

Alternative behavioral measures of post-conflict affiliation

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ABSTRACT

Animals are known to affiliate after conflicts rather than avoid each other. Affiliation can occur between former opponents or between a former opponent and a third-party, and is more common between individuals with high quality relationships. We investigate post-conflict affiliation in three species of corvid (crows) to examine how both sociality and analysis method influence this behavior. We hypothesized that 1) there will be no former opponent affiliation because the highest quality relationships in these species are between mates who never fight, therefore eliminating the need to repair this relationship; and 2) colonial rooks and jackdaws will show third-party affiliation with partners, whereas the territorial Eurasian jays will not show this behavior because they lack high quality relationships outside of the breeding season when their data were collected. Post-conflict affiliation is generally analysed using the latency to first affiliative contact, however this method has limitations. We explore two different measures: the frequency and duration of affiliation across each observation session. There was no evidence of former opponent affiliation in rooks or jays, but some in jackdaws according to affiliation durations. Rooks and jackdaws showed third-party affiliation with mates according to affiliation frequencies and durations, and jays showed third-party affiliation according to affiliation durations, but with any individual, not just mates. We suggest that post-conflict affiliation is best investigated using more than first affiliation latencies, and that the frequency and duration of affiliation may indicate whether affiliation is used to address post-conflict stress.

Keywords: post-conflict affiliation, analysis method, corvid, consolation, reconciliation, sociality

INTRODUCTION

Social species that have conflicts usually have some form of conflict management behavior to reduce the associated costs (Aureli et al. 2002). These behaviors can involve pre-conflict management (e.g., conflict avoidance, using greetings and grooming to reduce tension to make aggression less likely), third-party interventions during conflicts (e.g., agonistic support), post-conflict affiliation (e.g., friendly interactions between former opponents [former opponent affiliation] or a former opponent and a bystander after a conflict [third-party affiliation]), and redirecting aggression to bystanders (e.g., to distract their opponent or manage dominance relationships; see reviews in Scucchi et al. 1988, Aureli et al. 2002, and Koyama and Palagi 2006).

We examine one conflict management behavior in detail, namely, post-conflict affiliation, and also consider post-conflict aggression. Post-conflict affiliation usually occurs between individuals that share a valuable relationship, which is one that provides fitness benefits (see review by Arnold et al. 2010). If individuals interact frequently and provide mutual benefits, affiliative interactions after fights can facilitate a full or partial return to a stable relationship and reduce conflict-related stress or aggression (Aureli et al. 2002, Fraser et al. 2009). In addition to relationship value, compatibility (the amount of affiliation exchanged) and security (the consistency of interactions between individuals) can influence the likelihood of occurrence of post-conflict affiliation (Cords and Aureli 2000; Fraser et al. 2009).

The costs and benefits of participating in post-conflict affiliation vary according to the role the individual played in the conflict (the aggressor or the victim) and the initiator of the affiliation. For example, the costs of conflicts can be higher for victims (the individual that was attacked) than aggressors (the individual that attacked the victim) because victims may be at a greater risk of receiving more aggression after conflicts, both from their former opponent and from bystanders (see review by Arnold et al. 2010). Victims can offset these costs using post-conflict affiliation: initiating

former opponent affiliation or affiliation with a bystander may appease the aggressor and/or bystander, thus reducing the likelihood of receiving further aggression (Arnold et al. 2010). Conflicts may cause stress for both aggressors and victims, and post-conflict affiliation (former opponent and/or third-party affiliation initiated by former combatants or third-parties) may function proximately to reduce this stress and ultimately to repair the relationship such that both individuals can continue to benefit from repeated interactions (Arnold et al. 2010). Bystanders can benefit from third-party affiliation with former opponents after conflicts to reduce stress and their risk of receiving aggression if former opponents are agitated after fights (Fraser et al. 2009). In addition, victims and aggressors may benefit by affiliating with their former opponent's affiliates to indirectly repair the relationship between the former combatants (Fraser et al. 2009). In this case, the bystander may benefit from indirectly repairing the relationship between the former combatants via kin selection if the affiliation occurs among close relatives (Koski and Sterck 2009).

