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An Overview of the Barbary Macaque, *Macaca sylvanus,* Vocal Repertoire

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Key Words
Barbary macaques · *Macaca sylvanus* · Acoustic · Communication · Repertoire · Vocalizations · Facial gestures

Abstract

This study provides an overview of the vocalizations of Barbary macaques, *Macaca sylvanus*. Spectrographic displays of calls are presented along with photographs of the accompanying facial gestures. We give a general description of the contexts in which the different calls are uttered, with special regard to the age and sex of the caller. The vocal repertoire of Barbary macaques mainly consists of screams, shrill barks, geckers, low-frequency pants and grunts, with gradation occurring within and between call types. The spectrograms document that typically, Barbary macaques produce series of several consecutive calls. The influence of habitat, social structure and phylogenetic descent on the morphology of the repertoire and call diversity are discussed in comparison to other species.

Introduction

Although quantitative analyses of behaviour are the gold standard in ethology, and rigorous hypothesis testing is viewed as the norm, detailed descriptions of the behaviour patterns of the species under study ('ethograms') still form the foundation for any behavioural analysis. In the gestural or social domain, such ethograms typically consist of lists in which the relevant behaviour patterns are described in as much detail as possible [1–4], whereas overviews of vocal gestures typically feature spectrographic displays of calls [5–11]. Ethograms fulfil three major functions: firstly, they promote the use of a single terminology for the different behaviours

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across different researchers, secondly, they form the foundations for comparative studies, and thirdly, they are useful for newcomers to a particular species who embark on a study of its behaviour.

In this paper, we aim to provide an overview of the vocal behaviour of Barbary macaques (*Macaca sylvanus* L.1758). Barbary macaques are the only members of the genus *Macaca* living in Africa. Based on fossil and morphological [12], and molecular evidence [13–15], Barbary macaques form a separate species group, placed at the base of the clade *Macaca*, being a sister group to all Asian macaques. Presently, their occurrence is restricted to the mountainous regions of Algeria and Morocco [16, 17]. Barbary macaques are largely terrestrial during the day, but climb into trees and sleeping cliffs during the night and also during day-time resting periods [18, 19]. Their variable diet, consisting of the leaves and bark of the evergreen cedar, fruit, seeds, annual herbs, and insects [20], enables them to survive in a variety of habitats. Adults reach a shoulder height of about 40 cm, their head-to-tail length is up to 60 cm. Fully grown males weigh about 18 kg, females 13 kg [21]. Barbary macaques live in female-bonded multi-male, multi-female social groups. Presumably as an adaptation to their habitat, Barbary macaques are seasonal breeders with a mating season in autumn, and a birth season in spring [22]. Females are assertive and frequently approach males to initiate copulations. Their mating system has been termed 'promiscuous' [23, 24].

In this paper, we present spectrographic displays of calls along with a general description of the contexts in which the different calls are uttered, with special regard to the age and sex of the caller. This documentation supplements detailed quantitative analyses of the acoustic morphology of the Barbary macaque vocal repertoire [25]. As this previous paper heavily focussed on the method to describe the acoustic morphology of the vocal repertoire, and the quantitative results, a more illustrative description was lacking. The purpose of the present paper is to make up for this shortcoming.

In the quantitative analysis, we had used a cluster analysis and found that some acoustic configurations occurred more frequently than others within a continuously distributed acoustic space, i.e. these configurations emerged as different clusters and could be defined as 'call types'. However, due to the probabilistic and graded structure of the repertoire, different cluster solutions were appropriate to partition the data set. Therefore, the Barbary macaque call system was viewed as a prime example of a 'graded signalling system' [26]. In the present paper, we aim to illustrate the characteristics of the Barbary macaque vocalizations with spectrographic displays of the calls used in different contexts. The spectrograms document that typically, Barbary macaques produce series ('bouts') of several consecutive calls. We have added photographs of facial gestures which accompany some of the calls presented below.

Method

We recorded the vocal behaviour of Barbary macaques living in an outdoor enclosure at Rocamadour, France (size: 15 ha). The enclosure is a visitor park where monkeys range freely while visitors are restricted to a path. Individuals are well habituated to human observers and are tattooed with an individual code on the inside of the thigh. The monkeys are provisioned with monkey chow provided in feeder huts, and with apples, grain, and seeds

which are spread throughout the park. For details on park management and park size, see Turckheim and Merz [27]. We established five age classes: (1) infants up to the age of 1 year, (2) young juveniles of 1–2 years, (3) older juveniles of 2–3.5 years, (4) subadults: females of 3.5–5 years and males of 3.5–7 years, and (5) adult females older than 5 years and adult males older than 7 years of age [28].

