Rook, but not jackdaw, post-conflict third-party affiliation reduces aggression for aggressors

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Running title: Rook post-conflict third-party affiliation reduces aggression

Word count: 5,373

9 ABSTRACT

10 Post-conflict (PC) affiliation refers to the positive social interactions that occur after fights. Al-

11 though this behavior has been widely studied, its functions are rarely tested. We examine a po-

12 tential function of PC third-party affiliation (affiliation between former opponents and bystand-

13 ers) in rooks and jackdaws by investigating the hypothesis that conflicts lead to further aggres-

14 sion and that PC third-party affiliation increases to reduce such aggression. The results show that

15 PC affiliation reduces PC aggression for rook aggressors who were less likely to receive aggres-

16 sion after conflicts when they were affiliating with another versus when they were alone. The op-

17 posite result was found for victims of both species who received more aggression after conflicts,

18 and this aggression was not reduced by the act of affiliating. Finally, for jackdaw aggressors, the

19 amount of aggression received after conflicts was not influenced by whether the individual was

20 affiliating or alone, indicating that PC third-party affiliation may serve a function that we did not

21 examine. These findings highlight the importance of investigating functional differences in post-

22 conflict affiliative behavior according to the role played in the conflict.

23 INTRODUCTION

24 Mammals (de Waal & Yoshihara 1983; Koski & Sterck 2009; Romero et al. 2009), birds (e.g.,

25 Seed et al. 2007; Fraser & Bugnyar 2010, 2011; Logan et al. 2012), and fish (Bshary & Wurth

26 2001; Bshary & D'Souza 2005) exhibit conflict management strategies such as making amends

27 with a former opponent (former opponent affiliation) and affiliating with a bystander (third-party

28 affiliation) after fights (see reviews by Fraser et al. 2009 and Arnold et al. 2010). The prevalence

29 of this behavior indicates its functionality across taxa and contexts, however the function of post-

30 conflict (PC) affiliation can vary according to the role in the conflict and the initiator of the affil-

31 iation, an issue that is rarely investigated (Fraser et al. 2009; Arnold et al. 2010). There are sever-

32 al non-mutually exclusive hypotheses for the function of PC third-party affiliation (see review by

33 Koski & Sterck 2009). It might function to signal the alliances between mated partners to other

34   group members, which could assist the pair in maintaining their dominance rank (Seed et al.

35   2007). It may serve to maintain long-lasting partnerships: pairs that affiliate more after conflicts

36   may have a longer and more stable relationship (Seed et al. 2007). It might also reduce the stress

37   caused by the conflict (Fraser et al. 2008) or reduce aggression after an initial conflict ('post-

38   conflict aggression'; Fraser & Bugnyar 2010).

39   PC affiliation has recently been discovered in corvids (birds in the crow family) and functions

40   are beginning to be explored (Seed et al. 2007, Fraser & Bugnyar 2010 & 2011, Logan et al.

41   2012). Two social corvids, rooks (*Corvus frugilegus*) and jackdaws (*Corvus monedula*), show PC

42   third-party affiliation (Seed et al. 2007, Logan et al. 2012), however the function of this behavior

43   is unknown. Here we examine the hypothesis that PC third-party affiliation functions to reduce

44   PC aggression in rooks and jackdaws.

45   It has been suggested that PC third-party affiliation may function to reduce PC aggression for

46   victims in ravens (*Corvus corax*; Fraser & Bugnyar 2010). It is important to assess the role the

47   subject played in the conflict because there is considerable variation for aggressors and victims

48   in the amount of aggression they experience after an initial conflict. For instance, it is not simply

49   the case that all victims necessarily experience more aggression than all aggressors (Koski et al.

50   2007). It is also important to distinguish among initiators of PC aggression. After conflicts, an

51   increase in non-conflict aggression (i.e., aggression that is much less severe than a conflict) may

52   be directed *to bystanders by former opponents* (i.e., redirected aggression), in which case third-

53   party affiliation can be initiated by bystanders to reduce their chances of becoming a recipient of

54   aggression (Fraser et al. 2009). Alternatively, aggression can be directed *to former opponents by*

55   *others* and here third-party affiliation initiated by former opponents may reduce the likelihood of

56   receiving this aggression (Das 2000; Call et al. 2002; Koski & Sterck 2009; Romero et al. 2009;

57   Romero et al. 2011). In either case, third-party affiliation might function to reduce aggression.

3   3

58   Evidence in support of this hypothesis comes from empirical work by Fraser and Bugnyar (2010)

59   who found that sub-adult raven victims initiated affiliation with bystanders to reduce post-con-

60   flict aggression between former opponents (i.e., renewed aggression).

