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# The curious case of rhesus macaques: despotism does not prevent third-party postconflict affiliation

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The ability to manage aggression in social animals is crucial for maintaining stable group dynamics. Triadic postconflict contacts (TC) are widespread behavioural strategies across mammal species consisting of affiliative contacts provided spontaneously by a third party or bystander towards the victim or the aggressor of a previous conflict (unsolicited triadic contacts, UTC) or upon request by one of them (solicited, STC). Depending on the target, the social context and the relationship quality shared by the interacting agents, TC's functions can range from bystander self-protection to victim comfort with the ultimate outcome of maintaining group cohesion. Evidence suggests that TCs are strongly affected by social styles, with despotic species engaging less frequently in such behaviours. Here, we tested hypotheses on the presence, modulation and possible functions of UTC and STC in a group of rhesus macaques, *Macaca mulatta*, a highly despotic species. For the first time, we found that bystanders spontaneously provided affiliation to both victims and aggressors. In contrast, we did not find any significant evidence for STC. Macaques seem to be sensitive to potential risks implied in providing postconflict affiliation to victims and aggressors (e.g. age, arousal). To some extent, UTC decreased the probability of bystanders being the target of redirection. UTC coincides with consolation when bystanders direct affiliation mainly towards 'friend' victims, when they perceive the negative affective state of the victim (measured by screaming), and when affiliation reduces the victim's distress (measured by self-scratching). Our data support the first two criteria but not the last one. Bystanders' spontaneous motivation to offer affiliation to victims of aggression in *M. mulatta* goes beyond the social constraints associated with the species' despotic style suggesting that several factors can affect the emergence of prosocial behaviours also in despotic-intolerant species.

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Agonistic interactions are nearly ubiquitous in human and nonhuman animals (Moynihan, 1998). Although aggression is part of group social dynamics and can enforce the stability of group hierarchies, it can often lead to increased stress and instability within the group, and its impacts can extend beyond the interacting individuals (Aureli & de Waal, 2000; de Waal, 1989). The ability to

manage the effects of aggression in social groups is crucial to ensure stable group dynamics (Aureli & de Waal, 2000; de Waal, 1989; Tibbetts et al., 2022). Unmanaged aggression can indeed lead to victims attacking other groupmates or being reattacked (Aureli et al., 1993; Palagi & Norscia, 2013), as well as to the spread of aggression among group members (Blood & Semple, 2023). Together with the establishment of dominance hierarchies, which reduce the frequency of overt aggression (Preuschoft & van Schaik, 2000; Tibbetts et al., 2022), a variety of postconflict management strategies are often used by social animals to maintain group cohesion (Aureli & de Waal, 2000). Triadic contact (TC), also known as third-party affiliation, is a behavioural strategy in which a bystander affiliates (e.g. grooming, body contact, touching gestures, embrace), either spontaneously (unsolicited TC, UTC) or in

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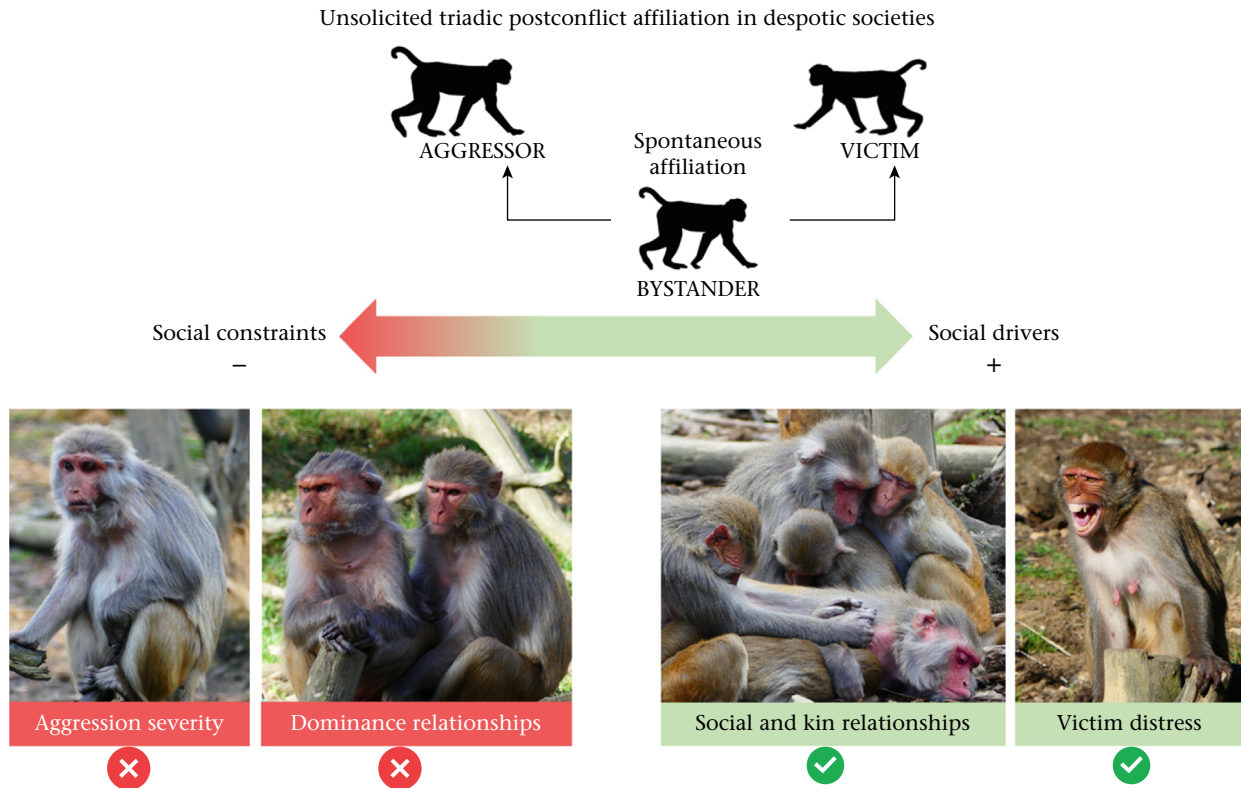
response to solicitation (solicited TC, STC), with one of the two opponents of the prior aggression (Palagi & Norscia, 2013). TC have been described in primate (*Pan* genus, Palagi & Norscia, 2013, Palagi et al., 2006; western lowland gorilla, *Gorilla gorilla gorilla*, Mallavarapu et al., 2006; gelada, *Theropithecus gelada*, Palagi et al., 2018; hamadryas baboon, *Papio hamadryas*, Romero et al., 2009; mandrill, *Mandrillus sphinx*, Schino & Marini, 2012; *Macaca* genus, Call et al., 2002, Katsu et al., 2018, Palagi et al., 2014) as well as nonprimate species (*Canis* genus, Cools et al., 2008, Palagi & Cordoni, 2009; pig, *Sus scrofa*, Cordoni et al., 2023; bottlenose dolphin, *Tursiops truncatus*, Yamamoto et al., 2020; rook, *Corvus frugilegus*, Seed et al., 2007), with varying functions and modalities. Despite the differences in motivation driving UTC and STC, the paucity of studies does not allow one to draw general conclusions on the possible mechanisms (e.g. risk mitigation, empathic propensity, kin relationships) leading to postconflict affiliation in the two postconflict strategies (McFarland & Majolo, 2012).

Possible differences emerge according to the target of the triadic postconflict affiliation. On the one hand, when provided to aggressors, such contacts can calm them limiting the risk of further aggression towards bystanders (e.g. appeasement, van Hooff, 1967; Pallante et al., 2018). On the other hand, TC can be provided to victims to protect them from further aggression (Palagi & Norscia, 2013), to reduce tension in the group (e.g. aggression spreading, Palagi et al., 2006) or to reduce the likelihood of bystanders being the victim of redirection (e.g. self-protection, Call et al., 2002; Schino & Marini, 2012). Within the plethora of postconflict tactics enacted by animals, third-party affiliation towards the victim seems to have a consolatory function when the contact is spontaneously directed by the bystander to the victim (e.g. bystander approaching the victim and providing affiliation), when it is directed to relatives/socially close subjects and when it reduces victims' distress (Palagi et al., 2014). However, disentangling the consolatory (immediately useful to the victim) and self-protective (immediately useful to the bystander) functions of TC is challenging because these contacts may serve both functions simultaneously. Some scholars suggest that the immediate factors underlying this behaviour involve bystanders being emotionally affected by the victim's negative state or cognitively perceiving the victim's distress and acting to alleviate it (emotional or cognitive empathy, de Waal & Preston, 2017; de Oliveira Terceiro et al., 2021). Others discuss the tendency to console victims in a more conservative way by linking such behaviour to risk evaluation processes (e.g. lower risk of redirection, retaliation in tolerant societies) and to the mere higher probability of interacting with a 'friend' due to spatial closeness (Puga-Gonzalez et al., 2014).