We conducted the recordings between 1987 and 2001 as part of a number of studies on the monkeys' vocal communication [overview in 29]. We used a Marantz cp 430, a Sony WM DC6, or a Sony DAT TCD-D3 or D100 cassette recorders with Sennheiser microphones (KN3 power module and ME80 or ME88 or K6 with ME66 with Sennheiser windscreen) at a distance of 1–10 m. Analogue recordings were subsequently transferred to a DAT tape (Sony TCD-D3 DAT recorder) for storage. We selected calls presented in this paper from a database containing more than 15,000 calls from 92 individually identified subjects, 40 males and 52 females. We used Avisoft (version 3.93, 2001, R. Specht, Berlin) to generate the spectrograms. When available, we complemented the spectrograms with photographs of the facial expressions accompanying the calls depicted. Note, however, that for technical reasons, the video recordings were taken at other times or from other animals than the sound recordings.

Results

Figure 1 shows examples of calls given in highly charged agonistic contexts by members of all age and sex classes. Overall, these calls exhibit a noisy structure. Figures 1a and b present call bouts given by an infant and a juvenile, respectively. Some of these calls show insertions of a periodic window in the otherwise noisy (chaotic) structure of the call [30]. Similarly, the calls depicted in figure 1d recorded from an adult female exhibit diagnostics of period-doubling bifurcations (insertions of subharmonic episodes with approximately $F_0/2$, $3F_0/2$ etc. [see 30 for details]). The juvenile screams presented in figure 1b were given while the subject appeared to recruit allies for support [31, 32], as she was turning her head and looking around. Figure 1e presents calls recorded from an adult male during a 'scream fight' during which a number of subjects sit in an area and scream loudly.

Figure 2 presents calls given in variety of aversive situations. Figure 2a shows calls recorded from an infant while in care of a male alloparent. These calls can be classified as undulated screams. In many cases, males will return infants to their mother either when the mother attempts to retrieve the infant or when the infant attempts to return to its mother [33]. Some males, however, restrain the infant for long periods of time, causing considerable distress for the infant and the mother [33, 34]. In such cases, the screams may also exhibit a more noisy structure, similar to the one depicted in figure 1a. Infant and juvenile screams are individually distinct [35] and mothers can make use of such calls when monitoring the infant's activity [36]. Figure 2b presents calls recorded from a half-year old at dusk during sleeping cluster formation while it was trying to gain access to the same sleeping cluster as the mother, but was being rejected by her [19]. This calling has been viewed as an expression of the parent-offspring conflict [37].

Figures 2c and d show tonal and complex screams recorded from adult females after being threatened and displaced by other group members, respectively. The last three calls of figure 2d exhibit some structural similarity with calls given after disturbances in the surroundings (see fig. 3), illustrating the view that similar sounding calls may be given in very different contexts. Figure 2e depicts a short series of

