Bystanders affect the outcome of mother–infant interactions in rhesus macaques

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Animal communication involves the transfer of information between a sender and one or more receivers. However, such interactions do not happen in a social vacuum; third parties are typically present, who can potentially eavesdrop upon or intervene in the interaction. The importance of such bystanders in shaping the outcome of communicative interactions has been widely studied in humans, but has only recently received attention in other animal species. Here, we studied bouts of infant crying among rhesus macaques (*Macaca mulatta*) in order to investigate how the presence of bystanders may affect the outcome of this signalling interaction between infants and mothers. It was hypothesized that, as crying is acoustically aversive, bystanders may be aggressive to the mother or the infant in order to bring the crying bout to a close. Consequently, it was predicted that mothers should acquiesce more often to crying if in the presence of potentially aggressive animals. In line with this prediction, it was found that mothers gave infants access to the nipple significantly more often when crying occurred in the presence of animals that posed a high risk of aggression towards them. Both mothers and infants tended to receive more aggression from bystanders during crying bouts than outside of this time, although such aggression was extremely rare and was received by less than half of the mothers and infants in the study. Mothers were also found to be significantly more aggressive to their infants while the latter were crying than outside of crying bouts. These results provide new insight into the complex dynamics of mother–offspring conflict, and indicate that bystanders may play an important role in shaping the outcome of signalling interactions between infants and their mothers.

Keywords: bystanders; audience; communication; crying; mother–offspring conflict; rhesus macaque

1. INTRODUCTION

The study of animal communication has tended historically to follow a rather rigid paradigm in which communication is seen as the transfer of information from a signaller to one or more receivers (Bradbury & Vehrencamp 1998). However, communication does not usually take place in isolation, but rather within a broader social context of third-party ‘bystanders’ (Johnstone 2001), and the importance of such individuals within a broader animal communication network has only quite recently received due attention (McGregor 2005). Work in this area has tended to focus on how bystanders may acquire and then act upon information about the participants in signalling interactions (Bonnie & Earley 2007). In this framework, individuals external to the dyadic interaction are viewed as eavesdroppers within the network (e.g. Doutrelant & McGregor 2000; Peake *et al.* 2002; Aquiloni *et al.* 2008).

Network members may have a more direct impact on signalling interactions, however. For example, Slocombe & Zuberbühler (2007) have recently documented an effect of bystanders on the acoustic structure of the calls made by wild chimpanzees. In this study, it was found that victims of

aggression, when in the presence of a third party dominant to the aggressor, modified their recruitment screams in such a way as to exaggerate the level of aggression being experienced. Bystanders may not just shape the behaviour of the signaller, but may also modify their behaviour towards either the signaller or the receiver in such a way as to affect the outcome of the interaction and the fitness benefits/losses incurred by each party. The extent to which bystanders influence the result of signalling interactions between pairs of individuals in this way is at present, however, very poorly understood in any species other than our own. Here we explore this issue, using infant–mother communication among rhesus macaques (*Macaca mulatta*) as a model signalling interaction.

Among non-human primate infants, crying represents the principal form of vocal communication (Maestripieri & Call 1996). Crying is particularly characteristic of interactions involving conflict between mother and offspring, such as when infants are rebuffed in their attempts to gain access to the nipple. While the function of such crying remains unresolved, it has been proposed that these calls have been selected to be deeply aversive to mothers (Todd 1988; Rendall & Owren 2002). Crying is, however, also likely to be perceptually noxious for other neighbouring

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animals. The highly aversive nature of infant crying may, in consequence, lead bystanders to be aggressive to the mother or the infant, in order to bring the crying bout to a close. Mothers of crying infants may as a result modify their response to crying according to their social environment; if dominant, potentially aggressive animals are close by, mothers would be predicted to be more likely to allow the infant access to the nipple than if no such animals are in proximity. We tested this prediction in a free-ranging population of rhesus macaques.