Among primates, macaques are an optimal model for a comparative study of TC as the *Macaca* genus includes species sharing similar group organization (multimale/multifemale groups with male exogamy and female philopatry, group size range 20–200 animals), but varying significantly in their social styles, ranging from highly despotic-intolerant to highly tolerant (Thierry, 2000, 2007). Despotic groups (e.g. rhesus macaque, *Macaca mulatta*, Japanese macaque, *Macaca fuscata*) compared to tolerant ones (e.g. Tonkean macaque, *Macaca tonkeana*) show steep and linear dominance hierarchies, more asymmetrical social relationships such as affiliation restricted to fewer kin subjects (Wu et al., 2018) and a lower tendency to deploy conflict resolution strategies (Thierry, 2007). Distinctions in macaque social styles mainly derive from data on female interactions (e.g. matriline), however, implying that possible intersex differences in the level of despotism can arise (Preuschoft et al., 1998). Importantly, even though there is some evidence for STC towards victims and aggressors in highly despotic macaques, UTC have never been observed in such groups (de Waal & Yoshihara, 1983; Katsu et al., 2018; Matheson, 1999;

Palagi et al., 2014; Schino et al., 2004), possibly because of the social constraints and associated risks (Puga-Gonzalez et al., 2014; Fig. 1). In moderately despotic macaques (crab-eating macaque, *Macaca fascicularis*, southern pigtailed macaque, *Macaca nemestrina*), TC seem to be present but mostly provided to aggressors, although no study has differentiated between STC and UTC (Das et al., 1997; Judge, 1991; Aureli and Schaik, 1991). Both STC and UTC seem to be present among moderately tolerant species (aggressors/victims, stump-tailed macaque, *Macaca arctoides*, Call et al., 2002; victims, Barbary macaque, *Macaca sylvanus*, McFarland & Majolo, 2012). Importantly, consolatory behaviours have so far been found only in the highly tolerant Tonkean macaque (Palagi et al., 2014). Clear-cut classification of despotic versus tolerant species based on the presence/absence of prosocial behaviours can, however, be reductive as cooperative behaviours can also emerge in despotic groups, although cooperation propensity in these species is generally affected by social and kin relationships (Japanese macaque, Bhattacharjee et al., 2023; Massen et al., 2010; rhesus macaque, Dubuc et al., 2012). Here we investigated the presence of postconflict triadic affiliation towards both victims and aggressors, and the factors potentially affecting the distribution of such contacts. In more detail, we then tested hypotheses on the potential functions of spontaneous third-party affiliation provided to victims, focusing on a large group of highly despotic rhesus macaques under naturalistic conditions.

For animals living in such despotic groups, spontaneously contacting one of the two opponents can expose third parties to new aggression either by the victim (redirection, Aureli et al., 1993) or by the aggressor (renewed aggression, Cordoni & Palagi, 2015). In this view, as TC solicited by one of the two opponents have already been found in another highly despotic macaque species (Katsu et al., 2018; Hypothesis 1), we expected STC to be present in our group (Prediction 1). UTC have never been reported in despotic macaques (de Waal & Yoshihara, 1983; Katsu et al., 2018; Matheson, 1999; Palagi et al., 2014; Schino et al., 2004). However, the presence of prosocial tendencies has also been reported in highly intolerant macaques when the risk of interaction is mitigated by social factors (e.g. close bonding, kinship; Bhattacharjee et al., 2023; Dubuc et al., 2012; Massen et al., 2010; Hypothesis 2). In this view, we expected that UTC towards victims or aggressors could also be present in our model species (Prediction 2a), but strictly under social situations implying low risks such as when the bystander and the target are both immature (Palagi et al., 2008; Prediction 2b) and/or share close social bonds (Palagi et al., 2014; Prediction 2c). Moreover, UTC should occur outside contexts of high arousal for the group such as during feeding times (Palagi et al., 2006; Prediction 2d) and less after aggression of high intensity (Prediction 2e). In such contexts of very high arousal, particularly in a despotic social system, all group members are exposed to a high risk of becoming a victim, and thus any provision of support is not encouraged. Finally, bystanders could limit the risk of postconflict contacts by actively avoiding interacting with higher-ranking subjects whether they are aggressors or victims (Prediction 2f). If the affiliative contact provided by the bystander serves to reduce its risk of being a victim of redirected aggression (Schino & Marini, 2012; Hypothesis 3), we first expected redirection to be present in our group (Prediction 3a) and bystander affiliation to decrease its probability (Prediction 3b). Moreover, bystander affiliation should be received from individuals who are frequently victims of redirection (Prediction 3c) and provided more to victims that often redirect aggression (Prediction 3d). If UTC towards victims have a consolatory function (Hypothesis 4), we expected them to be directed by bystanders mainly towards socially close victims (Prediction 4a). Moreover, to exclude the possibility that such a



**Figure 1.** Graphical representation of possible constraints (red) and drivers (green) for the emergence of unsolicited triadic postconflict affiliation in despotic societies such as those characterizing rhesus macaques, *Macaca mulatta*. Photos: Elisabetta Palagi.

preference is simply a by-product of the higher probability of initiating contact with preferred grooming partners (e.g. spatially close subjects, Puga-Gonzalez et al., 2014), we expected UTC to be mainly directed towards a ‘friend’ when it is a victim and not an aggressor (Prediction 4b). To support its consolatory function, UTC should also be mainly directed towards victims showing stress-related signals such as vocalizations at the end of the aggression or scratching in the postconflict period (Prediction 4c). For instance, the triggering factors activating the consolatory contact can be vocal signals (e.g. screams associated with the temper-tantrum) performed by the victim at the end of the aggressive event (bonobos, *Pan paniscus*, Heesen et al., 2022; olive baboons, *Papio anubis*, Lemasson et al., 2008). Finally, the consolatory function of UTC implies there will be a reduction in the victim’s distress (measured with scratching, Prediction 4d).

## METHODS

### Ethical Note

The study only involved the recording of macaques at a distance; it was purely observational and conducted without any contact or manipulation of animals. Therefore, the ethics committee of the University of Pisa waived the need for a permit.

### Study Group and Data Collection

The study group was hosted at Planète Sauvage (France). The enclosure, approximately 6110 m<sup>2</sup>, features a broad grassy area with trees interconnected by ropes, rope nets, and various wooden and metal shelters. The animals received a diet of commercial primate pellets at 0930 hours and a mixture of fruits, vegetables

and bread at 1430 hours. Water was always accessible from a water tank. Video cameras (Panasonic HC-V785 full-HD 25x, HC-V180 full-HD 200x) were used simultaneously in the data collection (August–October 2022), in the morning (0900–1300) and afternoon (1300–1700). Before data collection, a 1-week training period allowed observers to become proficient in animal recognition and in the identification of playful, grooming and aggressive behaviours. The group was composed of 122 captive-born macaques (59 males, 63 females; see Supplementary Table S1) and had been stable for the 2 years before the data collection (i.e. no new entries in the group). All animals were individually recognized based on facial and body characteristics (e.g. hair/skin colour, scars, tail shape, size). Kin relationships (e.g. matriline) among group members are unknown. Using data available by the zookeepers and following literature on the species (Berghänel et al., 2016; Hudson et al., 1996; Liao et al., 2018), we classified the animals into two age categories (males: 16 adults, 43 immatures; females: 42 adults, 21 immatures; adult sex ratio comparable to wild settings, Liao et al., 2018): (1) adults were animals showing fully developed and evident sexual traits ( $\geq 6$  years old for males,  $\geq 5$  years old for females); (2) immatures (males  $< 6$  years old; females  $< 5$  years old), comprised both subjects that had fully developed traits but were smaller than adults and subjects that spent a lot of time close to the mother, often breastfeeding or in nipple contact. Sampling techniques adhered to the all-occurrence and focal sampling method (Altmann, 1974; de Waal & Yoshihara, 1983). In total, about 120 h of video recording were collected. Focal animals, representing various subjects, were tracked daily at different times to ensure a balanced acquisition of daily data. We recorded all social interactions (e.g. social play, aggression, affiliation, proximity, resting periods) by focusing on the different subgroups of macaques randomly visible to the researchers, following these smaller groups

regardless of age or sex composition. We followed macaques to record the whole duration of the interactions. Importantly, both observers simultaneously recorded distinct subgroups of animals in different sections of the enclosure. These subgroups showed frequent and fluid changes in their composition, allowing for the collection of data on a considerable number of interacting subjects. By the end of the fieldwork, the video recordings showed a relatively even distribution among the subjects.

To calculate the recording time for each subject, during the video analysis we stopped the video every 5 min and coded the identities of the animals in the frame (generally 2–15 animals; i.e. scan sampling method, [Altmann, 1974](#)). For videos lasting less than 5 min, we stopped the video at halfway and coded the identities of all subjects. At the end of the video analyses, we summed all the scans obtained for each animal and then assessed the individual recording time (e.g. 60 scans in which a subject was recorded in total = 300 min of recording time for that subject; mean recording time  $\pm$  SE: 6.66  $\pm$  0.22 h; see [Supplementary Table S1](#); [Facondini et al., 2024](#)). In total (both focal and all-occurrences recording), 123.5 h of videos were collected.

### Video Coding

Two observers (S.A., G.F.) conducted frame-by-frame video analysis using PotPlayer 1.7.21305 (<https://potplayer.it.softonic.com>) to code the timing and duration of each behavioural pattern (precision of 0.02 s). For social grooming interactions the identity of the subjects and the exact time of beginning/end of the interactions were coded. A social grooming session was an interaction without pauses longer than 10 s ([Palagi et al., 2014](#)). Agonistic behavioural patterns (see Appendix [Table A1](#) for a detailed ethogram) were derived from published ethograms on rhesus macaques ([Partan, 2002](#); [Thierry, 1985](#)), as well as other macaque species ([Thierry et al., 2000](#)). For all aggressive encounters we coded the (1) ordinal number of the interaction, (2) day and time, (3) victim and aggressor identity, (4) behavioural patterns (Appendix [Table A1](#)), (5) outcome of the interaction (clear versus unclear winner/loser role; cases with retaliation or counterattack or absence of flee behaviour or submission by the victim were classified as unclear), (6) identity of all bystanders/third-parties (any individual apart from the victim and the aggressor) visible from the beginning of the aggression and that could perceive the interaction (generally at a distance of a maximum of 10 macaque body lengths from the two opponents when aggression occurred), (7) intensity of the aggression ('high intensity' when including physical contact between opponents with patterns such as slapping, pulling, pushing and in particular biting; 'low intensity' when not including physical contact between opponents but mostly threatening, chasing, fleeing) and (8) feeding condition (feeding lasting 30 min, 'prefeeding' = 30 min period before feeding, 'postfeeding' = 30 min period after feeding, 'control' = observations more than 30 min from a feeding event, [Palagi et al., 2007](#)). An aggressive event ended when no agonistic interaction between the aggressor and the victim occurred for more than 30 s ([McFarland & Majolo, 2012](#)). Only dyadic aggressive interactions were considered for the analyses. All cases with unclear victim/aggressor roles were excluded from the analyses.