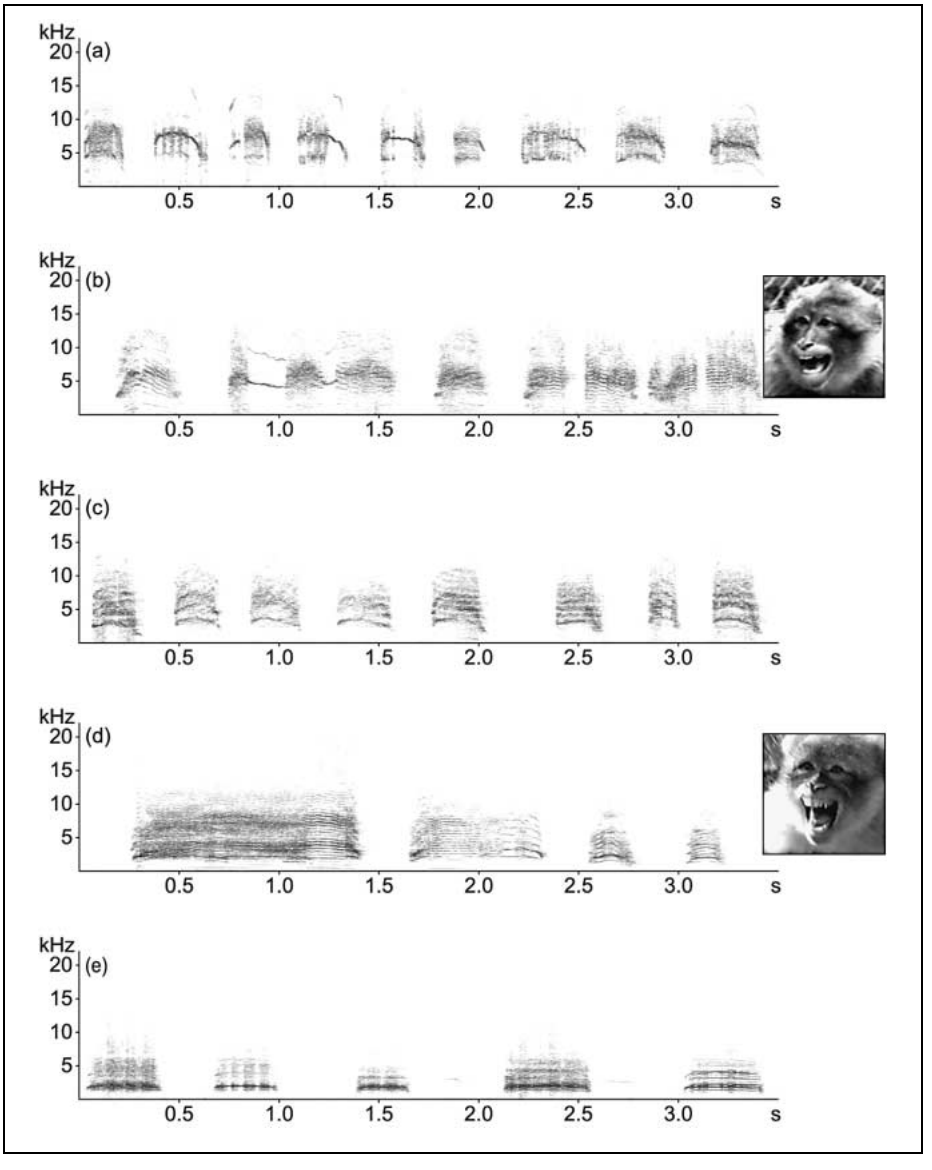

Fig. 1. Noisy and complex screams. Spectrograms (frequency on the y-axis, time on the x-axis) showing (**a**) noisy and complex screams recorded from an infant bitten by its mother; (**b**) complex screams from a 3.5-year-old male who challenged a female and appeared to recruit support from allies. The photograph presents a 4.5-year-old male in a similar situation; (**c**) noisy arched screams recorded from an adult female. She had been threatened by an adult male who was holding her infant, after she had tried to approach him to retrieve it; (**d**) complex screams recorded from an adult female who had been harassed and chased by several other group members. Note the period doubling in the second call from the left. The photographs shows a subadult female screaming; (**e**) noisy and complex screams uttered by an adult male during a male-male scream fight.

