ethology international journal of behavioural biology

Ethology

RESEARCH PAPER

Rook, But Not Jackdaw, Post-Conflict Third-Party Affiliation Reduces Aggression for Aggressors

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Received: November 26, 2012
Initial acceptance: January 7, 2013
Final acceptance: February 11, 2013
(L. Fusani)

doi: 10.1111/eth.12078

Abstract

Post-conflict (PC) affiliation refers to positive social interactions that occur after fights. Although this behavior has been widely studied, its functions are rarely tested. We examine a potential function of PC third-party affiliation (affiliation between former opponents and bystanders) in rooks and jackdaws by investigating the hypothesis that conflicts lead to further aggression and that PC third-party affiliation increases to reduce such aggression. The results show that PC affiliation reduces PC aggression for rook aggressors who were less likely to receive aggression after conflicts when they were affiliating with another vs. when they were alone. The opposite result was found for victims of both species who received more aggression after conflicts, and this aggression was not reduced by the act of affiliating. Finally, for jackdaw aggressors, the amount of aggression received after conflicts was not influenced by whether the individual was affiliating or alone, indicating that PC third-party affiliation may serve a function that we did not examine. These findings highlight the importance of investigating functional differences in PC affiliative behavior according to the role played in the conflict.

Introduction

Mammals (de Waal & Yoshihara 1983; Koski & Sterck 2009; Romero et al. 2009), birds (e.g., Seed et al. 2007; Fraser & Bugnyar 2010, 2011; Logan et al. 2013), and fish (Bshary & Wurth 2001; Bshary & D'Souza 2005) exhibit conflict management strategies such as making amends with a former opponent (former opponent affiliation) and affiliating with a bystander (third-party affiliation) after fights (see reviews by Fraser et al. 2009 and Arnold et al. 2010). The prevalence of this behavior indicates its functionality across taxa and contexts; however, the function of post-conflict (PC) affiliation can vary according to the role in the conflict and the initiator of the affiliation, an issue that is rarely investigated (Fraser et al. 2009; Arnold et al. 2010). There are several non-mutually exclusive hypotheses for the function of PC third-party affiliation (see review by Koski & Sterck 2009). It might function to signal the alliances between mated partners to other group members, which could assist the pair in maintaining their dominance rank (Seed et al. 2007). It may serve to maintain long-lasting partnerships: pairs that affiliate more after conflicts may have a longer and more stable relationship (Seed et al. 2007). It might also reduce the stress caused by the conflict (Fraser et al. 2008) or reduce aggression after an initial conflict ('PC aggression'; Fraser & Bugnyar 2010).

PC affiliation has recently been discovered in corvids (birds in the crow family), and functions are beginning to be explored (Seed et al. 2007; Fraser & Bugnyar 2010, 2011; Logan et al. 2013). Two social corvids, rooks (*Corvus frugilegus*) and jackdaws (*Corvus monedula*), show PC third-party affiliation (Seed et al. 2007; Logan et al. 2013); however, the function of this behavior is unknown. Here, we examine the hypothesis that PC third-party affiliation functions to reduce PC aggression in rooks and jackdaws.

It has been suggested that PC third-party affiliation may function to reduce PC aggression for victims in ravens (*Corvus corax*; Fraser & Bugnyar 2010). It is important to assess the role the subject played in the conflict because there is considerable variation for aggressors and victims in the amount of aggression they experience after an initial conflict. For instance, it is not simply the case that all victims necessarily experience more aggression than all aggressors (Koski et al. 2007). It is also important to distinguish among initiators of PC aggression. After conflicts, an increase in non-conflict aggression (i.e., aggression that is much less severe than a conflict) may be directed to bystanders by former opponents (i.e., redirected aggression), in which case third-party affiliation can be initiated by bystanders to reduce their chances of becoming a recipient of aggression (Fraser et al. 2009). Alternatively, aggression can be directed to former opponents by others, and here, third-party affiliation initiated by former opponents may reduce the likelihood of receiving this aggression (Das 2000; Call et al. 2002; Koski & Sterck 2009; Romero et al. 2009, 2011). In either case, third-party affiliation might function to reduce aggression. Evidence in support of this hypothesis comes from empirical work by Fraser & Bugnyar (2010) who found that subadult raven victims initiated affiliation with bystanders to reduce PC aggression between former opponents (i.e., renewed aggression).