Post-conflict aggression can occur between the former opponents (renewed aggression) or between a former opponent and a bystander (redirected aggression) and can provide an alternative or an additional mechanism to post-conflict affiliation for offsetting the costs of the conflict. A former opponent that renews aggression with the individual it just fought with may benefit from the ability to access a resource or succeed in winning and reap the potential benefits that may follow (Wittig and Boesch 2003b). A former opponent may direct aggression toward bystanders after conflicts, which could reduce stress or reduce the receipt of further aggression (Wittig and Boesch 2003b). In addition, bystanders may direct aggression toward a former opponent, which could help the bystander beat an opponent that has already been weakened by a previous conflict or gain access to a resource (Wittig and Boesch 2003b). There are also costs involved with engaging in further aggression, including damaged relationships, expending energy, and physical injury (see review by Wittig and Boesch 2003a).

The use of post-conflict affiliation strategies varies among taxa and may depend on the number of quality relationships individuals have. Species in which individuals have many stable, and therefore important, relationships use both former opponent and/or third-party affiliation depending on the willingness of former opponents to affiliate, as well as the willingness and availability of bystanders - a willingness that will depend on the quality of their relationship (humans: Fujisawa et al. 2006; non-human primates: see Das 2000, Koski and Sterck 2007; domestic dogs: Cools et al. 2008; wolves: Cordoni and Palagi 2008, Palagi and Cordoni 2009; horses: Cozzi et al. 2010; and sub-adult ravens: Fraser and Bugnyar 2010, Fraser and Bugnyar 2011). In contrast, rooks use only third-party affiliation, which may be due to the limited number of high quality relationships resulting from their long-term monogamous mating strategy (Seed et al. 2007). The rook findings raise the question of whether other corvid species with similar social structures show only third-party affiliation or whether this is peculiar to rooks.

We investigated whether post-conflict affiliation is restricted to social species by studying three species of corvid: colonial rooks (*Corvus frugilegus*) and jackdaws (*C. monedula*), which have similar social structures, and territorial Eurasian jays (*Garrulus glandarius*). To place post-conflict affiliative behavior in context, we also examined post-conflict aggression to determine whether it increases in frequency or has shorter latencies after conflicts. Individuals of all three species were the same age and housed under similar conditions. Seed and colleagues (2007) found that rooks show third-party affiliation between mates, but no former opponent affiliation. Since mated pairs had by far the strongest bond in the group and since mates never fought with each other, it is possible that when an individual fought with a non-mate, this relationship was not important enough to repair through former opponent affiliation, or the conflict may not have damaged the relationship (Seed et al. 2007). Based on previous findings by Seed and colleagues (2007) on rooks, we hypothesized that there would be no former opponent affiliation in any of the species in this study because they all form monogamous pair bonds which are the core units in the group (note that this is only

true for jays during the breeding season; Goodwin 1951; Röell 1978; Goodwin 1986; Snow and Perrins 1998; Emery et al. 2007). Since post-conflict affiliation has never been studied in jackdaws and jays, it was necessary to confirm the absence of former opponent affiliation rather than assuming this to be the case based on the rook data. We also quantified which relationships were of the highest quality by examining each relationship component empirically.

Furthermore, we hypothesized that jackdaws, which live in colonies and have a similar social structure to rooks, would also demonstrate third-party affiliation with their mates. While post-conflict affiliation is predicted to only occur in social species (Aureli et al. 2002), this has not explicitly been tested in a species as asocial as the jays. Therefore, we examined this hypothesis by investigating post-conflict affiliation in territorial jays who were expected not to show signs of post-conflict affiliation. Their data were collected only outside of the breeding season for welfare reasons. As mates primarily affiliate with each other during the breeding season, however, and since post-conflict affiliation should depend on the presence of social bonds, our hypothesis that these birds should not have post-conflict affiliation is plausible. Their lack of a high quality relationship to go to after a fight outside of the breeding season would eliminate the option of having post-conflict third-party affiliation.

Through studying the social influences on corvid post-conflict affiliation, we aimed to expand post-conflict affiliation analysis methodology. Current methods primarily analyse the timing of the first affiliative interaction in the post-conflict observation session and compare it with the timing of the first affiliative interaction in matched controls. If the first affiliative behavior occurs sooner after conflicts than in matched controls then post-conflict affiliation is thought to occur (de Waal and Yoshihara 1983). However, there are a number of reasons to look beyond the first affiliative contact to include all of the data in the observation sessions, which will allow an understanding of the broader patterns of post-conflict affiliation. For instance, some species might use post-conflict ag-

gression before switching to post-conflict affiliation (Wittig and Boesch 2003b), thus delaying their time to first affiliative contact such that it occurs later than in the matched control, making it appear that post-conflict affiliation did not occur. In this case, there exists a possibility that both the aggression and the affiliation were used in response to the conflict. Post-conflict affiliation would still occur, but the pattern of results would appear different from the standard pattern that is commonly investigated, thus resulting in a false negative conclusion. As well, only examining the influence of one affiliative interaction (the first) on post-conflict affiliative behavior may not be enough to observe an obvious difference in behavior, particularly if the affiliative event is of short duration or if more than one contact is necessary to reduce tension, if stress reduction is one of the functions of post-conflict affiliation.