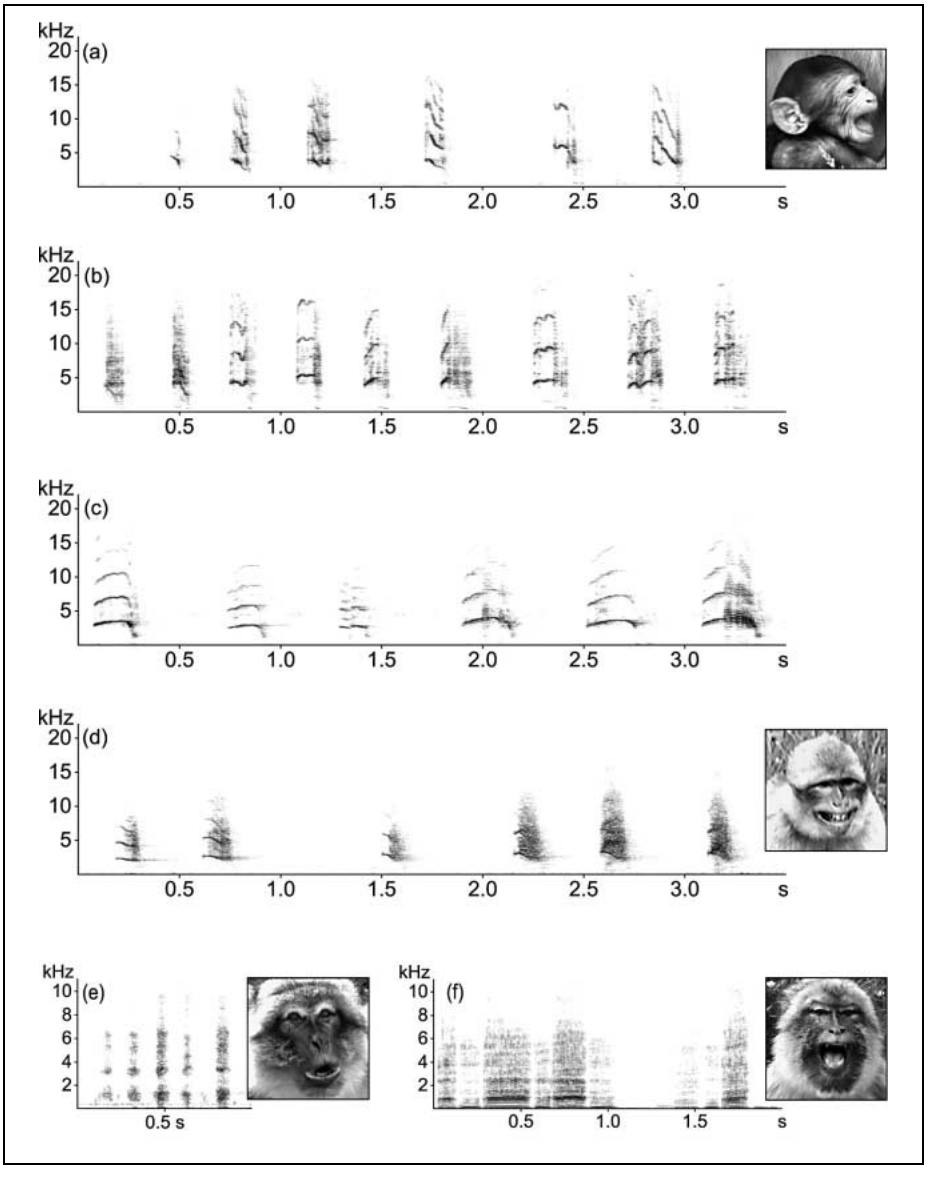

Fig. 2. Modulated and complex screams, pants, and rasping calls. (**a**) Modulated tonal screams recorded from a 2-month-old infant in care of an adult male. The male prevented the infant from returning to its mother by holding it at the ankle; (**b**) squeaks and modulated tonal screams recorded from a yearling who attempted to establish contact with its mother during sleeping cluster formation at dusk. The mother had repeatedly rejected the yearling; (**c**) tonal screams recorded from a 3-year-old female after she had been threatened by an adult male. Note the phase shift in the last call of the sequence; (**d**) complex screams recorded from an adult female who had been displaced from a feeder hut by an adult male. The photograph shows a 3-year-old female with a scared-threat grimace that can accompany such calls. The mouth is open and the teeth are visible; (**e**) pants recorded from an adult

