Standard Scientific Research and Essays Vol 8(11): 344-369, November 2020 (ISSN: 2310-7502)
http://www.standardresearchjournals.org/journals/SSRE

Research Article

Vocal, gestural repertoire and multimodal communication in wild Barbary macaques

***Faical Boutlib[1, 2], Hichame Dahdouh[2] and Varvara Vladimirova[2]**

[1]Department of Mammology and Primatology, Centre National Scientific Institute, Rabat, Morocco
[2]Moroccan Association for Protection of Heritage and Barbary Macaques, Fez, Morocco

*Corresponding Author E-mail: faysalbo@gmail.com, telephone: +212- 771574255

Accepted 10 May, 2020

Abstract

Multimodal communication, as well as vocal and gestural repertoire were investigated in a group of wild Barbary macaques (*Macaca sylvanus*) living in the Middle Atlas mountains of Morocco. Thirty minutes continuous focal animal samples were collected daily for five months consisting of the compilation of all gestures and facial expressions, occurrences and the recording of all vocalisations. Spectrograms were produced to clarify variations in the different call types and contexts for each call type were determined. The analyses revealed that there is a peak of calls' utterance in infancy while adults communicate more with gestural and facial signals. Infants are able to utter all call types but tend to combine it with a higher and more diversified rate than adults do. Moreover, analyses showed that some calls are sex-specific. Regarding multimodal signals, they were formed for the most part by facial expressions and communicated mostly during agonistic interactions. The discovery of new gestures and the development of infants' vocal repertoire are discussed. The results suggest that wild populations give a more and new accurate picture of the species' natural repertoire.

Keywords: Macaques, Multimodal communication, Gesture and Facial expression, Vocal repertoire.

INTRODUCTION

Research on non-human primate communication allows a better understanding of the emergence of human language as its evolution is one of the hardest mystery in science. Knowing the function of vocalisations, gestures and facial expressions are necessary to draw insights on which modality is the precursor of human language (Liebal et al., 2013). Chimpanzees, our closest relatives, are the most studied species for this issue although monkey communication systems can highlight language properties that evolved earlier during phylogeny. Barbary macaques are the least studied species in the genus *Macaca* that originated in Africa although all current sister groups are Asian. I am not aware of any previous literature on multimodal communication in Barbary macaques and before introducing the topic, I will highlight previous studies on gestural communication and I will then discuss findingsof their vocalisations.

Gestural communication

In the genus *Macaca*, gestures play a significant role in communication. They are used in many different contexts, for example, to engage a grooming interaction, to play, while mating or to get agonistic support (Maestripieri,1997). Throughout the years, the definition of gesture has been debated and authors do not agree of a universal one. For this master thesis, I will use the following definition: a gesture is "a behaviour that, unlike an action, is motorically ineffective, is produced in the presence of an audience and is tailored to the attention of the audience" (Liebal et al., 2013, p.78). The differentiation between a gesture that has a communicative intention and an action that has a non-communicative goal can be tricky, for example, when an individual wipes its nose (Liebal et al., 2013). A gesture can be audible as the chest beat of gorillas or tactile as when an individual slaps another (Liebal et al., 2013). Some authors, such as Hesler and Fischer (2007),consider facial expressions and postures as gestures, while Genty et al. (2009) do not.

Two types of mechanism affect the expression of a gesture: proximate and developmental (Liebal et al., 2013). Only a few studies have considered gestures present from birth (Liebal et al., 2013) and onto genetical development of gestural repertoire in Barbary macaques is not well thorough. Hesler and Fischer (2007) summarised it in their study on captive Barbary macaques and concluded that gestural repertoire expands with age. While infants are able to perform five gestures, adults can achieve 31. Interestingly, this is different for great apes, such as chimpanzees, where infants are able to perform more gestures than adults (Tomasello et al., 1997). Infants Barbary macaque are able to execute gestures, such as touch genitalia, touch body, head-flag, teeth-chatter and relaxed open mouth face (Hesler and Fischer, 2007). Every species has its own gestural repertoire, though apes and monkeys share some, such as embrace, grab, touch, bite, and slap or pull (Hesler and Fischer, 2007). Hesler and Fischer's (2007) research is the only one to my knowledge about the entire gestural repertoire of Barbary macaques. Other studies have focused on a specific gesture as Mehlman (1996) on branch shaking display or Faraut, Northwood and Majolo(2015)on non-reproductive mounts. Gestural repertoires of apes and monkeys are quite flexible and Hesler and Fischer (2007) emphasised flexibility in Barbary macaques' use of gestures. Flexibility means that the same gesture has several meanings or that different gestures are performed to reach the same goal. For instance, bared-teeth can mean a submissive or affiliative behaviour and open mouth, ground slap or stare are shown for a threat. Despite a thorough knowledge on gestures' function, little is known about what a recipient understands when a gesture is expressed by a conspecific (Liebal et al., 2013). To answer this issue, it is essential to have a complete knowledge of the gestural repertoire of a species.

Vocal communication

Vocal communication of Barbary macaques has been studied wider compared to their gestural repertoire. However, only a score of studies was carried out and all of them on captive populations on tourist sites. The Barbary macaques' vocal repertoire is graded and discrete (Hammerschmidt and Fischer, 1998b; Hammerschmidt and Todt, 1995).Their vocalisations mainly consist of noisy and modulated screams, pants, grunts, geckers and girneys divided into six call types (Fischer and Hammerschmidt, 2002). These call types are not context specific and individuals from all age-classes are able to produce them (Hammerschmidt and Fischer, 1998b). In Barbary macaques, research has focused on copulation calls, alarm calls, playing vocalisation and dusk chorus. The structure of their vocalisations is influenced by age, body weight and the sex. Despite diverse research on their calls, it is not clear if the classification of the vocal repertoire by Fischer and Hammerschmidt (2002) is perceptually salient to the individuals (Hauser, 1996).To extend research on this subject and complementary issues, it is crucial to identify the function of vocalisations and their meaning.

Multimodality

Humans talk in a multimodal fashion incorporating vocal, gestural and facial signals in their communication and the suggestion that animals communicate by integrating signals from different modalities was expressed by Darwin in 1872 (Higham and Hebets, 2013; Semple and Higham, 2013). Insects as honeybees, spiders, frogs, lizards, fowls, pigeons, squirrels and primates commonly use multimodal signals (Higham and Hebets, 2013; Liebal et al., 2013). A signal is multicomponent when it contains several stimuli of one sensory modality and multimodal when it contains several stimuli from different sensory modalities (Rowe, 1999). A multimodal signal is considered as redundant if the different components have similar connotations and as no redundant if the components have diverse significations (Liebal et al., 2013; Partan and Marler, 1999). Multimodal communication has its benefits for both the signaller and the recipient of a signal. Considering that multimodal communication carries a message through several sensory systems at the same time, it can be hypothesised that it increases the amount of information perceived (available) by the receiver (Liebal et al., 2013). Furthermore, the psychological research identified that multimodal communication allows better detectability, a faster answer from the receiver compared to unimodal signals, improves memorability and decreases ambiguity in signal comprehension (Liebal et al., 2013). Albeit multimodal communication brings benefits to the receiver and the signaller, it can lead to some drawbacks as well (Liebal et al., 2013). For instance, a multimodal message may further expose individuals to predators and the signaller and the recipient may spend more energy (Partan & Marler, 2005)to elicit and to process a multimodal rather than a unimodal signal. Moreover, multimodal signals are suitable for short-distance rather than long-distance communication (Partan and Marler, 2005). This means that they are more appropriate for intra-group communication (Partan and Marler, 2005).

A progress occurred on multimodal communication research in the years 2000 although there is still paucity in the number of investigations and the range of species studied. Indeed, the studies on multimodal communication in nonhuman primates are marginalised with only 5% that examined multimodal communication in an integrated fashion(Slocombe et al., 2011). Research on multimodal communication can be achieved at two levels, through the investigation of brain areas involved when a multicomponent signal is expressed and through the observation of specie's behaviour.

On a neural level, Arbib et al. (2008)emphasise that "aphasia of signed and spoken languages may result from lesions to Broca's area" (Pp.1053). This makes clear that Broca's area should be associated with multimodal language generation instead of vocal communication solely (Arbib et al., 2008). In chimpanzees, Taglialatela et al. (2011) showed that Broca's area homologue is involved in gestural and vocal signals. In Broca's area, mirror neurons exhibit activity both when an individual (human or animal) performs an action and when it observes another individual (especially of its kind) perform the same action or even when he imagines such action. This discovery might be strategic to understand auditory actions and language evolution(Kohler et al., 2002; Gazzola et al., 2006) and revealed a large intricacy of communication (Arbib et al., 2008). Since neural methods are invasive, the behavioural methods are a requirement to study wild animals.

On a behavioural level, an experiment by Ghazanfar & Logothetis(2003) showed that rhesus monkeys (*Macaca mulatta*) are able to match the vocalisation to the correct facial expression. This demonstrates that it is important to consider communication as its entirety involving all modalities to understand accurately multicomponent signals. Furthermore, these studies elicit a shift of interpretation from a unimodal to a multimodal origin of language, commonly gestural coupled to vocal, but the combination could also include facial communication (Slocombe et al., 2011). Indeed, language may have developed by means of «an integrated combination" of the three (Slocombe et al., 2011, Pp.923). Other studies usually report an isolated behaviour, such as multicomponent lip-smacking in crested macaques (*Macaca nigra*)(Micheletta et al., 2013) or examine the frequency and the nature of multimodal signals as in captive chimpanzees (Taglialatela et al., 2015). Primate communication is often multimodal and unimodal research tells only part of the answer (Slocombe et al., 2011) so it is necessary to expand research.

METHODS

Study site and subjects

This study was conducted on a wild group of Barbary macaques living in a deciduous forest of cedars (*Cedrus atlantica*) and holm oaks (*Quercus ilex*).The study site (33°24'N 005°09'W) is situated in Ifrane National Park, in the Middle Atlas mountains of Morocco near the city of Azrou, at an altitude between 1700 and 2100 meters above sea level. The home range for the group was much larger than what has been mentioned in the literature, around 2000 hectares (ha) while it is usually about 18.4ha (Fooden, 2007). The group consisted of Fifty one (51) individuals at the end of the study: seven (7) adult males, four (4) adult females, six (6) sub adult males, twelve (12) sub adult females, fourteen (14) juveniles and eight (8) infants when I left it. When I finished data collection at the end of March 2016, two (2) females gave birth, one (1) baby was born and one was stillbirth and there are currently fourteen (14) babies. Individuals were divided into fourage-classes according to their morphology: infants, juveniles, sub adults and adults (**Error! Reference source not found.**). I refer to babies as individuals who were born in March 2016. Infants were distinguished from juveniles by size and juveniles were distinguished from sub adults by size and hindquarters. Seasons were divided as follows: mating season from September to December identified by female copulation calls, mating-birth season from January to March when female copulation calls finished, birth season from March to July when the first infant born and birth-mating season from July to September after the last baby is born. Information on kinship was not available for the study group.

Table 1. The composition of the study group

Age-classes	Sex	Age (years)	N
Infants		<1	8
Juveniles		1 to <4	14
Sub adults	Females	4 to <5	12
	Males	4 to <7	6
Adults	Females	5	4
	Males	7	7

Habituation and identification

The research focused on a wild group not well habituated to humans. The habituation process I conducted with a Ph.D. student lasted several months from July 2015 until October 2016, five days a week. At the end of the study, not all the individuals were fully habituated, especially the adult females, but this did not affect data collection. Habituation consisted of approaching the group as close as possible and when the monkeys started to scream, the Ph.D. student and I stopped moving immediately to not disrupt their welfare. We were fully visible so the monkeys were never surprised by our presence and I took the habit to clear my throat so they would learn to identify and get used to us. I identified adult males, adult females, and sub adult males only with the help of binoculars and a video camera. For the sub adult females, it was not possible because of their large number and physical similarity. Because dominance rank is not well established in infants and juveniles and because they are difficult to follow, I did not identify them either. Natural marking such as scars, moles and fur or skin color pattern facilitated the recognition of identified individuals.