61   Based on the results for ravens (Fraser & Bugnyar 2010), PC third-party affiliation might also

62   function to reduce aggression in rooks and jackdaws given that both species show third-party af-

63   filiation and non-conflict aggression is common after conflicts. Our study is the first to examine

64   PC aggression in rooks and jackdaws. Therefore, we specified the following four broad predic-

65   tions which allowed us to investigate all interactions that might be occurring according to the

66   'Reduction of Aggression hypothesis': 1) an increase in non-conflict aggression after conflicts

67   either between former opponents or between a former opponent and a bystander, 2) an increase

68   in third-party affiliation after conflicts, 3) an effect of frequency and/or duration of affiliation on

69   the frequency of aggression received by former opponents from former opponents or bystanders,

70   4) an increase in aggression directed toward former opponents when they are alone rather than

71   when affiliating with another (i.e., the proximity of another individual directly reduces aggres-

72   sion). If an initial conflict increases the probability of further aggression between between

73   former opponents (prediction 1), a former opponent affiliating with a bystander might be expec-

74   ted to reduce such aggression received by that individual because the act of affiliating may deter

75   attacks from others (prediction 4; note that there is no strong evidence for former opponent affili-

76   ation in rooks and jackdaws [Logan et al. 2012], therefore former opponents are not expected to

77   affiliate with each other to reduce aggression). If an initial conflict increases the probability of

78   further aggression between a former opponent and a bystander (prediction 1; note that this would

79   likely not be the same bystander the former opponent is affiliating with since they affiliate

80   mostly with their mates who rarely aggress against each other; Logan et al. 2012), then affiliation

81   (with the mate) might be expected to reduce such aggression for the recipient of the aggression

82   (predictions 2-4), regardless of whether the recipient is the former opponent or the bystander. In

83   both cases, affiliation would serve a self protective function.

84   METHODS

85   Rooks (n=13) and jackdaws (n=14) were housed in a large outdoor aviary (20m x 10m x 3m), in-

86   dividually marked with color leg bands, and observed by CJL from November 2008 through

87   April 2011 from huts adjacent to the aviary (see Logan et al. 2012 for more details). Post-conflict

88   affiliation (results presented in Logan et al. 2012) and aggression data were collected using the

89   post-conflict matched control method (PC-MC method; de Waal & Yoshihara 1983). After a con-

90   flict ended, either the aggressor or the victim was observed for 10 min, and all behaviors and

91   their initiators were recorded using The Observer (Noldus Technologies, Inc.). On the next pos-

92   sible day, at the same time as the PC, a 10 min matched control (MC) was carried out on the

93   same individual, again recording all behaviors and their directions. The MC was canceled if a

94   conflict occurred during or in the 10 min prior to the MC to ensure the subjects were not engaged

95   in post-conflict behavior (see Logan et al. 2012 for detailed methods and ethogram).

96   All post-conflict aggression referred to in this study was aggression of a much lesser intensity

97   than the initial conflicts (non-conflict aggression). Conflicts were defined as aggressive physical

98   contact resulting in the one or both individuals leaving the area. Non-conflict aggression was

99   defined as aggressive encounters which either did not involve physical contact or which, in the

100   cases with physical contact, did not result in either individual leaving the area. Thus, non-conflict

101   aggression primarily involved displacements (a bird approaching another causing this bird to

102   move while the first one takes its place in the space) and threats (pecking at or lunging at another

103   bird; see full ethogram in Logan et al. 2012). We refer to both the initiators and winners of con-

104   flicts as 'aggressors' because initiators usually also win conflicts (Logan et al. 2012) and to indi-

105   viduals that initiate non-conflict aggression as 'initiators of aggression'. Note that non-conflict

106   aggression could occur in matched controls as well as in observation sessions after conflicts (Fig.

107   1), and in the latter case, could be initiated by conflict victims, conflict aggressors, or bystanders.

108   Data were collected on 108 PC-MC pairs in rooks and 116 PC-MC pairs in jackdaws. Aggressors

109   were followed in 42 PC-MC pairs in rooks and 62 PC-MC pairs in jackdaws, and victims in 66

110   rook PC-MC pairs and 54 jackdaw PC-MC pairs (data deposited in the Dryad Repository:

111   http://dx.doi.org/ *insert the rest of the URL here after the data is deposited*). Rooks had 6 and

112   jackdaws had 5 PCs with no affiliation, and there were no MCs without any affiliative contact.

113   Affiliative behaviors included sitting in proximity to another or contact sitting, allopreening, bill

114   twining, active food sharing, and bow displaying (see Logan et al. 2012 for full ethogram). PC

115   and MC aggression data were normally distributed according to the Anderson-Darling normality

116   test ($p > 0.05$), therefore parametric tests were used for analyses. Each test model (a model with

117   all of the factors of interest) was specifically chosen to fit a specific prediction, therefore we se-

118   lected the model of best fit by comparing the test model with a base model (a model with none of

119   the factors of interest). We did not examine intermediate models (i.e., models with some, but not

120   all of the factors in the test model) which were irrelevant to the prediction (Burnham & Ander-

121   son 2002). The model of best fit was selected by comparing a base model (response variable~1)

122   against the test model (response variable~explanatory variables) and choosing the model with the

123   lowest AICc (Akaike's Information Criterion for small samples; Akaike 1981) value and highest

124   Akaike weight using dredge and subset functions (R package: MuMIn, Akaike 1981, Burnham &

125   Anderson 2002). Akaike weights range from 0-1 with the sum of the weights of the models

126   equalling 1. Models with an Akaike weight equal to or greater than 0.9 are strongly supported

127   and can be relied upon to make inferences about the system in question (Burnham & Anderson

128   2002). Models with Akaike weights less than 0.9 indicate that inferences suggested by compet-

129   ing models cannot be ruled out (Burnham & Anderson 2002). Generalized linear mixed models

130   (GLMM) were applied in R using a Poisson distribution and log link (R Development Core

131 Team 2011, R package: lme4). The base model of each GLMM is indicated by ''' to which each

132 other factor level is compared in the results.