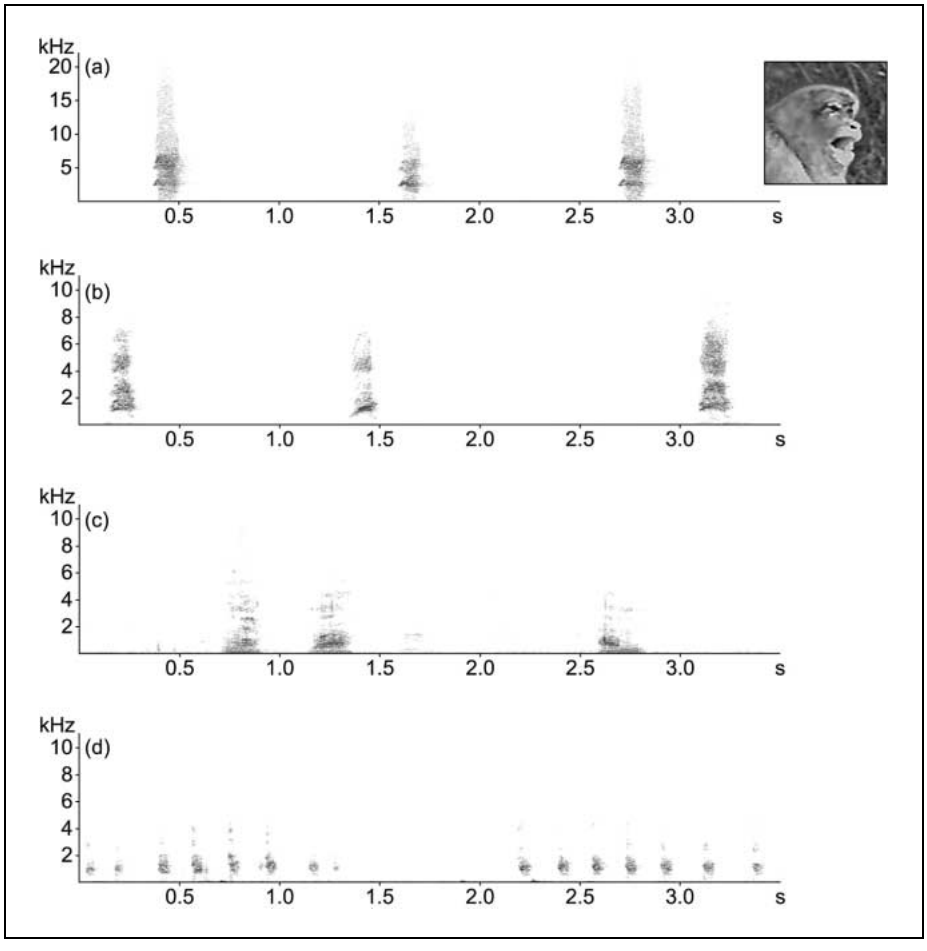

Fig. 3. Shrill barks. (**a**) Shrill barks recorded from an adult female after the animals had been disturbed on their sleeping trees at night. The photograph shows a male sitting in a tree who had spotted a dog and gave shrill barks; (**b**) shrill barks recorded from a juvenile male given in response to a dog in the monkeys' vicinity; (**c**) rasping calls recorded from an adult male given in response to a vulture flying towards a group of monkeys sitting at the edge of a cliff; (**d**) clucking barks recorded from a subadult male given in response to a snake.

female who was threatening another female. The accompanying photograph shows the threat grimace of an adult male: the lips are protruded and the eyebrows are raised; (**f**) rasping call recorded from an adult female who observed a fight in a distance, with the accompanying facial expression: The jaw is dropped and the corners of the mouth are not retracted.

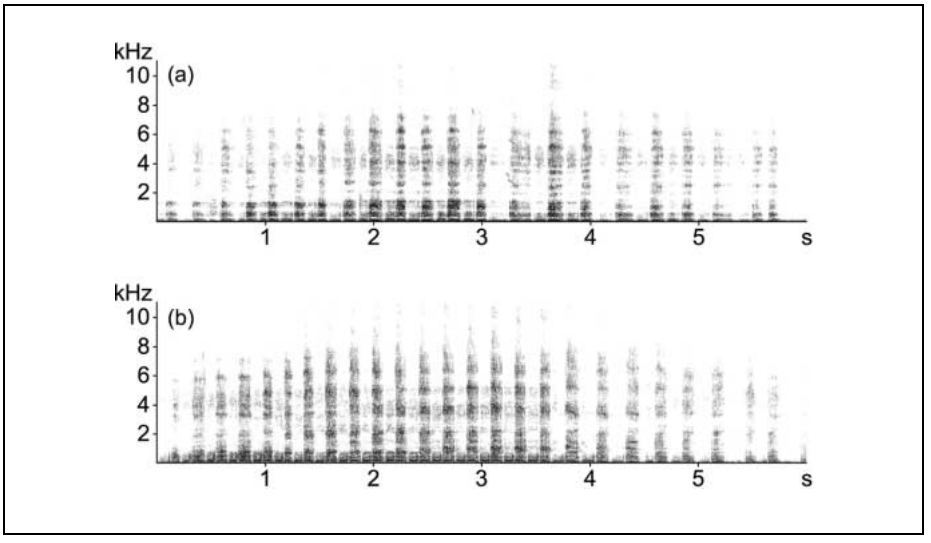

Fig. 4. Oestrus calls. (**a**) Rhythmic pant-grunts recorded from an adult female in oestrus; (**b**) rhythmic pant-grunts recorded from an adult female during copulation.

threat pants given by an adult female. While mild threat displays consist of a stare with the eyebrows slightly raised, a more intense form involves protruding the lips and forming a round opening, often, but not always accompanied by threat pants. These threat pants have a staccato-grunt structure, and the single units making up the call resemble the units of the mating call (see below).

Barbary macaques do not only call when they participate in interactions with other group members, but also when they observe interactions between third parties. In some cases, it appears as if they are supporting one of the parties. Interestingly, these calls may also be given from more than 50 m away from the agonistic interaction. One such call bout is presented in figure 2f, a rasping call recorded from an adult female while watching an agonistic interaction in the distance.

Figure 3 presents examples of calls given in response to different disturbances in the monkey's surroundings. These calls have been described as high-pitched shrill barks [38–40]. An acoustic analysis of this general call type revealed significant variation in relation to the stimulus that elicited the calling. Playback experiments also showed that the subjects themselves were able to discriminate calls given in response to different stimuli [39, 40]. In some cases, animals also emit lower frequency rasping calls (fig. 3c). This is often the case when animals approach the source of the threat and mob it.