Data collection

Data were collected daily between 08:00 and 17:00 in the winter and between 06:00 and 21:00 in the summer, ideally five (5) days a week. Data were collected during five (5) months from November 8th, 2015 until March 31st, 2016, using an iPod PCs loaded with Pendragon Forms Version 5.1 (Pendragon Software Corporation, Chicago, IL, U.S.A.). The study was entirely observational and my data collection was not invasive. Thirty (30) minutes continuous focal animal samples(Altmann, 1974) were collected several times a day on a daily basis following three observation blocks: between 6.00am and 10.15am, between 10.16am and 13.30pm and between 13.31pm to 16.45pm(Table 1). Since the group's activity varied throughout the day with resting periods, it avoids bias in communicative rates. Because of the hilly terrain and forest density, I had to stop occasionally a focal sampling because I could not follow the individual. If this happened for less than 5 minutes, I continued the focal until it reached 30 minutes in total, which I added to the first observation block. If the individual was out of sight for more than 5 minutes, I discarded the sample. I collected all signals performed by the focal individual, even those not targeted, and only considered a recipient if the focal animal looked to a co specific. By signal, I mean "the entire set of communicative features ("components") of an animal's behaviour, [be they gestures, vocalisations or facial expressions] that occur [alone or] simultaneously" (Partan and Marler, 2005, Pp.232)followed by a pause of >1s. In every focal, all occurrences of gestures given and received were recorded (for a complete description of the gestural repertoire of Barbary macaques, see the ethogram p.viin the appendices). To avoid confusion with previous studies, I considered facial expressions as gestures in this research to be able to compare my results with prior outcomes. I considered tactile signals (Partan and Marler, 2005) as touch body, pull, push and so on as manual gestures. Regarding multimodality, I classified a signal as such only if it consisted of at least two components from different modalities (gestural, vocal) expressed at the same time. I only considered the occurrence of simultaneous combinations of signals and not the production of signals into sequences. When a focal animal expressed a signal, the context associated was the one occurring during the communicative event or, failing that, immediately preceding it.

Table 1. Observation blocks respected for the data collection, number and duration in hours for the focal scans

Age class	Sex	Individual identity	Observation blocks (number of 30 min focals)			Total (in hours)
			6.00 – 10.15	10.16 – 13.30	13.31 – 16.45	
Adults	Males	DI	2	2	2	3
		MA	2	2	2	3
		OL	2	2	2	3
		PA	2	2	2	3
		KE	2	2	2	3
		CY	2	2	2	3
		NO	2	2	2	3
	Females	AD	2	2	2	3
		FA	2	2	2	3
		BI	2	2	2	3
		YU	2	2	2	3
Sub adults	Males	SA	2	2	2	3
		DA	2	2	2	3
		JA	2	2	2	3
		GA	2	2	2	3
		UC	2	2	2	3
		HU	2	2	2	3
	Females	-	8	8	6	11
Juveniles	Males	-	1	1	1	1.5
	Females	-	1	2	1	2
Infants	-	-	-	-	-	-
Total focals' number			44	45	42	65.5

Dominance hierarchy

Dominance rank is important when studying monkey behaviour (Baker et al., 2015). In macaques societies, the approach-avoidance system ("approach-retreat interactions", Maestripieri, 2005) allows determining individual's rank.

In my study group, I inferred the hierarchy by observing dyadic agonistic interactions between individuals *ad libitum* (Altmann, 1974; Deag, 1977). I recorded agonistic behaviours (aggression: open mouth display, lunge, ground slap, stare, slap, bite; submission: present, bared teeth display, teeth-chatter) including combinations of two or more components aforementioned. An interaction was taking into account only if the result was clear-cut. Usually, kinship knowledge helps to establish a hierarchy (Bernstein, 1976) but it was not known for this group.

Definitions, acoustic

The definition I use for multimodal communication is based on the channel (physical property) exploited by the signaller to convey a signal (Higham and Hebets, 2013) because my study was based on signallers' signal transmission. I did not investigate olfactory communication because its occurrence was too limited. Besides, I did not include visual signals as swellings or colors in my study because it is too challenging to construe outcomes on recipients and signallers. I considered only free multimodal signals where every component is unimodal (independent, isolated) contrary to fixed multimodal signals that cannot be divided such as lips movements (Higham and Hebets, 2013).I considered multimodal the association between scream face and fear scream only if the scream face was unvocalised before or after the vocalisations was uttered. If the individual opened his mouth just to utter the fear scream, I did not consider it as multimodal.

In addition to multimodal communication, this study construes call variations that are discussed scantily in previous research. All vocalisations uttered and received by the focal animal were recorded with a Marantz PMD661 and a Sennheiser microphone (ME 88). By vocalisations, I mean calls "that form a temporally coherent acoustic pattern" (Todt et al., 1995, Pp.145). To interpret vocalisations I recorded, I realised my spectrograms with Raven Pro 1.5 Beta Version and then I did an auditory-visual assignment with the help of spectrograms from previous work on Barbary macaques completed by Fischer and Hammerschmidt (2002).For sake of clarity, I present my results in a fashion similar to Fischer and Hammerschmidt (2002) otherwise, it would be confusing. I consider a call type as "a cluster of calls that are identical or at least similar in their acoustic shape (Todt et al., 1995, p.145). Vocalisations can be combined in series, where two or more calls are uttered with a pause inferior to 1 second between each vocalisation.

Because of background noise, I discarded vocalisations (N=24) of the study for which the type could not be specified. Acoustic disturbances originated from logging trucks and woodcutters talking, shepherds with sheep and dogs barking, birds' song, planes or helicopters passing by, the wind, when I can hear my footsteps in the snow, when the snowmelts and falls from the trees and when several animals vocalised at the same time. Besides, during data collection, I could not record all types of vocalisations. In the first place, I could not gather material on females giving birth because it happens during the night when I cannot be present on the field. Hammerschmidt and Ansorge (1989) managed to in captivity. Moreover, I could not record dusk chorus since I had to leave the field site before sunset when individuals are not yet in the trees to sleep. I do not have any playing vocalisationin my recordings because I could not get really close to individuals due to their wildness and as playing vocalisations are of low frequency, I was often too far with the microphone (around 10 meters away minimum from the individual). Furthermore, considering that gestures and vocalisations come together quickly during a playing interaction, it was usually impossible to attribute the vocalisation to the signaller.

Statistic analysis

The data has been analysed by IBM SPSS 21.For check whether the various categories of a factor differ significantly or not, we evaluate effects of age-sex classes (adult males, adult females, sub adult males, sub adult females) on mean gestures' rate per hour via a Linear Mixed Model analysis (LMM). Mean gestures' rate per hour was the dependent variable. Age- sex classes were entered as fixed variables. Individual Identity was entered as random factors (nominal variables). We tested each combination involving the variables of interest .spanning from a single-variable model to a model including all the fixed factors (full model).

For the vocalisations, I used a Linear Mixed Model analysis (LMM).For investigate if age-classes have significant effects on mean calls' rate per, I chose mean calls' rate per the dependent variable. Age- sex classes were entered as fixed variables. Individual Identity was entered as random factors (nominal variables). Then, I used to determine the significant differences between the groups' means (age-classes) via Linear Mixed Model analysis (LMM). The significance level was set at 0.05 for all tests. The box plots and graphs were carried out with SPSS Statistics 21 as well.

$$Y_{ij} = \underbrace{x_{ij}{}^t\beta}_{\text{fixed}} + \underbrace{u_{ij}{}^t\gamma_i}_{\text{random}} + \underbrace{\epsilon_{ij}}_{\text{random}}$$

$$i = 1, \ldots, m; j = 1, \ldots, n_i$$

With: Y_{ij} = response of j-th member of cluster i, i = 1, . . . ,m, j = 1, . . . , ni, m = number of clusters, n_i = size of cluster i, x_{ij} = covariate vector of j-th member of cluster i for fixed effects, $\in R^p$, β = fixed effects parameter, $\in R^p$, u_{ij} = covariate vector of j-th member of cluster i for random effects, $\in R^q$, γ_i = random effect parameter, $\in R^q$

For the vocalisations, I used a MANOVA (Multiple Analysis of Variance) to investigate if age-classes have significant effects on mean calls' rate per hour. Then, I used Tukey HSD test to determine the significant differences between the groups' means (age-classes). The significance level was set at 0.05 for all tests. The box plots and graphs were carried out with SPSS Statistics 21 as well.

RESULTS

Dominance hierarchy

Rank could be determined for adults of both sexes and sub adults males. I classified individuals into one of three categories: high, middle or low ranking depending on their dyadic interactions with conspecifics (Table 2). I could not differentiate sub adult females because they were similar and numerous (N=12). There is no rank hierarchy for infants and it is uncertain for juveniles. Thus, when doing the statistical analysis with the rank data involved, only adult males, adult females and sub adult males were considered.

Table 2.Every two letters code represent one individual. 1 This individual left the group on November 13th, 2015. 2 This individual migrated in the group on December 05th 2015

Age-classes	Adults		Sub adults
Ranks	Males	Females	Males
High	DI, MA, QU[1]	AD	DA, SA
Middle	PA, OL[2]	FA, BI	JA, GA
Low	NO, CY, KE	YU	UC, HU

See table 2 for more details on individuals

Communication

I collected N=131 focals, which represents 65.5 hours (124 focalsexcluding juveniles, for a total of 62 hours). I did not do focals on infants because they are difficult to follow and the group is protective towards them. However, since there were eight of them, they are substantially present in the data. The chance of an infant walking near a focal animal was 27% (8 infants /29 focal animals).

Gestural signals

In total, I recorded N=1287 gestures (N=1246 excluding juveniles), N=1148 without gesture combinations. This section includes data about gestures given and received by the focal animal although gesture combinations are not included and are presented below. Gestures received by infants are included in the total but since their sex and rank were unidentified, they are not present in most of the analysis. These gestures are classified as facial expressions and movements, manual gestures or postures.

Contexts that induced most gestures were vigilance (N=353), feeding (N=290), affiliative (N=183) and traveling (N=163). Facial expressions and movements are the most common gestures communicated by individuals (N=573), followed by postures (N=350) and manual gestures (N=218). Facial expressions are the most common type of gesture expressed by individuals in most contexts, except during mating. Males (N=726) expressed more gestures than females (N=381). High-ranking individuals communicated more gestures (N=336) than low-ranking (N=284) and middle-ranking individuals (N=261).

Concerning mean gestures' rate per hour, it varied from 7 to 25 per individual for a grand total of 16.23for all individuals (Table A and figure a p.i in the appendices).

The Type III of Fixed effects (Table 3) represent overall test of significance for age-sex classes included in the model. These F tests are especially useful to investigate when looking at omnibus tests of significance for age sex classes. Therefore, the Type III F test for the interaction between sex-age classes and mean gestures' rate per hour (without facial expression) is significant at the 5% level, suggesting that the age-sex classes have an effect on mean gesture rate per hour (F(1, 142.14)= 257.174 , p=0.000***).

Table 3. Tests of Fixed Effect for the interaction between age-sex classes' and men gestures' rate per hour of wild population of Barbary macaques

	Numerator df	Denominator df	F	Sig.
Intercept Fixed Factors	1	53.579	67.548	0.0000
Relationship quality	1	24.978	25.154	0.0053
mean gestures' rate/h	1	324.145	245.475	0.0007
age-sex classes	1	142.140	329.727	0.0145
age-sex classes X mean gestures' rate/h	2	15.157	257.174	**0.0000**

The Estimates of Fixed effects represent the maximum likelihood estimates of the fixed effect parameters (or regression coefficient) in the LMM being fitted. There is significant positive linear relationship of sub adults, with the estimated fixed effect being 0.455, and this fixed effect is significantly different from 0 based on the t test (There is also a significant interaction between age-sex classes and mean gestures' rate per hour, with a low mean by 0.167 for Adults and 0.289 by sub adults (Table 4). That meaning the sub adults expressed more gestures per hour than adults (p=0.0075) (

Figure 1).

