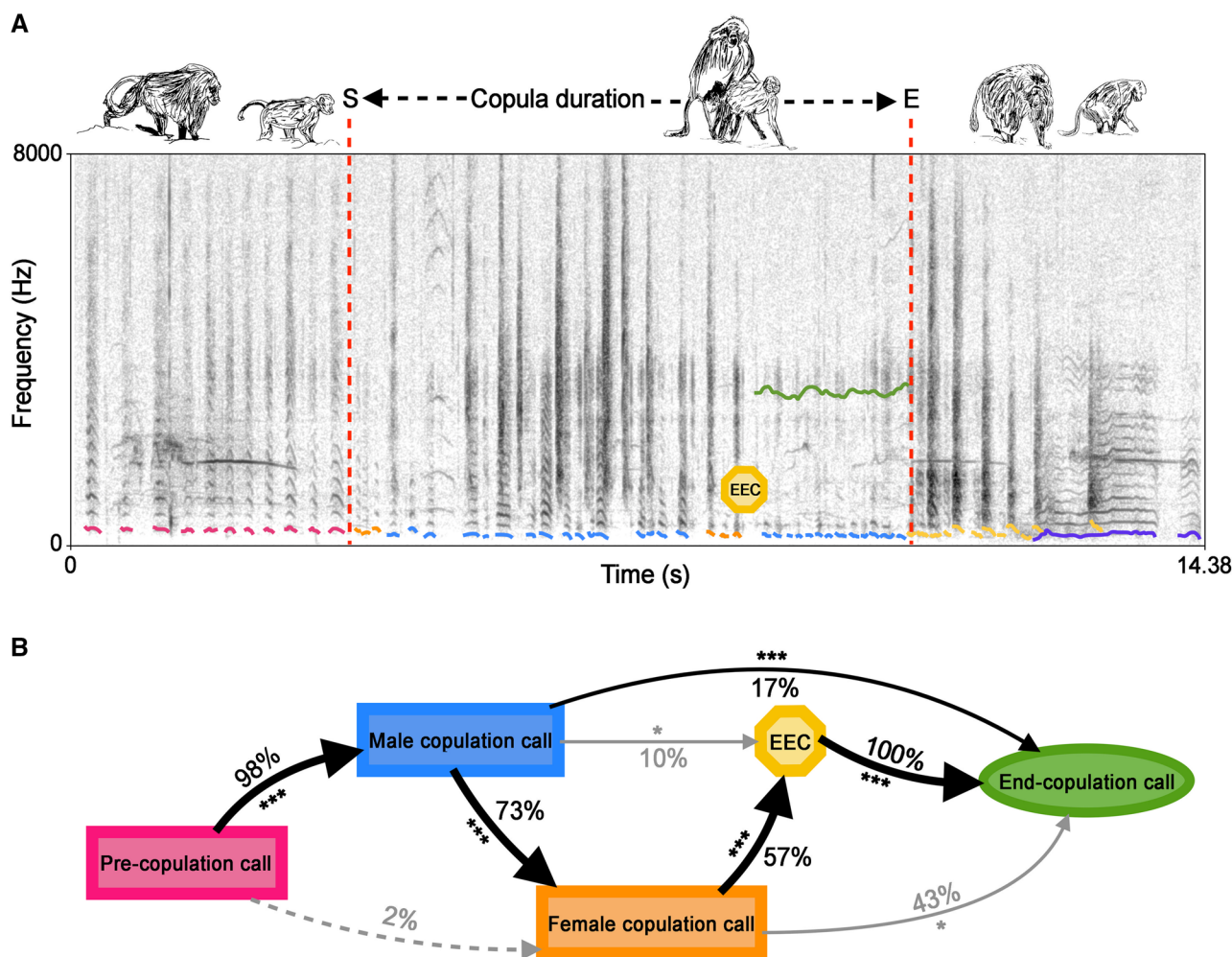


Figure 2. Scatter plot showing the relationship between the Logarithm of the Copula Duration and the Number of pre-copulation calls. Dots' shape represents the presence (triangles) and the absence (circles) of the end-copulation call. The blue line and the light blue area represent the linear regression and the confidence interval. On the upper x-axis, a density plot shows the Number of pre-copulation calls in presence (yellow density curve) and absence (blue density curve) of the end-copulation call. Individual observations are presented under the density curves with pipe symbols.