2. MATERIAL AND METHODS

(a) Study site and subjects

This study was carried out in the free-ranging population of rhesus macaques on the island of Cayo Santiago, Puerto Rico. Data were collected during observations of one group of animals (group S). Within this group, 11 adult females had dependent infants throughout the study period. The mean age of these infants at the start of data collection was 271 days (range 145–324 days). The group consisted of seven matriline, with matriline defined here as a group of animals all directly descended from the same currently living female, as well as that female herself.

(b) Data collection

Focal and *ad libitum* data were collected from 10 September 2005 to 17 January 2006, between the hours of 07.00–14.30. Nine mothers were selected at random as focal animals and data were collected for each of these animals until the birth of their new infant (or the end of the study if no infant was born). The order in which focal animals were followed was randomized daily. 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. Focal watches lasted 60 min, during which all occurrences of a number of key behaviours were noted. Any instances of aggression directed to the focal mother or her infant, including both non-contact (open mouth or vocal threats, lunge, charge or chase) and contact (push, hit, grab, bite and attack), were noted, along with the time of occurrence and the type of aggression.

All crying bouts of the focal mother's infant were recorded using a Marantz PMD670 solid-state recorder in conjunction with a Sennheiser MKH416 microphone. In addition, a range of contextual data for the crying bout were spoken onto the recording after the infant was silent. These data were as follows: time of the start of the bout; whether the infant made contact with the nipple or not (and the time at which contact occurred if applicable); the number and identity of any bystanders, defined as animals within 2 m of the focal mother; the occurrence of aggression towards the mother or the infant during the crying bout as well as the nature of the aggression and the identity of the aggressive animal. The data collected on whether contact was made with the nipple reflect the implicit assumption of this study that during each crying bout, the infant was attempting to gain access to the nipple; this assumption is strongly supported by our observations in the field. If the mother was moving during the crying bout, this was also noted and data on bystanders were not collected for this crying bout. Occasionally, an infant would make contact with the nipple, then lose it again and recommence crying. In this case, access was scored and only data related to the first crying bout were analysed.

If during a focal watch a nearby, clearly visible infant began crying, this bout was recorded along with the contextual data as described above. If during this bout the focal infant started crying, recording switched to that infant. In this way, the data provided by focal infants' crying bouts were supplemented with the data recorded *ad libitum* during these focal samples.

Each crying bout was classified according to whether there were (i) no bystanders; (ii) only bystanders subordinate to the mother, or dominant to but in the same matriline as the mother; or (iii) at least one bystander dominant to and not in the same matriline as the mother. Category (ii) was considered to contain bystanders that posed a low risk of aggression to the mother, as the only dominant animals in such groups were in her matriline, and thus unlikely to make a serious attack on her. Category (iii) was considered to contain animals that posed a high risk of aggression to the mother, as such animals could show high-level aggression towards her. For ease, categories (i)–(iii) will be abbreviated to 'no bystanders', 'low-risk bystander(s)' and 'high-risk bystander(s)', respectively.

(c) Statistical analysis

Two different statistical tests were used. For comparisons across the three bystander categories, the dataset contains missing values and therefore Mundry's (1999) permutation test for related samples with missing values was employed, maintaining the position of the missing values and running 10 000 permutations. This test is a variant of Friedman one-way ANOVA, and is appropriate for analyses of datasets with missing values, in which sample sizes are small, data are not normally distributed and the same individuals are used in the different pairwise comparisons (Mundry 1999). The same test was used for the *post hoc* pairwise comparisons between bystander categories; as three such comparisons were carried out (no bystanders versus low-risk bystanders, no bystanders versus high-risk bystanders and low-risk bystanders versus high-risk bystanders), we controlled the type I error rate by sequential Bonferroni tests (Rice 1989), using a Bonferroni adjustment (k) equal to 3. Mundry's (1999) permutation test was also employed for single pairwise comparisons that involved missing values, in which circumstances it provides a powerful alternative to Wilcoxon matched pairs signed-rank test. It is important to note that the sample size associated with this permutation test is the total number of animals in the dataset analysed in each case, rather than the number for whom data are available for all/both bystander categories. Single pairwise comparisons of data with no missing values were carried out using Wilcoxon matched-pair signed-rank tests, with exact significances reported due to the small sample sizes (Siegel & Castellan 1988; Mundry & Fischer 1998).