Table 4. Estimates of Fixed Effects for the interaction between age-sex classes' and men gestures' rate per hour of wild population of Barbary macaques

Parameter	Estimate	SE	*df*	*t*	*p*
Intercept	16.152436	0.998461	24.984	16.177	.000
Age-sex classe	0.455	0.087068	24.655	9.165	.000
AG=(Male Ad)	0.3	0.747242	24.714	3.457	.0745
AG=(Female Ad)	0.289	1.564289	24.984	.808	.129
AG=(Sub Ad	0.476	0.136409	24.655	2.362	**.0075**
Random factor	0	0			

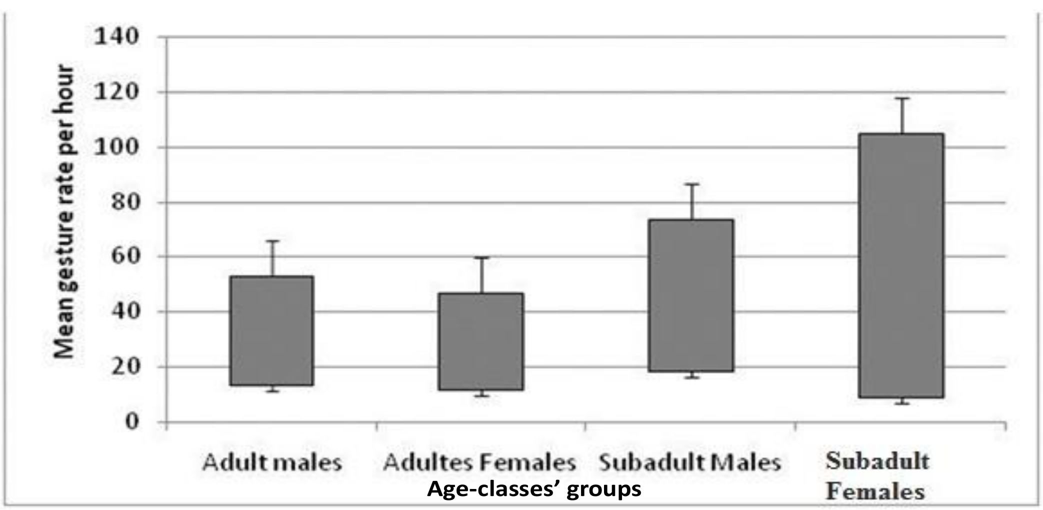


Figure 1. Mean gesture rate per hour in relation to sex and age-class. Only gestures given by the focal animal are considered but not gestures received

The Estimates of Covariance Parameters (Table 5) represent the maximum likelihood estimates of the covariance parameters (variances of the random effects, covariances of the random effects, variances and covariance's of the random errors, etc.) in the LMM that is being fitted. There are two covariance parameters defining the error covariance

structure in the model for the growth study data: the variance of the random errors [AR1, diagonal in the AR (1) covariance structure], and the correlation of adjacent errors (in terms of the amount of time between adjacent measures, or 2 years; this is AR1 rho). The variance of the random errors is estimated to be 1.19, which means that random errors associated with the growth observations (taking the fixed effects into account) are sampled from a normal distribution with variance 1.19. The estimates suggest that adjacent errors in the model actually have a negative correlation (0.473), which means that when conditioning on the fixed effects and random effects in this model, errors associated with observations from the same child at adjacent time points have a negative correlation; this might bring the covariance structure into question, prompting investigation of alternative covariance structures.

Table 5. Estimates of Covariance Parameters of the interaction between age-sex classes' and men gestures' rate per hour of wild population of Barbary macaques

Parameter		Estimate	SE	Wald Z	Sig.
Repeated Measure	AR1 Diagonal	1.192410	0.235547	5.062	.000
	AR rho	**-0.473280**	0.187112	-2.529	.011
Intercept + Id	UN(1.1)	11.377451	4.928971	2.308	.021
	UN(1,2)	- 0.814984	0.415695	-1.961	.050

Although, I did not collect focal scans on infants, I was able to observe that their gestural repertoire was developed to a greater extent. Infants were capable of displaying bared teeth, bite, yawn, slap at hands, push, grab, headstand, expose belly, head bob and branch shake (Table B p.ii in the appendices). Besides, I identified mounting between infants in a playing context. In total, they are able to express 16 gestures of a repertoire consisting of 40, which represents 40%.
There are four gestures missing in my data. First of all, I have never seen "drag a hind leg" on the study group which is a gesture that was observed occasionally in captive populations (Hesler and Fischer, 2007). In semi-free groups, the occurrence of "push and pull" was periodic although I did not witness it within the study group. I do not have "staring open mouth pant face" or "check-look" in my focals but I have seen it regularly during conflicts in the study group. These two expressions are quite hard to see because it happens mainly during aggressive interactions.

Gesture combinations

I did not consider gesture combinations as multimodal communication but rather as "multiple components [signals] within one sensory modality" (Higham and Hebets, 2013, Pp.1384).This section includes juveniles in the analyses except when the rank and the sex was a component of the analysis. In total, I recorded N=126 occurrences of gesture combinations made up of 62 different combinations (Table Cp. in appendices). The most frequent gestures' combination was "open mouth" coupled with "stare" (N=55) and "open mouth" accompanied by "stare" and "ground slap" (N=19).As single gestures, gesture combinations are essentially facial expressions and movement coupled (N=59), coupled with manual gestures (N=47) or coupled with postures (N=19). Gesture combinations were mostly expressed in a feeding context.

New gestures

I also observed novel gestures not mentioned in the previous literature. The first signal is when males, especially adults, gave a small "push" in the back of females who were sitting to make them getting up and inspect their hind quarters. This behaviour occurred often during the mating and birth seasons. This cod behaviour was a sub adult female "clapping in her hands" in front of an adult male to get his attention in the aim of having sex with him. The third signal I noticed several times is an individual teeth-chattering to himself or chattering at his body parts presumablyas an expression of high-stress levels. Finally, I observed homosexual mounts between females on several occasions, although this does not strictly qualify as a gesture. The mounts involved two sub adult females, an adult female on a sub adult female or even a sub adult female on a sub adult male.

Vocal signals

In total, I recorded N=1860 vocalisations (N=1833 excluding juveniles). This does not include 33 series of vocalisations for which I was unable to count the number of single calls. Among these 33 series, the type of 18 vocalisations could be identified. Among the 1860 vocalisations, eleven could not be identified. This section includes data about vocalisations given and received by the focal animal. Calls received by infants and juveniles were included in the total but when an analysis factor was about sex or rank, they were excluded from the analysis. Likewise, sub adult females were excluded from the analysis when the rank was involved as a statistical factor.

Contexts that induced most vocalisations were vigilance (N=384), feeding (N=334) and affiliative (N=199). Females (N=640) uttered more vocalisations than males (N=94) (infants excluded). Modulated and complex screams, pants, and rasping calls (vocalisations of type 2) are the most diversified in term of acoustic structure and include nine distinct subtypes. Compared to Fischer & Hammerschmidt (2002), I added three new subtypes g, h and i. g subtype characterises grunts, h characterises yawning and i characterises panting-grunts. Grunts (type 2g) are the most uttered 2 type calls by both sexes (N= 46 for females and N=36 for males). Moreover, it seems like some calls as 2c and 2f types are sex-specific, with only females uttering it. Regarding utterance of several call types in the same series of vocalisations, it is worth noting that infants combine several call types in a same series of vocalisations the most (N=390 vocalisations). The number of different combinations made of several call types in the sameseries decreases with age.

Concerning mean calls' rate per hour, it varied from zero to 66.33 per individual for a grand total of 8.80 for all individuals (Table D and figure B p.iv in the appendices). Females expressed more vocalisations per hour than males (**Error! Reference source not found.**).

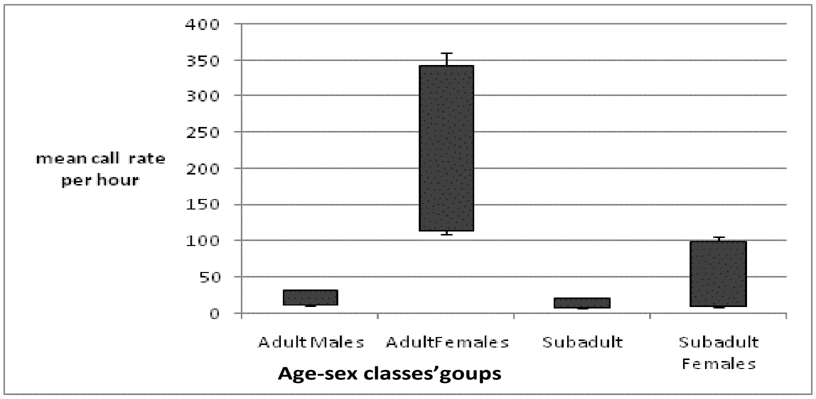


Figure 2. Mean call rate per hour in relation to sex and age-class. Only vocalisations uttered by the focal animal are considered but not vocalisations received

The Type III of Fixed effects (Table 6) represent overall test of significance for age-sex classes included in the model. These F tests are especially useful to investigate when looking at omnibus tests of significance for age sex classes. Therefore, the Type III F test for the interaction between sex-age classes and mean call rate per hour is significant at the 5% level, suggesting that Age-classes have an effect on mean call rate per hour (F(1,138.547)=70.08, df=138.547, p=0.000***).

Table 6.Tests of Fixed Effect for the interaction between age-sex classes' and men call rate per hour of wild population of Barbary macaques

	Numerator df	Denominator df	F	Sig.
Intercept Fixed Factors	1	57.8	67.548	0.0000
Relationship quality	1	80.1	25.154	0.0053
mean call rate per hour	1	324.145	1767.0	0.0007
age-sex classes	1	118.9	329.72	0.0145
age-sex classes X mean call rate per hour	2	138.547	257.1747	**0.0000**

The Estimates of Fixed effects represent the maximum likelihood estimates of the fixed effect parameters (or regression coefficient) in the LMM being fitted. There is significant positive linear relationship of sub adult males and females, with the estimated fixed effect being 0.62, and this fixed effect is significantly different from 0 based on the t test. There is also a significant interaction between age-sex classes and mean call rate per hour, with a low mean by 0.3 for Adults and 0.476 by sub adults. That meaning the sub adults and female adult's expressed more call per hour than adults Male (p=<0.0005) (**Error! Reference source not found.**).

Table 7.Estimates of Fixed Effects for the interaction between age-sex classes' and men call rate per hour of wild population of Barbary macaques

Parameter	Estimate	SE	df	*t*	*p*
Intercept	14.02	0.197452	18.245	14.222	.000
Age-sex classes	0.455	0.087068	7.1745	25.42	.000
AG=(Male Ad)	0.3	1.564289	24.5752	3.457	.0157

AG=(Female Ad)	1.264698	.457572	12.2145582	.62	**<0.0005**
AG=(Sub Ad	0.476	0.04544	42.25633	.62	**<0.0005**
Random factor	0	0			

The Estimates of Covariance Parameters (Table 8) represent the maximum likelihood estimates of the covariance parameters (variances of the random effects, covariances of the random effects, variances and covariance's of the random errors, etc.) in the LMM that is being fitted. There are two covariance parameters defining the error covariance structure in the model for the growth study data: the variance of the random errors [AR1, diagonal in the AR (1) covariance structure], and the correlation of adjacent errors (in terms of the amount of time between adjacent measures, or 2 years; this is AR1 rho). The variance of the random errors is estimated to be 4.63, which means that random errors associated with the growth observations (taking the fixed effects into account) are sampled from a normal distribution with variance 4.63. The table 4 shows that the random id is 11.377451.That suggest that adjacent errors in the model actually have a positive correlation, which means that when conditioning on the fixed effects and random effects in this model, errors associated with observations from the same child at adjacent time points have a positive correlation; this might bring the covariance structure into question, prompting investigation of alternative covariance structures.