Figure 4 shows calls that were given in the mating season. During copulation, females utter a rhythmic series of low-frequency grunts. Males, in contrast, typically remain silent. While in oestrus, females sometimes utter a call that sounds similar to the mating call although the female is not engaged in any mating activity. An analysis revealed that there are structural differences in the single units accord-

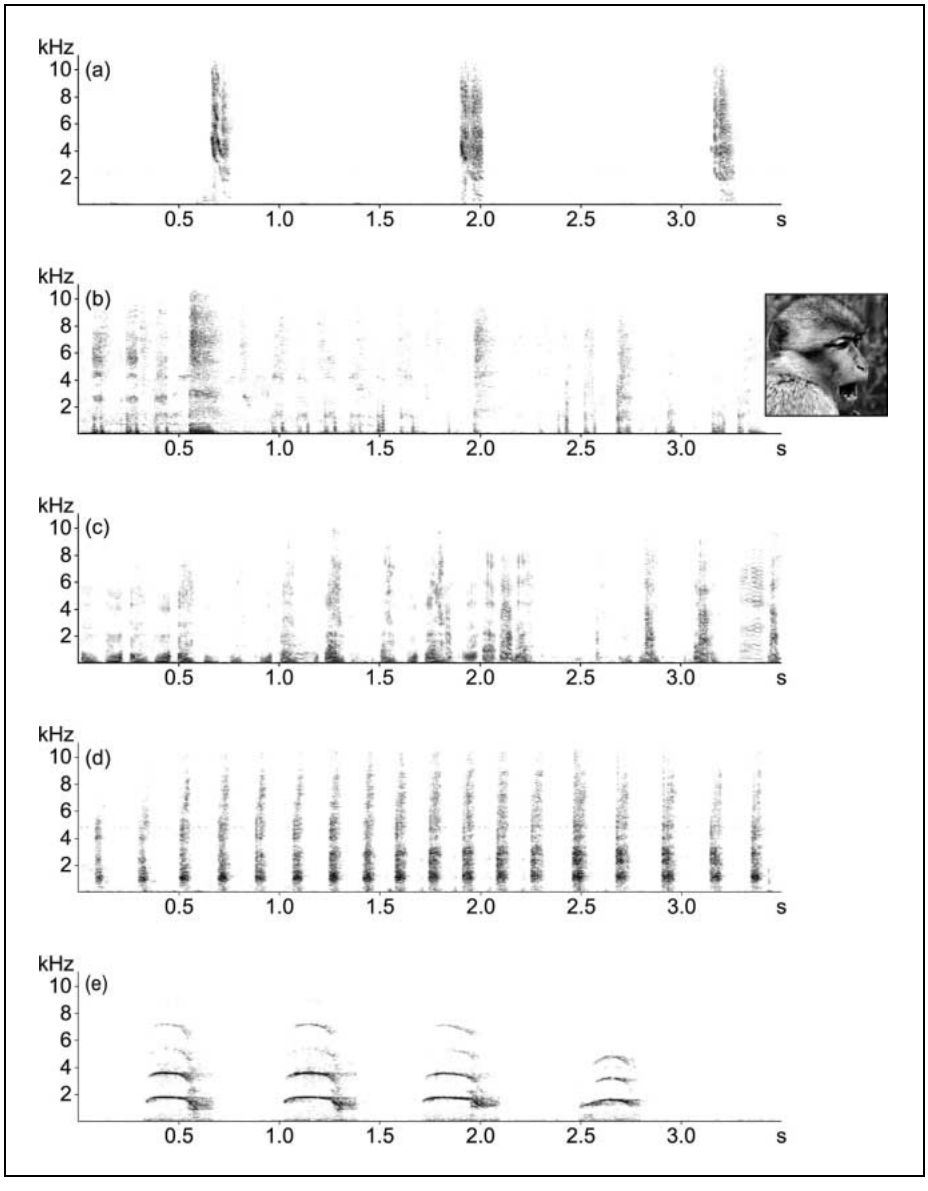

Fig. 5. Squeaks, pants and tonal calls. (**a**) Squeaks uttered by a 3-month-old infant that made its first attempts to climb a branch; (**b**) pants recorded from a group of juvenile males during rough-and-tumble play with the accompanying relaxed open-mouth play face. The lips cover the teeth, and the jaw is dropped.; (**c**) low frequency soft pants given by a subadult female who observed an interaction with a young infant; (**d**) pant barks recorded from an adult female who observed an interaction with a young infant; (**e**) clear calls uttered from an adult female in search of her infant.

