Sex differences in vocal communication among adult rhesus macaques ☆

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Abstract

In female-bonded primate species, females invest more time in grooming than males, and the majority of this grooming occurs in intra- rather than intersexual interactions. These clear sex differences in sociability reflect females' need to forge and maintain complex networks of social relationships with other females in the group. Increasing evidence indicates that vocal signals can have a similar function to grooming in mediating social interactions and relationships, and sex differences in patterns of use of vocal communication comparable to those seen for grooming might therefore be expected to occur. In this study of free-ranging adult rhesus macaques, we tested for such patterns, focusing on the frequency of utterance of three types of vocalisations given during close-range social interactions: coos, grunts, and girneys. As predicted, we found that females gave such calls significantly more frequently than males and also directed more of these vocalisations towards other females than to males; males' rate of vocalising towards the two sexes was not significantly different. To our knowledge, these results provide the first evidence for a sex difference in the rate of production of social vocalisations among adult nonhuman primates. The finding that increased sociability is associated with increased reliance on vocal communication may have important implications for theories of language evolution.

1. Introduction

In female-bonded primate species, adult females spend significantly more time involved in grooming than adult males and also devote a much higher proportion of their time to same-sex rather than mixed-sex grooming interactions (e.g., Cooper & Bernstein, 2000; Kaplan & Zucker, 1980; Sugiyama, 1971). These differences reflect the fact that in such social systems, females need to spend more time in servicing networks of social relationships and do so particularly with animals of their own sex (Seyfarth, 1977). These social networks are the fundamental constituents of the social system (Dunbar, 1988); understanding the way they are maintained is therefore essential for understanding the evolution of primate sociality. While studies of primate social networks have typically focussed very strongly on grooming as the key social bonding mechanism, grooming is not the only means by which primates may regulate their social interactions (Seyfarth & Cheney, 1993). Indeed, an increasing body of work indicates that primate vocal signals can fill a very similar niche to grooming in mediating social exchanges and relationships (Silk, 2002).

Bauers and de Waal (1991), for example, found evidence that the coo vocalisations of female stumptailed macaques (*Macaca arctoides*) facilitate positive social interactions; approaches preceded by coos were significantly more likely to lead to friendly contact than if no such call had been given. Similarly, observational studies of rhesus macaques (*Macaca mulatta*) by Silk, Kaldor, and Boyd (2000) suggest that the grunts and girneys given by females when approaching others signal benign intent, with calling during approaches associated with both a lower likelihood of aggression from the approaching animal and reduced numbers of submissive gestures by the animal being approached. A study by

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Cheney, Seyfarth, and Silk (1995) indicated that the post-conflict grunts of female chacma baboons (*Papio hamadryas ursinus*) play a role in reconciling opponents after aggression. Female subjects who had recently been attacked by a more dominant female responded less strongly to playback of the scream of the attacker if that female had grunted to them following the attack, indicating that these post-aggression grunts serve to mollify defeated opponents. These studies, along with many others of a similar nature (e.g., Mori, 1975; Palombit, Cheney, & Seyfarth, 1999), highlight the importance of vocalisations—in addition to grooming—in mediating primates' social interactions and, ultimately, their relationships.

If vocal communication is important in supporting social networks and supplements grooming in this respect, it would be predicted that we should see patterns of intersexual variation in the use of vocal signals similar to those seen for grooming. In the case of female-bonded species, adult females should not only vocalise more than adult males but also vocalise more often towards members of their own than the opposite sex. To our knowledge, no study has yet tested for these patterns of variation in vocal communication. A sex difference in overall rate of vocalisation (also known as volubility) was identified in infant vervet monkeys by Locke and Hauser (1999), who found that females vocalised significantly more often than males. In their study, however, most vocalisations were care elicitation calls directed at mothers; whether the sex difference in infant volubility translates into a similar bias in adulthood, when social networks are fully established, is unknown.