Table 8. Estimates of Covariance Parameters (Random effect) for the interaction between age-sex classes' and men call rate per hour of wild population of Barbary macaques

Parameter		**Estimate**	**SE**	**Wald Z**	**Sig.**
Repeated Measure	AR1	4.63	0.235547	5.062	.000
	Diagonal AR rho	4.25.473280	0.187112	-2.529	.011
Intercept + Id		**11.377451**	3.94492	2.5523	**<0.0005**

In summary, Age-classes have an effect on mean call rate per hour .In order to determine the significant differences between group means, we found that age-sex classes sub adult males and female have significantly affect the distribution of the mean call rate per hour.

There are types of call missing in my data. I did not have the occasion to record clucking barks, a subtype of alarm call when individuals encounter a snake. Regarding calls from type 5, I did not record pants, low-frequency soft pants and clear calls.

In general terms, to compare gestures and calls' frequencies, the frequency of gestures increases with age and frequency of vocalisations decreases from infants to juveniles' class and then increases up to adulthood (

Figure 1). Infants utter much more vocalisations than adults do and there is a significant decrease of utterance from infants to juveniles' class. Regarding gestures, there is a peak frequency of use in sub adults and a slight decrease from sub adults to adults' class. To sum up, infants express much more vocalisations than gestures and adults express more gestures than vocalisations.

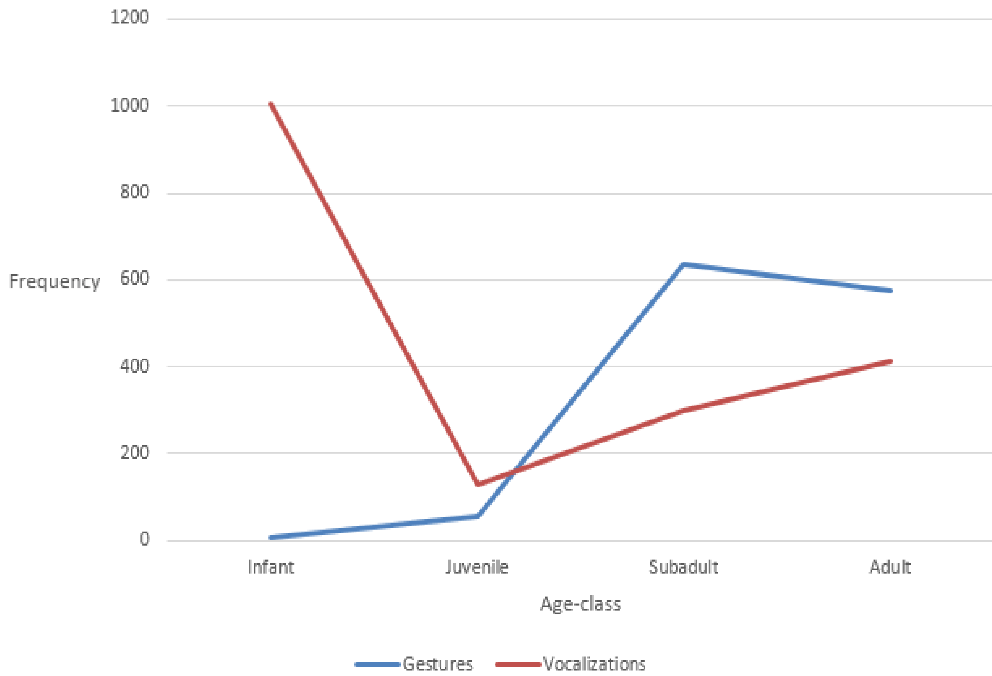


Figure 2. The frequency of gestures and vocalisations in relation to the age-class of the signaller. Newborns are not included in this graph. Gestures' rate includes combinations. Signals are given and received

Contexts of the calls

The analysis revealed that the function of many callsis unknown. Furthermore, most call types are uttered in various contexts. However, some calls as modulated tonal screams (type 2a) were expressed exclusively in an agonistic context. Grunts (type 2g) and complex screams (type 2d) are the most unspecific calls since they were uttered in eight different contexts. The results about contexts in which the calls were uttered are summarised in table 10 below.

Table 9.Contexts of theutterance of the calls.Call names in yellow were not recorded during data collection. V means that the call type was uttered in the corresponding context. Call names highlighted in bold are new compared to previous studies

Call types	Call subtypes	Call names	Agonistic	Sexual	Travelling	Feeding	Vigilance	Playing	Resting	Grooming	Affiliative
1	a	Noisy and complex scream			v	v	v	v	v	v	v
	b	Complex scream	v			v	v		v	v	
	c	Noisy arched scream								v	
	d	Complex scream	v		v	v	v			v	v
	e	Noisy and complex scream	v				v			v	
2	a	Modulated tonal scream	v								
	b	Squeak and modulated tonal scream			v	v	v	v		v	v
	c	Tonal scream	v		v	v	v				
	d	Complex scream	v		v	v	v	v	v	v	v
	e	Pant	v		v	v	v		v	v	
	f	Rasping call	v		v	v				v	
	g	Grunt	v	v	v	v	v		v	v	v
	h	Yawning							v		
	i	Panting-grunt			v						
3	a	Shrill bark (alarm call)									
	b				v		v				
	c	Rasping call			v						
	d	Clucking bark									
4	a	Oestrus call (copulation call) Rhythmic pant-grunt		v	v	v	v				
	b			v	v	v				v	v
5	a	Squeak								v	v
	b	Pant									
	c	Low-frequency soft pant									
	d	Pant bark				v					
	e	Clear call									
6	a	Gecker				v	v			v	v
	b	Girney				v					

Call Variations

I present call variations in a table structure classified by types. For every vocalisation, I put a spectrogram, the recorded sound, which individuals uttered and received the call, I tried to identify what exactly triggered the calls and I commented when it was necessary.

Boutlib et al 355

Table 10.Call type N°1

Call type N°1				
Call subtype	Spectrogram	Sound recording	Context	Comments

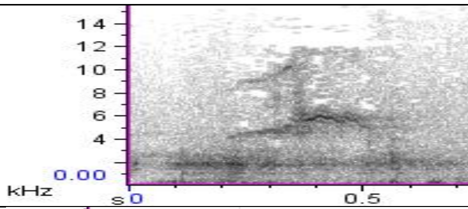
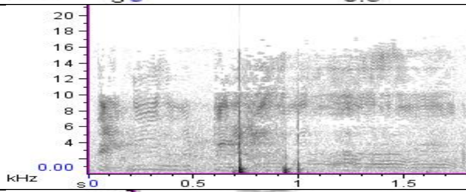
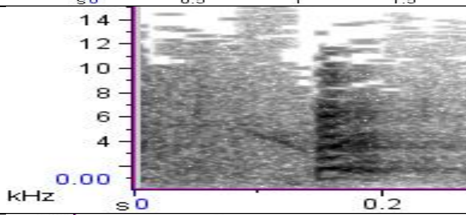
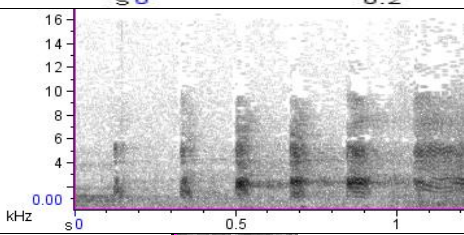
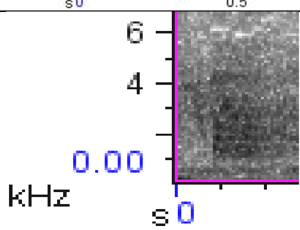
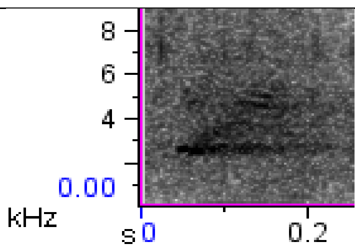
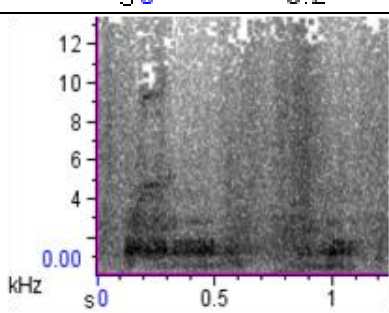
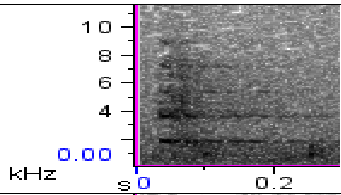
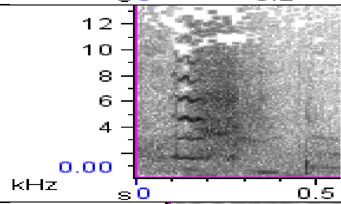
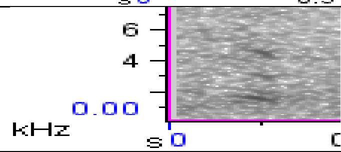
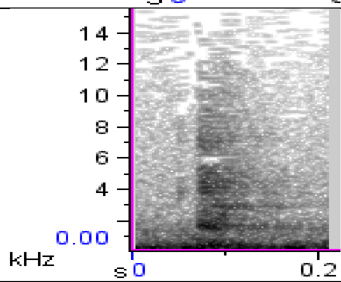
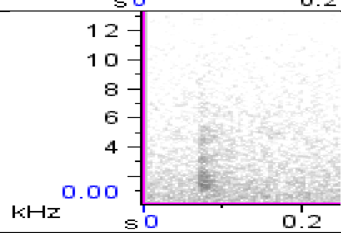
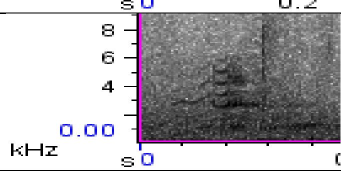
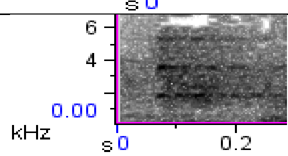
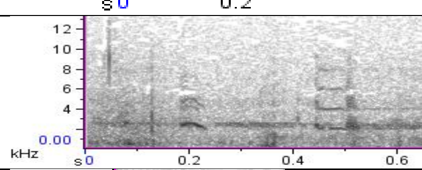
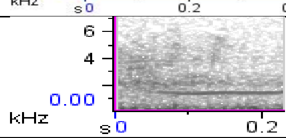
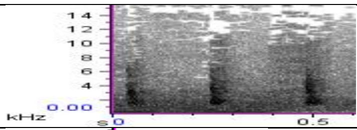
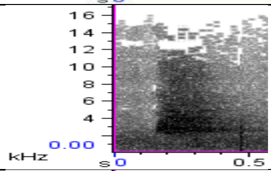
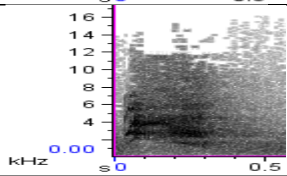
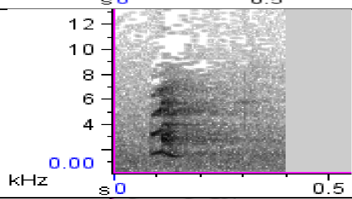
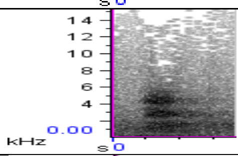
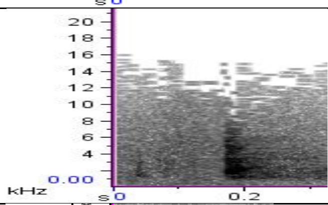
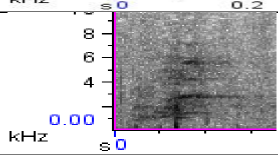
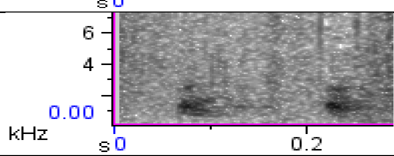
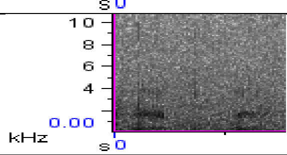
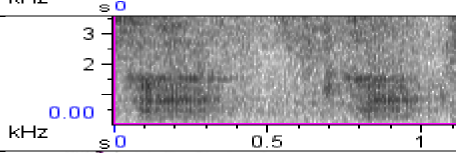
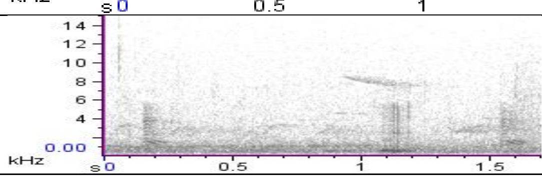
b		250316SAFRY.aif	Shriek uttered by a sub adult female to a sub adult male. The event that triggered the call is unknown in a feeding context.	It looks like a call uttered by an infant.
d		131215AD_IFRY.aif	Calls uttered by an infant after being slapped by its mother while it wanted to suckle in an affiliative context.	
d		280316HU_IFCW5.aif	Call uttered by an infant to a sub adult male. I think the infant wanted to be carried by the sub adult male n a feeding context.	Shorter than usual.
d		211115PA_FARYdebut.aif	Calls uttered by an adult female because she was harassed by an adult male in a vigilance context.	These vocalisations can be long or short.
d		270316AD1stcall3emeserie.aif	Noisy scream uttered by an adult female aggressed by an adult male who wanted to take its infant in a feeding context.	Lower frequency than usual.
e		280116JF3emeserie2ndcall.aif	Call uttered by a juvenile female after she has been severely aggressed (bitten) by an adult female. The adult female wanted to be groomed but did not give further notice before her actions in a feeding context.	
e		270116ADserie3.aif	Calls uttered by an adult female witnessing an aggression with a sub adult female during a grooming interaction.	