Table 5. Results of Model 2 showing the effect of female pre-copulation calls on the occurrence of the female end-copulation call

Fixed effect	Estimate	SE	df	z value	P-value
(Intercept)	-2.606	0.339	^a	-7.684	^a
No. of pre-copulation calls	0.059	0.016	1	3.578	0.000

Significant *P*-values are shown in bold.

^aNot shown as not having a meaningful interpretation.

always followed by the end-copulation call ($n = 17$; percentage of occurrence = 100%; $P < 0.001$). A flow diagram with all the possible behavioral transitions is shown in Figure 1B.

Discussion

In this study, we investigated whether gelada females emit vocalizations associated with mating as the mere result of an arousal state or tactically to manage mating by improving inter-sexual communication and possibly copulation success (i.e., ejaculation). Before and during copulations, females produce 3 different vocalizations. In addition to the well-described pre-copulation and copulation calls (Aich et al. 1990;

Gustison et al. 2012), we identified and quantitatively classified a call emitted during the final stage of the copulation, the “end-copulation call” (Figure 1A; Tables 1–3; Supplementary Video S1). Gelada pre-copulation calls are derived vocalizations that females usually emit as a proceptive display to attract males' attention (Mori and Dunbar 1985; Gustison et al. 2012; Roberts et al. 2017). Despite the debate on the emission of pre-copulation calls in the different reproductive stages (i.e., exclusively during estrus: Moos-Heilen and Sossinka 1990; Dunbar 2014; not only during estrus period but in highest proportion during cycling: Roberts et al. 2017), there is a general agreement on considering such calls as reliable indicators of estrus (Mori and Dunbar 1985; Moos-Heilen

Table 6. Results of Model 3a and Model 3b showing the effect of female pre-copulation calls, male and female copulation calls, EEC, and female end-copulation calls on female copulation calls and male copulation calls, respectively

Fixed effects	Estimate	SE	df	z value	P-value
Female copulation calls					
(Intercept)	0.642	0.329	a	1.954	a
No. of pre-copulation calls	0.002	0.006	1	0.355	0.722
No. of male copulation calls	-0.060	0.009	1	-6.984	0.000
EEC (presence) ^{b,c}	-0.095	0.193	1	-0.495	0.621
End-copulation call (presence) ^{b,c}	-0.704	0.256	1	-2.755	0.006
Male copulation calls					
(Intercept)	2.553	0.106	a	24.057	a
No. of pre-copulation calls	0.003	0.002	1	1.338	0.181
No. of female copulation calls	-0.035	0.006	1	-5.813	0.000
EEC (presence) ^{b,c}	-0.351	0.091	1	-3.845	0.000
End-copulation call (presence) ^{b,c}	0.195	0.069	1	2.809	0.005

Significant *P*-values are shown in bold.

^aNot shown as not having a meaningful interpretation.

^bEstimate ± SE refers to the response difference between the reported level of this categorical predictor and the reference category of the same predictor.

^cThese predictors were dummy coded, with the “EEC (Absence)” and “End-copulation call (Absence)” being the reference categories.