A common assumption in post-conflict affiliation literature is that the first affiliative contact after the conflict defines the post-conflict affiliative behavior. This assumption stems from the first study on post-conflict affiliation by de Waal and Roosmalen (1979) who showed that, after conflicts, the behavior used for the first affiliative contact was a different type than subsequent affiliative behaviors in chimpanzees. The logic is that, after a conflict occurs, the first affiliative event (the unique behavior) is a response to the conflict, whereas the second affiliative event (the non-unique behavior) is a response to the first affiliative event, only occurring because the first unique behavior had performed the supposed function of post-conflict affiliation (i.e., repairing the relationship). While first affiliative behaviors differ from subsequent affiliative behaviors after conflicts for some species (e.g., de Waal and van Roosmalen 1979; de Waal and Yoshihara 1983; Ren et al. 1991), other species do not show such differences, yet they still show post-conflict affiliation because affiliation occurs sooner after conflicts than in matched controls (e.g., Björnsdotter et al. 2000; Arnold and Barton 2001; Leca et al. 2002). This indicates that the conflict can influence not only the first affiliative event, but also subsequent affiliative events, which may not simply be a response to the previous affiliation, but a combined response to the conflict. Examining the first affiliative contact af-

ter conflicts will result in the detection of post-conflict affiliation only in those species where differences between first and subsequent post-conflict affiliative behaviors differ.

Although the traditional logic that only the first affiliative behavior is important in a post-conflict context, evidence to support this assumption is rarely provided (i.e., examining the differences between the first and subsequent affiliative behaviors after conflicts). More often, investigations examine whether certain types of affiliative behavior occur more as the first affiliation after conflicts versus their occurrence throughout controls (e.g., Gust and Gordon 1993; Castles and Whiten 1998; Judge and Mullen 2005; Berman et al. 2006; Cooper et al. 2007), which would illuminate only the first post-conflict affiliative behavior versus their overall baseline behavior, saying nothing about how affiliation changes over the course of the post-conflict observation period. Some studies examine whether first affiliative contacts after conflicts occur more than the first affiliative contacts in controls (Swedell 1997; Verbeek and de Waal 1997), which is similar to the previous analysis method only more limited. Other studies examine only the first affiliative contacts in the post-conflict observation session to determine whether one or a few behaviors occur significantly more often (e.g., Grüter 2004; Palagi et al. 2004; Leone and Palagi 2010; Norscia and Palagi 2011). This method is interesting if certain behaviors are predominantly used after conflicts, but does not account for control behavior, thus is not very informative.

Another common analysis is to determine whether certain types of affiliative behavior occur more throughout the whole post-conflict observation period compared with the whole control observation period (e.g., York and Rowell 1988; Schino 1998; Westlund et al. 2000; Koyama 2001; Wahaj et al. 2001; Radford 2008; Palagi and Cordoni 2009; Schino and Marini 2011). This analysis overlooks differences between first and subsequent affiliative behavior after conflicts, assumes the post-conflict response may occur beyond just one affiliative event, and compares all post-conflict behavior with all behavior in the control period. Given that some species do not use different behaviors

for their first affiliative post-conflict contact, it is important to examine the whole post-conflict period and compare it with the control period to determine what, if any, post-conflict affiliative patterns occur. Whether or not first and subsequent affiliative behaviors differ after conflicts does not discount the fact that the subsequent affiliation could still be responding to the conflict. The theoretical framework for analyzing post-conflict affiliation in this way has not been put forth yet, which is something we aim to address here.

We argue that post-conflict affiliation should be affected by the internal state (i.e., the stress of engaging in a conflict) of the individual who should respond behaviorally until the internal state has returned to baseline levels. If the individual is physiologically affected by the conflict through an increase in stress, and it requires a certain period of time or a certain amount of affiliation to decrease this stress, then we would expect affiliation to continue to respond to the physiological increase in stress until levels return to baseline. Therefore, multiple affiliative events may respond to the initial stressor (the conflict), thus constituting the post-conflict affiliative behavior, rather than defining the post-conflict affiliative behavior by the first affiliative contact and ignoring subsequent affiliative interactions.