Table 11 .Call type N°2

Call type N°2

Call subtype	Spectrogram	Sound recording	Context	Comments
B		280116BI_IFtype2bnew.aif	Call uttered by an infant to its mother, an adult female, during a grooming interaction.	
B		280116GA_IF2b.aif	Call uttered by an infant to a sub adult male because the infant wanted to be carried in an affiliative context.	
B		280316SAF_IFCW3.aif	Call uttered by an infant to its mother, a sub adult female, because he wanted to suckle in an affiliative context.	
B		290116SAF_IFpart13emeserie.aif	Call uttered by an infant to its mother, a sub adult female, because he wanted to suckle in a grooming context.	This call is grading towards type 1d.
B		141115SA_SAFunknown.aif	Call uttered by a sub adult female to a sub adult male in an affiliative context. The event that triggered the call was unknown.	
C		270116UC_SAFunknown.aif	Tonal scream uttered by a sub adult female to a sub adult male after he aggressed her by a lunge in a feeding context.	
C		270316AD_newtype2c.aif	Call uttered by an adult female after an adult male tried to take her infant in a feeding context.	Even if these calls are of the same type and subtype and spectrograms look similar, they sound really different.
C		281115FARYpart1stserie.aif	Calls uttered by an adult female because she was harassed by an adult male in a feeding context.	
c		291115ADFS15.aif	Call uttered by an adult female witnessing a males' fight.	This call is formed by the fundamental frequency only.

Continuation Table 12 .Call type N°2

d		270116UC_JU.aif	Calls uttered by a juvenile to a sub adult male after he aggressed him by a lunge in a feeding context.
d		270116UC_SAF2d.aif	Call uttered by a sub adult female to a sub adult male after he aggressed her by a lunge in a feeding context.
d		270116UC_SAFRY4.aif	Call uttered by a sub adult female to a sub adult male after he aggressed her by a lunge in a feeding context.
d		270116UC_SAFRY5.aif	Call uttered by a sub adult female to a sub adult male after he aggressed her by a lunge in a feeding context.
d		270116UC_SAFRY2.aif	Call uttered by a sub adult female to a sub adult male after he aggressed her by a lunge in a feeding context.
d		300116DI_ADRY1.aif	Call uttered by an adult female to an adult male after he aggressed her by a lunge in a feeding context.
d		300316HU_IF2dtype.aif	Call uttered by an infant to a sub adult male. The event that triggered the call is unknown in an affiliative context.
d		300316UC_HU2dnew.aif	Calls uttered by a sub adult male to another sub adult male because he was grabbed by him in a feeding context.
f		241215AD_GR1&2.aif	Calls uttered by an adult female to a sub adult female during a grooming interaction. The event that triggered the call was unknown.
g		260316CYGR1&2.aif	Rough grunts uttered by an adult male witnessing a group agonistic interaction from 60 meters away in a resting context.
g		260316SAFGR.aif	Tonal grunts at 0.2 and 1.6 seconds uttered by a sub adult female in a feeding context. The event that triggered the calls was unknown, as well as the recipient of these calls.

Continuation Table 13 .Call type N°2

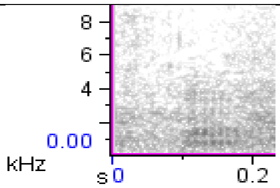
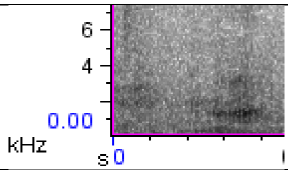
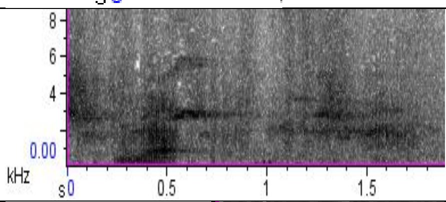
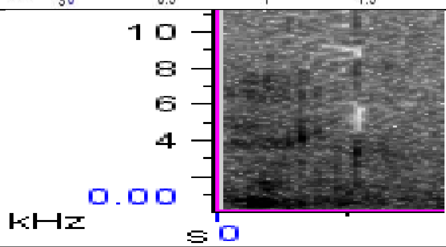
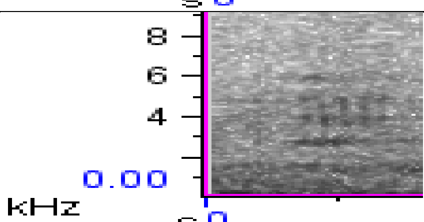
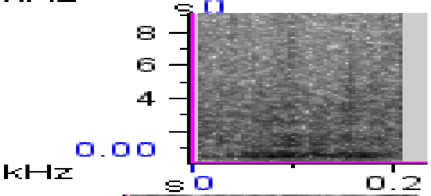
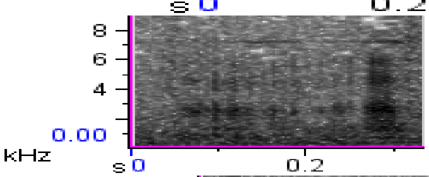
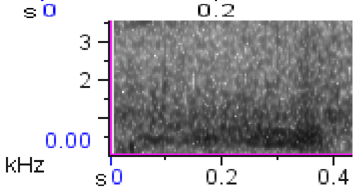
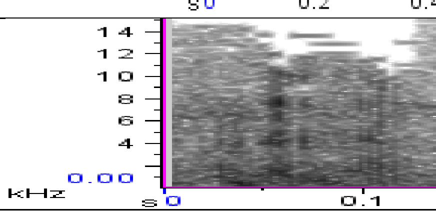
g		280116BI_GR.aif	Rough grunt uttered by an adult female in an affiliative context. The event that triggered the calls was unknown, as well as the recipient of these calls.
g		280316OLfoodGR.aif	Food grunt uttered by an adult male in a feeding context. He did not have neighbours when he grunted. This call is considered as a rough grunt.
g		280316PAGR3&4.aif	Two rough grunts uttered by an adult male while he was witnessing an aggression between other group' members in a vigilance context. The recipient of these calls was unknown.
g		300116GAGR.aif	High-frequency rough grunt uttered by a sub adult male in a vigilance context. The event that triggered the call was unknown, as well as the recipient of this call.
g		310316GA_GR1.aif	Rough grunt uttered by a sub adult male while he was witnessing an aggression between other group' members in a vigilance context. The recipient of this call was unknown.
g		080116HU_GR1.aif	Rough grunt uttered by a sub adult male in a vigilance context. The event that triggered the call was unknown, as well as the recipient of this call.
g		030316UC_SAFrGR.aif	Rough grunt uttered by a sub adult female to a sub adult male because he aggressed her by a lunge in a feeding context.
h		300116GAyawn.aif	Low-frequency vocalisation uttered by a sub adult male when yawning in a resting context.
i		310316GAGR3.aif	Panting grunt uttered by a sub adult male in a traveling context. The event that triggered the call was unknown, as well as the recipient of this call.

Table 14. Call type N°3

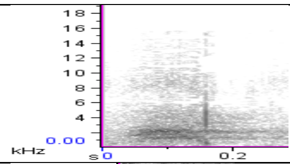
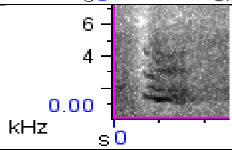
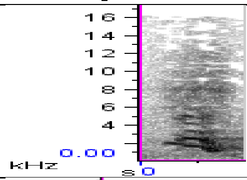
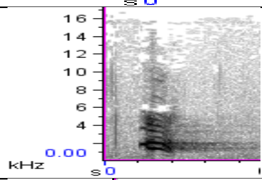
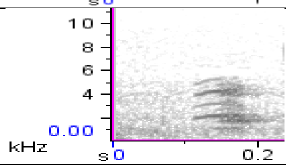
Call subtype	Spectrogram	Sound recording	Context	Comments
		Call type N°3		
b		131215YU_AC1.aif	Alarm call uttered by an adult female to the group because there were dogs around 150 meters away in a vigilance context.	. For the same disturbance, the same individual uttered different alarm calls in the structure, even if they seem to be of the same type
b		281115FAAC4.aif	Alarm call uttered by an adult female to the group because there were dogs several hundred meters away in a vigilance context	
b		281115FAAC6.aif	Alarm call uttered by an adult female to the group because there were dogs several hundred meters away in a vigilance context	
b		281115FAAC11.aif	Alarm call uttered by an adult female to the group because there were dogs several hundred meters away in a vigilance context	
c		131215YUAC8.aif	Alarm call uttered by an adult female to the group because there were dogs around 150 meters away in a traveling context.	

Table 15. Call type N°4

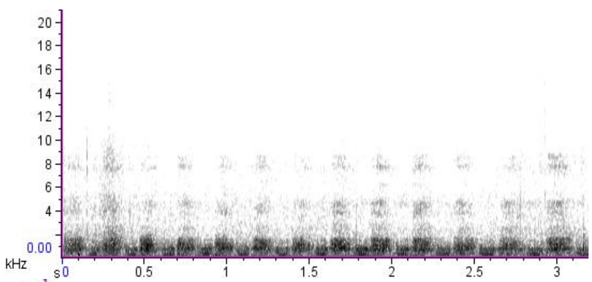
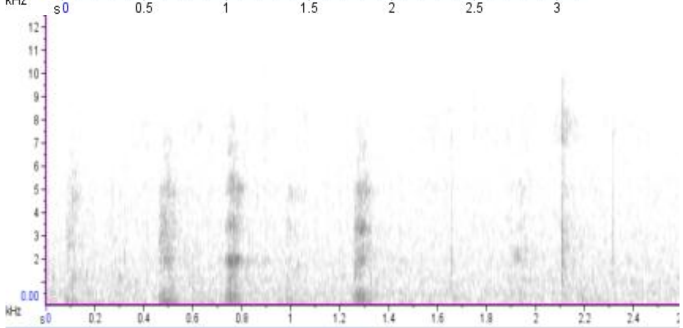
Call subtype	Spectrogram	Sound recording	Context	Comments
		Call type N°4		
a		061215SAF_CCO.aif	Oestrus calls uttered by a sub adult female to a sub adult male to attract him in a vigilance context.	
b		061215MA_BICC.aif	Copulation calls uttered by an adult female to an adult male during copulation.	Pant-grunts are not always rhythmic.

