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Opinion Article

Why are bystanders friendly to recipients of aggression?

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The escalation of conflicts of interest into aggressive conflict can be costly in terms of increased post-conflict stress and damage to the opponents' relationship. Some costs may be mitigated through post-conflict interactions. One such type of interaction is affiliative contact from a bystander to the recipient of aggression. This type of interaction has been suggested to have a number of functions, including stress reduction and opponent relationship repair. It may also protect bystanders from redirected aggression from the original recipient of aggression. Here we review the evidence for such functions and propose a framework within which the function and occurrence of post-conflict affiliation directed from a bystander to the recipient of aggression is related to the quality of the relationships between the individuals involved and the patterns of behavior expressed.

Introduction

Aggressive conflict can be very costly in terms of risk of injury, loss of time and energy, as well as loss of benefits afforded by the relationship between the opponents¹⁻⁵ and increased post-conflict levels of stress (behavioral^{6,7} and hormonal^{8,9} measures). Post-conflict interactions mitigate some of the costs of aggressive conflict.^{7,10} The majority of research on post-conflict behavior has focused on reconciliation, the affiliative post-conflict interaction between former opponents, 11,12 but important post-conflict interactions may also occur between the opponents and bystanders uninvolved in the previous conflict. 13,14 In particular, a number of recent studies have demonstrated the phenomenon of post-conflict affiliation directed from a bystander to the recipient of aggression in a variety of species from primates¹⁵⁻²⁵ to dogs²⁶ and rooks.²⁷ This review focuses on bystander to recipient interactions and examines the variations in their patterns, which are consistent with a number of different functional explanations.

When reconciliation was first documented in chimpanzees (*Pan troglodytes*) at Arnhem Zoo by de Waal & van Roosmalen, ²⁸ it was also shown that the recipient of aggression was more likely to engage

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in an affiliative interaction with an uninvolved bystander than by chance. Such interactions were labeled 'consolation', assuming that the interaction had a calming function. De Waal and van Roosmalen,²⁸ however, did not test this assumption, nor did they differentiate between affiliative interactions initiated by bystanders and those initiated by the recipient of aggression. In offering postconflict affiliation to the recipient of aggression, bystanders may provide a benefit in stress-reduction to the recipient, while putting himself or herself at risk of receiving aggression. In fact, they may become targets of aggression either directly, by receiving redirected aggression from the initial recipient of aggression, or indirectly, by becoming involved in renewed aggression between the former opponents while offering post-conflict affiliation. In responding to affiliation solicited by the recipient of aggression, however, the bystander faces little or no risk of redirected aggression. Thus, post-conflict bystander affiliation directed towards the recipient of aggression may be qualitatively different from affiliation by the recipient of aggression towards the bystander, and thus a differentiation is frequently made between 'unsolicited affiliation', initiated by the bystander, and 'solicited affiliation', initiated by the recipient of aggression.²⁹ Such a differentiation has been further supported by the fact that a number of studies have found evidence for the occurrence of post-conflict bystander affiliation solicited by the recipient of aggression but not for similar affiliation offered by the bystander, 29-31 or for the occurrence of unsolicited affiliation but not affiliation solicited by the recipient of aggression. 16,17,19,20

The role of the conflict participant may also be important in discriminating between different post-conflict interactions involving bystanders. 13,14 Whereas de Waal and van Roosmalen 28 focused on recipients of aggression only, many later studies did not differentiate between recipients of aggression and aggressors. The recipient of aggression is more likely to experience higher levels of post-conflict stress, 19,32,33 and thus the potentially stress-alleviating effect of bystander affiliation may offer higher benefits to the recipient of aggression than to the aggressor. Furthermore, the risks of aggression for the bystander on approaching the aggressor may differ from those on approaching the recipient of aggression after a conflict. Moreover, affiliating with the aggressor after a conflict may prove more successful or meaningful with respect to certain potential functions, such as providing encouragement or the strengthening of bonds between allies¹⁴ than affiliating with the recipient of aggression. Nevertheless, some, if not all, of the functions of bystander affiliation discussed in this review may be applicable to both post-conflict interactions directed from bystanders to aggressors and those directed towards recipients of aggression, but our focus is only on the latter.