### Postconflict and Matched-Control observations

After the last aggressive patterns of each agonistic interaction, we conducted 3 min focal observations on the victim and aggressor of the prior encounter (Postconflict observation, PC), when both subjects could be followed ([de Waal & Yoshihara, 1983](#); [Palagi et al., 2014](#)). Each PC was matched with a Matched-Control focal observation (MC) of the same duration for the victim and the

aggressor (when both subjects could be followed during the PC). As victims/aggressors could not always be followed for the entire 3 min PC (e.g. after aggression, victim is visible for only 2 min,  $N = 69$  cases), we did a focal MC of the same duration (e.g. victim followed for a 2 min MC observation). The MC was carried out on the earliest available day, at a time closely matching the original PC, focusing on the same individual. We made sure that the MC did not follow agonistic interactions (at least 3 min after any agonistic interaction occurring in the group, [de Waal & Yoshihara, 1983](#)). The large size of the enclosure allowed macaques to scatter, making it difficult always to follow the animals for the whole PC duration. However, as the observers could enter the enclosure, this maximized the possibility of following the animals. During PCs and MCs, we coded all affiliative contacts between the focal individual and bystanders (see Appendix [Table A1](#)). We focused our analysis on both STC and UTC. STCs were coded when the victim or the aggressor actively approached or requested an affiliative contact (e.g. exposing parts of the body to be groomed, [Ueno et al., 2014](#)). UTC were coded when the bystander spontaneously approached, initiated contact and/or initiated an affiliative interaction with the victim or the aggressor. The few cases where the bystander spontaneously approached the victim ( $N = 2$ ) or the aggressor ( $N = 1$ ) and received affiliation (e.g. grooming, see [Supplementary Video 1](#)) were also scored as UTC. This is supported by literature showing that providing grooming, as well as receiving it, reduces distress ([Aureli & Yates, 2010](#)) and improves the affective states of both groomees and groomers ([Crockford et al., 2013](#)).

While we acknowledge the possibility of more subtle forms of invitation in primates such as calls ([Cheney et al., 2010](#)), we never observed such vocalizations in our study. For each minute of each PC and MCs we recorded the (1) minute of observation (first, second, third), (2) ordinal number of the observation, (3) day and time of the observation, (4) identity of prior opponents for PC and MC observations, (5) presence and type of affiliative contacts (see Appendix [Table A1](#); the first of such contacts was coded as UTC/STC), (6) identity of the bystander providing TC, (7) feeding condition (feeding, prefeeding, postfeeding, control), (8) number of subjects around the victim/aggressor (all the subjects at a distance of a maximum of 10 macaque body lengths from the focal subject were counted at the beginning of each minute; these subjects could have a higher probability of interacting with the focal one) and (9) self-scratching of victim/aggressor.

### Redirection

Redirection of aggression was coded in all PC periods when the victim of the former aggression attacked another group member (different from the aggressor).

### REDINDEX and VREDINDEX

For each subject, we computed an index that gives us a measure of the likelihood of redirecting aggression towards other group members (REDINDEX). This was determined by dividing the number of instances where the subject redirected aggression by the total number of times the subject had been sampled as a victim (i.e. the occasions when the subject could have redirected aggression, [Schino & Marini, 2012](#)). Then, for each subject, we computed an index that gives us a measure of the probability of becoming a victim of redirected aggression from other group members (VREDINDEX). This was calculated by dividing the number of times a subject was a victim of redirection by the times the subject had been sampled as a bystander. Both indices assume that all the bystanders on average experience similar conditions (e.g. number of subjects present during aggression and relationship quality between bystanders and victim/aggressor).

### Social bonds

We assessed social bond strength for each dyad of subjects by calculating an index based on social grooming data (Palagi et al., 2014; Schino & Marini, 2012). This index was derived as the ratio of the time (s) two individuals groomed each other to the total time (s) they appeared in the same frame thus having the opportunity to interact. For the calculation of the time in which two individuals were observed together, during video analysis we stopped the video every 5 min and coded all the IDs of the macaques in the frame. Then, we summed all the scans for each dyad (scans where the two subjects were together) and estimated the observation time for the dyad (e.g. 50 scans in which two subjects were recorded together = 250 min observation for the dyad). The index provides a proxy of the likelihood of two subjects engaging in grooming when they are in proximity.

### Interobserver agreement

We assessed interobserver reliability on about 15% of the videos independently coded by two observers using Cohen's Kappa coefficient (Cohen, 1968). This was always higher than 0.80 (subject identification:  $K = 0.94$ ; aggression intensity:  $K = 0.88$ ; decided or undecided aggression:  $K = 0.96$ ; presence of unsolicited/solicited triadic contacts during PC/MC and presence of further redirected aggression:  $K_{\min} = 0.83$ ,  $K_{\max} = 0.87$ ; scratching during PC/MC:  $K = 0.83$ ; number of subjects around victims and aggressors in the PC/MC:  $K = 0.95$ ).

### Statistical Analyses

#### Dominance hierarchy

We used the average dominance index (ADI, Saccà et al., 2022) to derive dominance hierarchy and ranking scores. This index overcomes substantial biases in the steepness of hierarchies, especially when numerous dyads within the groups have no interactions (a crucial consideration when studying large groups; Saccà et al., 2022). All aggressive events with doubtful valence or not clear winner/loser roles were excluded. We tested the hierarchy linearity with the triangle transitivity ( $t_{\text{tri}} = 1$ , perfect linearity, Shizuka & McDonald, 2012). To better understand the distribution of power, we compared individual ADI values according to age (immature versus adult) or sex (female versus male), and computed the female dominance index (FDI, Hemelrijk et al., 2008), which can range from 0 (complete male dominance) to 1 (complete female dominance). Nonparametric tests were conducted to compare two groups (Wilcoxon rank sum test), following the verification of the non-normal distribution of variables through the Shapiro–Wilk test (Ghasemi & Zahediasl, 2012) and visual inspection (e.g. histograms).

#### Models

The first four models (Models 1–4) investigated the possible presence of both unsolicited (UTC) and solicited (STC) triadic postconflict affiliation towards victims/aggressors. In these models we had both PC and MC observations. Models 5 and 6 used observations of the different possible dyads of victim–bystander and aggressor–bystander under PC conditions to test the effect of predictors related to their relationship on the likelihood of triadic affiliation. Models 7 and 8 only used PC observations to test the effect of aggression characteristics on the likelihood of triadic affiliation. Each model is described below.

*Solicited triadic contact with the victim: Model 1.* To understand which factors affected the likelihood of STC to the victim, we ran a generalized linear mixed model (GLMM, glmmTMB 1.2.5042) with STC as response variable (presence/absence of STC to the victim, binomial error distribution). The ID of the victim and the PC–MC pair

ID (the ordinal numbers indicating the PC/MC; all the minutes referred to each PC–MC pair were associated with the same ID to prevent pseudoreplication) were included as random factors. The fixed factors considered were the (1) Condition (PC versus MC), (2) Number of subjects around the victim, (3) Victim ADI, (4) Victim age (immature versus adult), (5) Victim sex, (6) Victim scratching rate during the PC/MC (seconds spent scratching/PC period of the observation), (7) Feeding condition (feeding, prefeeding, postfeeding, control).

*Unsolicited triadic contact with the victim: Model 2.* To understand which factors affected the likelihood of UTC to the victim, we ran a GLMM with UTC as response variable (presence/absence of UTC to the victim, binomial error distribution). The ID of the victim and the PC–MC pair ID (ordinal number indicating the PC/MC pair) were included as random factors. The fixed factors considered were the (1) Condition, (2) Number of subjects around the victim in each minute of observation, (3) Victim ADI, (4) Victim age, (5) Victim sex, (6) Victim scratching rate and (7) Feeding condition.

*Solicited triadic contact with the aggressor: Model 3.* To understand which factors affected the likelihood of STC to the aggressor, we ran a GLMM with STC as response variable (presence/absence of STC to the aggressor, binomial error distribution). The ID of the aggressor and the PC–MC pair ID (ordinal number indicating the PC/MC pair) were included as random factors. The fixed factors considered were the (1) Condition, (2) Number of subjects around the aggressor, (3) Aggressor ADI, (4) Aggressor age, (5) Aggressor sex, (6) Aggressor scratching rate, (7) Feeding condition and (8) Aggressor scratching rate (seconds spent scratching/PC period of the observation).

*Unsolicited triadic contact with the aggressor: Model 4.* To understand which factors affected the likelihood of UTC to the aggressor, we ran a GLMM with UTC as response variable (presence/absence of UTC to the aggressor, binomial error distribution). The ID of the aggressor and the PC–MC pair ID (ordinal number indicating the PC/MC pair) were included as random factors. The fixed factors considered were the (1) Condition, (2) Number of subjects around the aggressor, (3) Aggressor ADI, (4) Aggressor age, (5) Aggressor sex, (6) Aggressor scratching rate (seconds spent scratching/PC period of the observation), (7) Feeding condition.

*Victim–bystander relationship: Model 5.* To understand whether factors related to the victim–bystander relationship affected the likelihood of UTC to the victim, we ran a GLMM with UTC as response variable for all the possible dyads of victim–bystander observed (presence/absence of UTC given by the bystander to the victim in at least one PC, binomial error distribution). The interaction between ID of the victim and ID of the bystander was included as random factor. The fixed factors considered were, for each victim – bystander dyad, the (1) Age combination (immature–immature, immature–adult, adult–adult), (2) Sex combination (male–male, female–female, male–female), (3) Social bond, (4) difference in ADI between victim and bystander ( $|\text{diffADI } v-b|$ ), (5) REDINDEX of the victim (likelihood of redirecting aggression towards other group members), (6) VREDINDEX of the bystander (probability of becoming a victim of redirected aggression).