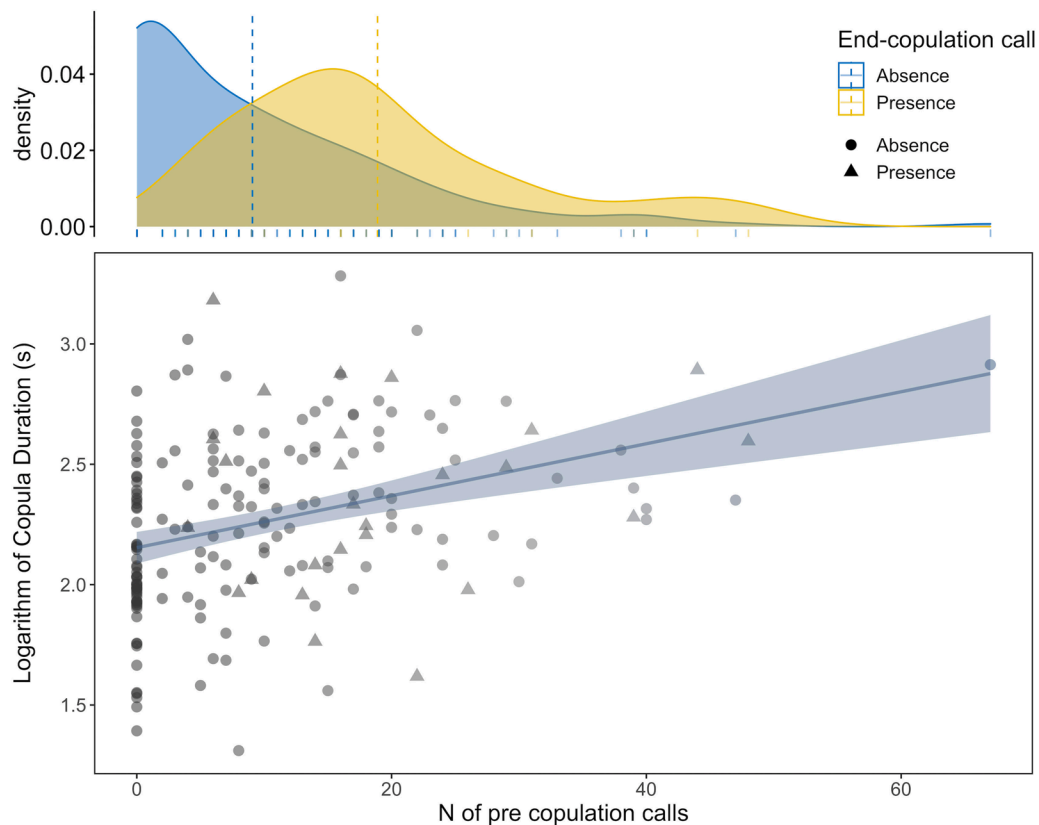


Figure 3. Scatter plot showing the relationship between the number of male copulation calls and female copulation calls. The blue line and the light blue area represent the linear regression and the confidence interval. Dots' shape represents the presence (triangles) and the absence (circles) of the end-copulation call. Dots' color represents the presence (yellow) and the absence (blue) of EEC. On the upper x-axis, a box plot shows the number of female copulation calls and absence (gray box) and presence (black box) of the end-copulation call. On the right y-axis, 2 box plots show the number of male copulation calls in absence (gray box) and presence (black box) of the end-copulation call, and in absence (blue box) and presence (yellow box) of EEC.

and Sossinka 1990; Roberts et al. 2017). By analyzing the number of pre-copulation calls emitted in a sequence, we found that longer sequences of such calls were followed by longer copulations (Figure 2) that suggests the higher the

female motivation to engage in sexual contact, the higher the likelihood of successful copulation. In addition, we found that longer sequences of pre-copulation calls were also followed by a higher probability of emission of the end-copulation call