133 *Prediction 1:* To determine whether initial conflicts increased the rate of further, non-conflict ag-

134 gression (displacements and threats, see Logan et al. 2012 for ethogram) in PCs versus MCs. We

135 examined the frequency of aggression per session (response variable) as influenced by treatment

136 (MC`, PC), and role in the conflict (aggressor`, victim; explanatory variables), and included

137 treatment and subject as random factors. One model was run for aggression between former op-

138 ponents and another for aggression between a former opponent and a bystander for these ana-

139 lyses. However, since there were few aggressive events between former opponents for both rooks

140 (n=36) and jackdaws (n=41), subsequent analyses included only aggression between a former

141 opponent and a bystander (n=145 rooks, n=120 jackdaws). *Prediction 2:* results are presented

142 from previous work by Logan et al. (2012) using GLMMs to determine whether the frequency or

143 duration of affiliation per session (response variable) was influenced by treatment, sex, role, af-

144 filiation initiator, relationship type, or age, with subject and treatment as random factors. *Predic-*

145 *tion 3:* GLMMs were carried out to test the frequency of aggression per session (response vari-

146 able) according to affiliation duration or frequency per session, role, and treatment (explanatory

147 variables; subject, treatment and affiliation duration as random factors). *Prediction 4:* we used a

148 GLMM to test the frequency of aggression per session (response variable) as influenced by

149 whether the subject was affiliating with another (others absent` [alone], others present [with an-

150 other bird]), treatment, and role (explanatory variables; subject and treatment as random factors).

151 RESULTS

152 *Prediction 1: did non-conflict aggression increase after conflicts?*

153 Overall, non-conflict aggression did not increase after conflicts relative to matched controls: the

154 overall frequency of aggression in PCs and MCs was similar (paired t-test: t=0.77, df=12,

155   p=0.45, 95% confidence interval=-0.05-0.10). However, non-conflict aggression was higher in

156   PCs than MCs for rook aggressors who increased non-conflict aggression toward victims

157   (Akaike weight=1.00; Table 1, Model 1a), which was reflected in the complementary model in-

158   dicating that victims received more aggression from aggressors in PCs than in MCs (Akaike

159   weight=1.00; Table 1, Model 2a). There was no evidence for an increase in aggression in jack-

160   daw victims or aggressors after conflicts.

161   *Prediction 2: did affiliation increase after conflicts?*

162   Post-conflict third-party affiliation occurred in both species. These results are reported in Logan

163   et al. (2012), however we summarize them here. The frequency and duration of post-conflict

164   third-party affiliation increased after conflicts relative to matched controls for rook victims of

165   both sexes (Logan et al. 2012, frequency: Table 5, test model AIC=408, base model AIC=444;

166   duration: Table 6, test model AIC=14830, base model AIC=18985). The frequency of affiliation

167   increased after conflicts for jackdaw aggressors (males) and victims (both sexes) relative to

168   matched controls (Logan et al. 2012, Table 5, test model AIC=388, base model AIC=389), and

169   the duration of affiliation lengthened after conflicts for aggressors (both sexes) and victims (fe-

170   males) relative to matched controls (Fig. 2; Logan et al. 2012, Table 6, test model AIC=17839,

171   base model AIC=25055). While both former opponents and bystanders initiated affiliation, it

172   was more likely to be initiated by the former opponent in rooks (Logan et al. 2012, Table 5,

173   GLMM estimate=4.57, se=4.03) and in jackdaw females (Logan et al. 2012, Table 5, GLMM es-

174   timate=1.59, se=2.83), while jackdaw males were more likely to have affiliation initiated by

175   bystanders (Logan et al. 2012, Table 5, GLMM estimate=-5.75, se=3.42).

176   *Prediction 3: does the frequency and/or duration of affiliation influence the frequency of receiv-*

177   *ing aggression?*

178 The frequency of aggression received by former opponents was not influenced by affiliation *dur-*

179 *ation* across the whole session because the base model was the model of best fit for both rooks

180 (base model Akaike weight=0.998) and jackdaws (base model Akaike weight=0.85), regardless

181 of their role in the conflict (Table 3, Model: Duration). The frequency of aggression received by

182 former opponents was also not influenced by affiliation *frequencies* in rooks because the base

183 model was the model of best fit (Akaike weight=0.993, Table 3, Model: Frequency). In contrast,

184 the frequency of aggression received by jackdaw former opponents was influenced by affiliation

185 frequencies (test model Akaike weight=0.998). After conflicts, victims received more aggression

186 with increasing frequency of affiliation (effect=0.24, se=0.21), while aggressors showed a negat-

187 ive relationship between aggression and affiliation frequencies (effect=-0.57, se=0.33). However,

188 the opposite pattern was found for victims and aggressors in MCs: a negative relationship

189 between affiliation and aggression frequencies for victims (effect=-0.06, se=0.17) and a positive

190 relationship for aggressors (effect=0.40, se=0.24; Table 3).