*Aggressor–bystander relationship: Model 6.* To understand whether factors related to the aggressor–bystander relationship affected the likelihood of UTC to the aggressor, we ran a GLMM with UTC as response variable for all the possible dyads of aggressor–bystander observed (presence/absence of UTC given by the bystander to the aggressor in at least one PC, binomial error distribution). The interaction between ID of the aggressor and ID of the bystander was included as random factor. The fixed factors considered were, for

each aggressor – bystander dyad, the (1) Age combination, (2) Sex combination, (3) Social bond and (4) difference in ADI between aggressor and bystander ( $|\text{diffADI a-b}|$ ).

In both Models 5 and Model 6, owing to the scarcity of events characterizing affiliation between aggressor and victim during the PC ( $N = 11$ ), we decided to exclude such cases from the analysis.

**Aggression intensity and victim distress: Model 7.** To understand whether the intensity of the aggression and the presence of victim vocal signals of emotional distress affected the likelihood of UTC to them, we ran a GLMM with UTC as response variable (presence/absence of UTC in each PC, binomial error distribution). The interaction between ID of the aggressor and ID of the victim was included as random factor. The fixed factors considered were, for each aggressor–victim dyad, the (1) Age combination, (2) Sex combination, (3) Social bond, (4) difference in ADI between aggressor and victim ( $|\text{diffADI a-v}|$ ), (5) Intensity of the aggression (low versus high) and (6) presence of screams by victims (open-mouth, bared-teeth) at the end of the aggression (last pattern coded in the aggressive interaction).

**Aggression intensity and UTC to aggressor: Model 8.** To understand whether the intensity of the aggression affected the likelihood of UTC to aggressors, we ran a GLMM with UTC as response variable (presence/absence of UTC in each PC, binomial error distribution). The interaction between ID of the aggressor and ID of the victim was included as random factor. The fixed factors considered were, for each aggressor–victim dyad, the (1) Age combination, (2) Sex combination, (3) Social bond (4) difference in ADI between aggressor and victim ( $|\text{diffADI a-v}|$ ) and (5) Intensity of the aggression.

**Scratching (Prediction 4d).** We compared victim scratching rates between PC-no contact (absence of UTC) and MC (Palagi et al., 2014), both for the whole duration and for each 30 s time slot. Then, we compared scratching rates across three conditions: PC-no contact (absence of UTC), PC-contact (after UTC, excluding cases with reconciliatory contacts) and MC. Only the events not characterized by conciliatory contacts were considered for this analysis.

**Self-protection hypothesis.** To determine whether redirection was present in the group (Prediction 3a), we first quantified the average rate of redirection (times a victim redirected an aggression/time the subject was a victim). To analyse the immediate consequences of providing or not providing UTC to victims of aggression (Prediction 3b), we compared the rate with which bystanders were victims of redirection after providing UTC (number of times the subject was a victim of redirection/the total number of times the subject was a bystander and gave UTC; if redirection occurred, we considered the presence of UTC before redirection) versus when not providing UTC to the victim (number of times the subject was a victim of redirection/the total number of times the subject was a bystander and did not give UTC).

For analysis of Predictions 3c and 3d: Do subjects that more often redirect aggression receive more UTC from bystanders (REDINDEX)? Do bystanders that are more often victims of redirection provide more UTC to victims (VREDINDEX)? see Victim–bystander relationship: Model 5.

#### General analysis

Multicollinearity in the GLMMs was assessed using the `check_collinearity` function (R package `performance` v 0.4.4) relying on variance inflation factors (VIFs). ‘Low correlation’ was found for all the fixed factors included in all models (VIF: 1.02–2.28). Model significance was evaluated by comparing the full model against a null model comprising only random effects, employing the likelihood ratio test (LRT) with the `Chisq` test argument (Dobson & Barnett, 2018). To determine the  $P$  value for

each predictor, separate LRTs were conducted between the full model and a model lacking that specific predictor, utilizing the Anova function (Barr, 2013). For calculating marginal and conditional  $R^2$  values, version 1.43.17 of the MuMIn package (Bartoń 2020) was utilized. Marginal  $R^2$  quantifies the proportion of variance in the response variable explained by the fixed factors alone, while conditional  $R^2$  captures the portion explained by both fixed and random factors (Nakagawa & Schielzeth, 2013). Relative odds ratios were employed to illustrate the actual impact of estimated effects. This was accomplished using the `confint()` function, where odds ratios (OR) represent the expected change in odds when all variables are held at reference values, and the fixed factor increases by one unit. For conducting pairwise comparisons involving factors with more than two levels in the models, the R package `emmeans` was utilized, and the Tukey test was performed (Bretz et al., 2016; Lenth, 2021). All the analyses were done in RStudio (<http://www.r-project.org>).

## RESULTS

### Preliminary Results and Group Dominance Hierarchy

A total of 1330 agonistic events were recorded and used for extrapolating the dominance hierarchy. The patterns used in the different third-party TC are reported in Appendix Table A2. We found a steepness of 0.965 and evidence for linearity in the dominance hierarchy (Appendix Fig. A1a; proportion of transitive triads among all triads,  $P_t = 0.978$ , triangle transitivity,  $t_{tri} = 0.911$ ,  $P < 0.001$ ; Shizuka & McDonald, 2012). Interestingly, no difference in terms of dominance ranking was found between males and females ( $W = 1852.5$ ,  $P = 0.978$ ; Fig. A1b) and the female dominance index (FDI, Hemelrijk et al., 2008) was in line with this result (FDI = 0.50 when considering all the subjects, FDI = 0.38 when considering only fully adult subjects), indicating no sex-biased dominance in the group. Dominance was age-biased, with adults being higher ranking than immatures ( $W = 2536.5$ ,  $P < 0.001$ ; Fig. A1c). Among the 1330 aggressive events, 199 were overt aggression; among these, we could follow the PC period for 150 events. We found 82 TC (48 UTC and 34 STC, to victims/aggressors) in 70 different PCs (see Appendix Table A2).

### Solicited Triadic Contact with the Victim

For Model 1 there were  $N = 290$  observations (145 PC/MC pairs). The full model differed significantly from the null one ( $X^2_9 = 44.78$ ,  $P < 0.001$ , marginal  $R^2 = 0.797$ , conditional  $R^2 = 0.798$ ). The variables Condition and Feeding condition had a significant effect on the likelihood of STC to the victim. Interestingly, the likelihood of STC was higher in the MC compared to the PC ( $X^2 = 5.259$ ,  $P = 0.022$ ). The Tukey test revealed that during feeding the likelihood of STC was significantly lower than far from feeding time, in control conditions ( $z = 4.20$ ,  $P = 0.0002$ ), whereas no difference was found between the other levels of the predictor. On the other hand, the Number of subjects around the victim, Victim ADI, Victim age, Victim sex and Victim scratching rate did not significantly affect the response variable (see Table 1 for full results).

### Unsolicited Triadic Contact with the Victim

In Model 2 there were  $N = 300$  observations. The full model differed significantly from the null one ( $X^2_9 = 41.87$ ,  $P < 0.001$ , marginal  $R^2 = 0.31$ , conditional  $R^2 = 0.39$ ). The variables Condition and Victim age had a significant effect on the likelihood of UTC to the victim. Specifically, the likelihood of UTC was about seven times higher (odds ratio = 7.05) in the PC than the MC period ( $X^2 =$