Based on the results for ravens (Fraser & Bugnyar 2010), PC third-party affiliation might also function to reduce aggression in rooks and jackdaws given that both species show third-party affiliation and non-conflict aggression is common after conflicts. Our study is the first to examine PC aggression in rooks and jackdaws. Therefore, we specified the following four broad predictions, which allowed us to investigate all interactions that might be occurring according to the 'Reduction of Aggression Hypothesis': (1) an increase in non-conflict aggression after conflicts either between former opponents or between a former opponent and a bystander; (2) an increase in third-party affiliation after conflicts; (3) an effect of frequency and/or duration of affiliation on the frequency of aggression received by former opponents from former opponents or bystanders; (4) an increase in aggression directed toward former opponents when they are alone rather than when affiliating with another (i.e., the proximity of another individual directly reduces aggression). If an initial conflict increases the probability of further aggression between former opponents (prediction 1), a former opponent affiliating with a bystander might be expected to reduce such aggression received by that individual because the act of affiliating may deter attacks from others (prediction 4; note that there is no strong evidence for former opponent affiliation in rooks and jackdaws [Logan et al. 2013], therefore former opponents are not expected to affiliate with each other to reduce aggression). If an initial conflict increases the probability of further aggression between a former opponent and a bystander (prediction 1; note that this would likely not be the same bystander the former opponent is affiliating with because they affiliate mostly with their mates who rarely aggress against each other; Logan et al. 2013), then affiliation (with the mate) might be expected to reduce such aggression for the recipient of the aggression (predictions 2–4), regardless of whether the recipient is the former opponent or the bystander. In both cases, affiliation would serve a self-protective function.

Methods

Rooks (n = 13) and jackdaws (n = 14) were housed in a large outdoor aviary (20 m × 10 m × 3 m), individually marked with color leg bands, and observed by CJL from November 2008 through April 2011 from huts adjacent to the aviary (see Logan et al. 2013 for more details). PC affiliation (results presented in Logan et al. 2013) and aggression data were collected using the post-conflict-matched control method (PC-MC method; de Waal & Yoshihara 1983). After a conflict ended, either the aggressor or the victim was observed for 10 min, and all behaviors and their initiators were recorded using the Observer (Noldus Technologies, Inc.). On the next possible day, at the same time as the PC, a 10-min-matched control (MC) was carried out on the same individual, again recording all behaviors and their directions. The MC was canceled if a conflict occurred during the MC or in the 10 min prior to the MC to ensure the subjects were not engaged in PC behavior (see Logan et al. 2013 for detailed methods and ethogram).

All PC aggression referred to in this study was aggression of a much lesser intensity (non-conflict aggression) than the initial conflicts. Conflicts were defined as aggressive physical contact resulting in one or both individuals leaving the area. Non-conflict aggression was defined as aggressive encounters, which either did not involve physical contact or which, in the cases with physical contact, did not result in either individual leaving the area. Thus, non-conflict aggression primarily involved displacements (a bird approaching another causing it to move, while the first one takes its place in the space) and threats (pecking at or lunging at another bird; see full ethogram in Logan et al. 2013). We refer to both the initiators and winners of conflicts as 'aggressors' because initiators usually also win conflicts (Logan et al. 2013) and to individuals that initiate non-conflict aggression as ‘initiators of aggression’. Note that non-conflict aggression could occur in matched controls as well as in observation sessions after conflicts (Fig. 1), and could be initiated by conflict victims, conflict aggressors, or bystanders.