Data on sex differences in patterns of vocal communication are also relevant to current ideas relating to language evolution. Dunbar (1993) has argued that the pressure to maintain social networks as group size increased during human evolutionary history may ultimately have driven the evolution of language as a novel social bonding mechanism. According to this theory, when group size reached a point where the time demands of grooming became unmanageable, language evolved as a more time-efficient 'vocal grooming' mechanism (Dunbar, 1993). Extending this line of logic, it has been proposed that the selective pressures driving language evolution would have acted more strongly on the nondispersing sex, the members of which needed to establish and service a larger and more complex network of long-term relationships (Dunbar, 1996). This latter hypothesis would be supported by evidence from nonhuman primates indicating that even in the absence of language, vocal communication is more important for the philopatric sex, members of which form the core of the group.

In this study, we set out to investigate whether sex differences in primate social communication, well documented in relation to grooming, extend also to vocal communication. The overall rate of production of three types of vocalisations given during close-range social interactions—coos, grunts, and girneys—was examined among free-ranging adult rhesus macaques (*M. mulatta*).

This rate was compared between males and females. Then, for each sex separately, the rate of vocalisation towards the two sexes was compared.

2. Methods

2.1. Study site and subjects

This study was carried out in a population of free-ranging rhesus macaques on the island of Cayo Santiago, Puerto Rico. This population is provisioned daily with monkey chow placed in one of three large feeding corrals, and water is available *ad libitum* from a number of drinking troughs around the island. Rhesus macaques live in multi-male, multi-female groups. Females are philopatric and consequently form the core of the social group with established social relationships and networks. Males, particularly sexually mature males, assume a more peripheral position in the social structure.

Data for this study were collected during observations of one group of rhesus macaques (Group S). Study subjects were 16 adult females and 7 adult males. Data were only collected from adult animals in this study as it is only in adulthood that social networks are fully established (Datta, 1988).

2.2. Data collection

Data were collected during 15 min focal follows from March 27 to June 12, 2006, between 0700 and 1430 h. A total of 182 and 46 h of data were collected for females and males, respectively. Throughout the study period, focal individuals (except oestrous females) were sampled at least once every 2 days. The order in which focal animals were followed was randomised each day, and focal observations of the chosen animal began on locating them, unless the subject was sleeping, in oestrus or in the feeding corral. The daily provision of food on Cayo Santiago meant that monkeys' vocalisation rates were significantly elevated during this time. Feeding in the corral was also highly competitive due to the nature in which it was carried out, making morning feeding time highly artificial, not resembling a natural setting. Animals were therefore not followed while in the feeding corral. Data were not collected from females while they were in oestrus, due to their unusual behaviour during this period (Sahi, 2003). If the subject was lost at any point during the focal watch, the observation was suspended until the animal was found again. The focal watch was abandoned if the subject was not found after 30 min.

Recordings of vocal bouts were made using a Marantz PMD670 solid-state recorder and Sennheiser MKH416 microphone to allow quantification of the rate of production of vocalisations. As this study relates to social communication, only grunts, coos, and girneys were recorded; these three types of calls are given in close-range—generally affiliative—social contexts (Erwin, 1975; Hauser, Evans, & Marler, 1993; Rowell & Hinde, 1962; Silk et al., 2000) and

are therefore most relevant to the hypothesis to be tested. Hereafter, we shall refer to all of these calls as 'social vocalisations'. Where the observer was confident that an individual animal was clearly the intended receiver of the vocalisation, based on the behaviour of signaller and (assumed) receiver, and in particular the direction of gaze of the signaller, the age class and sex of this animal were noted.

2.3. Assessment of rate of production of social vocalisations

Acoustic analysis was carried out using Raven Lite 1.0 software (Bioacoustics Research Program, Cornell Lab of Ornithology). Each individual's overall rate of production of social vocalisations was calculated from the recordings made during their focal watches. A bout was determined as a single vocalisation or a train of vocalisations in which calls were separated from others by <0.1 s; a gap greater than this was judged to be sufficiently long as to represent a break between bouts. This classification was based on initial inspection of the spectrograms and was used to provide an objective and repeatable measure of what constituted a vocal bout.