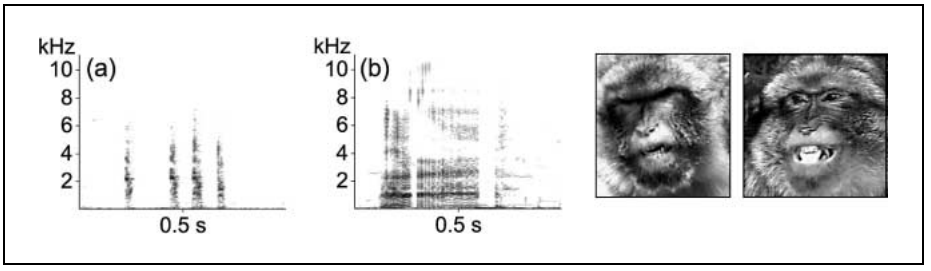

Fig. 6. Gecker and girney. (**a**) Geckers uttered by a 3-year-old juvenile who attempts to make contact with a group of other animals huddling on the ground after descent from the sleeping trees in the morning; (**b**) girney recorded from an adult female during interaction with an infant. This call exemplar also exhibits a grumbling component. The photographs show an adult female and an adult male producing a girney with a chewing jaw movement and the tongue flapping.

ing to whether the call was uttered during copulation or in another situation [29]. Further analysis of the temporal and spectral characteristics of these calls also indicates that there are differences in relation to the phase of the oestrus during which the call is emitted [41]. Playback experiments showed that this variation is perceptually salient to males [41, 42].

Figure 5 presents calls that were given during a variety of situations. Figure 5a shows calls recorded from an infant in a non-social situation while it attempted to climb a branch. Figure 5b presents vocalizations emitted during play, consisting of staccatos of soft aspirated low-frequency grunts. During play, animals typically display a relaxed open-mouth round face [43] while they vocalize [S. Kipper and D. Todt, unpubl. data]. Vocalizations of a similar acoustic structure are also given by adults when they watch infants (fig. 5c). As mentioned before, Barbary macaques vocalize during interactions between other group members. Figure 5d presents an example of a series of pants that were given while the subject was observing a triadic interaction involving an infant (see below). Figure 5e depicts four clear calls recorded from a female whose infant was out of sight with an alloparent. Similar calls could be recorded from females whose dead infant had been removed by the park staff.

Figure 6, finally, shows two call types given while the callers were in close contact with other group members. Figure 6a presents a series of geckers that were recorded from a juvenile who was part of a huddle that broke apart. Such calls may also be recorded from animals who try to establish contact with such a huddle. Figure 6b depicts a 'girney' recorded from an adult female who participated in a so-called 'triadic interaction', also known as 'agonistic buffering' [24, 44–47]. Before and during such episodes, animals proceed through an elaborate greeting procedure that predominantly consists of retraction of the lips and rapid teeth-chattering, while often also rapidly flapping the tongue with the mouth half open. Occasionally, animals also retract the scalp or shake their heads. This behaviour has also been characterized as 'smacking' [21], and may grade into the 'silent bared-teeth display' [43]. Interestingly, girneys can also be heard when the group travels into another area of the park.

Discussion

The vocal repertoire of Barbary macaques can be characterized as variations on a few themes, namely screams, shrill barks, geckers, and low-frequency pants. Occasionally, Barbary macaques produce tonal 'coo'-like calls, and nasally sounding girneys. Intergradations occur frequently, and in our quantitative analysis [25], no unique cluster solution emerged. According to this analysis, we defined as 'call types' those call exemplars that represented cluster centres. However, the delineations between clusters were not always obvious. As we illustrate in this present paper, there was no clear-cut relationship between call types and the situations in which they occurred. For instance, pant calls are given in agonistic encounters when one animal is threatening another, but also when a subject observes an interaction between group members and an infant, clearly an affiliative situation. Likewise, tonal calls were recorded from females that were threatened as well as from females who were in search of their infant. Although noisy and complex screams were most often observed in highly charged contexts such as contact aggression, it is important to keep in mind that this context category encompasses a wide variety of situations. Some call types, for instance noisy screams, are given by members of all age-sex classes. The same is true for shrill barks, with the exception that infants do not produce them. Highly undulated screams, in contrast, are most frequently given by infant and juvenile macaques, and only rarely by members of older age classes [25].