**Table 1**  
Estimated parameters and results of the likelihood ratio tests ( $\chi^2$ ) of the GLMMs (Models 1–4)

Fixed effects	Coefficient	SE	$\chi^2$	df	P
<b>Solicited triadic contact (STC) to the victim (Prediction 1): Model 1</b>					
Intercept	-1.098	0.633	–	–	–
Tested variables					
Condition <sup>a</sup> (PC)	-0.993	0.433	5.259	1	<b>0.022</b>
No. of subjects around victim	0.089	0.090	0.998	1	0.318
Victim ADI	-0.662	0.920	0.518	1	0.472
Victim scratching rate	7.233	7.270	0.990	1	0.372
Victim sex <sup>a</sup> (Male)	-0.310	0.492	0.397	1	0.529
Victim age <sup>a</sup> (Adult)	-0.633	0.540	1.372	1	0.241
Feeding condition <sup>a</sup>	–	–	20.579	3	<b>&lt;0.001</b>
Feeding condition (Feeding)	-2.835	0.675	–	–	–
Feeding condition (Postfeeding)	-1.698	0.789	–	–	–
Feeding condition (Prefeeding)	-19.541	9.546e+03	–	–	–
<i>N</i> <sub>observations</sub> =290. Random factors: Victim ID (variance=0.028, SD=0.15) and PC-MC pair ID (variance= 3.7e-09, SD=6.08e-05)					
<b>Unsolicited triadic contact (UTC) to the victim (Prediction 2a, 2d, 4c): Model 2</b>					
Intercept	-3.830	0.885	–	–	–
Tested variables					
Condition <sup>a</sup> (PC)	1.953	0.885	16.426	1	<b>&lt;0.001</b>
No. of subjects around victim	0.081	0.059	1.879	1	0.170
Victim ADI	0.379	0.864	0.192	1	0.661
Victim scratching rate	0.760	7.535	0.010	1	0.920
Victim sex <sup>a</sup> (male)	-0.641	0.449	2.037	1	0.154
Victim age <sup>a</sup> (immature)	1.308	0.556	5.530	1	<b>0.019</b>
Feeding condition <sup>a</sup>	–	–	6.153	3	0.104
Feeding condition (feeding)	-1.007	0.480	–	–	–
Feeding condition (postfeeding)	0.334	0.573	–	–	–
Feeding condition (prefeeding)	0.490	0.862	–	–	–
<i>N</i> <sub>observations</sub> =300. Random factors: Victim ID (variance=2.010e-09, SD=4.477e-05) and PC-MC pair ID (variance=0.429, SD=0.655)					
<b>Solicited triadic contact (STC) to the aggressor (Prediction 1): Model 3</b>					
Intercept	-0.944	0.579	–	–	–
Tested variables					
Condition <sup>a</sup> (PC)	-0.045	0.362	0.016	1	0.901
No. of subjects around aggressor	-0.054	0.096	0.319	1	0.572
Aggressor ADI	-0.613	0.986	0.387	1	0.534
Aggressor scratching rate	-5.289	5.734	0.851	1	0.356
Aggressor sex <sup>a</sup> (male)	0.379	0.495	0.586	1	0.444
Aggressor age <sup>a</sup> (adult)	0.533	0.506	1.111	1	0.292
Feeding condition <sup>a</sup>	–	–	16.244	3	<b>0.001</b>
Feeding condition (feeding)	-2.059	0.545	–	–	–
Feeding condition (postfeeding)	-1.420	0.689	–	–	–
Feeding condition (prefeeding)	-1.954	1.219	–	–	–
<i>N</i> <sub>observations</sub> =286, random factors: Aggressor ID (variance=0.64, SD=0.80) and PC-MC pair ID (variance= 1.98e-08, SD=1.41e-04)					
<b>Unsolicited triadic contact (UTC) to the aggressor (Prediction 2a, 2d): Model 4</b>					
Intercept	-1.496	0.660	–	–	–
Tested variables					
Condition <sup>a</sup> (PC)	1.206	0.525	5.281	1	<b>0.022</b>
No. of subjects around aggressor	0.127	0.129	0.962	1	0.327
Aggressor ADI	-1.624	1.111	2.136	1	0.144
Aggressor scratching rate	4.447	4.218	1.111	1	0.292
Aggressor sex <sup>a</sup> (male)	-1.650	0.668	6.098	1	<b>0.013</b>
Aggressor age <sup>a</sup> (adult)	-0.510	0.554	0.849	1	0.357
Feeding condition <sup>a</sup>	–	–	8.686	3	<b>0.034</b>
Feeding condition (feeding)	-2.962	1.120	–	–	–
Feeding condition (postfeeding)	-0.351	0.706	–	–	–
Feeding condition (prefeeding)	1.167	0.939	–	–	–
<i>N</i> <sub>observations</sub> =288. Random factors: Aggressor ID (variance=2.85e-09, SD=5.34e-05) and PC-MC pair ID (variance=1.79e-11, SD=4.23e-06)					

–: not applicable; ADI: average dominance index; PC: postconflict period; MC: matched-control period. Significant *P* values are in bold.

<sup>a</sup> These variables were dummy coded.

16.426,  $P < 0.0001$ ; Fig. 2a). Immature victims had a higher likelihood of receiving triadic affiliation than adults ( $X^2 = 5.530$ ,  $P = 0.019$ ; Fig. 2b). On the other hand, the Number of subjects around the victim, Victim ADI, Victim sex, Victim scratching rate and Feeding condition did not significantly affect the response variable (see Table 1 for full results).

#### Solicited Triadic Contact with the Aggressor

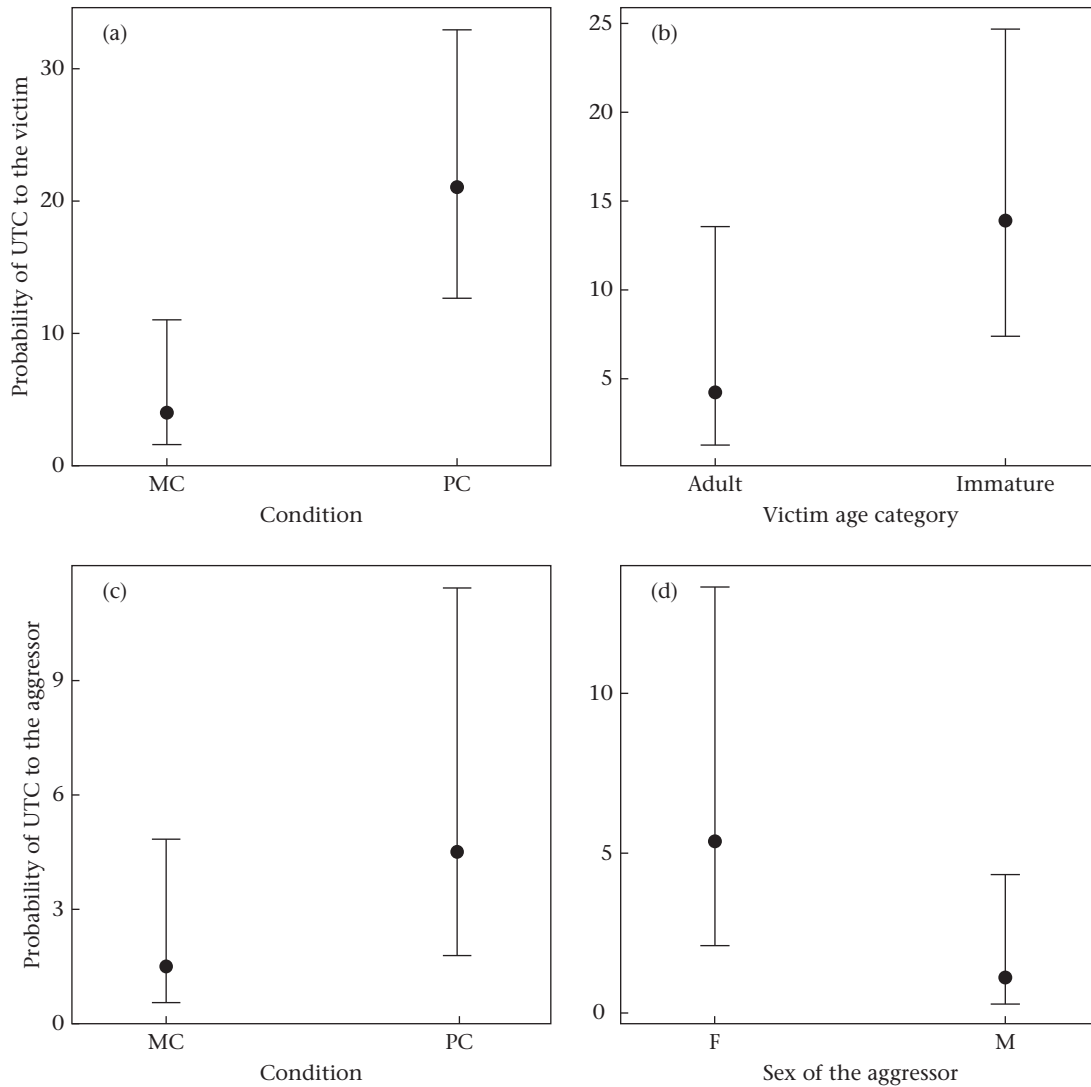
Model 3 included  $N = 286$  observations. The full model differed significantly from the null one ( $X^2_9 = 26.36$ ,  $P = 0.002$ , marginal  $R^2 = 0.21$ , conditional  $R^2 = 0.34$ ). The variable Feeding condition had a significant effect on the likelihood of STC to the aggressor. The

Tukey test revealed that during feeding the likelihood of STC to the aggressor was significantly lower ( $X^2 = 16.244$ ,  $P = 0.001$ ) than in control conditions ( $z = 3.78$ ,  $P = 0.001$ ), whereas no significant difference was found between the other levels of the predictor. On the other hand, the Condition, Number of subjects around the aggressor, Aggressor ADI, Aggressor age, Aggressor sex and Aggressor scratching rate did not affect the response variable (see Table 1 for full results).

#### Unsolicited Triadic Contact with the Aggressor

Model 4 included  $N = 288$  observations. The full model differed significantly from the null one ( $X^2_9 = 38.77$ ,  $P < 0.001$ , marginal  $R^2$





**Figure 2.** The effect of (a) Condition (postconflict period, PC, versus matched–control period, MC) of the observation and (b) Victim age on the probability of unsolicited triadic contacts, UTC, to the victim and of (c) Condition of the observation and (d) Aggressor sex (F: female; M: male) on the probability of UTC to the aggressor. Error bars represent 95% confidence intervals. The values on the Y axis indicate percentages.

= 0.545 =  $R^2$  conditional). The variables Condition, Aggressor sex and Feeding condition had a significant effect on the likelihood of UTC to the aggressor. Specifically, the likelihood of UTC was more than three times higher (odds ratio = 3.34) in the PC than the MC ( $X^2 = 5.281$ ,  $P = 0.022$ ; Fig. 2c). The likelihood of giving UTC to the aggressor was higher when this was a female ( $X^2 = 6.098$ ,  $P = 0.013$ ; Fig. 2d). The Tukey test revealed that during feeding the likelihood of UTC was significantly lower than in prefeeding ( $z = 2.644$ ,  $P = 0.041$ ) and control periods ( $z = -2.821$ ,  $P = 0.025$ ) whereas no difference was found between the other levels of the predictor. On the other hand, the Number of subjects around the aggressor, Aggressor ADI, Aggressor age and Aggressor scratching rate did not significantly affect the response variable (see Table 1 for full results).