191 *Prediction 4: did former opponents receive more aggression when alone rather than when affili-*

192 *ating with another?*

193 In PCs, rook conflict aggressors received less aggression when they were affiliating with another

194 than when they were alone (Akaike weight=1.00, Fig. 3, Table 4, test model). Jackdaw conflict

195 aggressors also received less aggression when affiliating in PCs than in MCs, however in PCs

196 the reduced aggression occurred regardless of whether they were affiliating or alone (Akaike

197 weight=0.96, Table 4, test model). In MCs, conflict aggressors from both species received more

198 aggression when affiliating than when alone (rooks: alone effect=-0.95, se=0.67, affiliating ef-

199 fect=-0.18, se=1.11; jackdaws: alone effect=-1.57, se=0.55, affiliating effect=0.58, se=0.87;

200 Table 4). Victims of both species received more aggression in PCs relative to MCs: for rooks this

201 was regardless of whether they were affiliating with another or alone (alone PCs: effect=0.36,

202 se=0.47, MCs: effect=-0.20, se=0.37; affiliating PCs: effect=0.37, se=0.87, MCs: effect=-0.51,

203   se=0.69), and for jackdaws the effect was stronger when alone (alone PCs effect=0.65, se=0.51,

204   MCs effect=0.35, se=0.33; affiliating PCs effect=0.46, se=0.81, MCs effect=-0.92, se=0.57;

205   Table 4). In MCs, jackdaw and rook conflict victims received less aggression when affiliating

206   than when alone (Table 4).

207   DISCUSSION

208   After an initial conflict, rook victims received more aggression from the conflict aggressor than

209   they received in matched controls (observation sessions without conflicts, which served as a

210   baseline; Table 5). Accordingly, while both aggressors and victims increased affiliation after con-

211   flicts, the effect was stronger for victims (Logan et al. 2012). Jackdaws did not increase aggres-

212   sion after conflicts, however there was an interaction between aggression and affiliation. If affili-

213   ation serves to reduce aggression, then individuals should show a positive relationship between

214   the frequency of aggression and affiliation: when individuals receive extensive aggression, they

215   should affiliate extensively to counter the aggression. This pattern held for jackdaw victims, but

216   not for aggressors. After an initial conflict, jackdaw victims received more aggression the more

217   they affiliated with another individual. In contrast, aggressors were less likely to receive aggres-

218   sion the more they affiliated with another individual.

219   Only for rook aggressors did post-conflict affiliation *directly* reduce aggression since they re-

220   ceived less aggression while they were affiliating than when they were alone. Victims of both

221   species directly reduced aggression when affiliating (compared to when alone) in matched con-

222   trols. Therefore, while rook and jackdaw victims may use affiliation to reduce aggression in a

223   non-post-conflict context, it is only the rook aggressors that receive the direct benefits of reduced

224   aggression after conflicts. This difference between rook aggressors and victims is unlikely to be

225   simply due to victims affiliating more after conflicts, and therefore receiving less aggression, be-

226   cause there aggressors and victims did not differ in the *duration* or *frequency* of affiliation. Affil-

227 iation might have a general aggression reducing function, perhaps the act of affiliating, namely,

228 sitting near or touching another individual, prevents others from directing aggression toward

229 either of these individuals because there are two potential adversaries rather than just one. In ad-

230 dition to the post-conflict context, the aggression reducing function of affiliation may serve dif-

231 ferent purposes. For instance, affiliation with partners may serve as a signal of an alliance to pre-

232 vent others from initiating aggression in any situation when the risk of receiving aggression is

233 high.

234 In jackdaws, affiliating only appears to serve a protective function for victims in MCs, therefore

235 the function of PC third-party affiliation is remains to be elucidated for victims and aggressors.

236 Jackdaw aggressors received the same amount of aggression after conflicts regardless of whether

237 they were affiliating or alone. It appears that the act of affiliating does not reduce aggression

238 after conflicts in this species. This could be due to the fact that there is no evidence for an in-

239 crease in aggression after conflicts relative to baseline conditions. If aggression does not in-

240 crease, there would be no need for PC third-party affiliation to decrease aggression. More invest-

241 igations must be conducted to determine the function of PC affiliation in jackdaws.

242 In addition to the *direct* benefits (as just discussed above) of affiliating that were investigated in

243 prediction 4 (affiliating with another will reduce the amount of aggression received), the act of

244 affiliating may also *indirectly* reduce aggression. Rook aggressors may have a stronger bond

245 with their partners (with whom most of their affiliation occurs) than victims or enjoy a higher

246 rank, potentially causing more immediate relief from aggression due to the signalling of their

247 bond or rank through affiliation.