(i) Do bystanders affect the outcome of the crying bout?

Crying bouts by infants led to one of two discrete outcomes: the mother either allowed the infant access to the nipple or did not allow such access. In the first step of the analysis, focal and *ad libitum* data were combined to calculate mean rates of gaining access to the nipple by infants according to whether there were no bystanders, low-risk bystander(s) or high-risk bystander(s). In an initial exploration of how mothers' responses to crying by their infants were related to the bystanders' presence or type, for each mother, the percentage of crying bouts in which access was given was calculated for each category of bystanders. Within each bystander category, a mean percentage was then calculated across mothers. These analyses provide an overview of how mothers' responses to

infants may be linked to the presence or type of bystanders. To examine the statistical significance of any difference identified in access rates between bystander categories, for each mother, the percentage of crying bouts in which access was given was calculated for the three bystander categories; this was done only where at least four bouts were available for a particular bystander category. Mundry's (1999) permutation test was used to compare access rates across the three bystander categories and between the three possible pairs of bystander category (no bystanders versus low-risk bystanders, no bystanders versus high-risk bystanders and low-risk bystanders versus high-risk bystanders).

(ii) *Does bystander number explain any effect of high-risk bystanders?*

One potential explanation for an apparent effect of the presence of high-risk bystander(s) on mothers' responses, if one is found, is that it is an artefact of groups containing high-risk bystander(s) having an effect on mothers simply because they happen to be larger than groups containing only low-risk bystander(s). In other words, there may be a bystander effect, but it is related to the number of bystanders rather than the presence of potentially aggressive animals *per se*. Two analyses were carried out to test this alternative explanation. For both analyses, focal and *ad libitum* data were combined, and mean values of bystander number were calculated for each mother either for each bystander category or according to the outcome of the bout. In the first analysis, bystander numbers were compared between low- and high-risk bystander groups, using Mundry's (1999) permutation test. In the second analysis, mean bystander group sizes were compared between crying bouts where access was given and those where access was not given using Wilcoxon matched-pair signed-rank tests.

(iii) *Does infant age explain any effect of high-risk bystanders?*

Another possible explanation for any effects of high-risk bystander(s) is that both the likelihood of mothers giving access and the presence of high-risk bystanders are negatively related to infant age. Younger infants may, in theory, spend more time in the presence of dominant bystanders unrelated to their mother (who may be attracted to such infants) and also experience less refusals by their mothers (due to their young age). This confounding effect of infant age could give rise to an apparent effect of high-risk bystanders on responses to crying bouts. To explore this possibility, we tested whether mean infant age differed between crying bouts (i) where high-risk bystander(s) were present and those where either no bystanders or only low-risk bystander(s) were present, and (ii) where access was given and those where it was refused. Focal and *ad libitum* data were combined for these analyses. Mundry's (1999) permutation test was used for the former analysis and the Wilcoxon matched-pair signed-rank test was used for the latter.

(iv) *Is crying associated with increased aggression from bystanders towards mothers or infants?*

If infant crying is highly aversive, we might expect to see mothers and/or infants receiving more aggression during crying bouts than outside of this time. This possibility was explored using exclusively the focal data, as it was only here that rates of aggression outside of, as well as during, crying bouts could be calculated. Small sample sizes, owing to the fact that only four mothers and four infants suffered aggression during crying bouts, preclude formal statistical analyses of these data;

therefore, only descriptive results are presented. Considering mothers first, for each focal mother, the rate of aggression received was calculated (i) per hour of crying bouts by their infant and (ii) per hour of observation time outside of crying bouts. The mean of these two rates across all focal females was then calculated and the mean rate of aggression during crying bouts was divided by the mean rate of aggression outside of this time. This gives an indication of how much more or less frequently aggression towards focal mothers occurred during crying bouts. Exactly the same procedure was then carried out for focal infants to quantify their relative rates of aggression received during and outside of crying bouts.