Data were collected on 108 PC-MC pairs in rooks and 116 PC-MC pairs in jackdaws. Aggressors were followed in 42 PC-MC pairs in rooks and 62 PC-MC pairs in jackdaws, and victims in 66 rook PC-MC pairs and 54 jackdaw PC-MC pairs (data deposited in the Dryad Repository: http://dx.doi.org/10.5061/dryad.r4jq1). Rooks had 6 and jackdaws had 5 PCs with no affiliation, and there were no MCs without any affiliative contact. Affiliative behaviors included sitting in proximity to another or contact sitting, allopreening, active food sharing, and bow displaying (see Logan et al. 2013 for full ethogram). PC and MC aggression data were normally distributed according to the Anderson-Darling normality test ($p > 0.05$); therefore, parametric tests were used for analyses. Each test model (a model with all of the factors of interest) was specifically chosen to fit a specific prediction; therefore, we selected the model of best fit by comparing the test model with a base model (a model with none of the factors of interest). We did not examine intermediate models (i.e., models with some, but not all of the factors in the test model), which were irrelevant to the prediction (Burnham & Anderson 2002). The model of best fit was selected by comparing a base model (response variable~1) against the test model (response variable~explanatory variables) and choosing the model with the lowest AICc (Akaike’s Information Criterion for small samples; Akaike 1981) value and highest Akaike weight using dredge and subset functions in R (R package: MuMIn [Bates et al. 2011]; R Development Core Team 2011; Akaike 1981; Burnham & Anderson 2002). Akaike weights range from 0 to 1 with the sum of the weights of the models equaling 1. Models with an Akaike weight equal to or greater than 0.9 are strongly supported and can be relied upon to make inferences about the system in question (Burnham & Anderson 2002). Models with Akaike weights less than 0.9 indicate that inferences suggested by competing models cannot be ruled out (Burnham & Anderson 2002). Generalized linear mixed models (GLMMs) were applied in R using a Poisson distribution and log link (R package: lme4, Bartoń 2012). The base model of each GLMM is indicated by ‘’’ to which each other factor level is compared in the results.

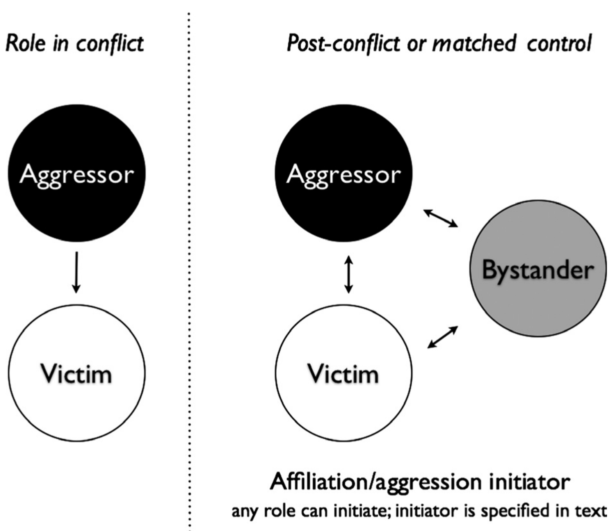

Fig. 1: Visualization of the possible interactions between aggressors, victims, and bystanders according to the role in the conflict and initiator of affiliation or aggression. A conflict occurs when an aggressor initiates (indicated by the direction of the arrow) a conflict with the victim. After the conflict (and in matched controls) the aggressor and victim maintain their titles. Aggressors and victims can be referred to collectively as former opponents to distinguish individuals that were involved in the conflict from bystanders, and they can engage in affiliation and/or non-conflict aggression with each other and/or bystanders.

Prediction 1: To determine whether initial conflicts increased the rate of further, non-conflict aggression (displacements and threats, see Logan et al. 2013 for ethogram) in PCs vs. MCs. We examined the frequency of aggression per session (response variable) as influenced by treatment (MC‘, PC), and role in the conflict (aggressor‘, victim; explanatory variables), and included treatment and subject as random factors. One model was run for aggression between former opponents and another for aggression between a former opponent and a bystander for these analyses. However, as there were few aggressive events between former opponents for both rooks ($n = 36$) and jackdaws ($n = 41$), subsequent analyses included only aggression between a former opponent and a bystander ($n = 145$ rooks, $n = 120$ jackdaws). Prediction 2: results are presented from previous work by Logan et al. (2013) using GLMMs to determine whether the frequency or duration of affiliation per session (response variable) was influenced by treatment, sex, role, affiliation initiator, relationship type, or age, with subject and treatment as random factors. Prediction 3: GLMMs were carried out to test the frequency of aggression per session (response variable) according to affiliation duration or frequency per session, role, and treatment (explanatory variables; subject, treatment, and affiliation duration were included as random factors). Prediction 4: we used a GLMM to test the frequency of aggression per session (response variable) as influenced by whether the subject was affiliating with another (others absent' [alone], others present [with another bird]), treatment, and role (explanatory variables; subject and treatment were included as random factors).