248 Affiliation seems to successfully reduce post-conflict aggression for rook aggressors, but not for

249 victims, which might explain why there was no overall increase in aggression in PCs compared

250   to MCs since the decrease for aggressors might have balanced out any increase for victims. If af-

251   filiation is used to *effectively* reduce the amount of aggression received, then the overall level of

252   aggression received should be low. An experimental manipulation of affiliation levels (for ex-

253   ample a condition with affiliation versus a condition with no affiliation between individuals)

254   would be required to test this hypothesis. However, this would require preventing affiliation

255   among free-flying birds without separating them from particular group members which might be

256   difficult to achieve in practice.

257   In summary, we have shown in two corvid species (rooks and jackdaws) that post-conflict affili-

258   ation likely serves more than one function. Victims and aggressors show differences in the

259   amount of aggression received after conflicts. Affiliating appears to reduce aggression for rook

260   and jackdaw victims under baseline conditions (MCs) and for rook aggressors after conflicts,

261   however rook victims lose the protective function of affiliation after conflicts. Thus, our results

262   suggest that while rook aggressors might use affiliation to reduce aggression, post-conflict affili-

263   ation might serve a different function for rook victims and jackdaw aggressors and victims.

264   While we have provided evidence for one function, the lack of support for this hypothesis in

265   jackdaws and in rook victims means that post-conflict affiliation serves a different function for

266   these individuals. This result emphasizes the necessity of investigating the functional differences

267   of post-conflict affiliation according to an individual's role in the conflict.

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14

317 Figure 1. Visualisation of the possible interactions between aggressors, victims, and bystanders

318 according to the role in the conflict and initiator of affiliation or aggression. A conflict occurs

319 when an aggressor initiates (indicated by the direction of the arrow) a conflict with the victim.

320 After the conflict (and in matched controls) the aggressor and victim maintain their titles. Ag-

321 gressors and victims can be referred to collectively as former opponents to distinguish between

322 individuals that had been involved in the conflict from bystanders, and they can engage in affili-

323 ation and/or non-conflict aggression with each other and/or bystanders.
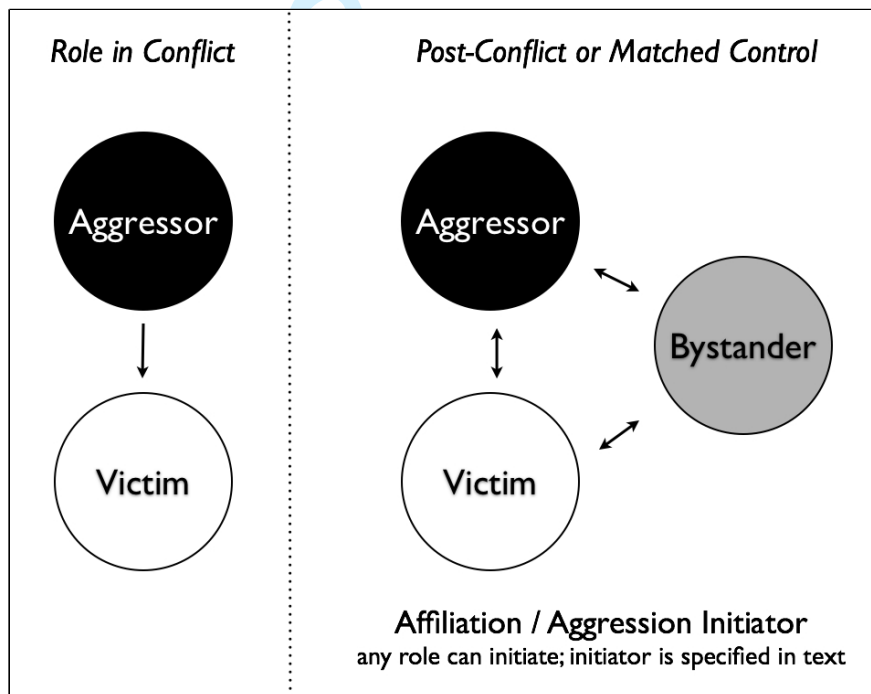
324   Figure 2. The total frequency (A) and duration (B) of affiliation per post-conflict (PC) or

325   matched control (MC) by species. Note that duration totals can add up to more than the observa-

326   tion session length (600s) because multiple affiliative states could occur at one time. Asterisks

327   (*) indicate effect size directions found in the GLMM analyses in Logan et al. (2012) and sum-

