



Effects of aggression on interactions between uninvolved bystanders in mandrills



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In group-living animals, aggression can have consequences that spread beyond the initial opponents. In this study, we observed a social group of mandrills, *Mandrillus sphinx*, focusing on the behaviour of uninvolved bystanders, i.e. those individuals that witnessed aggression without being directly involved. In the aftermath of aggression, uninvolved bystanders directed both increased affiliation and increased aggression to other bystanders. They also showed increased scratching, a behavioural indicator of anxiety. Bystanders affiliated preferentially with the kin of the original aggressor when they were related to the victim. Contrary to predictions, affiliating with another bystander had no effect on either the probability of aggression or the rate of scratching. The increase in postconflict aggression between bystanders may be explained by social facilitation. The increase in affiliation may represent a form of indirect reconciliation.

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Thirty-five years of research on conflict management in group-living animals have revealed surprisingly complex processes (Aureli, Fraser, Schaffner, & Schino, 2012; Thierry, 2013). Most research has focused on the immediate consequences of aggression, and has shown how an initially dyadic event such as an aggressive confrontation can extend its consequences to a number of other individuals beyond the initial aggressor and victim. While research has traditionally concentrated on postconflict interactions involving the original contestants (Aureli, Cords, & van Schaik, 2002; Aureli & de Waal, 2000), recent studies have shown how aggression can also affect uninvolved bystanders, so that simply witnessing an aggressive event (without being in any way involved in the aggression) can alter the behaviour of bystanders towards other uninvolved groupmates.

Judge and Mullen (2005) were the first to show that witnesses of aggression engage in increased affiliation with other bystanders, especially with those individuals that were generally their closer associates. This finding was later confirmed by De Marco, Cozzolino, Dessi-Fulgheri, and Thierry (2010), but not by Leone, Mignini, Mancini, and Palagi (2010). Judge and Mullen (2005)

hypothesized that aggression engenders groupwide social tension, and that individuals not involved in the original aggressive event (bystanders, hereafter) engage in affiliation in order to reduce such tension. This interpretation was supported by the observation of increased displacement activities (a behavioural indicator of anxiety: Maestripieri, Schino, Aureli, & Troisi, 1992; Troisi, 2002) among bystanders and by a calming effect (i.e. a reduction in displacement activities) following affiliation.

All of the above studies excluded from their analyses any postconflict observations in which the focal subject (i.e. the bystander) was involved in an aggressive interaction. Although this choice allowed a possible confounding factor to be excluded, it also limited the range of the bystander's behavioural responses available for analysis. In fact, by focusing on affiliative interactions only, a biased picture of the behavioural responses that bystanders can show after witnessing an aggressive interaction is obtained.

There is indeed some indication that witnessing an aggressive event can elicit aggression between bystanders. Cheney and Seyfarth (1986) and Aureli, Cozzolino, Cordischi, and Scucchi (1992) showed that in vervet monkeys, *Chlorocebus pygerythrus*, and in Japanese macaques, *Macaca fuscata*, the kin of victims of aggression can later attack the kin of the aggressor. Aggression between bystanders may thus represent a form of family revenge driven by kin selection. These observations support the notion of a spread of aggression across the group, although they are silent with

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regard to the occurrence and function of affiliative interactions between bystanders. An alternative explanation for the spread of aggression (but not for kin-biased aggression) is that it is a consequence of social facilitation, a widespread but often neglected phenomenon (Clayton, 1978). Clearly, social facilitation may explain increased aggression, but not affiliation between bystanders.

In this paper, we present the results of a study of captive mandrills, *Mandrillus sphinx*, that explored the consequences of witnessing an aggressive event by focusing on both affiliative and aggressive responses. We quantified both aggressive and affiliative interactions between witnesses of an aggressive event and investigated their functional consequences. Our analyses proceeded as follows.

First, we described interactions between bystanders and the two original opponents (the aggressor and the victim of the aggression that started the postconflict observation). Observations focused on bystanders are not best suited to address these issues (which are instead best addressed by observations focused on the victim and/or the aggressor), so that we only present these data in order to describe the framework within which interactions between bystanders occur. Second, we examined whether witnessing aggression was associated with increases in both affiliative and aggressive interactions with other bystanders. Third, we tested the following predictions about the functional significance of affiliative and aggressive interactions between bystanders.