Results

Prediction 1: Did Non-Conflict Aggression Increase After Conflicts?

Overall, non-conflict aggression did not increase after conflicts relative to matched controls: the overall frequency of aggression in PCs and MCs was similar for rooks and jackdaws (paired *t*-test: rooks: t = 1.04, df = 107, p = 0.30, 95% confidence interval = −0.28 to 0.91; jackdaws: t = 1.08, df = 115, p = 0.28, 95% CI = −0.17 to 0.59). However, non-conflict aggression was higher in PCs than MCs for rook aggressors who increased non-conflict aggression toward victims (Akaike weight = 1.00; Table 1, Model 1a), which was reflected in the complementary model indicating that victims received more aggression from aggressors in PCs than in MCs (Akaike weight = 1.00; Table 1, Model 2a). There was no evidence for an increase in aggression in jackdaw victims or aggressors after conflicts (Tables 1 and 2).

Prediction 2: Did Affiliation Increase After Conflicts?

Post-conflict third-party affiliation occurred in both species. These results are reported in Logan et al. (2013); however, we summarize them here. The frequency and duration of post-conflict third-party affiliation increased after conflicts relative to matched controls for rook victims of both sexes (see Tables 5 and 6 in Logan et al. 2013: frequency: Table 5, test model AIC = 408, base model AIC = 444; duration: Table 6, test model AIC = 14830, base model AIC = 18985). The frequency of affiliation increased after conflicts for jackdaw aggressors (males) and victims (both sexes) relative to matched controls (Table 5 in Logan et al. 2013: test model AIC = 388, base model AIC = 389), and the duration of affiliation lengthened after conflicts for aggressors (both sexes) and victims (females) relative to matched controls (Fig. 2; Table 6 in Logan et al. 2013: test model AIC = 17839, base model AIC = 25055). While both former opponents and bystanders initiated affiliation, it was more likely to be initiated by the former opponent in rooks (Table 5 in Logan et al. 2013: GLMM estimate = 4.57, se = 4.03) and in jackdaw females (Table 5 in Logan et al. 2013: GLMM estimate = 1.59, se = 2.83), while jackdaw males were more likely to have affiliation initiated by bystanders (Table 5 in Logan et al. 2013: GLMM estimate =−5.75, se = 3.42).

Prediction 3: Does the Frequency and/or Duration of Affiliation Influence the Frequency of Receiving Aggression?

The frequency of aggression received by former opponents was not influenced by affiliation duration across the whole session because the base model was the model of best fit for both rooks (base model Akaike weight = 0.998) and jackdaws (base model Akaike weight = 0.85), regardless of their role in the conflict (Table 3, Model: Duration). The frequency of aggression received by former opponents was also not influenced by affiliation frequencies in rooks because the base model was the model of best fit (Akaike weight = 0.993, Table 3, Model: Frequency). In contrast, the frequency of aggression received by jackdaw former opponents was influenced by affiliation

Table 1: Prediction 1: GLMM results for the frequency of non-conflict aggression between former opponents after initial conflicts (estimate, standard error). Models 1a (test model) and 1b (base model) refer to aggression directed from the former opponent that was the focal subject toward the other former opponent, and models 2a (test model) and 2b (base model) refer to aggression directed from the non-focal former opponent toward the focal former opponent. Subject and treatment were specified as random factors in all models. Column headers in parentheses are implicit levels of that factor, agg denotes the aggressor in the conflict