To support this argument, it must first be shown that conflicts increase physiological stress, which is confirmed in greylag geese (Wascher et al. 2010) and mice (Keeney et al. 2006). Conflicts increased heart rate and stress-indicating behavior in greylag geese, and the effect strengthened after conflicts of longer duration and higher intensity (Wascher et al. 2010). Mice who lost conflicts had increased plasma corticosterone levels for up to 60 minutes after the conflict (Keeney et al. 2006), indicating that conflicts induce prolonged physiological stress responses which are unlikely to be influenced by one affiliative behavior, especially if it is of a short duration. Next, affiliation after conflicts should decrease this physiological response (stress) over a prolonged period of time, which is shown in pigtail (Boccia et al. 1989) and rhesus macaques (Bernstein 1964). Agonistic be-

haviors in a pigtail macaque increased the heart rate, and the subsequent receipt of allogrooming (for a minimum of 2 minutes) decreased the heart rate more than other behaviors (Boccia et al. 1989). This shows that prolonged affiliative contact elicited a physiological change by decreasing stress levels, and implicates the duration of affiliation as a potential measure of post-conflict affiliative behavior. Stress increased in rhesus macaques as a result of the introduction of new group members; consequently both aggression and affiliation increased, however aggression required only two days to return to baseline levels while affiliation took longer (Bernstein 1964). This indicates that it requires more than just one affiliative event to restore stress levels to baseline, and may suggest the frequency of affiliation as an effective measure of post-conflict affiliation.

We propose that analysing post-conflict affiliation data according to the frequency and duration of affiliation are useful in detecting and understanding the overall patterns of this behavior. An increase in stress correlates with an increase in activity levels in great tits (Carere et al. 2003). If conflicts increase stress, then the frequency of affiliation and other behaviors should also increase after conflicts in response to the stress. If the frequency of affiliation increases preferentially over other behaviors then the subjects could be using affiliation as way to reduce the stress induced by the conflict. The cause of the increase in activity levels could also be explained by some external factor occurring near the time of the conflict, however, if sample sizes are large enough (i.e., data are collected on enough conflicts and their matched controls) then external noise should be eliminated since it likely would not occur near every conflict. Additionally, the duration of affiliation may play a role in post-conflict affiliative behavior: if affiliative events last longer after conflicts, subjects may use the extended contact to reduce stress.

The frequency and duration of affiliation are likely not independent of each other, however, if post-conflict affiliation is occurring, then these variables may show different patterns. Affiliation frequency and duration may interact to create a constellation of post-conflict affiliative behavior. If the

frequency of affiliation increases, but duration decreases or stays the same after conflicts relative to matched controls, then the conflict will have increased activity levels and it will be important to determine whether affiliation is the preferred activity (which would allow the possibility for it to reduce stress) or if activity in general increased (which would not indicate that post-conflict affiliation occurred). An increase in both the frequency and duration of affiliation after conflicts would indicate a rise in activity levels with longer periods of social contact, lending more support to the hypothesis that affiliation functions to reduce stress (though it would not be a direct test of this hypothesis). Additionally, affiliation frequencies may increase and durations may decrease soon after conflicts, while later in the post-conflict observation session the reverse relationship may occur if early affiliative events reduce stress and/or activity levels.

While studies have occasionally used the frequency of affiliation (e.g., de Waal and van Roosmalen 1979; Gust and Gordon 1993; Cheney and Seyfarth 1997; Björnsdotter et al. 2000; Call et al. 2002; Sommer et al. 2002; Fraser and Aureli 2008; Majolo et al. 2009) and one study used the duration of affiliation (de Marco et al. 2010) as a measure of post-conflict affiliative behavior, we will examine the effectiveness of using affiliation frequencies and durations to detect post-conflict affiliative behavior in three species.

MATERIALS AND METHODS

Study site

Captive rooks (N=13; 10 females, 3 males), jackdaws (N=14 until May 2010, N=13 until January 2011, N=11 thereafter; initially 6 females, 8 males), and jays (N=10 until March 2009, N=9 thereafter; initially 6 females, 4 males) were observed in large outdoor aviaries, in which birds were able to fly freely, at the University of Cambridge Sub-Department of Animal Behaviour in Madingley, U. K. Rooks and jackdaws were housed in the same aviary (20 x 10 x 3m) and jays in an adjacent aviary (20 x 6 x 3m). All areas of the aviaries were observable from the observation huts, except for

one small section of the rook and jackdaw enclosure that was seldom visited by the birds. All birds had free access to food and water at all times, and aviaries were enriched with objects, dirt, grass, plants, rocks, and branches. The maintenance diet consisted of fruit, vegetables (raw and cooked), dog food, soaked dog and cat biscuits, bread, cheese, eggs, and Mazuri® Zoo A (E) Mini pellets (<http://www.mazuri.com/PDF/5635.pdf>). Birds were observed when they were not being disturbed by caregiving activities (*i.e.*, feeding, aviary cleaning, and de-worming) and individuals were identified by unique colour ring combinations on their legs. Upon conclusion of this investigation, all subjects remained in the aviary for further study by other researchers.