Table 15. Call type N°5

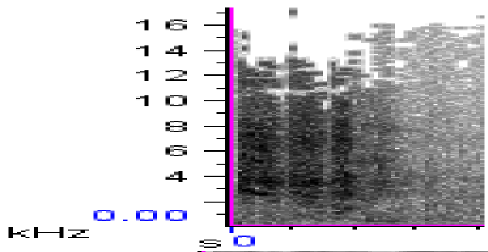
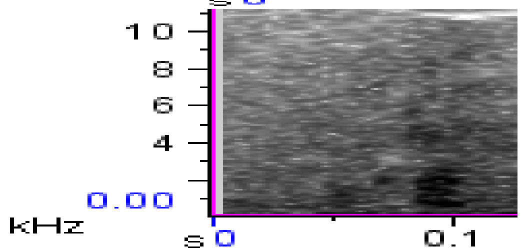
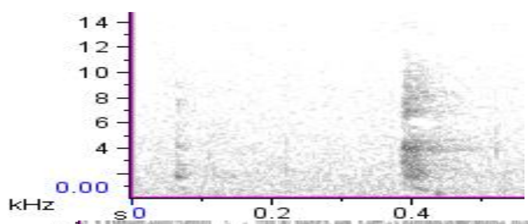
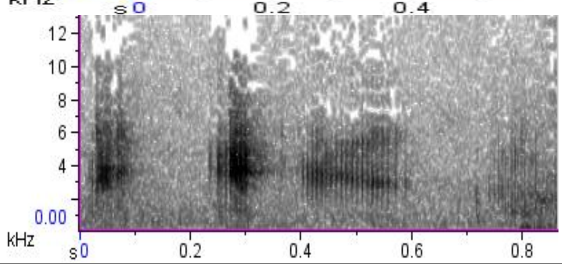
Call subtype	Spectrogram	Sound recording	Context	Comments
		Call type N°5		
a		280116GA_IFSQ1.aif	Squeak uttered by an infant to a sub adult male because he wanted to ride him in an affiliative context.	
d		080116HU_IFCW3.aif	Pant bark uttered by an infant to a sub adult male in a traveling context. The event that triggered the call was unknown	

Table 16. Call type N°6

Call subtype	Spectrogram	Sound recording	Context	Comments
		Call type N°6		
a		261115FA_IF1st&2call.aif	Gecker calls uttered by an infant to its mother, an adult female, because he wanted to suckle in a grooming context.	
b		060116OL_IFunknown.aif	Girney uttered by an infant to an adult male in an affiliative context, during dorsal carriage.	Infants are capable of uttering girney and it is very similar to adults.

Multimodal signals

In total, I recorded N=30 occurrences of seven different multimodal signals. This section includes given and received signals by the focal animal. The context that induced multimodality the most was agonistic (N=13). The multimodal signals were formed the most by facial expressions (N=25), followed by manual gestures (N=4) and postures (N=1). Adult (N=26) expressed more multimodal signals than sub adult (N=4). I did not observe juveniles or infants communicated multimodal signals. Females (N=18) expressed more multimodal signals than males (N=12). High-ranking individuals communicated more multimodal signals (N=14) than middle-ranking (N=8) and low-ranking individuals (N=7). The most frequent gesture was unvocalised scream face (N=18) (Table E p.v in the appendices).Twenty-three signals were composed of type 2 vocalisations, five were composed of type 4 vocalisations and two signals had their call types not identified. Tonal screams (vocalisations of type 2c, N=11) and grunts (vocalisations of type 2g, N=7) were the most uttered in multimodal signals.

DISCUSSION

Principal findings

Gestural communication

This research allowed to discover new gestures as "push the back" to inspect female sexual swellings. The most surprising were the manifestation of homosexual behaviours between females. Barbary macaques communicate more with vocalisations at a young age and adults express more gestures. Infants have a limited gestural repertoire though they are able to express 16 gestures of a repertoire consisting of 40, which represents 40%. Adults communicate on average with 16.23 gestures per hour, with facial expressions prevailing in all contexts, except sexual. Facial expressions expressed as unimodal gesture or part of gesture combinations are communicated the most by males and especially high-ranking individuals. Regarding sub adults, they are the age-class that expresses gestures the most surpassing adults with sub adult females expressing more gestures than sub adult males.

Vocal communication

In Barbary macaque, there is a peak of calls utterance in infancy. Infants are able to utter all call types but tend to combine it with a higher and more diversified rate than adults do. Adults and sub adults communicate on average with 8.80 vocalisations per hour with females vocalising much more than males. It seems that call types as 2c and 2f are sex-specific, with only females uttering it. Vocalisations of type 2are the most diversified in term of acoustic structure and include nine distinct subtypes. Among these calls, grunts (type 2g) are the most uttered calls by both sexes and in various contexts.

Multimodal communication

Multimodal signals were formed for the most part by facial expressions and communicated mostly during agonistic interactions. Adults and especially high-ranking individuals expressed scream face coupled with vocalisations of type 2 to a greater extent.

Relations with previous work

Gestures

Research on gestural communication is lacking in wild environments (Liebal et al., 2013)and most of the studies on gestural repertoire were conducted on captive populations (Liebal et al., 2013; Slocombe et al., 2011).In the wild group, adult males communicated the majority of facial expressions, certainly because the great part of facial expressions communicate threats and males are superior to females in the hierarchy. For the same reason, high-ranking individuals expressed more gestures. The fact that sub adults are the age-class that expresses gestures the most could be explained by their strategic link in the network, playing with juveniles and learning from adults, which makes them having the most social interactions in the group. Since sub adult females express more gestures than sub adult males that could be explained by matri lines. Indeed, females may have stronger links between them because they are linked genetically.

Infants communicate more by vocalisations though their gestural repertoire was more developed that what Hesler and Fischer (2007) asserted. The possible interpretation for this variation in the repertoire between captive and wild individuals could be the distinction in environmental conditions. For instance, predators are numerous for wild individuals being one of the driving forces of dexterity's stimulation that could lead to a faster repertoire's expansion compared to captive populations. This implies that captive animals would take an extended time to acquire gestural repertoire.

Gesture combinations

Gestures' combinations are frequent in the communication of Barbary macaques and they are redundant signals (Partan and Marler, 1999, 2005) for the most part, meaning that every component taken unimodally elicits an equivalent response from the receiver. Thus, threat gestures will be associated together, as well as affiliative and agonistic gestures. However, it is not clear if gesture combinations are more likely to elicit a response than a gesture elicited alone (Liebal et al., 2013).

New gestures

The most surprising gesture discovered was the manifestation of homosexual behaviours between females. Homosexual interactions are well documented in most Anthropoidea species. Wolfe (1981) observed females having homosexual interactions in Japanese macaques and mounting between females has been observed in stumptail macaques (*Macaca arctoides*) (Maestripieri, 1997). To my knowledge, it has never been reported that females Barbary macaques practice mounting between each other. I observed several times sub adults female mounting each other or a female mounting a sub adult female. This can be an approach to attract males in the aim of copulation. Moreover, I witnessed a sub adult female mounting a sub adult male. This can be to encourage the male to start copulation (Maestripieri, 1997) or to appease tensions afterward an agonistic interaction.

"Push" the back occurred often during the mating and birth seasons, certainly to have cues on females' fertile phase in the first case and to get an olfactory indication about gestation in the second case.

Vocalisations

Vocal repertoire of Barbary macaques is complex and not fully puzzled out yet. Todt et al., (2005) asserted that frequency of vocalisations decreases with age although I identified a slight increase between juveniles and adult stages. In the adults, middle-ranking and low-ranking female's uttered copulation calls the most. This could mean that copulation calls are a strategy to attract a mate since the highest-ranking female uttered only one vocalisation. Among type 2 calls, grunts (type 2g) were the most uttered calls by both sexes. Even if this type of vocalisation is largely mentioned in the literature (Fischer and Hammerschmidt, 2002; Hammerschmidt and Fischer, 1998b), there is no explicit information about it. To my knowledge, even in reviews (Fischer and Hammerschmidt, 2002), there is no spectrogram or description for this call type. I think that grunts are uttered sometimes as a form of greeting but it is hard to assess and I am not aware of previous literature about this issue in Barbary macaques. Grunts are used for greeting alone of coupled with facial expressions in pigtail macaques (Maestripieri, 1997). Even if it was asserted that Barbary macaques do not vocalise when discovering food (Hauser, 1996), I could observe at least one occasion when an adult male uttered food grunts when foraging. Since Barbary macaque grunt a lot, it is challenging to assess the contexts, the function and the recipients of these calls.

Multimodality

To my knowledge, this is the first study on multimodal communication in Barbary macaques. Multimodal signals justified the *signal redundancy hypothesis* rather than the simultaneous message hypothesis (Rowe, 1999).Contrary to chimpanzees (Taglialatela et al., 2015), Barbary macaques in most cases perform signals directed to a conspecific. They were not numerous which could be explained by the fact that wild Barbary macaques have various predators. Because multimodal signals expose individuals more than unimodal signals, this could justify the reason why Barbary macaques do no express it often. Since I observed multimodal communication in adults and sub adults exclusively, it seems that mechanisms involved in multimodality require a certain level of cognition that younger individuals have not developed yet (Liebal et al., 2013).

Because the main contexts in multimodal communication were aggression and sexual, we can theorise that it evolved from these two peculiar contexts to be ubiquitous in human communication. During aggressive and sexual contexts, individuals need to be in a high attentional state and multimodality can facilitate the transfer of information and understanding by the receiver. This fits with the "evolutionarily urgent contexts" hypothesis emphasised by Liebal et al. (2013, p.118).

In Barbary macaques, the vocalisations studied in more depth are the calls utter during the mating season. When it occurs, females give oestrus calls to attract males and copulation calls ("mating calls", Pohl and Todt, 1984) during or immediately after mounting (Pfefferle et al., 2011). At several occasions during copulation, females combined copulation calls with a gesture, "mountee reaches back". This combination could have an impact on the reproduction's outcome. Perhaps it could increase male mating success (Partan and Marler, 2005)because the combination would be more attractive for the male.

LIMITATIONS

Facial expressions in Barbary macaques are characterised by several features as scream face when the monkey pulls its eyebrows and scalp, flattens its ears against the head, pulls up its lips, shows its teeth and usually its gums. In some studies about multimodal communication, all these components are taken separately in the analysis but it was too challenging to do so in my research. With the same idea, some studies on multimodal signals record the number of gestures, facial expressions and vocalisations as part of the same communicative units. To be accurate, I think this should be recorded on videotapes because the sequences are fast. I was able to record unit for vocalisations only and I collected occurrences of gesture combinations, facial expression combinations and combinations of both gestures and facial expressions.

An accurate manner to define multicomponent signals is to understand how the receiver perceives signals (Rowe, 1999). This study was focused on multimodal signals expressed by signallers but not on the response of recipients or audience. However, I witnessed many occurrences of individuals who "commented" interactions between other individuals, especially during agonistic and mating contexts.

FUTURE RESEARCH

Further studies should investigate how recipient answers to multimodal signals to identify a potential stronger response compared to unimodal signals, as well as how the recipient receives, interprets, and integrates these signals (Higham and Hebets, 2013).

Future research should investigate the presence of *accessory cues*(Rowe, 1999) before a vocalisation, a gesture or a multimodal combination is uttered. For instance, a gesture or a call may be uttered before a multimodal communication to get the attention of the recipient so he is more likely to receive a stronger message. Besides, since multicomponent signals are more detectable (Rowe, 1999), perhaps they are used as accessory cues themselves so the signaller has the full attention of the recipient to convey the main message.

Bibliography

Alcock J(1972). The evolution of the use of tools by feeding animals. *Evolution*, 26:464-473

Altmann J(1974). Observational study of behaviour: sampling methods. *Behaviour*, 49:227–267.