Species	Model	Intercept (agg, MC)	Victim (MC)	PC (agg)	PC* Victim	df	loglik	AICc	Akaike Weight
Rook	1a. Test	−0.89, 1.31	−0.15, 0.79	20.95, 3871.60	−19.55, 3871.60	6	−21	55	1.00
	1b. Base	−1.42, 0.54				3	−32	71	0.00
	2a. Test	−4.08, 2.02	2.00, 1.04	0.23, 2.47	0.14, 1.27	6	−25	65	1.00
	2b. Base	−0.16, 0.17				3	−38	82	0.00
Jackdaw	1a. Test	−0.85, 0.99	−0.59, 0.70	0.95, 1.13	−0.03, 0.85	6	−29	72	0.40
	1b. Base	−1.23, 0.46				3	−32	71	0.60
	2a. Test	−0.08, 0.81	−0.57, 0.56	−1.26, 1.02	1.11, 0.70	6	−46	105	0.15
	2b. Base	−0.70, 0.27				3	−48	102	0.85

Table 2: Prediction 1: GLMM results for the frequency of non-conflict aggression between a former opponent and a bystander after initial conflicts (estimate, standard error). Models 1a (test model) and 1b (base model) refer to aggression directed from a former opponent toward a bystander, and models 2a (test model) and 2b (base model) refer to aggression directed from bystanders toward former opponents. Subject and treatment were specified as random factors in all models. Column headers in parentheses are implicit levels of that factor, agg denotes the aggressor in the conflict

Species	Model	Intercept (agg, MC)	Victim (MC)	PC (agg)	PC* Victim	df	loglik	AICc	Akaike Weight
Rook	1a. Test	0.08, 0.23	−0.17, 0.20	−0.52, 0.21	0.42, 0.29	6	−168	342	0.68
	1b. Base	−0.31, 0.22				3	−166	344	0.32
	2a. Test	−0.66, 0.55	−0.07, 0.29	0.02, 0.65	0.23, 0.37	6	−146	304	0.21
	2b. Base	−0.57, 0.31				3	−148	301	0.79
Jackdaw	1a. Test	−1.65, 0.55	0.28, 0.33	−0.43, 0.74	0.35, 0.45	6	−111	233	0.36
	1b. Base	−1.15, 0.17				3	−113	232	0.65
	2a. Test	−0.81, 0.44	0.10, 0.27	−1.15, 0.64	0.69, 0.38	6	−138	288	0.68
	2b. Base	−0.71, 0.16				3	−142	290	0.32

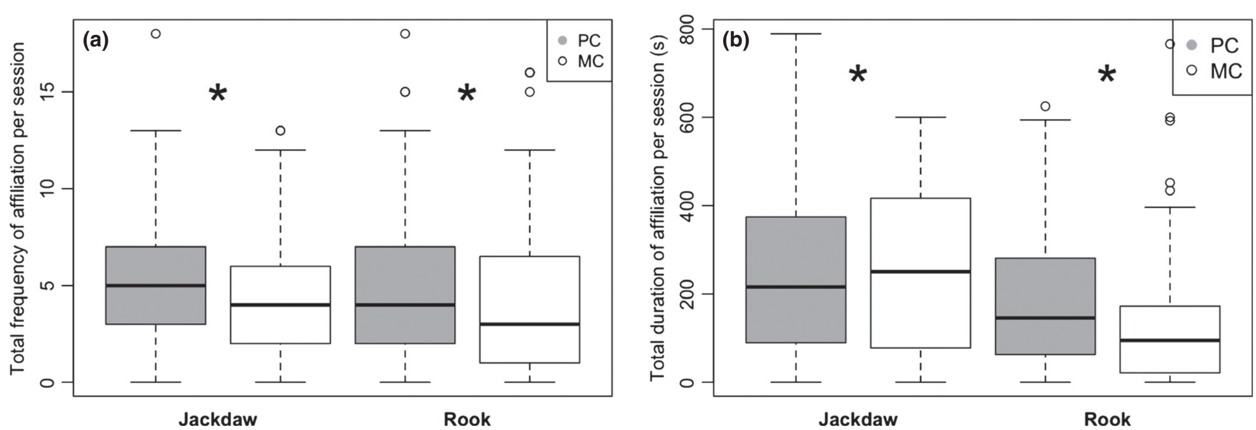

Fig. 2: Prediction 2: The total frequency (a) and duration (b) of affiliation per post-conflict (PC) or matched control (MC) by species. Note that duration totals can add up to more than the observation session length (600s) because multiple affiliative states could occur at one time. Asterisks (*) indicate effect size directions found in the GLMM analyses in Logan et al. (2013), which are summarized in the text. Figure reproduced from Logan et al. (2013).

frequencies (test model Akaike weight = 0.998). After conflicts, victims received more aggression with increasing frequency of affiliation (effect = 0.24, se = 0.21), while aggressors showed a negative relationship between aggression and affiliation frequencies (effect = −0.57, se = 0.33). However, the opposite pattern was found for victims and aggressors in MCs: a negative relationship between affiliation and aggression frequencies for victims (effect = −0.06, se = 0.17) and a positive relationship for aggressors (effect = 0.40, se = 0.24; Table 3).