328   marized in the text. Figure reproduced from Logan et al. (2012).
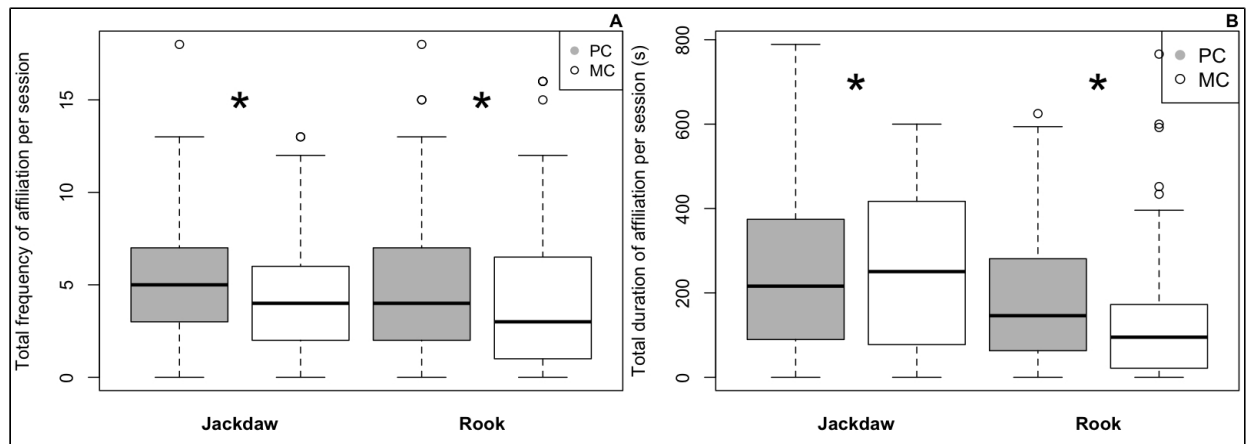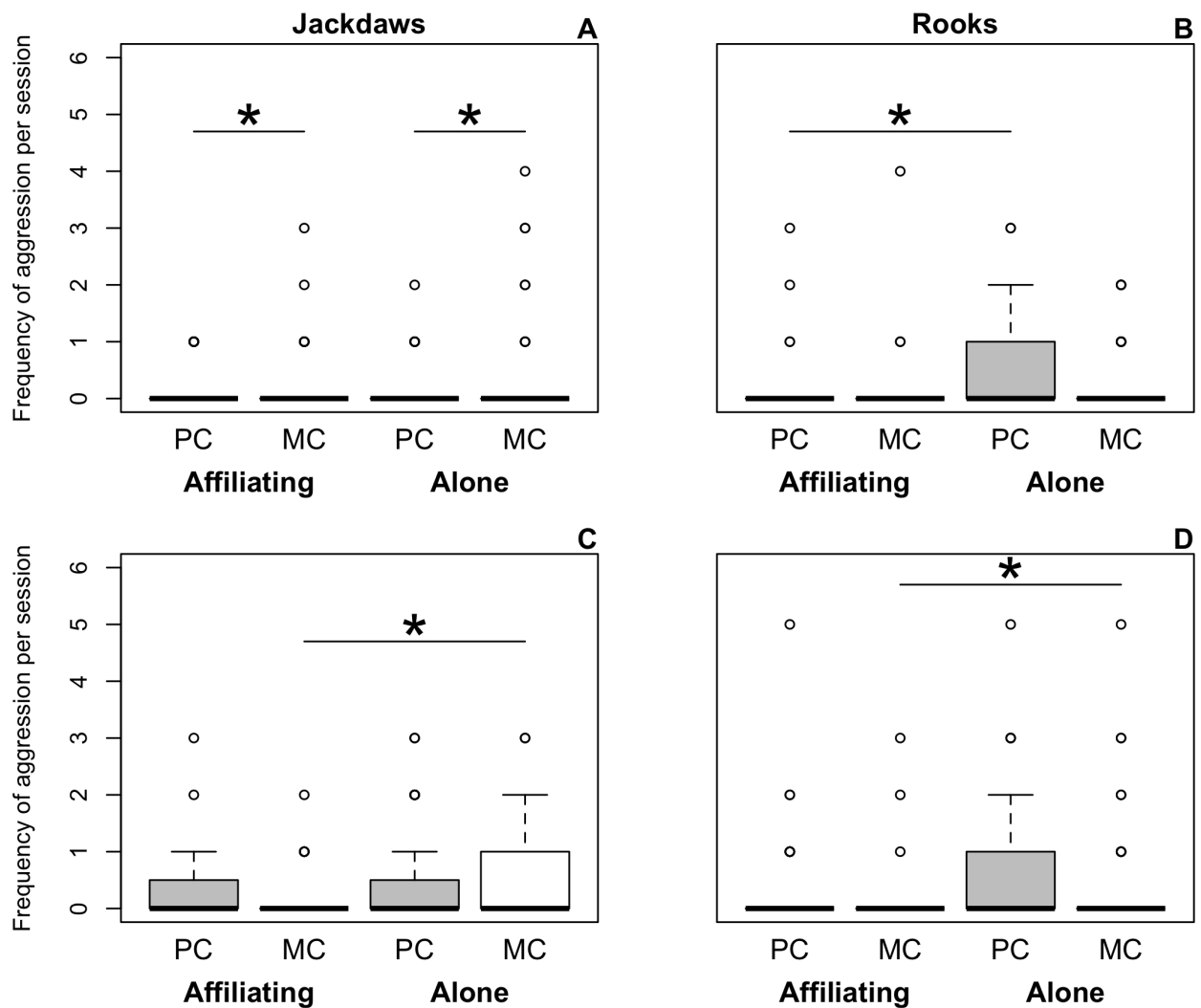
Figure 3. The total frequency of post-conflict third-party initiated aggression per post-conflict (PC) or matched control (MC) for conflict aggressors (A and B) and victims (C and D) when jackdaw (A and C) and rook (B and D) former opponents were affiliating with another versus when they were alone. 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 described in the text.