Following de Waal & Roosmalen's²⁸ study, the occurrence of postconflict affiliation initiated by the bystander received further attention when de Waal & Aureli³⁴ compared its patterns in chimpanzees with previously published findings in four macaque species. 35-39 Post-conflict bystander affiliation directed towards the recipient of aggression was found to occur in chimpanzees but not in macaques. One possible interpretation of this result is that monkeys may not have the requisite cognitive capacity for this interaction, known as the 'cognitive constraints hypothesis'. 34 In order for bystanders to 'console' a recipient of aggression, they are expected to recognize that the recipient is distressed and be able to respond appropriately to alleviate that distress, and thus the absence of 'consolation' in monkeys may be due to a difference in empathy attribution in monkeys and apes. 40 Japanese macaque mothers do not shows signs of distress or increase affiliative contacts with their offspring when their offspring are targets of aggression,⁴¹ suggesting that the mothers may not perceive their offspring's need for distress alleviation and supporting the hypothesis that monkeys are not cognitively capable of 'consolation'. The degree to which apes are capable of empathy, however, is under debate. 40,42-46 While differences in cognitive ability may explain differences in the relative occurrence of bystander affiliation in different species when a stress-reduction function is applicable, this should not impact the occurrence of bystander affiliation if and when other functions apply, for which such cognitive abilities are not required.

While simply demonstrating the occurrence of post-conflict interactions may not in itself tell us about their functions, their relative occurrence across species may help us to understand their functional significance. Although some other studies did find evidence for post-conflict affiliation between conflict opponents and bystanders in monkeys, those studies either made no distinction between the aggressor and recipient of aggression⁴⁷⁻⁴⁹ or did not differentiate between solicited and unsolicited bystander affiliation.³⁹ The stress reduction function was not tested in those studies, but a different function for post-conflict affiliation between bystanders and conflict participants was proposed. Such affiliation was proposed to function as 'triadic reconciliation' ³⁹ given that the bystander involved was the opponent's kin. In such cases, the bystander was proposed to act as a proxy for their kin, thus contacts between a conflict participant and their opponent's kin could potentially fulfill the same functions as reconciliation, namely relationship repair and distress alleviation. Although no firm conclusions can be drawn from these studies about the function of post-conflict affiliation directed from the bystander to the recipient of aggression as distinctions between the roles of the conflict participant were not made and/or the initiator of the contact was not identified, it seems possible that a relationship repair function could apply to such affiliation.

The first, and indeed the only, study to definitively demonstrate the occurrence of post-conflict bystander affiliation directed towards the recipient of aggression in primate species other than apes (although such contacts have been recently demonstrated in domestic dogs²⁶ and rooks²⁷), did so only by analyzing different types of affiliative behaviors separately.²⁵ Stumptailed macaque (*Macaca arctoides*) victims were found to receive an increased level of post-conflict affiliation from bystanders in the form of sociosexual behaviors, but not allo-grooming. The authors argued that if the

function of such contacts were stress reduction, as is implied by the term 'consolation', allo-grooming would be expected to increase, as this behavior has been shown to reduce heart rate and tension-related activities. ^{50,51} Furthermore, as kin are likely to have a valuable relationship and valuable partners are more likely to be responsive to each others' distress, kin would be expected to be most likely to provide consolation. However, kin of the recipient of aggression did not provide the post-conflict affiliation. The authors instead proposed another function for post-conflict bystander affiliation directed towards the recipient of aggression: self-protection. One way for the recipient of aggression to reduce post-conflict stress is to redirect aggression towards other group members. ^{38,52} Thus, by affiliating with the recipient of aggression, the bystander may be attempting to appease them and reduce the likelihood of becoming a target of redirected aggression.