Prediction 4: Did Former Opponents Receive More Aggression When Alone Rather Than When Affiliating With Another?

In PCs, rook conflict aggressors received less aggression when they were affiliating with another than when they were alone (Akaike weight = 1.00, Fig. 3, Table 4, test model). Jackdaw conflict aggressors also received less aggression when affiliating in PCs than in MCs; however, in PCs, the reduced aggression occurred regardless of whether they were affiliating or alone (Akaike weight = 0.96, Table 4, test model). In MCs, conflict aggressors from both species received more aggression when affiliating than when alone (rooks: alone effect = −0.95, se = 0.67, affiliating effect = −0.18, se = 1.11; jackdaws: alone effect = −1.57, se = 0.55, affiliating effect = 0.58, se = 0.87; Table 4). Victims of both species received more aggression in PCs relative to MCs: for rooks this was regardless of whether they were affiliating with another or alone (alone PCs: effect = 0.36, se = 0.47, MCs: effect = −0.20, se = 0.37; affiliating PCs: effect = 0.37, se = 0.87, MCs: effect = −0.51, se = 0.69), and for jackdaws the effect was stronger when alone (alone

Table 3: Prediction 3: GLMM results for the frequency of a former opponent receiving aggression from a bystander in relation to the duration and frequency of affiliation (estimate, standard error). Subject, treatment, and affiliation duration were specified as random factors in all models. Column headers in parentheses are implicit levels of that factor; columns labeled 'Affiliation' indicate either the duration or frequency depending on which model is being considered; agg denotes the aggressor in the conflict

Species	Model	Intercept (agg, MC)	Victim (MC)	Affiliation (agg, MC)	Affiliation * Victim (MC)	PC (agg)	PC* Victim	PC* Affiliation (agg)	PC* Affiliation* Victim	df	loglik	AICc	Akaike Weight
Rook	Duration	−5.57, 6.35	−0.34, 3.69	0.006, 0.04	−0.005, 0.03	−3.50, 9.58	2.31, 5.68	0.005, 0.05	−0.001, 0.03	11	−54	132	0.002
	Base	−6.03, 0.93								4	−55	119	0.998
	Frequency	−4.91, 5.33	−0.38, 3.29	0.09, 0.86	−0.07, 0.64	−4.06, 8.34	1.98, 5.01	0.41, 1.09	−0.08, 0.76	11	−53	129	0.007
	Base	−6.03, 0.93								4	−55	119	0.993
Jackdaw	Duration	0.18, 1.42	−1.68, 0.96	−0.004, 0.004	0.003, 0.003	−1.10, 1.96	0.89, 1.24	−0.001, 0.006	0.0008, 0.004	11	−71	166	0.16
	Base	−2.03, 0.26								4	−77	163	0.85
	Frequency	−4.37, 2.12	0.28, 1.36	0.40, 0.24	−0.06, 0.17	3.16, 2.58	−0.97, 1.63	−0.57, 0.33	0.24, 0.21	11	−63	150	0.998
	Base	−2.03, 0.26								4	−77	163	0.002

Table 4: Prediction 4: GLMM results for the frequency of aggression when affiliating with another (present) or alone according to treatment and role for former opponents that were recipients of aggression (estimate, standard error). Subject and treatment were specified as random factors in all models. Column headers in parentheses are implicit levels of that factor, agg denotes the aggressor