Data collection: relationship quality

Data were collected to determine which relationships were the most valuable (mated pairs), compatible (frequency of affiliative exchanges) and secure (consistency of aggressive exchanges and the fluidity of dominance hierarchies; see Table 1 for definitions of all behaviors recorded). These data were collected *ad libitum* (Altmann 1974) from 1 November 2008 through 5 April 2011 by CJL in collaboration with Ljerka Ostojic and Gabrielle Davidson (data collection effort was distributed 77%, 16%, and 6% respectively). We observed the birds for 324 hours in total. However, we chose 16 random hours per season (off season and pre-breeding season for jays, pre-breeding and breeding season for rooks and jackdaws) per aviary for analysis to equalise observation time among species. Random numbers were generated at www.random.org and assigned to observation sessions until a total of 32 hours per aviary per year had been chosen (multiplied by 3 years = 96 hours for rooks and jackdaws, and 96 hours for jays). Observations were recorded as events with The Observer 5.0 (Noldus Information Technology) and analysed with The Observer 5.0, MatMan 1.1 (Noldus Information Technology), and R 2.8.1 (R Development Core Team 2011). While more behaviors were recorded, particular attention was given to affiliative and aggressive interactions: if these interactions were observed, they were recorded with priority over other behaviors that might be happening at the same time. Proximity measures were coded using the nearest neighbour.

Relationship *value* was measured by those individuals that formed mated pairs because this was the only relationship that contributed directly to fitness. Rook and jackdaw mated partners were determined by identifying the nesting pairs, which included building and defending the nest, incubating eggs, or guarding the nest site. Since jays had to be separated during the breeding season, we inferred that those birds that could be housed together and those that shared food with each other were partners. To measure relationship *compatibility*, the frequency of affiliative exchanges between partner dyads and non-partner dyads was analyzed using Mann-Whitney U tests.

Relationship *security* was measured with aggressive and dominance interactions. The frequency of aggressive exchanges between partner dyads and non-partner dyads was analyzed with Mann-Whitney U tests as with affiliation above. The relationship between affiliation and aggression within a dyad was used to measure security, with the prediction that mated partners would have high affiliation frequencies and low or no aggression frequencies, thus representing a consistent, low risk relationship indicating high security. Dominance hierarchies were determined for each species according to the number of aggressive interactions an individual initiated or received. Individual dominance rank was calculated as the number of aggressive interactions initiated by a subject divided by the total number of aggressive interactions in which this subject was involved (*i.e.*, when the subject was the initiator and recipient of aggression). To test whether the dominance hierarchy was linear, Landau's linearity index, h , was applied using actor-receiver matrices of aggressive behavior in MatMan 1.1. Dominance hierarchy properties may indicate relationship security as well. If dominance hierarchies are fluid (*i.e.*, having many rank changes over time), then counter-aggression by subordinates is tolerated to some degree, indicating a less risky social environment that may promote post-conflict affiliation due to the more negotiable nature of their relationships (Thierry 1985, Aureli et al. 1997; Fraser et al. 2009). However, if dominance hierarchies are rigid (*i.e.*, few or no

rank changes over time), then aggression may be more severe and unidirectional, therefore increasing the risk of engaging in post-conflict affiliation.

Data collection: post-conflict affiliation

All data were collected from 1 November 2008 to 22 April 2011 between 09:30 and 17:15 by CJL from observation huts next to the aviaries using the Post-Conflict-Matched Control (PC-MC) method (de Waal and Yoshihara 1983) for a total of 713 hours (573 hours with the rooks and jackdaws, and 140 hours with the jays). This resulted in 242 PC-MC pairs (108 rook PC-MC pairs, mean conflicts per bird \pm standard deviation=8.3 \pm 3.6; 116 jackdaw PC-MC pairs, 8.3 \pm 2.6; and 18 jay PC-MC pairs, 1.8 \pm 1.2). Data were not collected on jays during the breeding season due to extremely intense fighting at this time which required separating the birds. Severe aggression (conflicts that lasted more than 30 seconds and recurred in quick succession between two individuals) was avoided by monitoring the birds and if aggression escalated, technicians were alerted who intervened to prevent further aggression by separating the birds. While severe aggression was excluded, the intensity of conflicts in this study ranged from mild (e.g., one bird lunges at and pecks another who leaves the area) to high (two birds wrestling on the ground while kicking and pecking at each other). There was an average of 0.33 conflicts per hour for jackdaws, 0.18 conflicts per hour for rooks, and 0.12 conflicts per hour for jays.