Arbib MA, Liebal K, Pika S (2008). Primate Vocalisation, Gesture, and the Evolution of Human Language. Current Anthropology, 49(6): 1053–1076. https://doi.org/10.1086/593015

Baker KR, Lea SEG, Melfi VA(2015). Comparative Personality Assessment of Three Captive Primate Species : Macaca nigra, Macaca sylvanus, and Saimiri sciureus. Pp. 625–646. https://doi.org/10.1007/s10764-015-9843-3

Beck BB (1980). Animal Tool Behaviour: the Use and Manufacture of Tools. New York: Garland STPM Press.

Bernstein IS(1976). Dominance , Aggression and Reproduction in Primate Societies, Pp. 459–472.

Breuer T, Ndoundou-hockemba M, FishlockV(2005). First Observation of Tool Use in Wild Gorillas, 3(11): 2–4. https://doi.org/10.1371/journal.pbio.0030380

Brumm H, Kipper S, Riechelmann C, Todt D(2005). Do Barbary macaques "comment" on what they see? A first report on vocalisations accompanying interactions of third parties. Primates, 46(2): 141–144. https://doi.org/10.1007/s10329-004-0107-7

Deag JM(1977). Aggression and submission in monkey societies. Animal Behaviour, 25(PART 2): 465–474. https://doi.org/10.1016/0003-3472(77)90021-5

Faraut L, Northwood A, Majolo B(2015). The function of non-reproductive mounts among male Barbary macaques (Macaca sylvanus). Amer. J. Primatology. 77(11): 1149–1157. https://doi.org/10.1002/ajp.22451

Fedigan LM, BaxterMJ (1984). Sex Differences and Social Organization in Free-ranging Spider Monkeys (Ateles geoffroyi). Primates, 25(3): 279–294.

Fischer J, Hammerschmidt K(2002). An Overview of the Barbary Macaque, Macaca sylvanus, Vocal Repertoire. Folia Primatologica, 73: 32–45.

Fischer J, Hammerschmidt K, Todt D(1995). Factors Affecting Acoustic Variation in Barbary macaque (Macaca sylvanus) Disturbance Calls. Ethology, 101(1): 51–66. https://doi.org/10.1111/j.1439-0310.1995.tb00345.x

Fischer J, Hammerschmidt K(2001). Functional referents and acoustic similarity revisited : the case of Barbary macaque alarm calls. Animal Cognition, 4: 29–35. https://doi.org/10.1007/s100710100093

Fischer J, Hammerschmidt K, Todt D(1998). Local variation in Barbary macaque shrill barks. Animal Behaviour, 56(1992): 623–629. https://doi.org/10.1006/anbe.1998.0796

Fooden J(2007). Systematic review of the Barbary macaque, Macaca sylvanus (Linnaeus, 1758). Fieldiana Zool, (113): 1–60.

Gazzola V, Aziz-Zadeh L, Keysers C(2006). Empathy and the somatotopic auditory mirror system in humans. Current Biology : CB, 16(18): 1824–9. https://doi.org/10.1016/j.cub.2006.07.072

Genty E, Breuer T, Hobaiter C, Byrne RW(2009). Gestural communication of the gorilla (Gorilla gorilla): Repertoire, intentionality and possible origins. Animal Cognition, 12(3): 527–546. https://doi.org/10.1007/s10071-009-0213-4

Ghazanfar AA, Logothetis NK(2003). Facial expressions linked to monkey calls. Nature, 423(6943): 937–938.

Hammerschmidt K, Ansorge V(1989). Birth of a Barbary macaque (Macaca sylvanus): Acoustic and behavioural features. Folia Primatologica, 52(1-2): 78–87. https://doi.org/10.1017/CBO9781107415324.004

Hammerschmidt K, Fischer J(1998). The vocal repertoire of Barbary macaques: a quantitative analysis of a graded signal system. Ethology, 104(3): 203–216. https://doi.org/10.1111/j.1439-0310.1998.tb00063.x

Hauser MD (1996). Vocal communication in macaques: causes of variation. In J. E. Fa & D. G. Lindburg (Eds), Evolution and ecology of macaque societies (Pp. 551-577). Cambridge, England: Cambridge University Press.

Hausfater G(1972). Intergroup Behaviour of Free-Ranging Rhesus Monkeys (Macaca mulatta). Folia Primatologica, 18: 78–107.

https://doi.org/10.1007/s13398-014-0173-7.2
Hesler N, Fischer J(2007). Gestural communication of Barbary macaques (Macaca sylvanus): An overview. In J. Call & M. Tomasello (Eds.), The Gestural Communication of Apes and Monkeys (1st ed., Pp. 264). Mahwah, New Jersey, London: Lawrence Erlbaum Associates, Inc., Publishers.
Higham JP, Hebets EA(2013). An introduction to multimodal communication. Behavioural Ecology and Sociobiology, 67(9): 1381–1388. https://doi.org/10.1007/s00265-013-1590-x
Hohmann G, Fruth B(2015). Culture in bonobos? Between-species and within-species variation in behavior. Current Anthropology, 44(4): 563–571.
Horwich RH(1983). Breeding behaviours in the black howler monkey (Alouatta pigra) of Belize. Primates, 24(2): 222–230.
In J. E. Fa & D. G. Lindburg (Eds), Evolution and ecology of macaque societies. (Pp. 527-550). Cambridge, England: Cambridge University Press.
Iriki A, Tanaka M, Iwamura Y (1996). Coding of modified body schema during tool use by macaque postcentral neurons. Neuro report, 7: 2325-2330
Kipper S, Todt D(2002). The use of vocal signals in the social play of barbary macaques. Primates; Journal of Primatology, 43(1): 3–17. https://doi.org/10.1007/BF02629572
Kohler E, Keysers C, Umilta MA, Fogassi L, Gallese V, Rizzolatti G(2002). Hearing Sounds, Understanding Actions : Action Representation in Mirror Neurons. Sci. 297(August): 846–848.
Liebal K, Waller BM, Burrows AM, Slocombe KE(2013). Primate communication, A multimodal approach (Vol. 1). New York: Cambridge University Press. https://doi.org/10.1017/CBO9781107415324.004
Lindburg DG(1971). "The rhesus monkey in North India: an ecological and behavioural study." Primate behaviour: developments in field and laboratory research, 2: 1-106.
Maestripieri D(1997). Gestural communication in macaques usage and meaning of non-vocal signals. Evolution of Communication, (1): 193–222.
Maestripieri D(2005). Gestural communication in three species of macaques (Macaca mulatta, M. nemestrina, M. arctoides): use of signals in relation to dominance and social context. Gesture, 5(1–2): 57–73. https://doi.org/10.1075/gest.5.1-2.06mae
Majolo B, McFarland R, Young C, Qarro M(2013). The Effect of Climatic Factors on the Activity Budgets of Barbary Macaques (Macaca sylvanus). Int. J. Primatology, 34(3): 500–514. https://doi.org/10.1007/s10764-013-9678-8
Mehlman PT (1996). Branch shaking and related displays in wild Barbary macaques. In J. E. Fa & D. G. Lindburg (Eds.), Evolution and ecology of Macaque societies (Pp.523- 526). Cambridge, England: Cambridge University Press.
Micheletta J, Engelhardt A, Matthews L, Agil M, Waller BM(2013). Multi component and multimodal lip smacking in crested macaques (Macaca nigra). Amer. J. Primatology, 75(7): 763–773. https://doi.org/10.1002/ajp.22105
Milich KM, Maestripieri D(2016). Sex or power ? The function of male displays in rhesus macaques. https://doi.org/10.1163/1568539X-00003340
Modahl KB, Eaton GG(1977). Display Behaviour in a Confined Troop of Japanese Macaques Macaca-Fuscata. Animal Behaviour, 25(3), 525–535.
Oppenheimer JR, Oppenheimer EC(1973). Preliminary observations of Cebus nigrivittatus (primates: Cebidae) on the Venezuelan Llanos. Folia Primatologica, 19(6), 409–436.
Partan SR, Marler P(1999). Communication goes multimodal. Science, 283(5406): 1272–1273. https://doi.org/10.1017/CBO9781107415324.004
Partan SR, Marler P(2005). Issues in the classification of multimodal communication signals. The American Naturalist, 166(2): 231–245. https://doi.org/10.1086/431246
Pfefferle D, Heistermann M, Pirow R, Hodges JK, Fischer J(2011). Estrogen and Progestogen Correlates of the Structure of Female Copulation Calls in Semi-Free-Ranging Barbary Macaques (Macaca sylvanus). Int. J. Primatology, 32: 992–1006. https://doi.org/10.1007/s10764-011-9517-8
Rowe C(1999). Receiver psychology and the evolution of multicomponent signals. Animal Behaviour, 58(5): 921–931. https://doi.org/10.1017/CBO9781107415324.004
Seltmann A, Majolo B, Schülke O, Ostner J(2013). The Organization of Collective Group Movements in Wild Barbary Macaques (Macaca sylvanus): Social Structure Drives Processes of Group Coordination in Macaques. PloS One, 8(6), e67285. https://doi.org/10.1371/journal.pone.0067285
Semple S, Higham JP(2013). Primate signals: Current issues and perspectives. Amer. J. Primatology, 75(7): 613–620. https://doi.org/10.1002/ajp.22139
Slocombe KE, Waller BM, Liebal K(2011). The language void: the need for multimodality in primate communication research. Animal Behaviour, 81(5): 919–924. https://doi.org/10.1016/j.anbehav.2011.02.002
St Amant R, Horton TE(2008). Revisiting the definition of animal tool use. Animal Behaviour, 75(4): 1199–1208. https://doi.org/10.1016/j.anbehav.2007.09.028
Sugiyama Y(1969). Social Behaviour of Chimpanzees in the Budongo Forest , Uganda 1), 225: 197–225.
Taglialatela JP, Russell JL, Pope SM, Morton T, Bogart S, Reamer LA, Hopkins WD(2015). Multimodal communication in chimpanzees. Amer. J.Primatology, 77(11): 1143–1148. https://doi.org/10.1002/ajp.22449
Taglialatela JP, Russell JL, Schaeffer JA, Hopkins WD(2011). Chimpanzee Vocal Signaling Points to a Multimodal Origin of Human Language. PloS One, 6(4): 1–7. https://doi.org/10.1371/journal.pone.0018852
Todt D, Hammershmidt K, Ansorge V, Fischer J(1995). The vocal behaviour of Barbary macaques (Macaca sylvanus): call features and their performance in infants and adults. In E. Zimmermann, J. D. Newman, & U. Jürgens (Eds.), Current topics in primate vocal communication (Plenum Pre, pp. 141–160). New York: Springer Science+Business Media, LLC.
Tomasello M(2008). Origins of human communication. Choice Reviews Online (MIT Press, Vol. 46). Cambridge, MA. https://doi.org/10.5860/CHOICE.46-3671
Tomasello M, Call J, Warren J, Frost GT, Carpenter M, Nagell K(1997). The ontogeny of chimpanzee gestural signals: a comparison across groups and generations. Evolution of Communication, 1(2): 223–259. https://doi.org/10.1075/eoc.l.2.04tom

Van Lawick-Goodall J(1970). Tool-using in primates and other vertebrates. In: Advances in the Study of Behaviour. Vol. 3 (Ed. by D. Lehrman, R. Hinde & E. Shaw), Pp. 195-249. New York: Academic.
Vessey SH(1968). Interactions between free-ranging groups of rhesus monkeys. Folia Primatologica, 8: 228–239.
Wacewicz S, Zywiczynski P(2016). The multimodal origins of linguistic communication. Language & Communication, in press, Pp. 1–8. https://doi.org/10.1016/j.langcom.2016.10.001
Wolfe LD(1981). Display behaviour of three troops of Japanese monkeys (Macaca fuscata). Primates, 22(1): 24–32. https://doi.org/10.1007/BF02382554
Yamagiwa J(1985). Socio-sexual Factors of Troop Fission in Wild Japanese Monkeys (Macaca fuscatayakui) on Yakushima Island, Japan. Primates, 26(2): 105–120.
Zeller A(1996). The inter-play of kinship organisation and facial communication in the macaques.