Species	Model	Intercept (agg, alone, MC)	Victim (alone, MC)	Present (agg, MC)	Present * Victim (MC)	PC (agg, alone)	PC* Victim (alone)	PC* Present (agg)	PC* Present* Victim	df	loglik	AICc	Akaike Weight
Rook	Test	−0.95, 0.67	−0.20, 0.37	−0.18, 1.11	−0.51, 0.69	−0.01, 0.81	0.36, 0.47	−0.56, 1.46	0.37, 0.87	10	−183	387	1.00
	Base	−1.35, 0.34								3	−200	405	0.00
Jackdaw	Test	−1.57, 0.55	0.35, 0.33	0.58, 0.87	−0.92, 0.57	−1.35, 0.88	0.65, 0.51	−0.003, 1.31	0.46, 0.81	10	−193.887	408	0.96
	Base	−1.39, 0.16								3	−204.257	416	0.04

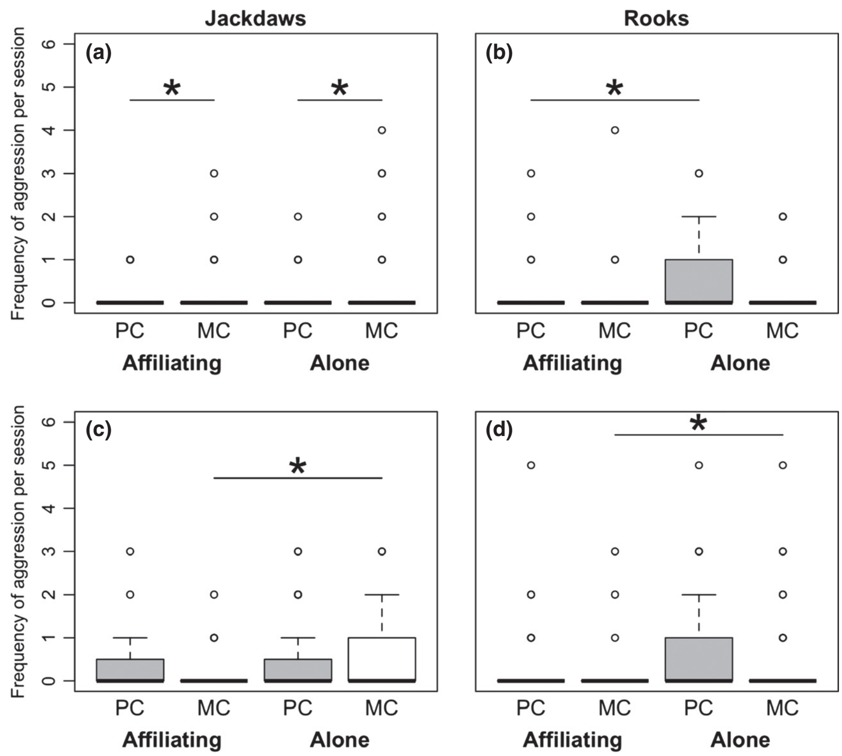

Fig. 3: Prediction 4: The total frequency of post-conflict third-party initiated aggression per post-conflict (PC) or matched control (MC) for conflict aggressors (a and b) and victims (c and d) when jackdaw (a and c) and rook (b and d) former opponents were affiliating with another vs. when they were alone. Boxes show the median and upper and lower quartiles (75% and 25%) of the data, and the whiskers show the maximum and minimum values. Asterisks (*) indicate effect size directions found in the GLMM analysis (Table 4) and are described in the text.

Table 5: Summarizing the predictions and results from the hypothesis that post-conflict third-party affiliation reduces aggression

Predictions	Rooks	Jackdaws
1. Did non-conflict aggression increase after conflicts?	Yes	No
2. Did affiliation increase after conflicts?	Yes	Yes
3. Does the frequency and/or duration of affiliation influence the frequency of receiving aggression?	No	Yes
4. Did former opponents receive more aggression when alone rather than when affiliating with another?	Yes	No

PCs effect = 0.65, se = 0.51, MCs effect = 0.35, se = 0.33; affiliating PCs effect = 0.46, se = 0.81, MCs effect = −0.92, se = 0.57; Table 4). In MCs, jackdaw and rook conflict victims received less aggression when affiliating than when alone (Table 4).