17

335   Table 1. Prediction 1: the frequency of non-conflict aggression *between former opponents* after

336   initial conflicts (estimate, standard error). Models 1a (test model) and 1b (base model) refer to

337   aggression directed from the former opponent that was the focal subject toward the other former

338   opponent, and models 2a (test model) and 2b (base model) refer to aggression directed from the

339   non-focal former opponent toward the focal former opponent. Subject and treatment were spe-

340   cified as random factors in all models. Column headers in parentheses are implicit levels of that

341   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

342   Table 2. Prediction 1: the frequency of non-conflict aggression *between a former opponent and a*

343   *bystander* after initial conflicts (estimate, standard error). Models 1a (test model) and 1b (base

344   model) refer to aggression directed from a former opponent toward a bystander, and models 2a

345   (test model) and 2b (base model) refer to aggression directed from bystanders toward former op-

346   ponents. Subject and treatment were specified as random factors in all models. Column headers

347   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

348 Table 3. Prediction 3: GLMM results for the *frequency of a former opponent receiving aggres-*
349 *sion* from a bystander in relation to the *duration* and *frequency* of affiliation (estimate, standard
350 error). Subject, treatment, and affiliation duration were specified as random factors in all models.
351 Column headers in parentheses are implicit levels of that factor; columns labeled "Affiliation"
352 indicate either the duration or frequency depending on which model is being considered; agg de-
353 notes 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

354   Table 4. Prediction 4: *frequency of aggression* when affiliating with another (*present*) or *alone*

355   according to treatment and role for former opponents that were *recipients* of aggression (estim-

356   ate, standard error). Subject and treatment were specified as random factors in all models.

357   Column headers in parentheses are implicit levels of that factor, agg denotes the aggressor.
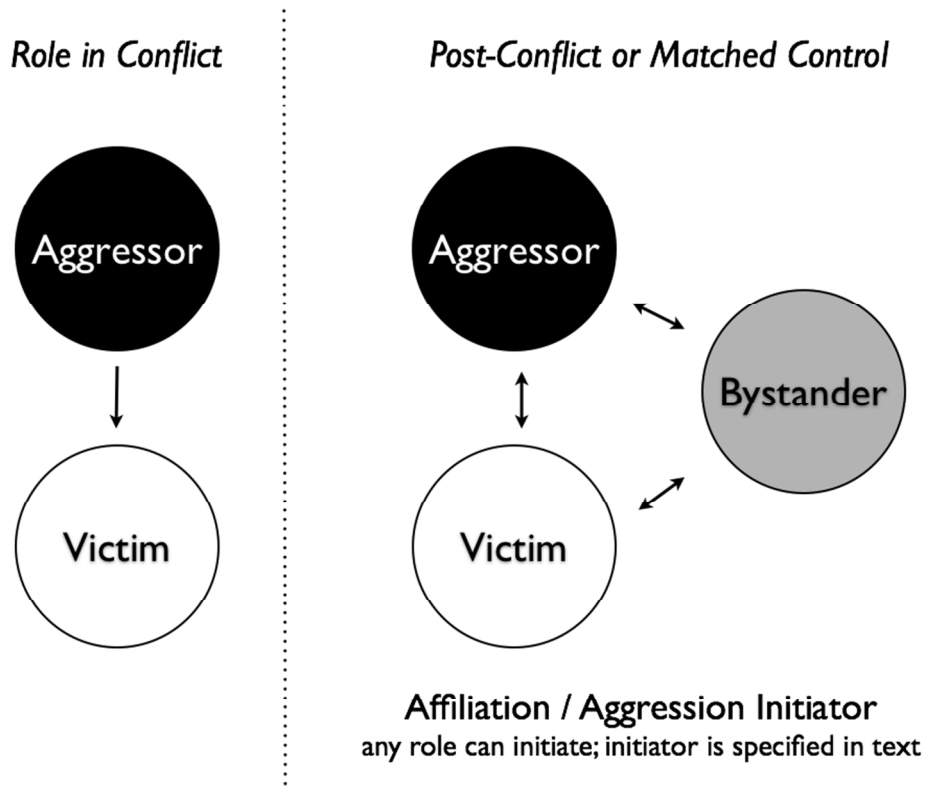
Species	Model	Intercept (agg, alone, MC)	Victim (alone, MC)	Present (agg, MC)	Present * Victim (MC)	PC (agg, alone)	PC* Victim (alone)	PC* Present (agg)	PC* Present* Victim	df	loglik	AICc	Akaike Weight
Rook	Test	-0.95, 0.67	-0.20, 0.37	-0.18, 1.11	-0.51, 0.69	-0.01, 0.81	0.36, 0.47	-0.56, 1.46	0.37, 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