We cannot rule out the possibility that extended periods of observations of wild Barbary macaques would reveal additional calls or differences in call usage. However, during a 4-week observation period on wild members of this species living in the Middle Atlas in Morocco, we found no differences in terms of the acoustic structure or usage of alarm calls and screams [19]. Also, Semple's description of the acoustic characteristics and usage of mating calls by Barbary macaques living in Gibraltar [41, 42] confirmed the view that our observations reflect species-typical vocal behaviour.

It still remains difficult to compare the repertoires of different species as there is no standard method to classify call types. Also, the characterization of calls either according to presumed function or context may vary from study to study. To date, there are few comprehensive studies on the vocal repertoires of other macaques species, for instance Green's study on Japanese macaques, *M. fuscata* [10], Palombit's description of the vocal repertoire of on long-tailed macaques, *M. fascicularis* [9], or Hohmann's overview of the calls of the lion-tailed macaques, *M. silenus* [11]. Most other studies addressing macaque vocal behaviour dealt with more specific aspects, for instance the use of 'food calls' in toque macaques, *M. sinica* [48], acoustic variation within and between contexts [32, 49], or relation to age and sex [50–52], and individual differences in vocalizations [53–55]. It is worth noting that in contrast to some other macaque species [48, 56], we never observed any vocalizations in the context of encountering food or highly preferred food. In sum, it seems that – despite the differences in the set-up and presentation of the above-mentioned studies – Barbary macaques, the only African macaques, use considerably more harsh and noisy vocalizations and have a very limited use of 'coo calls' compared to the Asian macaques. This seems also to be true in comparison with another terrestrial macaque, the stump-tailed macaque, *M. arctoides* [57].

The investigation of the structure of vocal repertoires of different species is particularly interesting in the light of the question of which factors underlie repertoire morphology. Traditionally, repertoires have either been described as 'graded' or 'discrete', or a mixture of the two [26, 58, 59]. A graded signal system is characterized by continuous acoustic variation between and/or within signal types, with no obvious distinct boundaries that allow a listener to discriminate easily between one signal type and another. Discrete repertoires, on the other hand, contain signals with no intermediates between call types. Marler [26, 59] hypothesized that graded vocal repertoires should evolve when individuals inhabit relatively open habitat and interact at high rates and at close range with conspecifics. In contrast, discrete vocal repertoires should be favoured when auditory signals must operate without accompanying visual or other contextual cues; for example, in forest habitats or when being broadcast over long distances. At first glance, the Barbary macaques' repertoire fits with Marler's hypothesis. However, Marler also hypothesized that long-distance calls should be acoustically distinct because other cues may be lacking. With regard to the Barbary macaques' shrill barks, this certainly is not the case.

By now, a number of studies have revealed that Marler's predictions are not always met. For instance, the alarm calls of female baboons grade into contact calls [60], and similarly, male baboon alarm wahoos grade into contest calls [61]. Both female barks and male wahoos are used in long-distance communication, and one would assume that there is some cost to ambiguity. Arboreal New World monkeys generally exhibit calls with a very different structure. Their repertoires mainly consist of high-frequency tonal calls, twitters, chucks and a variety of peeps [8, 62]. Yet, at the same time, these calls exhibit pronounced inter- and intra-call type variation [63]. To make matters even more complicated, the repertoire of the arboreal squirrel monkeys, *Saimiri sciureus*, consists not only of call types that are typical for arboreal species, such as chatters and twitters, but also of a large variety of calls that are typically attributed to terrestrial monkeys, i.e. screams, barks, caws, growls and cackles [6, 64]. Furthermore, there is considerable variation within and between call types [65]. Similar 'mixed' vocal repertoires could be found in arboreal Old World monkeys, such as many guenons [66]. Another example are the semi-terrestrial red-fronted lemurs, *Eulemur fulvus*, which produce a number of vocalizations that can typically be attributed to terrestrially living species, for instance croaks, grunts, and woofs [67]. However, during close contact social interaction, they also utter high-frequency tonal peeps [C. Fichtel and K. Hammerschmidt, unpubl. data]. Possibly, the habitat type does not so much determine the extent of gradation within call types, but rather the overall diversity of call types [52]. A systematic comparison would surely be warranted.

Currently, it seems that no single factor can account for the variation in repertoire diversity. Other factors such as body size, phylogenetic descent, and social structure presumably also play a role in shaping a species' repertoire [11, 68]. As these factors are also related to one another, it will be difficult to extract the primary driving forces. Nonetheless, we believe that a systematic study of the diversity and variability of different non-human primate repertoires could provide important insights into the selective pressures and evolutionary constraints operating on the vocal behaviour of our closest living relatives.

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