Post-conflict bystander affiliation directed towards the recipient of aggression may therefore have a number of different functions. Hence, the functional label 'consolation' first attributed to this type of post-conflict interaction may not always be appropriate, and should only be used where a stress-alleviating function has been shown. More neutral terms such as post-conflict triadic or third-party affiliation have been used in recent studies. 17,19,25,53 As these terms do not specify the direction of the interaction or the role of the conflict participant, we have chosen to use the term 'post-conflict bystander affiliation directed towards recipients of aggression' (hereafter referred to as 'bystander affiliation', with the implicit assumption that we are only referring to affiliation initiated by the bystander and directed towards the recipient of aggression). In order for the occurrence of bystander affiliation to be determined in a population, the distribution and latency of affiliative contacts during post-conflict periods and during matched control observations must be compared separately according to the initiator of the interaction and the role of the conflict participant. Bystander affiliation is demonstrated in a population when it can be shown that bystanders are likely to initiate affiliative contact with the recipient of aggression earlier in the post-conflict periods than in control periods. Using this definition, bystander affiliation has thus far only been demonstrated in chimpanzees, bonobos, gorillas, stump-tailed macaques, rooks and dogs (see Table 1), although its occurrence has been investigated, but not found, in a number of other species. 13 Although studies of bystander affiliation initially focused primarily on the demonstration of the interaction, the attention has now shifted more towards the functional aspects of bystander affiliation, and therefore the importance of distinguishing the role of the conflict opponent and the initiator of bystander affiliation has only relatively recently become apparent. Thus, comparisons among different 'types' of bystander affiliation, i.e., among instances of bystander affiliation fulfilling (at least potentially) different functions, have not yet been made. Below, we review evidence for the different functions of bystander affiliation in light of recent developments in the field, and propose a predictive framework for the occurrence of these functions.

Stress Reduction

Consolation, the original term used for bystander affiliation, implies a stress reduction function, but for almost 30 years it was not formally tested. The first study to actually investigate this function found no evidence that bystander affiliation reduces behavioral

Table 1 Species in which post-conflict affiliation directed from a bystander to the recipient of aggression has been demonstrated and the suggested function of such interactions

Species	Location	Suggested function [†]
Pan troglodytes	Chester Zoo ^{20,47}	Stress reduction
	Arnhem Zoo ^{19,66,68}	Self-protection
	Taï Forest ^{16,67}	Relationship repair
	Mahale ¹⁷	
	ZooParc de Beauval ¹⁸	Reduces social stress and aggression in entire group
	Yerkes Regional Primate Research Center ³⁴	Stress reduction
Pan paniscus	Apenheul Primate Park ²³	Stress reduction
Gorilla gorilla beringei	Zoo Atlanta ²²	
	Apenheul Primate Park ²¹	Stress reduction
Macaca arctoides	Yerkes Regional Primate Research Center ²⁵	Self-protection
Papio hamadryas ursinus [‡]	Moremi Game Reserve, Botswana ²⁴	Relationship repair
Canis domesticus	Versele-Laga, Deinze, Belgium ²⁶	
Corvus frugilegus*	University of Cambridge ²⁷	Strengthen partner bonds

[†]Functions are in italics if they were tested in the study. Cells are empty for cases where no function was suggested. [‡]The occurrence of bystander affiliation was not demonstrated but experimentally manipulated bystander affiliation was shown to increase tolerance between opponents to baseline levels. ^{*}The occurrence of bystander initiated post-conflict affiliation with the recipient of aggression was demonstrated, but affiliation initiated by the recipient of aggression and initiated by the bystander were combined for analyses on the patterns of bystander affiliation and thus conclusions about the likely function refer to bystander affiliation initiated by either party.