358   Table 5. Summarizing the predictions and results from the hypothesis that post-conflict third-

359   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

Role in Conflict | *Post-Conflict or Matched Control*

Aggressor

Victim

Aggressor

Bystander

Victim

**Affiliation / Aggression Initiator**
any role can initiate; initiator is specified in text

Visualisation 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 between individuals that had been involved in the conflict from bystanders, and they can engage in affiliation and/or non-conflict aggression with each other and/or bystanders.
337x266mm (72 x 72 DPI)
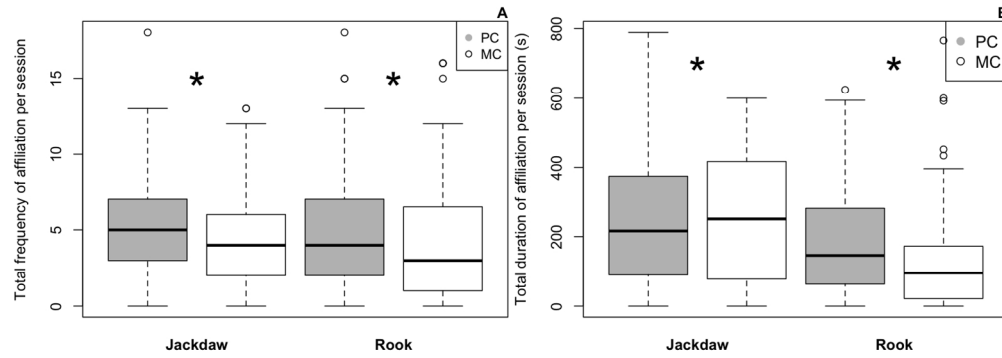
The total frequency (A) and duration (B) of affiliation per post-conflict (PC) or matched control (MC) by species. Note that duration totals can add up to more than the observation session length (600s) because multiple affiliative states could occur at one time. Asterisks (*) indicate effect size directions found in the GLMM analyses in Logan et al. (2012) and summarized in the text. Figure reproduced from Logan et al. (2012).
135x48mm (300 x 300 DPI)
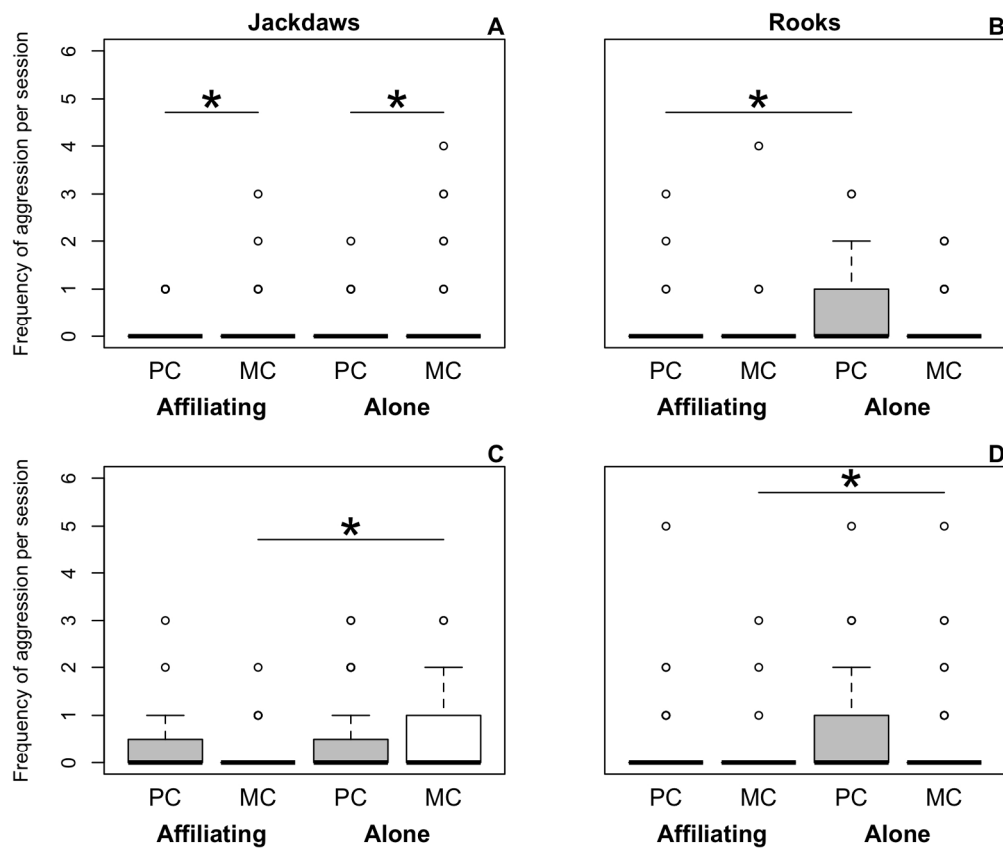
The total frequency of post-conflict third-party initiated aggression per post-conflict (PC) or matched control (MC) for conflict aggressors (A and B) and victims (C and D) when jackdaw (A and C) and rook (B and D) former opponents were affiliating with another versus when they were alone. Boxes show 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 described in the text.

177x151mm (300 x 300 DPI)