(v) *Is crying associated with increased aggression from mothers towards their own infants?*

Finally, if crying by infants is aversive to mothers and may also lead to aggression directed to mothers and infants, it would be expected that mothers might try to punish noisy infants to whom they are not willing to provide access. Such physical punishment may in the long run condition infants to cease crying. This was again tested using the focal data only, for the reasons described above. To give an indication of how much more or less frequently aggression by mothers to their infants occurred during crying bouts, the mean rate of aggression by mothers to infants during crying bouts was divided by the mean rate of aggression outside of this time. As most focal mothers were aggressive at least once to their infant, the difference between these time periods could be tested statistically. Mundry's (1999) permutation test was used to compare mean rates of aggression by mothers during and outside of crying bouts. It should be noted that this comparison does not take into account proximity of the infant to the mother and thus results should be treated accordingly. Crying infants are invariably very close to mothers while non-crying infants may be further away and often out of sight of mothers, and are therefore potentially less likely to be the target of maternal aggression.

All statistical analyses were carried out using SPSS v. 15; all tests were two-tailed.

3. RESULTS

Data were recorded on 149 crying bouts that occurred during the 220 hours of focal watches (mean rate of occurrence = $0.68 \text{ bouts h}^{-1}$) and on 159 additional bouts that were recorded *ad libitum*. Crying bouts lasted a mean of 46.0 s (range 1.1–430.0 s).

(a) High-risk bystanders appear to affect the outcome of the crying bout, but low-risk bystanders do not

It was found that when no bystanders were present within 2 m, mothers gave access to the nipple following an average of 39.4 per cent of crying bouts. When only low-risk bystanders were present, an average of 53.5 per cent of crying bouts led to access. When at least one high-risk bystander was present, access was given during an average of 81.8 per cent of bouts. There was significant variation across bystander categories in the likelihood of access being given (permutation test: $n = 11$, $p = 0.002$). Pairwise comparisons revealed that, compared with when no bystanders were present, the presence of only low-risk bystanders did not affect the likelihood of access to the nipple (permutation test: $n = 11$, $p = 0.288$; figure 1a). By contrast, access was significantly more likely to be

Figure 1. (a–c) Percentage of crying bouts in which mothers gave crying infants access to the nipple, according to the presence or type of bystanders. Each line represents data for one mother, and only mothers for whom data are available for both bystander categories are shown (data are not available for all mothers for all bystander categories).

given when high-risk bystanders were present than when no bystanders were present (permutation test: $n=11$, $p=0.002$; figure 1b). In addition, access was significantly more likely to occur in the presence of high-risk bystanders than when only low-risk bystanders were present (permutation test: $n=11$, $p=0.025$; figure 1c). The latter two significant results remain significant after Bonferroni correction.

(b) Bystander number does not explain the apparent effect of high-risk bystanders

Mean bystander group sizes were not significantly larger for high-risk bystander groups compared with low-risk bystander groups (permutation test: $n=11$, $p=0.378$). Moreover, there was no significant difference in bystander group sizes between bouts where access was given and those where it was denied (Wilcoxon matched-pair signed-rank test: $Z=-0.306$, $n=11$, $p=0.793$).

(c) Infant age does not explain the apparent effect of high-risk bystanders

There was no significant difference in infant age between crying bouts where no bystanders, only low- or high-risk bystanders were present (permutation test: $n=11$, $p=0.297$). In addition, there was no difference in infant age between crying bouts where access was given and those where access was denied (Wilcoxon matched-pair signed-rank test: $Z=-0.890$, $n=11$, $p=0.400$).