(Figure 2). As in several primate species, females can vocalize during male ejaculation (e.g., van Lawick-Goodall 1968; Dixon et al. 1975; Deputte and Goustard, 1980; Thompson-Handler et al. 1984; O'Connell and Cowlshaw 1994; Todt et al. 1995; reviewed in Maestriperi and Roney 2005; Brewer and Hendrie 2011; Dixon 2015; Prokop 2021), the timing of end-copulation call recorded in our females suggests that such call could be emitted in conjunction with ejaculation. These results confirm the proceptive function of pre-copulation calls (Mori and Dunbar 1985; Moos-Heilen and Sossinka 1990; Roberts et al. 2017) and unveil a more specific role of these calls that is prolonging the copula duration, thus ensuring its successful completion (Prediction 1 supported). The social organization of the species can explain this peculiar behavior (Snyder-Mackler et al. 2012). Being the gelada social system based on reproductive OMUs, the male access to reproductive females is guaranteed as soon as it has control over the group. Thus, gelada males do not need to upset the basic pattern of their social interactions to ensure access to a preferred sexual partner. Females, on the other hand, must compete to be such a partner (Dunbar and Dunbar 1975). Although further studies are needed to verify the exact matching between ejaculation and female end-copulation call, the discovery of this new vocalization not only expands the vocal repertoire of geladas but also allows understanding that communication during mating in this species is more sophisticated than previously thought.

Furthermore, our findings show that females can fine-tune the emission of copulation calls and end-copulation calls, possibly to maintain male arousal and motivation to complete the copula (Prediction 2 supported). When females decreased copulation calls and increased the emission of end-copulation call, male copulation calls, indicating arousal (Dixon 2015), increased. In addition, EEC, mainly initiated by females (Zanoli et al. 2021), further contributed to increase the number of copulation calls emitted by the male (Figure 3). These results corroborate the well-known crucial role of EEC in the regulation of sexual contact (Dixon, 2015; Zanoli et al. 2021) and suggest that the coordinated use of female vocal and visual signals can further modulate male sexual arousal, expressed through vocalizations (Dixon 2015). Consistently, the sequential analysis on the vocal and visual signals showed that the concatenation of displays with the highest likelihood of occurrence includes the entire visual and acoustic repertoire and shows the most complex degree of coordination between partners (Figure 1B). In particular, the pre-copulation call attracts the attention of the male, which starts emitting the copulation calls as the pelvic thrusting begins. Subsequently, the female maintains the male sexual arousal by emitting copulation calls, engaging in EEC and, finally, uttering the end-copulation call to possibly signal the positive conclusion of the copula (Supplementary Video S1).

These findings are especially important considering the social structure of geladas. By living in OMUs, leader males do not need to mate as frequently as primates living in multi-male groups where the male intra-sexual competition is high. Even if extra group paternity may occur in highly dense gelada populations (Miller et al. 2021), usually, a male has exclusive sexual access to the females of its group, with a low risk of sperm competition from other males (Dunbar 2014). As a result, contrary to other Papionini species, gelada females actively solicit sexual interactions (Dunbar 1978) and strengthen the social bond by grooming the male after

mating (Zanoli et al. 2021). Our study endorses the role of female geladas in managing the occurrence and the outcome of copulations and provides support for the hypothesis that vocalizations emitted during mating are signals specifically intended for the partner (Pfefferle 2016). By considering the social organization of geladas and the timing of emission of vocalizations around mating we found that female call types are not the simple automatic expression of arousal. Female geladas possess the ability to well integrate acoustic and visual communication before and during mating in a flexible way to improve inter-sexual coordination.

Data Accessibility Statement

Data are available at <https://doi.org/10.5281/zenodo.5483682>.

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Authors' Contributions

All authors conceived and designed the paper; A.Z. made the data collection; I.N. and E.P. carried the field training for behavioral data collection; A.Z., M.G., and A.L. embedded the methodology for bioacoustics data collection and performed the acoustics and statistical analysis; A.Z. and E.P. wrote the draft and all authors improved the text. All authors revised and approved the final manuscript.

Conflicts of Interest Statement

The authors declare that they have no conflict of interest.

Supplementary Material

Supplementary material can be found at <https://academic.oup.com/cz>.

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