indicators of stress in chimpanzees. 19 More recently, however, another study on chimpanzees found that bystander affiliation did reduce levels of behavioral indicators of stress,54 suggesting that bystander affiliation does have a stress reduction function, at least in some cases. Both of these studies used levels of self-directed behavior (self-scratching and/or self-grooming) to measure levels of stress. While direct evidence that these behaviors are linked to stressrelated physiological changes is lacking, there is a growing body of circumstantial evidence that suggests that self-directed behaviors are reliable indicators of stress and anxiety in primates. 55,56 Indirect physiological evidence is provided by the fact that allo-grooming reduces both self-directed behaviors⁵⁰ and heart rate.^{51,57} There is also pharmacological evidence to support the link, as anxiogenic and anxiolytic drugs selectively increase and decrease levels of self-directed behavior respectively. 58,59 Furthermore, levels of self-grooming and self-scratching have been used successfully in a number of studies across primate species to investigate the stress-inducing and stressalleviating effects of aggressive conflict and post-conflict interactions and variations in stress levels therein. 32,33,60-65 Moreover, the stressalleviating effect of reconciliation in human children assessed using levels of self-directed behavior⁶⁴ has now been confirmed based on analysis of salivary cortisol levels.⁸ As the evidence for the stress

alleviation effect is still limited, more studies are needed to address the link between post-conflict bystander affiliation and stress reduction, preferably using both behavioral and physiological measures of stress in the same study.

Self Protection

Call et al.²⁵ suggested that bystander affiliation in stumptailed macaques might serve a self-protective rather than stress-reducing function on the basis that such contacts consisted of socio-sexual behaviors, which are not likely to alleviate stress, and were not provided by the recipient of aggression's kin, which are expected to be the partners most likely to provide stress alleviation. No evidence was found, however, that the recipients of aggression redirected aggression towards bystanders after conflicts. In contrast, Koski and Sterck⁶⁶ found that in chimpanzees, bystanders were less likely to become targets of redirected aggression if they affiliated with the recipient of aggression after a conflict. Original recipients of aggression were equally likely to redirect aggression after receiving affiliation from bystanders, but directed aggression towards group members other than the bystander from whom they received postconflict affiliation.66 As bystander affiliation was not shown to reduce behavioral indicators of stress in this group of chimpanzees, 19 it seems unlikely that it simultaneously serves a self-protection and stress-reduction function, but rather that these functions represent separate post-conflict strategies. Moreover, when bystander affiliation was shown to have a self-protective function, it was unlikely to be provided by kin,66 whereas, in another group of chimpanzees, bystander affiliation with a stress-reducing function was offered by valuable partners.54

The social constraints hypothesis³⁴ predicts, as an alternative to the cognitive constraints hypothesis, that inter-species differences in the occurrence of bystander affiliation are due to the differential risk of aggression for potential bystanders on approaching the original recipient of aggression. Following this hypothesis, bystander affiliation is more likely to occur in species with more tolerant social systems, where the risks of further aggression involving the recipient are lower. The apparent intra-specific differences in functions of bystander affiliation in chimpanzees may provide support for the social constraints hypothesis. Bystander affiliation provided by valuable partners was shown to reduce levels of behavioral indicators of stress in one group of chimpanzees, where redirected aggression was virtually absent,⁵⁴ whereas a stress-alleviating effect was not found in a group of chimpanzees with a relatively higher rate of redirected aggression,¹⁹ and bystander affiliation in that group was likely to be offered by those most at risk of becoming targets of redirected aggression.66 Thus, differences in the function of bystander affiliation may stem from a differential risk of aggressive conflict for the bystanders.

Opponent Relationship Repair

Affiliative post-conflict interactions between a conflict participant and their opponent's kin, or triadic reconciliations, have been well documented. 13,14,39,47-49 They have been suggested to function as a substitute for reconciliation when the risk of renewed aggression between the opponents is too high. 16 Thus, relatives of a conflict participant may approach and affiliate with its former opponent and in doing so act on its behalf, potentially repairing the former

opponents' relationship and reducing post-conflict stress. In most studies it was unclear whether such interactions were initiated by bystanders or conflict participants, and directed towards the recipient or initiator of aggression. The only study that distinguished between the aggressor and recipient of aggression found post-conflict affiliative interactions only between aggressors and their opponents' kin.³⁹ A recent study, however, has shown that bystander affiliation directed from the aggressor's kin to the recipient of aggression may indeed repair the opponents' relationship.²⁴ Using an experimental set-up that exploited baboons' (Papio hamadryas ursinus) use of affiliative vocalizations for reconciliation, playback recordings of affiliative vocalizations from the aggressor's kin after a conflict lead to the recipient of aggression displaying increased tolerance for the aggressor's presence. Thus, bystander affiliation may function not only as a stress-alleviating or self-protecting mechanism, but may also function to repair the opponents' relationship.²⁴