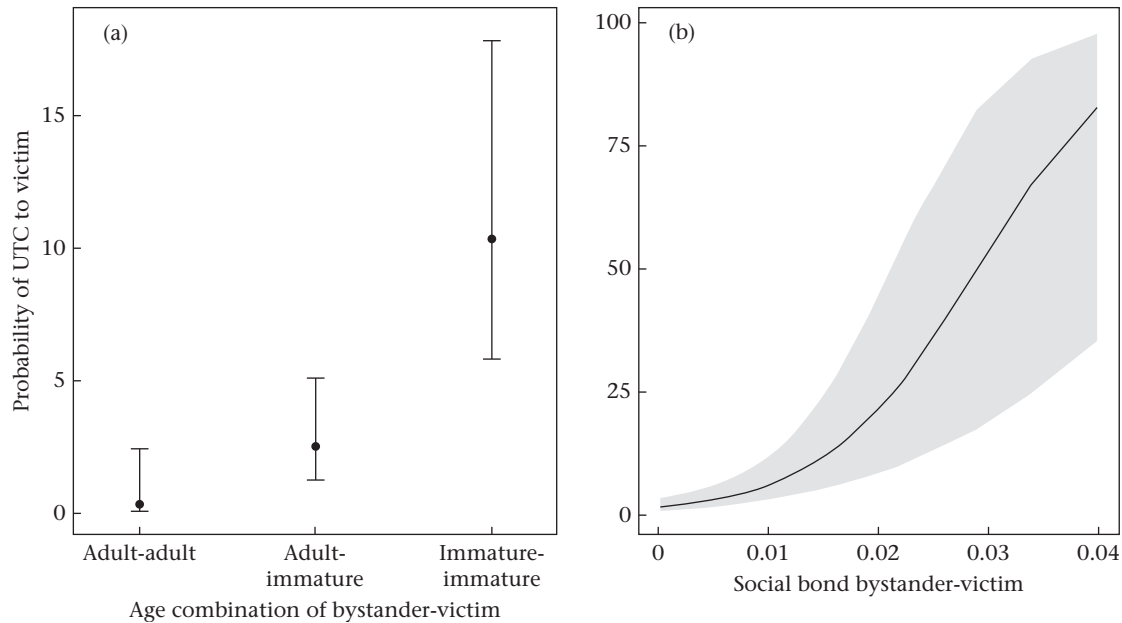
#### Victim–bystander Relationship

In Model 5 there were  $N = 633$  victim–bystander dyads (each observation of the model refers to a different dyad). The full model (fixed variables) differed significantly from the null one ( $X^2 = 45.52$ ,  $P < 0.001$ , marginal  $R^2 = 0.404 = R^2$  conditional). Social bond and

Age combination had a significant effect on the response variable. UTC contacts to the victim were more likely to occur when bystander and victim were both immatures ( $X^2 = 15.99$ ,  $P = 0.0003$ ; Tukey test result, immature–immature versus adult–adult:  $t_{622} = -3.25$ ,  $P = 0.004$ ; immature–immature versus immature–adult:  $t_{622} = -3.13$ ,  $P = 0.005$ ; adult–adult versus immature–adult:  $t_{622} = -1.95$ ,  $P = 0.125$ ; Fig. 3a). Importantly, the stronger the social bond, the higher the likelihood of UTC ( $X^2 = 21.32$ ,  $P < 0.001$ ; Fig. 3b). Notably, neither the victim's probability of redirecting aggression (i.e. REDINDEX) nor the bystander's probability of being a victim of redirection (i.e. VREDINDEX) affected the tendency to provide victims with UTC. Similarly, neither the |diffADiv-b| nor Sex combination significantly affected the response variable (see Table 2 for full results).

#### Aggressor–bystander Relationship

In Model 6 there were  $N = 569$  dyads of bystander aggression (each observation in the model refers to a different dyad). The full model (fixed variables) investigating whether the aggressor–bystander relationship affected the likelihood of having



**Figure 3.** The effect of (a) the age combination of victim and bystander and (b) the social bond between victim and bystander on the probability of a bystander providing unsolicited triadic contacts, UTC, to the victim. Error bars and shaded areas represent 95% confidence intervals. The values on the Y axis indicate percentages.

given at least one UTC to the aggressor (in PCs) did not differ from the null one ( $X^2 = 11.28$ ,  $P = 0.08$ ).

#### Victim Scratching Rate

We found no difference in scratching rates between PCs (without UTC) and MCs (PC without UTC versus MC:  $W = 6508.5$ ,  $P = 0.865$ ). We divided PCs/MCs into time slots of 30 s (up to six time slots for observations of 3 min), comparing the scratching rates between PCs without UTC and MCs but no difference was detected for the six comparisons ( $P > 0.05$  for all Wilcoxon rank sum tests). When we added the group of PCs with UTC, still no difference was detected between the three groups (PC without UTC versus MC versus PC with UTC, Kruskal–Wallis test:  $X^2_2 = 0.981$ ,  $P = 0.612$ ).

#### Aggression Intensity and Victim Distress

In Model 7 there were  $N = 144$  PCs. The full model differed significantly from the null one ( $X^2 = 25.33$ ,  $P = 0.001$ , marginal  $R^2 = 0.287 = R^2$  conditional). Victim scream and Sex combination had a significant effect on the response variable. UTCs to the victim were more likely to occur when aggressor and victim were both females ( $X^2 = 10.62$ ,  $P = 0.005$ ; Tukey test results: female–female versus female–male:  $t_{134} = 3.04$ ,  $P = 0.008$ ; female–female versus male–male:  $t_{134} = 2.26$ ,  $P = 0.06$ , female–male versus male–male:  $t_{134} = -0.244$ ,  $P = 0.97$ ). Importantly, the presence of victim screams at the end of the aggression increased the chance of bystanders receiving UTCs ( $X^2 = 8.56$ ,  $P = 0.003$ ; Fig. 4). On the other hand, Age combination, Social bond,  $|\text{diffAD}|_{v-a}$  and the Intensity of the aggression did not affect the response variable (see Table 2 for full results).

#### Aggression Intensity and UTC to the Aggressor

Model 8 included  $N = 144$  PC observations. The full model did not differ from the null one ( $X^2 = 7.97$ ,  $P = 0.24$ ).

#### Self-protection Hypothesis

##### Rates of redirection in the group (Prediction 3a)

Of 90 total victims of aggression, 23 showed redirection at least once. Considering only subjects that were victims of at least two aggressive interactions ( $N = 50$  animals), 15 showed redirection at least once. The mean level of redirection (considering  $N = 50$  animals) was  $11.30\% \pm 2.67$  SE, and when calculated only on those 15 subjects who redirected at least once, this increased to  $37.68\% \pm 3.40$  SE.

##### Does providing UTC reduce the likelihood of being a victim of redirection (Prediction 3b)?

Bystanders ( $N = 45$ ) were never victims of redirection after providing UTC. On average, bystanders were victims of redirection on  $4.23\% \pm 1.21$  SE of times when they did not provide UTC to the victim (Appendix Fig. A2). Excluding bystanders who never provided UTC and who were never victims of redirection ( $N = 33$ ), bystanders were victims of redirection on  $16\% \pm 0.159$  SE of times when they did not spontaneously affiliate with the victim.

##### Risk of redirected aggression and UTC (Predictions 3c, 3d)

Neither the victim's probability of redirecting aggression (i.e. REDINDEX) nor the bystander's probability of being a victim of redirection (i.e. VREDINDEX) affected the tendency to provide victims with UTC. See Model 5 for full results.

## DISCUSSION

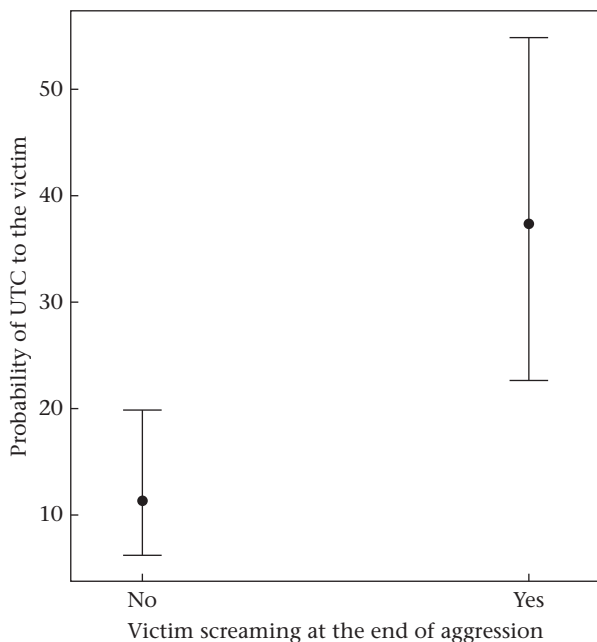
Here we found clear evidence for the presence of postconflict unsolicited triadic contacts (UTC) in rhesus macaques (Prediction 2a supported). The presence of this strategy may come as a surprise as UTC have never been reported in despotic macaque species (Judge, 1991; Katsu et al., 2018; Matheson, 1999; Palagi et al., 2014), not even between mothers and their infants (Japanese macaque, Schino et al., 2004). This result suggests that comparative studies on despotic-intolerant species can unveil the presence of phenomena thought to be exclusively present in more tolerant species