The jay average is inflated because there were rarely conflicts outside of the breeding season, in which case they were anecdotally observed from the rook and jackdaw observation hut until conflicts began when the breeding season approached, which then triggered direct observation of the jays. Just before the onset of the breeding season, jay conflicts would suddenly increase in frequency and intensity with the birds staying locked together while fighting on the ground or one bird would repeatedly chase another. If one of these intense conflicts was observed, the birds were separated and technicians consulted regarding care, which resulted in examinations by the veterinarian if

injuries were suspected. No birds were injured during the mild aggression that occurred during observation sessions for this study. In one instance there was repeated aggression by one rook toward another and in this case CJL intervened, separated the birds, and the victim was examined by the veterinarian.

Immediately after a conflict ended (which was obvious because birds separated from each other), a 10-minute post-conflict (PC) observation session began in which either the victim or aggressor was the focal subject and all behaviors were recorded as well as who initiated and terminated each interaction (Altmann 1974). Post-conflict aggression, such as displacements and threats which did not involve physical contact (see Table 1), could occur in PCs or MCs. Since non-conflict aggression was very mild and common, while conflicts were more severe and rare, we collected data on non-conflict aggression assuming it did not simulate a conflict situation. Observations were equalised as much as possible between victims (rooks: N=66 PC-MC pairs; jackdaws: N=54 PC-MC pairs, jays: N=9 PC-MC pairs) and aggressors (rooks: N=42 PC-MC pairs; jackdaws: N=61 PC-MC pairs, jays: N=9 PC-MC pairs), while those individuals least represented were prioritised to ensure at least five PC-MC pairs per subject (hence the lack of equality between sample sizes for roles).

Ten-minute matched controls (MC) were conducted using focal follows on the same individuals as those in the PC they were matched to. MCs were matched to the same time of day as the PC and usually conducted within one week of the PC, and always within the season in which the PC occurred to ensure similar behavior patterns for the MC. The MC was preceded by a 10-minute focal follow to determine if the subject was involved in a conflict before the MC. If there was conflict before or during the MC it was cancelled. Subsequent MCs were carried out until there was no observed conflict before or during an MC to ensure a control with presumed baseline stress levels for comparison with the PC that was assumed to involve elevated stress levels due to the conflict. Certain behaviors (co-feeding and proximity) were recorded 5-sec after an individual was observed to

begin that activity to ensure the subject was participating in that activity (e.g., co-feeding rather than traveling). Affiliation was separated into two categories: active, which involved being nearer than 5 cm or touching another individual, and passive, where individuals were between 5 and 30 cm of each other (see Table 1).

Data were recorded onto a digital voice recorder (Olympus Digital Voice Recorder VN-2100) and transcribed into Microsoft Excel 2007 (Microsoft Corporation) from 7 to 26 November 2008. After 26 November 2008, data were recorded using The Observer XT 7.0 and 9.0, entered into Microsoft Excel 2007, and analysed in R 2.8.1 (R Development Core Team 2011). The affiliation data (the proportion of attracted versus dispersed PC-MC sessions per subject, the frequency of affiliation per minute in PCs and in MCs, and the duration of affiliation per 10-minute session) contained a mixture of normal and non-normal distributions (Anderson-Darling normality test: $P > 0.05$ and $P < 0.05$). A visual check using histograms confirmed this result. Therefore, non-parametric statistics were used on all affiliation data for consistency and comparability.

Conflicts

Aggressors and victims of conflicts were classified as such according to the initiator of the fight (aggressors were the initiators). In some cases, we were not able to see who initiated a fight because the birds moved so quickly that identification of individuals by their colour rings was not possible until after the fight had begun. When the conflict initiator was unknown, we relied on information regarding the outcome of the fight (winner or loser) to assign the role of aggressor or victim. For rooks and jackdaws, conflict outcome is an accurate proxy for predicting the initiator of the conflict because aggressors usually won and victims primarily lost fights (Pearson's chi-square test for homogeneity; rooks: $X^2_3=81.8$, $P < 0.001$; jackdaws: $X^2_3=14.6$, $p=0.002$). Therefore, when the initiator was unknown, winners were classified as aggressors and losers as victims. There was only one instance in which both the conflict initiator and outcome was unknown. This data was included in the

analysis when possible (i.e., when it was not necessary to the analysis to identify the focal animal's role in the conflict). For jays, the conflict outcome was not the ideal proxy for predicting the initiator of the conflict since winners did not always initiate conflicts ($X^2_3=7.3$, $p=0.06$). However, since we do not analyze the jay data according to the role in the conflict (due to their small sample sizes), this should not pose a problem.