Such a function may not be limited to bystander affiliation from the aggressor's kin. In species in which high-value relationships exist between unrelated individuals, valuable partners may also be able to act on the aggressor's behalf. In chimpanzees, bystander affiliation has been shown to occur between aggressors' valuable partners and recipients of aggression.⁶⁷

Other Functions

While the stress-reduction, self-protection and relationship-repair functions of bystander affiliation have received the most attention, they are almost certainly not its only functions. That aggressive conflict affects the behavior of individuals other than those directly involved in the conflict is well known, but post-conflict interactions may also have a wider effect than is immediately apparent. Bystander affiliation in chimpanzees has been found to reduce the likelihood of further aggression among group members, ¹⁸ and thus might function to prevent the diffusion of conflict throughout the group.

Research on corvids has lead to the suggestion that bystander affiliation may also function to show support for valuable partners or to strengthen bonds between allies and advertise that bond to others,²⁷ although in these cases affiliation was initiated by either the bystander or the recipient of aggression.

Interdependency of Bystander Affiliation & Reconciliation

Bystander affiliation is only one of a number of post-conflict interactions, 16,68 and as such we may be able to understand more about the functions of bystander affiliation by examining it in the context of post-conflict strategies as a whole rather than in isolation. The stress-reduction and relationship-repair functions of bystander affiliation, in particular, overlap with those of reconciliation, and thus it seems likely that the occurrence of reconciliation and bystander affiliation (at least when those functions are applicable) are linked. Reconciliation is expected to be the first priority for opponents, as it is likely to be most effective in mitigating the negative consequences of aggressive conflict, by repairing the relationship between opponents and reducing post-conflict stress. Reconciliation does, however, entail risks of renewed aggression,⁷ and thus may not occur when the value of the opponents' relationship is low or the risk of renewed aggression is high, as the costs would outweigh the benefits.^{7,69} Bystander affiliation may thus, under some circumstances, function as an alternative to reconciliation in situations when approaching the former

opponent is likely to result in renewed aggression. ¹⁶ Accordingly, interdependency of post-conflict interactions is expected when the functions of bystander affiliation and reconciliation overlap. Indeed bystander affiliation was found to be more likely to occur in the absence of reconciliation and vice-versa when a stress-reduction function²⁰ and a relationship-repair function¹⁶ were likely, suggesting that bystander affiliation under those circumstances occurs when reconciliation is too risky. A similar interdependence between bystander affiliation and reconciliation was found when bystander affiliation was shown to reduce further aggression in the whole group, ¹⁸ and when a function was not determined. ²³

As the self-protection function of bystander affiliation primarily benefits the bystander rather than the recipient of aggression, the effects of this form of bystander affiliation and reconciliation might not be linked. Indeed, no interdependency between the two events was found when a self-protection function was shown in chimpanzees.⁶⁸ However, a more subtle form of interdependency may be present. As self-protective bystander affiliation functions to reduce the chances of redirected aggression, the patterns of interdependency between self-protective bystander affiliation and reconciliation may be mediated by the occurrence of redirected aggression. Thus, if the occurrence of redirected aggression and reconciliation are interdependent, as has been found in some species,³⁸ then bystander affiliation occurring when the risks of redirected aggression are high may be indirectly linked to the occurrence of reconciliation. When multiple post-conflict interactions occur after a single conflict, however, the likelihood that once a post-conflict interaction takes place, any subsequent interactions occur as a result of the first post-conflict interaction, rather than as a direct result of the preceding conflict, should be considered.