(d) Crying is associated with increased aggression from bystanders towards mothers and infants

Evidence that bystanders found crying bouts aversive is revealed by a trend for increased aggression towards both mothers and infants during crying bouts compared with outside of these times. In total, five instances of aggression towards the mother and eight instances of aggression towards the infant during crying bouts were seen during focal watches; 12 instances of aggression (six to the mother and six to the infant) during crying bouts were seen during *ad libitum* sampling. On average, therefore, aggression to either the mother or the infant occurred in 8.1 per cent (25 out of 308) of all crying bouts. In all 25 cases where aggression was seen, the aggressive animal was dominant to the mother and not in the same matriline as the mother, supporting the use of a bystander category considering animals that are dominant and unrelated to the mother, rather than simply dominant to her.

Mothers received aggression during five of the 149 crying bouts that occurred during focal follows. One mother received aggression during two of her infant's bouts, on each occasion by an adult female, and three other mothers received aggression once each, on each occasion by an adult male. The mean rate of aggression during crying bouts calculated across all focal mothers (including therefore those who were never aggressed during crying bouts) was 27.98 instances per hour. By contrast, outside of crying bouts, the mean rate of aggression towards focal mothers was 0.79 instances per hour. On average, therefore, mothers received aggression at a rate 35.42 times higher during crying bouts than outside of this time.

If infant crying bouts are perceptually unpleasant for bystanders, we might also expect to see infants receiving more aggression from such animals during their crying bouts than outside of this time. Eight instances of aggression from bystanders (two from adult males and six from subadult or adult females) towards infants were seen during the 149 focal crying bouts, with four infants in total being aggressed: one infant was aggressed on three different occasions; two infants were aggressed on two occasions; and one infant was aggressed once. The mean rates of aggression received by infants were 15.69 instances per hour of crying bout, and 0.52 instances per hour outside of this time. Therefore, on average, infants received aggression from bystanders at a rate 30.17 times higher during crying bouts than when they were not crying.

(e) Crying is associated with increased aggression from mothers towards their own infants

Aggression by the nine focal mothers towards their infants was seen in 30 (20.1%) out of the 149 focal crying bouts, with 46 instances of aggression seen in total (in some

bouts, multiple instances of aggression occurred). Using the total number of 46 aggressive incidents to calculate the rates of aggression, it was found that, on average, mothers were 460.88 times more aggressive to their infants during crying bouts (mean = 36.87 instances of aggression per hour) than they were outside of this time (mean = 0.08 instances of aggression per hour). Comparing rates of aggression for individual mothers between these two times reveals that mothers were aggressive significantly more often during their infants' crying bouts (permutation test: $n=9$, $p=0.018$).

4. DISCUSSION

In this study, the presence of bystanders that posed a high potential risk of aggression was associated with an increased likelihood of rhesus macaque mothers allowing their offspring access to the nipple. There was a trend for both mothers and infants to receive more aggression during crying bouts than outside of this time. Mothers were also found to show aggression to their infants at much higher rates when they were crying than not crying. These results indicate that the outcome of infant–mother communication in this species is affected by the presence and nature of bystanders, and that this effect may be linked to potential or actual aggression from these individuals. This further highlights the importance of considering complex audience effects on animal signalling interactions.

Studies of the effects of an audience on primate vocal communication have most frequently examined how the presence of conspecific receivers affects the behaviour of signallers, for example with respect to whether calling occurs or not (Wich & Sterck 2003), latency to calling (Di Bitetti 2005) or the rate of call production (Caine *et al.* 1995; Brosnan & de Waal 2003). In their study of wild chimpanzees, Slocombe & Zuberbühler (2007) found that, while victims of aggression exaggerated their recruitment screams when in the presence of a third party dominant to the aggressor, this modification of call structure did not have a significant effect on the likelihood of bystanders providing support. Our study documents a different bystander effect: an impact of nearby animals on the actual outcome of the interaction between a signaller (infant) and an assumed receiver (the mother). To our knowledge, this is the first evidence among non-human primates of an impact of bystanders 'external' to the dyadic interaction on receivers' responses to signallers. Such effects are, however, well documented in our own species (Locke 2005) and these findings therefore indicate further common ground between the communicative interactions of human and non-human primates.