We examined the number of conflicts per dyad, and whether aggressors were always the dominant and victims the subordinate individual of the former opponents using a chi square test (data were a mix of normal and non-normal distributions according to the Anderson Darling normality test, therefore non-parametric statistics were used; $p>0.05$ and $p<0.05$, respectively).

Corrected conciliatory tendencies and triadic contact tendencies

First affiliative contacts between former opponents and between former opponents and third-parties in PCs and MCs were analysed as follows: a PC-MC pair was considered 'attracted' if the first affiliative behavior occurred sooner in the PC than the MC, 'dispersed' if affiliative behavior occurred sooner in the MC than the PC, and 'neutral' if no affiliative behavior occurred in either the PC or MC or if it occurred at the same time in both (de Waal and Yoshihara 1983). A corrected conciliatory tendency (CCT) was calculated per bird to determine the degree to which former opponents engaged in post-conflict affiliative contacts (de Waal and Yoshihara 1983; Veneema et al. 1994). The CCT is the number of attracted minus the number of dispersed PC-MC pairs divided by the total number of PC-MC pairs. The triadic contact tendency (TCT) determines the degree to which third-parties affiliate with former combatants and is calculated in the same way as the CCT, however attraction is defined as affiliative interactions occurring sooner between a former combatant and a third-party in the PC than in the MC (Call et al. 2002).

First affiliation latencies

Wilcoxon signed rank tests were used to determine if the proportion of attracted PC-MC pairs was higher than the proportion of dispersed PC-MC pairs for active affiliation, passive affiliation, and all affiliation (active and passive combined). If a higher proportion of PC-MC pairs are attracted, this indicates a shorter latency to first affiliation after fights than in matched controls and provides evidence for former opponent or third-party affiliation after conflicts. All tests were two-tailed. Generalised linear mixed models (GLMM; R package: lme4) were used to determine whether particular categories of affiliation were more likely to have attracted PC-MC pairs (also termed selective attraction). The response variable was the proportion of attracted PC-MC pairs per subject, and the explanatory variables included the proportion of attracted PC-MC pairs by initiator (former combatant, third-party), sex (female, male), role (aggressor, victim), affiliating with (other, partner), and affiliation type (active, all, passive), with subject as a random factor. Aside from affiliation type, all variables were continuous proportions with a binomial distribution and GLMMs were run with a logit link. The base model is denoted by ‘‘’, which is reported in the analysis as the intercept and to which all other factor levels are compared. Each test model was compared against a null model (response variable~1), which included the random factor from the test model. The most parsimonious model (model of best fit) was selected by taking the full model (including all of the factors of interest) and reducing it by its least significant factor (based on p-values) repeatedly until the model with the lowest AIC was achieved (Akaike 1981). If the least significant factor was part of a significant interaction, then it was kept in the interaction, but dropped as a separate factor from the model, unless the factor was involved in many interactions, in which case this was considered the best model if the AIC value was lower than the null model. Only the null model and model of best fit are shown in the accompanying tables for brevity. This analysis was not carried out on the jays who only had four attracted PC-MC pairs, thus it would not be prudent to further subset this data for analysis.

Frequency of affiliation

To examine the frequency of third-party affiliative interactions in PCs and MCs (not just the first affiliative contact in each), data were analysed with GLMMs using a Poisson distribution and log link. The model of best fit was selected as above. We examined the influence of the following explanatory variables on the frequency of affiliation: treatment (MC`, PC), sex (female`, male), role in the conflict (aggressor`, victim), affiliation initiator (self`, third-party), and relationship to the subject (other`, partner). Subject was considered a random factor because observations from the same individual could be correlated. Treatment was included as a fixed factor and a random factor because PCs and MCs were matched and thus not independent of each other. Data (affiliation residuals) were normally distributed. To examine whether overall activity levels or specifically affiliation increased, aggression rates were analysed for comparison using paired t-tests on aggression rates per bird in PCs versus MCs (data were normal according to the Anderson Darling normality test).