Bystander Affiliation and Relationship Quality

Our review has highlighted that post-conflict affiliation directed from a bystander to a recipient of aggression can have multiple functions. These functions are not species-specific, but rather this behavior may have different functions within the same species and even within the same group. Relationship quality may be the key to understanding the function of each occurrence of bystander affiliation. The quality of the relationship between the opponents determines the costs and benefits of reconciliation, which in turn may determine the costs and benefits of bystander affiliation from the recipient's point of view. Similarly, the relationship between the bystander and the recipient may determine the costs and benefits of affiliation from the bystander's point of view. Thus, in order to understand the functions and determinants of bystander affiliation, it is important to investigate the quality of the relationships involved. In this context it is useful to view relationship quality as consisting of three separate components, relationship value, compatibility and security.⁶⁹ Value refers to the benefits afforded by the relationship. Compatibility is a measure of the general tenor of social interactions, or the tolerance of the dyad. Security refers to the predictability of a partner's behavior, or is a measure of the consistency of interactions between partners over time.

Bystander affiliation is likely to function as consolation, or have a stress reduction function, when conflict has lead to elevated stress levels and when reconciliation is less likely to occur. Thus, in these circumstances the relationship between opponents is likely to be of low value, and thus not worth repairing, and/or of low compatibility, leading to an increased risk of renewed aggression. Furthermore, the relationship between the bystander and the recipient of aggression is likely to be highly valuable when bystander affiliation has a stress reduction function, as valuable partners are expected to be more responsive to each other's distress. 70 Moreover, valuable partners are likely to exchange affiliation reciprocally, and as such may be more likely to offer stress-reducing bystander affiliation, as bystanders are unlikely to gain direct benefits from such interactions. Indeed, Fraser et al.⁵⁴ found that bystander affiliation was most likely to be offered by those who shared a valuable relationship with the recipient of aggression in chimpanzees, and bystander affiliation in rooks occurs only between mating partners.²⁷ If the stress reduction function of bystander affiliation applies mainly to valuable partners, it seems likely that it would be difficult to detect a stress reduction effect if such an effect were investigated across the group as a whole rather than within just those dyads who share valuable relationships. This may have happened in the case of Koski & Sterck's 19 study in which a stress-reduction function for bystander affiliation was not found (see below), although a stress reduction effect was not found even when only bystander affiliation provided by kin was considered. That bystander affiliation is provided by valuable partners and reduces stress levels⁵⁴ supports the hypothesis that 'consolation' may be an expression of empathy. The mechanism behind bystander affiliation, however, cannot be determined by examining its function, and more needs to be understood about the benefits afforded to the bystander by consoling the recipient of aggression for us to understand the bystander's motivation to console.

The self-protection function of bystander affiliation is likely to apply when the relationship between the bystander and the recipient of aggression is of low value and low compatibility, leading to a high probability that the bystander will become the target of redirected aggression. The relationship between the opponents is likely to depend on the functions and patterns of redirected aggression. If redirected aggression provides an alternative stress-alleviation mechanism to reconciliation, 60 then the relationship between opponents is likely to be of low compatibility as the risks of renewed aggression upon reconciliation may be too high. However, as redirected aggression may lead to an increased likelihood of reconciliation,³⁸ the value of the opponents' relationship may be high as the benefits of reconciliation appear to outweigh the risks once redirected aggression has occurred. Thus, the occurrence of self-protective bystander affiliation is likely linked to risks of aggressive conflict for both the original recipient of aggression and for the bystander. Interestingly, when a self-protection function was likely for most cases of bystander affiliation in a chimpanzee group, it seemed unlikely to apply to bystander affiliation offered by kin of the recipient of aggression, as the risks of redirected aggression towards those individuals was very low.⁶⁶ Thus, while bystander affiliation offered by those at risk of becoming targets of redirected aggression may function as a self-protective mechanism, bystander affiliation from kin may serve another function, such as distress alleviation.