The lack of an effect of low-risk (i.e. subordinate, or dominant but closely related) bystanders on mothers' rate of giving access to crying infants, and the suggestion that both mothers and infants are more likely to receive aggression during a crying bout than outside of this time, suggests that mothers may take into account the risk of aggression from bystanders when deciding how to respond to crying bouts. The rarity of the occurrence of aggression from bystanders to mothers or infants in the present study, making meaningful statistical comparisons impossible, precludes anything other than very tentative inferences from the data presented here. As a minimum, however, these results do suggest that the risk of aggression from

bystanders may need to be considered when exploring the evolution and dynamics of mother–offspring conflict in gregarious animal species. Systematically quantifying the impact of crying on the aggressive behaviour of bystanders represents a key area for future research.

When considering the bystander effect seen in this study, it is important to consider alternative explanations to that in which mothers modify their behaviour due to their perceived risk of aggression from nearby animals. First, it is possible that infants modify their crying behaviour in the presence of high- but not low-risk bystanders, and, as a consequence, the response of mothers to this signal is affected. This explanation is not mutually exclusive to one in which mothers alter their response in accordance with the nature of bystanders; both infant calling and mothers' decision-making could be affected such that infants call differently—perhaps more aversively—in the presence of high-risk bystanders, further increasing the already elevated probability of their mothers giving in to their crying in such social contexts. This alternative explanation would require understanding by infants of third-party relationships, namely the dominance relationship between mothers and bystanders. A more subtle alternative therefore needs to be considered: that mothers behave differently—perhaps more nervously—in the presence of potentially aggressive animals and that infants respond to their mothers' behaviour and call differently as a result, in turn prompting a greater likelihood of being given access to the nipple. Distinguishing between these explanations would require simultaneous and fine-grained temporal analysis of the behaviour of both mothers and infants, and the interactions between them; such analysis is not possible in the current study.

Irrespective of the mechanism linking bystanders to the outcome of crying bouts, the results of this work have important implications for studies using measures of maternal responsiveness to explore parent–offspring conflict in non-human primates. Maestripieri (1995) highlighted the importance of studying mothers' responses to offspring signals for understanding the proximate and ultimate mechanisms underlying the parent–offspring relationship. Hauser (1993) used such data on maternal responsiveness to crying infants among vervet monkeys (*Cercopithecus aethiops*) to test the hypothesis that cries reflect honest signals of offspring need. Maestripieri (1995) similarly quantified changes over time in mothers' responses to infant distress calls among stump-tail macaques (*Macaca arctoides*), in this case to explore the temporal dynamics of the mother–infant relationship. The present work suggests that maternal responsiveness to crying can be dramatically affected by the social environment, and future studies quantifying this aspect of maternal behaviour should therefore take into account potential bystander effects.

Finally, the results of this study indicate that crying by rhesus macaque infants is associated with a high risk of aggression from mothers. Such aggression may reflect an attempt by mothers simply to stop the production of this highly aversive signal; a complementary explanation is that mothers' increased aggression reflects a maternal strategy to minimize aggression from bystanders to themselves or their offspring. Maestripieri *et al.* (2000) documented a similar link between crying and maternal aggression in

rhesus macaques, providing evidence that crying by abused infants may increase the likelihood of further physical abuse from mothers. In humans, it is well documented that crying sometimes elicits negative reactions from mothers and can in some cases be the triggering event for abuse of infants (Reijneveld *et al.* 2004; Lee *et al.* 2007). Further exploration of the proximate mechanisms underlying mother–infant aggression during crying in non-human primates may therefore provide important insights into the biological basis of child maltreatment in our own species (Maestripieri 1999).

This research adhered to the Association for the Study of Animal Behaviour/Animal Behavior Society Guidelines for the Use of Animals in Research, the legal requirements of the country in which the work was carried out and all institutional guidelines. This work was approved by the Institutional Animal Care and Use Committee of the University of Puerto Rico.

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