2.4. Statistical analysis

Data were tested for normality using a Kolmogorov–Smirnov test and found not to differ significantly from a normal distribution. One-way analysis of variance was used to compare the rate of production of social vocalisations of males and females. In addition, three separate sets of analyses were carried out to test for differences between the sexes with respect to whom they directed their calls towards. In the first analysis, for each sex, paired t tests were used to compare the rate of production of social vocalisations towards all males and females (regardless of age) in the group. This first analysis was then repeated using data on vocalisations directed only towards adult animals. Finally, this second analysis was repeated with the data on vocalisations towards adults only, having been corrected for the different numbers of adults of each sex available as potential receivers of the signal. For this, data on males' rate of vocalising towards males were multiplied by 16/6 (the number of adult females to whom they could vocalise divided by the number of other adult males) and data on females' rate of vocalising to males were multiplied by 15/7 (the number of other adult females to whom they could vocalise divided by the number of adult males). This adjustment took account of the fact that a higher rate of vocalisation to adult females compared to adult males might be expected, purely as a result of the fact that there were more adult females in the group to whom an individual could potentially vocalise. As six separate tests were carried out to look at differences within sexes in rate of vocalisation to males and females, we controlled the type I error rate by sequential Bonferroni tests (Rice, 1989), using a Bonferroni adjustment (k) equal to six. All analyses were carried out using SPSS v15; all tests are two tailed.

3. Results

There were marked sex differences in the rate of production of social vocalisations, with females vocalising significantly more often than males [ANOVA: $F(1,21)=28.58$, $p<.001$, Fig. 1]. For vocal bouts where the animal towards which the vocalisation was directed could confidently be inferred, females vocalised significantly more frequently to females than to males [mean to females=3.13 bouts/h; mean to males=0.14 bouts/h; paired t test: $t(15)=7.54$, $p<.001$, Fig. 2A]. This difference remained when only vocalisations directed at adults were examined [mean to adult females=2.72 bouts/h; mean to adult males=0.08 bouts/h; paired t test, $t(15)=6.78$, $p<.001$] and after correcting these data for the relative numbers of adult males and females in the group [mean to adult females=2.72 bouts/h; corrected mean to adult males=0.17 bouts/h; paired t test: $t(15)=6.36$, $p<.001$]. The results of these three t tests remain significant after Bonferroni correction. By contrast, males did not direct significantly more social vocalisations towards either sex [mean to females=0.13 bouts/h; mean to males=0.04 bouts/h; paired t test: $t(6)=1.97$, $p=.096$, Fig. 2B]. This lack of difference remained when only vocalisations directed at adults were considered [mean to adult females=0.11 bouts/h; mean to adult males=0.04 bouts/h; paired t test: $t(6)=1.46$, $p=.194$] and after correcting for the relative numbers of adult males and females in the group [mean to adult females=0.11 bouts/h; corrected mean to adult males=0.08 bouts/h; paired t test: $t(6)=0.65$, $p=.538$].

4. Discussion

This study investigated sex differences in the rate of production of social vocalisations—grunts, coos, and girneys—among adult rhesus macaques. Significant variation was found between the sexes, with females vocalising
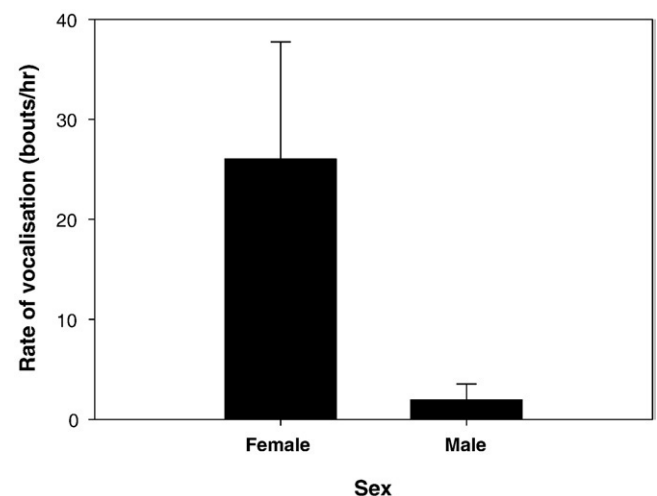