Discussion

After an initial conflict, rook victims received more aggression from the conflict aggressor than they received in matched controls (observation sessions without conflicts, which served as a baseline; Table 5). Accordingly, while both aggressors and victims increased affiliation after conflicts, the effect was stronger for victims (Logan et al. 2013). Jackdaws did not increase aggression after conflicts; however, there was an interaction between aggression and affiliation. If affiliation serves to reduce aggression, then individuals should show a positive relationship between the frequency of aggression and affiliation: when individuals receive extensive aggression, they should affiliate extensively to counter the aggression. This pattern held for jackdaw victims, but not for aggressors. After an initial conflict, jackdaw victims received more aggression the more they affiliated with another individual. In contrast, aggressors were less likely to receive aggression the more they affiliated with another individual.

Only for rook aggressors did PC affiliation directly reduce aggression since they received less aggression while they were affiliating than when they were alone. Victims of both species directly reduced aggression when affiliating (compared with when alone) in matched controls. Therefore, while rook and jackdaw victims may use affiliation to reduce aggression in a non-PC context, it is only the rook aggressors that receive the direct benefits of reduced aggression after conflicts. This difference between rook aggressors and victims is unlikely to be simply due to victims affiliating more after conflicts, and therefore receiving less aggression, because there aggressors and victims did not differ in the duration or frequency of affiliation. Affiliation might have a general aggression reducing function: perhaps the act of affiliating, namely sitting near or touching another individual, prevents others from directing aggression toward either of these individuals because there are two potential adversaries rather than just one. In addition to the PC context, the aggression reducing function of affiliation may serve different purposes. For instance, affiliation with partners may serve as a signal of an alliance to prevent others from initiating aggression in any situation when the risk of receiving aggression is high.

In jackdaws, affiliating only appears to serve a protective function for victims in MCs; therefore, the function of PC third-party affiliation is remains to be elucidated for victims and aggressors. Jackdaw aggressors received the same amount of aggression after conflicts regardless of whether they were affiliating or alone. It appears that the act of affiliating does not reduce aggression after conflicts in this species. This could be due to the fact that there is no evidence for an increase in aggression after conflicts relative to baseline conditions. If aggression does not increase, there would be no need for PC third-party affiliation to decrease aggression. More investigations must be conducted to determine the function of PC affiliation in jackdaws.

In addition to the direct benefits (as just discussed above) of affiliating that were investigated in prediction 4 (affiliating with another will reduce the amount of aggression received), the act of affiliating may also indirectly reduce aggression. Rook aggressors may have a stronger bond with their partners (with whom most of their affiliation occurs) than victims or enjoy a higher rank, potentially causing more immediate relief from aggression due to the signaling of their bond or rank through affiliation.

Affiliation seems to successfully reduce PC aggression for rook aggressors, but not for victims, which might explain why there was no overall increase in aggression in PCs compared with MCs because the decrease for aggressors might have balanced out any increase for victims. If affiliation is used to effectively reduce the amount of aggression received, then the overall level of aggression received should be low. An experimental manipulation of affiliation levels (for example, a condition with affiliation vs. a condition with no affiliation between individuals) would be required to test this hypothesis. However, this would require preventing affiliation among free-flying birds without separating them from particular group members, which might be difficult to achieve in practice.

In summary, we have shown in two corvid species (rooks and jackdaws) that PC affiliation likely serves more than one function. Victims and aggressors show differences in the amount of aggression received after conflicts. Affiliating appears to reduce aggression for rook and jackdaw victims under baseline conditions (MCs), and for rook aggressors after conflicts, however, rook victims lose the protective function of affiliation after conflicts. Thus, our results suggest that while rook aggressors might use affiliation to reduce aggression, PC affiliation might serve a different function for rook victims and jackdaw aggressors and victims. While we have provided evidence for one function, the lack of support for this hypothesis in jackdaws and in rook victims means that PC affiliation serves a different function for these individuals. This result emphasizes the necessity of investigating the functional differences of PC affiliation according to an individual's role in the conflict.

Acknowledgements

We thank Dieter Lukas for analysis assistance and Rachael Shaw for discussions. We are grateful for financial support from the Gates Cambridge Scholarship and Murray Edwards College (CJL), and the BBSRC, the Royal Society, and the University of Cambridge (NSC). The authors declare no conflicts of interest.

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