**Table 2**  
Estimated parameters and results of the likelihood ratio tests ( $\chi^2$ ) of the GLMMs (Models 5 and 7)

Fixed effects	Coefficient	SE	$\chi^2$	df	P
<b>Victim–bystander relationship (Prediction 2b, 2c, 2f, 3c, 3d, 4a): Model 5</b>					
Intercept	-5.905	1.145	–	–	–
Tested variable					
Social bond v-b	143.287	31.035	21.317	1	<b>&lt;0.001</b>
diffADI v-b	0.540	0.810	0.444	1	0.505
Sex combination v-b <sup>a</sup>	–	–	2.943	2	0.230
Sex combination v-b (F–M)	0.184	0.463	–	–	–
Sex combination v-b (M–M)	-1.176	0.832	–	–	–
Age combination v-b <sup>a</sup>	–	–	15.993	2	<b>&lt;0.001</b>
Age combination v-b (A–I)	2.130	1.090	–	–	–
Age combination v-b (I–I)	3.634	1.118	–	–	–
REDINDEX	-0.847	2.636	0.103	1	0.748
VREDINDEX	-0.919	0.921	0.995	1	0.319
<i>N</i> <sub>observations</sub> =633. Random factor: Victim ID (variance= 9.94e-42, SD=3.15e-21) * Bystander ID (variance=3.48e-32, SD=1.87e-16)					
<b>Intensity of aggression and victim distress (Prediction 2e, 4c): Model 7</b>					
Intercept	-2.467	0.739	–	–	–
Tested variable					
Victim scream <sup>a</sup> (Yes)	1.535	0.525	8.564	1	<b>0.003</b>
Intensity <sup>a</sup> (low)	1.149	0.627	3.356	1	0.067
Social bond v-a	9.085	30.869	0.087	1	0.769
diffADI v-a	0.031	0.998	0.001	1	0.975
Sex combination v-a <sup>a</sup>	–	–	10.622	2	<b>0.004</b>
Sex combination v-a (F–M)	-1.753	0.577	–	–	–
Sex combination v-a (M–M)	-1.579	0.697	–	–	–
Age comb v-b <sup>a,b</sup>	–	–	2.869	2	0.238
Age combination v-a (A–I)	1.063	0.650	–	–	–
Age combination v-a (I–I)	0.479	0.662	–	–	–
<i>N</i> <sub>observations</sub> =145 random factor: Victim ID (variance=2.76e-30, SD=1.66e-15) * aggressor ID (variance=7.88e-30, SD=2.81e-15)					

--: not applicable. F: female; M: male; A: adult; I: immature; ADI: average dominance index; |diffADI v-a|: difference in ADI between victim and bystander, REDINDEX: index indicating the likelihood of a victim of prior aggression redirecting aggression towards other group members; VREDINDEX: index indicating the probability of a bystander becoming victim of redirected aggression (see Methods). Significant *P* values are in bold.

<sup>a</sup> These predictors were dummy coded.



**Figure 4.** The effect of the presence of victim screams at the end of the aggression on the probability of unsolicited triadic contacts, UTC, to the victim. Error bars represent 95% confidence intervals. The values on the Y axis indicate percentages.

(Schino et al., 2004; Scopa & Palagi, 2016), as recently shown for other behaviours such as rapid facial mimicry in rhesus macaques (Facondini et al., 2024) in contrast to what was posited by Scopa and Palagi (2016). In our case, analysing intergroup variability in despotic macaques can tell us more about how prosocial attitudes

can also be present in despotic species but under specific social conditions (Bhattacharjee et al., 2023; Dubuc et al., 2012; Massen et al., 2010). Importantly, this does not mean that our group is an exception, as our data on the group dominance hierarchy are in line with the despotic nature already reported for rhesus macaques. Triadic contacts were provided to both victims and aggressors only spontaneously. Indeed, in our study group we did not find solicited triadic contacts (STC) to be statistically more frequent during the postconflict compared to the control period (Prediction 1 not supported). The spontaneous nature of contacts provided by bystanders can be indicative of a case-by-case risk and convenience evaluation of a given action, and not of a simple response to a mere request. Our interpretation is in line with recent evidence showing that macaques are able to evaluate the payoff of their behavioural choices and the social context under conflict situations (Ballesta & Meunier, 2023).

Our results only partially support those theoretical frameworks ascribing differential postconflict strategies to risk-sensitive reactions (Puga-Gonzalez et al., 2014). Although we found the highest frequency for UTC when both the bystander and the victim were immature and socially close (Predictions 2b and 2c supported for UTC to victim), neither the arousal level of the context (i.e. aggression intensity, temporal distance from feeding) nor the relative hierarchical ranking of the subjects affected UTC towards the victim (Predictions 2d, 2e, 2f not supported). Similarly, UTCs towards the aggressor were more likely far from highly competitive contexts such as feeding (Prediction 2d supported for UTC to aggressor) but were not modulated by any of the other factors indicating possible risks or benefits. See Table 3 for the summary of the outcomes.

We found only partial support for the self-protection hypothesis (Schino & Marini, 2012) predicting that triadic postconflict affiliation towards the victim serves to decrease the probability of the bystanders being the target of redirection. The notable rates of

**Table 3**

Summary of outcomes related to the presence or absence of the different types of triadic contacts resulting from their relative frequency in postconflict compared to matched-control conditions (Models 1–4)

Factors modulating bystander response towards the target	STC towards aggressors (absent)	STC towards victims (absent)	UTC towards aggressors (present)	UTC towards victims (present)
Social bond	NA	NA	No	Yes
Feeding condition	NA	NA	Yes	No
Age combination	NA	NA	No	Yes
Sex combination	NA	NA	Yes	No
Distance in dominance ranks	NA	NA	No	No
Intensity of aggression	NA	NA	No	No
Victim distress	NA	NA	NA	Yes

UTC: unsolicited triadic contacts; STC: solicited triadic contacts; NA: not applicable since the phenomenon is not present.

redirection in rhesus macaques compared to more tolerant monkeys (gelada, Palagi et al., 2018; Tonkean macaque, Palagi et al., 2014; Prediction 3a supported) and the absence of redirection experienced by the bystander after providing UTC (Prediction 3b supported) are in line with the self-protection hypothesis. Yet, the risk of being a victim of redirection did not affect the likelihood of providing UTC (Prediction 3c not supported, Prediction 3d not supported). It must be noted that an alternative strategy of bystanders could simply be to get away from the victim, considering the large space available to our group (6110 m<sup>2</sup>).

Consolation arises from a sense of sympathetic concern, characterized by an emotional response triggered when witnessing someone else's distress (Pérez-Manrique & Gomila, 2018). In this view, UTC can assume a consolatory function when (1) a bystander perceives the affective negative state of the victim (e.g. vocal distress signals), (2) the affiliative action resolves the victim's distress and (3) it is directed towards 'friend' victims. Among monkeys, consolation has been conclusively proven only in Tonkean macaques (Palagi et al., 2014) and marmosets, *Callithrix jacchus* (de Oliveira Terceiro et al., 2021).

It has been hypothesized that the tendency to provide postconflict affiliation could simply be a byproduct of the higher tendency to groom 'friends' and kin outside the agonistic context (Puga-Gonzalez et al., 2014). In our group, whereas bystanders spontaneously provided affiliation more often towards 'friend' victims (Prediction 4a supported), they did not more often provide postconflict grooming to 'friend' aggressors (Prediction 4b supported) ruling out the 'byproduct' nature of postconflict affiliation. Thus, for a bystander, contacting a victim seems to have a different affective valence than contacting an aggressor.

In an elegant experiment, Whitehouse et al. (2016) demonstrated that macaques perceive the arousal conveyed by conspecifics' scratching possibly to monitor the negative affective state of groupmates. In contrast to most studies (Aureli and Schaik, 1991; McFarland & Majolo, 2012; Palagi & Norscia, 2013; Palagi et al., 2014, 2018), in our victims self-scratching did not increase in the minutes following a conflict compared to a control condition (Prediction 4d not supported). Two explanations are possible: either self-scratching is not a good indicator of the individual's anxiety state, or the agonistic events are not sufficient to perturb the affective homeostasis across the postconflict period. Other types of signals such as vocalizations can also be important in expressing emotional distress in mammals (Briefer, 2012, 2018). Hearing socially close groupmates screaming (i.e. an emotionally valent vocal signal) can elicit consolatory acts by bystanders rather than cause their flight response to limit the possible risks of the aggression. This has been recently found by Heesen et al. (2022)

studying consolation in bonobos. Evidence also exists in olive baboons, which reacted promptly after hearing screaming from socially valuable females (Lemasson et al., 2008). Similarly, we found that vocal distress signals produced by rhesus macaque victims at the end of the aggression attracted, more than distancing, bystanders (Prediction 4c partially supported). Although it is not always simple to distinguish solicited from unsolicited affiliation, the fact that third parties rarely provided affiliation when the victim directly approached them but did so when there were no apparent requests supports the spontaneous nature of UTCs. Future studies will also need to investigate the role of subtler forms of request such as gazing or vocalizations.

It is worth noting that while sympathetic concern (underlying consolation) is, at a proximate level, primarily driven by altruistic motives (e.g. alleviating distress in a victim), it can also result in personal benefits (Batson, 2010). Hence, the consolatory and self-protective functions are difficult to disentangle to explain the occurrence and modality of UTC towards victims in both human and nonhuman mammals (Batson, 2010; Burkett et al., 2016). Although the data set should be expanded to more conclusively support or discard any hypothesis about the function of postconflict affiliation in rhesus macaques, our data suggest new comparative intergroup studies on postconflict management strategies in this group of primates.

In conclusion, the surprising discovery of bystanders' motivational autonomy in providing postconflict affiliation in rhesus macaques challenges previous evidence about the difficulty of overcoming the social constraints imposed by despotic styles. Such constraints might assume less importance when the affective states of strongly bonded groupmates are involved.

### Author Contributions

**Alban Lemasson:** Writing – review & editing, Writing – original draft, Supervision, Investigation, Conceptualization. **Elisabetta Palagi:** Writing – review & editing, Writing – original draft, Supervision, Project administration, Formal analysis, Conceptualization. **Giulia Facondini:** Writing – review & editing, Data curation. **Luca Pedrucci:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Formal analysis, Conceptualization. **Martin Böye:** Writing – review & editing, Resources. **Simone Aere:** Writing – review & editing, Writing – original draft, Methodology, Data curation.

### Data Availability

Full data sets used for the analyses are available as [Supplementary material](#).

### Declaration of Interest

The authors declare no conflict of interest of any kind.

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### Supplementary Material

Supplementary material associated with this article is available in the online version at <https://doi.org/10.1016/j.anbehav.2024.10.036>.