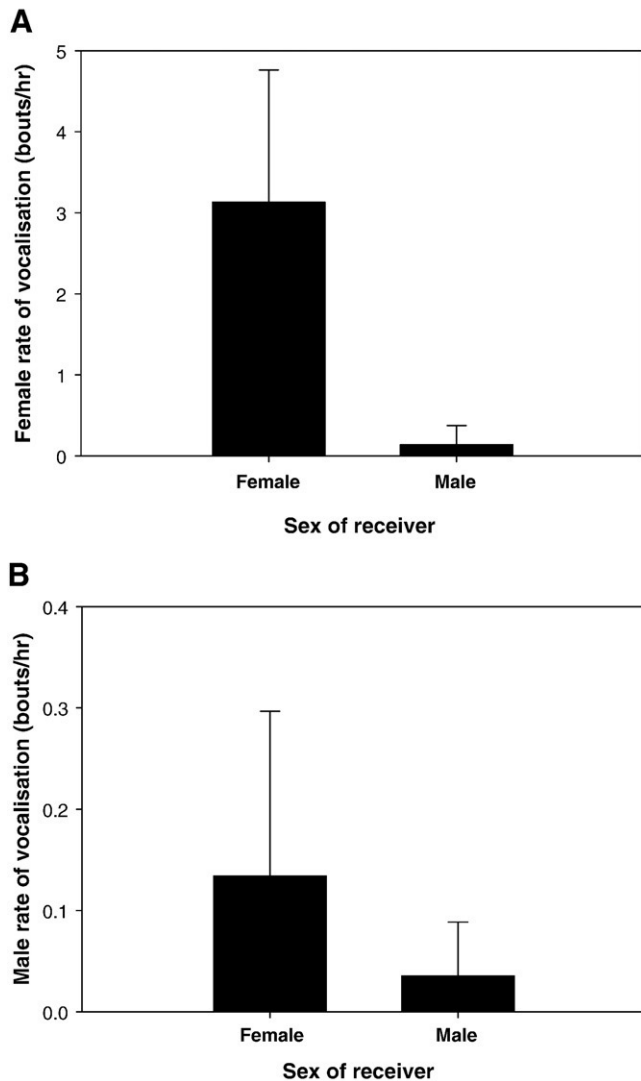Fig. 1. Comparison between male and female volubility. Error bars indicate mean+1 S.D.

A

B

Fig. 2. Comparison between volubility towards female and male receivers for (A) female and (B) male subjects. Error bars indicate mean+1 S.D.

markedly more often than did males. Females also directed more of their vocalisations towards other females than to males, whereas males' rate of vocalisation towards the two sexes was not significantly different. Our results complement a body of literature from female-bonded primate species that indicates, based on grooming data, that females are by far the more sociable sex. For rhesus macaques at least, these clear sex differences in sociability extend to vocal as well as tactile modalities of social communication.

These findings suggest, firstly, that the pressure to service social networks leads to an increased dependence on vocal communication. This provides support to Dunbar's (1996) idea that during human evolution, selection for advanced vocal abilities acted more strongly on the sex that forms the core of the society than on the dispersing sex. Grooming and vocalisations differ in important ways; perhaps most importantly, time constraints may limit the amount of grooming that can be done in a day and the number of

grooming partners but are very unlikely to affect how many vocal signals can be produced or the number of individuals to which vocal signals can be directed. As a result, social vocalisations may be used to regulate relations with a much broader range of individuals than is possible by grooming alone. In addition, the time and opportunity costs of grooming contrast markedly with the low-cost nature of affiliative vocal signals (Silk, 2002). Seyfarth and Cheney (1993) have highlighted the urgency of evaluating the relative importance of vocalisations and grooming in the maintenance of primate social networks, and this remains a key challenge in the study of primate sociality.

The sex differences in adult rhesus macaques' rate of vocalisation documented here contrast markedly with the lack of evidence for such differences in our own species. Mehl et al. (2007) recently debunked the idea that in Western cultures, women talk more than men; their data revealed no significant variation between the sexes with respect to the number of words spoken per day. This lack of difference may reflect the fact that modern humans are not female-bonded in the sense that this term is used to describe nonhuman primate social structure. Data on daily word use among traditional societies where female kin networks are strong, and matrilocality is the norm, are needed to assess whether the link between sociality and reliance on vocal communication seen in the present study is relevant also to humans.

Further data on a range of female-bonded primate species are now needed to assess the broader generality of the findings of the present study. Perhaps the most critical test will be to examine male-bonded primate species, in which it would be predicted that males would show a higher rate of production of social vocalisations than females. Such studies will provide invaluable data to test the idea that increased sociability is associated with increased reliance on vocal communication and, in consequence, will have implications for theories that link language evolution to the size or complexity of the social group.

Acknowledgments

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