When opponent relationship repair is the likely function of bystander affiliation, the relationship between the bystander and the aggressor is valuable enough to serve as a proxy for the recipient. It is also likely that the relationship between the opponents is of low compatibility, and thus the risks of renewed aggression are too high for direct reconciliation to take place. The relationship between opponents is nevertheless likely to be valuable enough for relationship repair to be worthwhile. The relationship between the bystander and the aggressor is also likely to be more valuable than the relationship between the bystander and the recipient of aggression, as was found when a relationship repair function was likely for bystander affiliation in chimpanzees.⁶⁷

Measuring Relationship Quality

The importance of each of the components of relationship quality, especially between opponents, in shaping post-conflict behavior is well established, 69,71 yet the methods used for measuring relationship quality components are varied and, for the most part, offer an incomplete view of the true quality of the relationship between partners.⁷² Common methods include assigning dyads to relationship quality classifications according to their sex- and/or age-combination 17,73-75 or according to whether they are kin or non-kin.^{39,76-79} While this can be effective, this method does not take into account the considerable variation in the quality of relationships that may exist within these broad categories. Furthermore, the class of relationship quality assigned to each category (such as classifying a particular sexcombination as having valuable relationships) is frequently chosen without adequate justification in the study group (e.g., on what basis are all dyads with that sex-combination thought to have more valuable relationships than other sex-combinations). Levels of certain behaviors deemed to represent certain components of relationship quality are also frequently employed, such as using agonistic support as a measure of relationship value.⁷¹ Single behaviors, however, may not provide enough information for a true evaluation of the quality of the relationship between individuals, and the assignment of behaviors to particular components can be contentious, as for example, grooming has be used to represent either relationship value⁸⁰ or compatibility.^{53,68} Thus, in order to gain more accurate, quantitative estimate of each of the relationship quality components, which is vital if the functions of bystander affiliation are to be fully understood, relationship quality must be measured using improved techniques. Wittig & Boesch⁸¹ suggested that relationship value is best reflected by a combination of several benefits that emerge directly from the value of the relationship and not from the frequency of affiliative interactions and based their measure on levels of both food-sharing and agonistic support. Fraser et al.⁷² went a step further towards obtaining composite, quantitative, behavioral measures for each component of relationship quality using principal component analysis. Their study showed that indeed relationship value, compatibility and security each describes a separate aspect of relationship quality and can be measured using different behavioral indicators.

Bystander Affiliation Form and Function

Examining the behaviors used for bystander affiliation may also provide clues as to its function, particularly for those species showing rich behavioral variation in the form of their post-conflict interactions. Call et al.²⁵ were only able to demonstrate the occurrence of bystander affiliation in stumptailed macaques when grooming and socio-sexual behaviors were analyzed separately. Only socio-sexual behaviors were used by the macaques for bystander affiliation, possibly because these behaviors would be more effective in achieving

the function of self-protection, while minimizing the risk of aggression, as these are brief behaviors that require the partners to spend only a very short period of time in contact with each other. Valuable partners can afford to use potentially more risky behaviors (i.e., those that involve close contact, exposure of sensitive parts of the body and those that make it difficult to flee), as the risk of being attacked is minimal. Thus, for bystander affiliation with a stress reduction function, reassuring, close affiliative contacts are likely to be used.²⁰

Conclusions

Post-conflict bystander affiliation directed at the recipient of aggression may have a number of functions, including, but not exclusively, stress-reduction, self-protection and opponent relationship repair. In addition to studying the consequences of the interaction, a key aspect to understanding these functions is the quality of the relationship within the triad (i.e., the former aggressor, the former recipient of aggression and the bystander). Variation in relationship quality, even within a population, seems to be strongly associated with different functions for what outwardly appear to be very similar behaviors. Thus far, very few studies have investigated the function of post-conflict bystander affiliation, and the occurrence of bystander affiliation in non-primate species is largely unknown. Many more studies, across a wide range of species, are needed before we can fully understand how and why bystanders affiliate with recipients of aggression after a conflict. Future studies should, where possible, investigate the functions of bystander affiliation separately according to qualities of the relationships between opponents and between the bystander and each opponent, as well as according to the forms of affiliative behaviors. Terminology used should reflect the potential for a number of different functions, and thus functional terminology, such as the use of the term 'consolation', should only be used where such a function has been demonstrated. Bystander affiliation is not a single post-conflict interaction, but represents a number of different strategies for the management of conflict, and the functions proposed here may also apply to post-conflict affiliation from bystanders to aggressors. As such, it is important that bystander affiliation is not investigated in isolation but in the context of post-conflict behavior as a whole.

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