APPENDICES

Tables and figures

Gestures

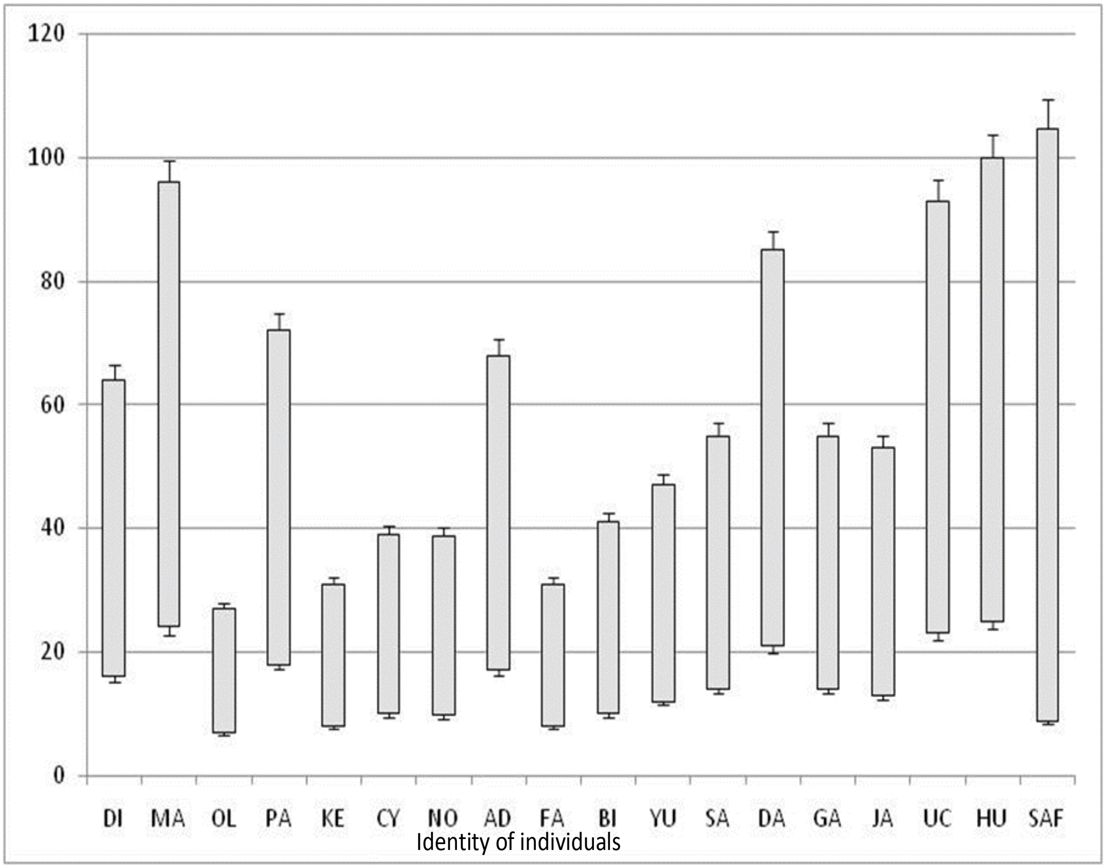


Figure A. Box plot representing gesture rates per individual per hour except for sub adult females (SAF) for which it is the whole age-class. Individuals are classified from highest to lowest ranking from left to right

Table A. The total number of gestures expressed by individuals and mean gesture rates per hour and individual. This table does not include situations when the individual who elicited the gesture was unknown and the gestures are all expressed by the focals, not received. Gesture combinations are included, with a combination counting as one gesture. Since sub adult females were not identified, the column "SAF" (sub adult females) represents the whole age-class and not a unique individual

Age-class	Individual identity	Total of gestures expressed by individuals	Mean gesture rate per hour
Adult males	DI	56	18.67
	MA	93	31
	OL	23	7.67
	PA	57	19
	KE	31	10.33
	CY	35	11.67
Adult females	NO	33	11
	AD	53	17.67
	FA	23	7.67
	BI	31	10.33
	YU	40	13.33
	SA	48	16
Sub adult males	DA	70	23.33
	GA	45	15
	JA	44	14.67
	UC	86	28.67
	HU	81	27
Sub adult females	-	100	9.09
Grand total		842	16.23

Table B. Age-classes in which gestures were observed updated from Fischer and Hesler (2007). "+" means frequently, "o" means rarely and "?" means unsure. In green are the differences I found compared to Fischer & Hesler (2007)

	Signal	Infant	Young Juvenile	Older Juvenile	Sub adult Female	Sub adult Male	Adult Female	Adult Male
Facial Expressions and Movements	relaxed open mouth face	+	+	+	+	+	o	o
	lip-smack		+	+	+	+	+	+
	teeth-chatter	+	+	+	+	+	+	+
	bared teeth display	+	+	+	+	+	+	+
	unvocalised scream face				+	+	+	+
	stare			+	+	+	+	+
	open mouth display		+	+	+	+	+	+
	staring open mouth pant face				+	+	+	+
	bite	+	+	+	+	+	+	+
	yawn	+	+	+	+	+	+	+
	chatter at body parts			+	+	+	+	+
	bared teeth gecker face					+	+	+
	chew-smack					+	+	+
Manual	touch body	+	+	+	+	+	+	+
	hug			+	+	+	+	+
	knead				+	+	+	+
	touch genitalia	+	+	+	+	+	+	+
	hip-touch		+	+	+	+	+	+
	slap at hands	+		+	+	+	+	+
	slap		+	+	+	+	+	+
	ground slap			+	+	+	+	+
	pull		+	+	+	+	+	+
	push	+	+	+	+	+	+	+
	push and pull							
	grab	+	+	+	+	+	+	+
	sweep							
	touch own genitalia				+	+	+	+
	mountee reaches back				+	+	+	+
	embrace			?	?	+	+	+
Postures	headstand	+		+		+	+	+
	head-flag	+			+	+	+	+
	expose belly	+		+		+		
	invitation to ride			+		+	+	+
	present			+	+	+	+	+
	mount	+			+	+	+	+
	lunge				+	+	+	+
	check-look				+	+	+	+
	head bob	+	+	+	+	+	+	+
	drag a hind leg							
	branch shake	+	+	+	+	+	+	+

Table C. Gesture combinations and their frequencies

Gesture combinations	Combinations' frequency
BI+GB	1
BI+TB	2
CBP+KN	1
HG+TC	2
HT+CBP	1
LU+SF	1
MRB+TC	1
OM+GS	1
OM+LU	2
OM+SL	3
OM+ST	55
OM+ST+GS	19
OM+TC	1
P+LS	1
SF+ST	3
SL+LU	1
ST+GS	7
TB+TC	1
TC+EM	2
TC+HT	1
TC+M	13
TC+P	2
TC+TOG	1
TG+CBP+EM	1
TG+TC	3
Grand total	**126**

Vocalisations

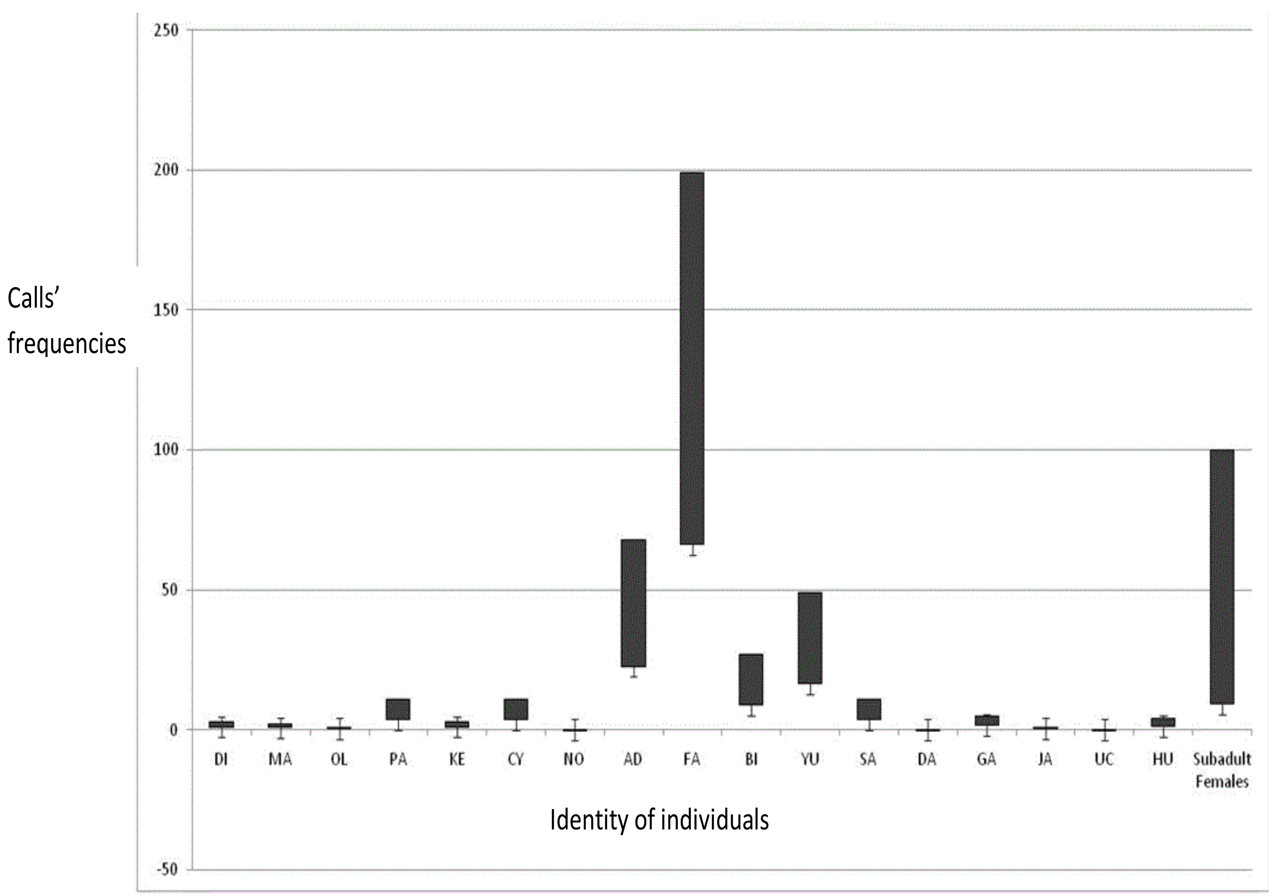


Figure B. Box plot representing call rates per individual per hour except for sub adult females (SAF) for which it is the whole age-class. Individuals are classified from highest to lowest ranking from left to right

Table D. The total number of calls uttered by individuals and mean calls' rate per hour per individual

Age-class	Individual identity	Total of vocalisations per individual	Mean call rate per hour
	DI	3	1
Adult Males	MA	2	0.66667
	OL	1	0.33333
	PA	11	3.66667
	KE	3	1
	CY	11	3.66667
	NO	0	0
Adult Females	AD	68	22.6667
	FA	199	66.3333
	BI	27	9
	YU	49	16.3333
	SA	11	3.66667
	DA	0	0
Sub adult Males	GA	5	1.66667
	JA	1	0.33333
	UC	0	0
	HU	4	1.33333
Sub adult Females	-	100	9.09091
Grand total		495	8.79735

This table does not include situations when the individual who elicited the call was unknown and the calls are all uttered by the focals, not received. Since sub adult females were not identified, the column "SAF" (sub adult females) represents the whole age-class and not a unique individual

Multimodality

Table E. Type of gestures and vocalisations involved in multimodal signals and their frequency. For an explanation about gestures, see the ethogram in appendices

Type of gesture / Type of vocalisation	2	4	Unknown	Grand total
MRB		4		4
M			1	1
OM+ST	1			1
SF	18			18
ST	2	1	1	4
TC	1			1
YA	1			1
Grand total	**23**	**5**	**2**	**30**