(1) If postconflict affiliation between bystanders is in fact a consequence of increased aggression between them (i.e. if it represents reconciliation after aggression between bystanders), then we expect to observe no increase in postconflict affiliation when observations that include aggression between bystanders are excluded from analysis (as was done in the previous studies described above).

(2) If postconflict affiliation between bystanders functions to reduce groupwide social tension, then we expect it to be associated with a reduction in aggression received from other bystanders and with a reduction in scratching. We also tested whether postconflict affiliation is directed to preferred partners.

(3) If postconflict affiliation between bystanders is a form of interfamily reconciliation (quadratic reconciliation; Judge & Mullen, 2005), then we expect bystanders to exchange affiliative contacts in relation to their own relatedness with the original contestants and to the relatedness of the original contestants with the other bystander.

(4) If postconflict aggression between bystanders is a form of family revenge driven by kin selection, then we expect bystanders to attack other bystanders in relation to their own relatedness with the victim of the original aggression and to the relatedness of the other bystander with the aggressor of the original aggression.

(5) If postconflict aggression between bystanders is simply due to some form of social facilitation, then we expect it to show no specific characteristics, and thus to be directed to those individuals that are usually the target of the bystander's aggression.

METHODS

Subjects and Housing

We studied a group of 15 sexually mature mandrills (five males and 10 females). Two more mature females that were present at the beginning of the observations died shortly after and the few data that had been collected on them were discarded. Two more

individuals were removed by the zoo staff for management purposes during the course of the study and are thus somewhat underrepresented in our data. The group was housed in the Rome zoo (Bioparco) in a 240 m² outdoor enclosure connected with a 30 m² indoor quarter.

We obtained information on maternal kinship from demographic records. The alpha male had no maternal relatives, while all other individuals belonged to one of three matriline (formed by three, five and six individuals, respectively).

Data Collection

Data were collected by M.S. from September 2012 to July 2013, between 1000 and 1700 hours, excluding feeding time. We adapted the PC-MC method of de Waal and Yoshihara (1983) and carried out focal animal observations immediately following an aggressive interaction (postconflict observations, PCs) and on the next possible day in the absence of aggression (matched-control observations, MCs). Observations focused on a witness of the aggressive event (a bystander, hereafter) who was not directly involved in the interaction. Bystanders were chosen randomly for observation among the individuals awake and apparently aware of the aggressive event. Bystanders were not chosen for observation if they joined the original aggressive event or were the target of aggression by the original aggressor or victim within 30 s. MC observations were carried out on the same subject observed in the PC observation, at the same time of day, up to a week later. Both PC and MC observations lasted 5 min, or until the focal subject entered the indoor quarters (this happened in 14.9% of the observations). Observations that lasted less than 1 min were discarded. A total of 296 PC-MC pairs of observation were recorded. All 15 members of the group were sampled as focal subjects (5–31 PC-MC pairs per subject; average 19.7).

Aggressive events that initiated PC observations included contact aggression (biting or grabbing), chases and threats (staring, open-mouth, head-bob, ground-slap). For each initial aggressive event we recorded the identity of the individuals involved, its intensity, whether it was dyadic or polyadic (i.e. whether it involved only two or more than two individuals) and whether it was unidirectional or bidirectional (i.e. whether the victim was aggressive to the aggressor or not). During PC and MC observations we recorded all aggressive (see above) and affiliative interactions (allogrooming, genital inspect, hand touch, mounting, muzzle contact, playing, sitting in contact, bared teeth and crest raise; see Schino & Marini, 2011 for definitions) in which the focal subject was involved, as well as the identity of its partners. We also recorded the subject's scratching (defined as in Schino, Scucchi, Maestripietri, & Turillazzi, 1988).

To assess overall affiliative relationships among group members, we also scanned the group every 15 min, for a total of 797 group scans. The identities of all visible individuals, of all dyads involved in grooming and of all dyads sitting in contact were recorded.

Being purely observational, this study did not require approval by an ethical committee.

Data Analysis

We relied on survival analysis (the log-rank test) to compare the timing of the first affiliative interaction (or aggressive interaction, in separate analyses) between bystanders and between bystanders and aggressors or victims in PC and MC observations (Cleves, Gould, Gutierrez, & Marchenko, 2008). We entered the identity of the subject as a 'stratification' variable in order to avoid pseudoreplication. Survival analysis was also used to test the effect of affiliative interactions on aggression received during PC

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