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## Appendix

**Table A1**

Detailed ethogram of aggressive and affiliative patterns used during aggression

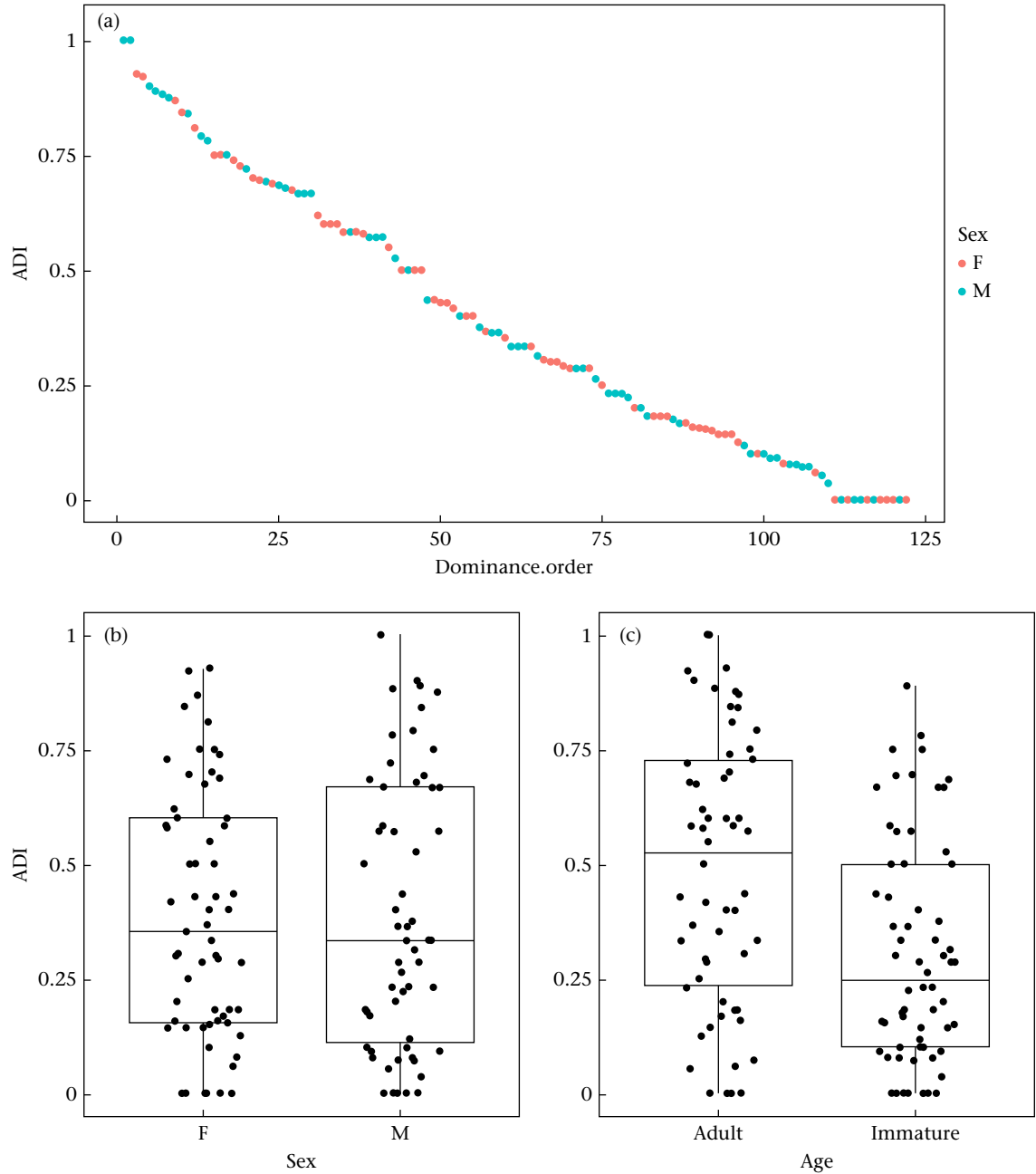
Behaviour	Description
Avoidance	An individual walks away when displaced, threatened, or attacked
Bite	An individual bites another, inducing flight, crouch, screaming or counterattack in it
Chase	An individual runs after a fleeing individual
Displacement	An individual approaches or contacts an individual, which simultaneously moves away
Grab	An individual vigorously grabs or pulls another
Half-open mouth	The mouth is slightly open with corners drawn back, the lower lip may be retracted, and the teeth are partly visible. This display is accompanied by staring. It is occasionally silent but is most often accompanied by rattle vocalization. This expression is associated with aggression and acts as a mild threat
Jump away	Jumps to get away from another individual with whom he was playing or having other types of interactions
Jump on	A subject jump onto a support (branch, hammock ...) or onto another individual
Open mouth bared-teeth scream	The mouth is open wide with corners retracted, exposing the teeth and sometimes the gums. This facial expression is accompanied by staring and screaming vocalizations (screams, screeches, chuckles, geckers). The display occurs in agonistic contexts. Depending on the vocalization, it may act as a threat or a protest and may be associated with an attack or a counterattack
Presentation	An individual raises or orients the hindquarters towards a nearby partner and may turn the head towards the partner. In intense presentations (e.g. in oestrous females), the head is lowered against the ground, with arms flexed and rump elevated. This may be an invitation to anogenital inspection or exploration, mount, play, grooming or a response to a threat (submission)
Pushing	An individual pushes away another using hand or body, transferring momentum. The partner may move or resist
Run after	Chasing someone to catch them
Run away	Run away from someone
Scalp retraction	The scalp is retracted, ears may be flattened against the head while the individual looks at a partner. This may be associated with physical approach. This is an invitation to play or an aggressive pattern
Silent bared-teeth	The upper lip or both lips are vertically retracted, exposing the teeth and sometimes the gums. The corners of the mouth may be drawn back. The jaw may be either closed or opened to various degrees. The scalp is often raised, and the ears flattened. This is an affiliative display; it is commonly observed during submissive behaviours from a subordinate to a dominant individual
Silent stare open mouth	An individual stares at another while standing with its mouth open without vocalizing
Slap	An individual hits another with the flat of its hand. This is an aggressive act
Stamping	A rhythmic trot or a jump followed by an abrupt landing with stiff limbs. This motion occurs in conditions of social tension, agonistic contexts or play. It may be followed by yawning. It is associated with arousal in the performer and may attract attention to it
Social play	Play performed by two or more individuals engaging in one or more activities, such as grabbing, pirouetting, pulling and/or pushing, slapping, wrestling, etc. (see full ethogram in <a href="#">Thierry et al., 2000</a> ; <a href="#">Yanagi &amp; Berman 2014</a> )
Embrace	An individual encircles another ventro-ventrally with arms. There is contact between heads or chests. Embracing may be mutual or unilateral. There may be a simultaneous grasping of the fur. This is an affiliative contact that may be accompanied by lipsmack. The contact may happen also laterally with each subject draping an arm over the other's hips or waist
Grooming	An individual cleans the skin or fur of a partner. The hair is brushed and parted using the hands. Particles are picked using hand or mouth, teeth or tongue. An individual grooms a passive partner or both mutually groom each other
Gentle touch	An individual contacts another lightly with hand in a region other than the hip. This affiliative contact does not involve pushing, grasping or pulling
Sit in contact	Two individuals sitting in contact with one another
Mount	An individual climbs ventrodorsally upon a standing partner. The mounter may or may not grip the legs of the partner. The behaviour may represent a copulation or an affiliative interaction

Ethograms from [Thierry et al., 2000](#); [Partan, 2002](#); [Yanagi & Berman 2014](#).

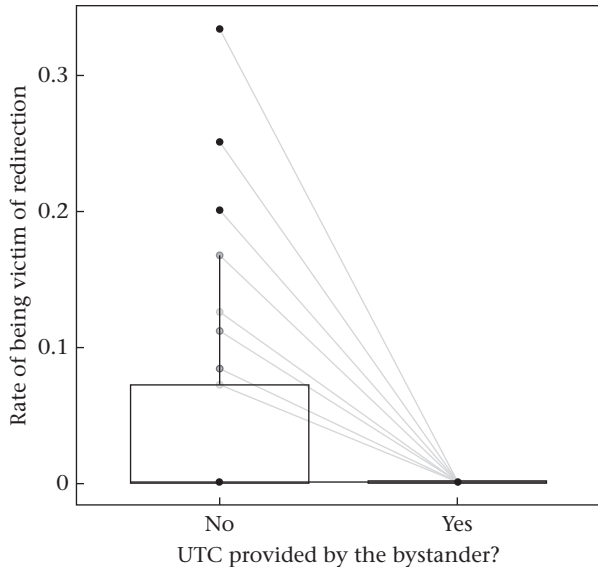
**Table A2**  
Affiliative patterns used by bystanders as triadic contacts

	STC (aggressor)		STC (victim)		UTC (aggressor)		UTC (victim)	
	MC	PC	MC	PC	MC	PC	MC	PC
Grooming	18	17	20	5	2	10	3	7
Embrace	0	0	0	2	0	0	0	9
Sit in contact	0	3	2	3	1	4	0	4
Social play	5	0	1	0	3	2	3	8
Gentle touch	0	1	0	1	0	2	0	1
Lips making	0	1	0	1	0	1	0	0

STC: solicited triadic contacts; UTC: unsolicited triadic contacts; PC: postconflict period; MC: matched – control period.



**Figure A1.** (a) Average dominance index (ADI) as a function of the dominance position of each individual (F: female; M: male), (b) ADI distribution according to males and females and (c) effect of age on ADI distribution. The box plots show the median and 25th and 75th percentiles; the whiskers indicate the values within 1.5 times the interquartile range and the circles are individual points.



**Figure A2.** Box plots comparing the rate of being a victim of redirection (for bystanders of aggression) after providing versus not providing an unsolicited triadic contact with the victim. The box plots show the median and 25th and 75th percentiles; the whiskers indicate the values within 1.5 times the interquartile range and the circles indicate individuals; each line linking the two box plots connects the two conditions for each subject (i.e. after providing or not providing unsolicited triadic contacts to the victim).