Duration of affiliation

The total duration of affiliative events in PCs and MCs was analysed with a GLMM (as in the frequency of affiliation analysis). We investigated whether the total duration of affiliation per 10-minute session (0-600 seconds) was influenced by the treatment (MC`, PC), with treatment and subject as random factors. Residuals were normally distributed. The mean duration of affiliative events was compared between the first five minutes and last five minutes of 10-minute PCs and MCs using Mann-Whitney U tests to determine whether longer durations of affiliation occurred later in PCs and to confirm that similar mean durations occurred in both halves of MCs (data were not normal according to the Anderson Darling normality test). Jay models were GLMs and not GLMMs because there was only one data point per individual, eliminating the ability to run subject as a random factor.

Post-conflict aggression

Aggression data were normally distributed and parametric tests were used for analysis (Anderson-Darling normality test: $P > 0.05$). To determine whether aggression occurs sooner and ‘survives’ longer after conflicts versus in matched controls, survival curves were created using accelerated failure-time models for former opponent-former opponent and former opponent-third-party aggression in PCs and MCs (R package: survival). First, the appropriate distribution was chosen by running the model with each distribution (Weibull, gaussian, logistic, and lognormal) and choosing the distribution from the model with the loglikelihood closest to zero. The Weibull distribution had the lowest loglikelihood in all cases except with the jackdaw former opponent-third-party aggression for which a gaussian distribution had the lowest loglikelihood. The models with the best fitting distribution were used for analysis. The survival curves were compared with a Wald test to determine whether PC and MC aggression curves differed.

RESULTS

Which are the highest quality relationships in each species?

Relationship value

Most individuals from all three of the species developed a pair-bond during the first year (rooks: 4 pairs out of 13 birds [note that one pair was female-female], jackdaws: 6 pairs out of 14 birds, jays: 4 pairs out of 9 birds). The rooks had an unbalanced sex distribution resulting in fewer pairs than there were available birds. All rook pairs maintained the same partner throughout this study, there was one partner change in the jackdaws, and three partner changes in the jays. Therefore, rook and jackdaw partnerships were stable over time, while jay pairs were not. This indicates that rooks and jackdaws are monogamous, and that there is serial monogamy in the jays who affiliate with one mate each breeding season and sometimes re-pair with the same individual the next year.

Relationship compatibility

Mated pairs in all three species exchanged higher frequencies of affiliation than non-partner dyads, thus showing the most compatibility (Mann-Whitney U test: rooks: mean frequency of affiliative contact per non-partner dyad \pm sd=18 \pm 8, mean per partner dyad=601 \pm 128, W=0, p=0.00001, 95% confidence interval=-725-(-447); jackdaws: mean per non-partner dyad=14 \pm 6, mean per partner dyad=307 \pm 116, W=0, p=0.00001, 95% CI=-362-(-232); jays: mean per non-partner dyad=5 \pm 4, mean per partner dyad=108 \pm 80, W=0, p=0.00005, 95% CI=-195-(-52)). However, not all jay mated pairs exhibited strong bonds during the time of data collection, which demonstrates that mates are more tolerant of each other mostly during the breeding season which was excluded from the data collection period due to intense fighting over territories.

Relationship security

Rook mated partners also had the highest relationship security because there was a lower frequency of aggression between partners than between non-partner dyads, (Mann-Whitney U test: mean frequency of aggressive contact per non-partner dyad \pm sd=10 \pm 7, mean per partner dyad=3 \pm 2, W=88, p=0.01, 95% confidence interval=1-9). The consistent lack of aggression in rooks represents a predictably affiliative response from the partner, thus high security. In contrast, rooks engaged in aggression with non-mates as well as affiliation (though much less than with the partner), indicating a lower level of predictability or relationship security. There were similar frequencies of aggression between partner dyads and non-partner dyads in jackdaws and jays, indicating no difference in relationship security (Mann-Whitney U test: jackdaws: mean frequency of aggressive contact per non-partner dyad=3 \pm 2, mean per partner dyad=2 \pm 2, W=101, p=0.64, 95% confidence interval=-1-2; jays: mean per non-partner dyad=10 \pm 8, mean per partner dyad=6 \pm 4, W=52.5, p=0.29, 95% CI=-3-11).

There was a significant linear dominance hierarchy within each species for each year and when all years were combined (Table 3; overall Landau's linearity index: rooks $h=0.88$, p=0.0001; jackdaws

$h=0.62$, $p=0.0001$; jays $h=0.93$, $p=0.0001$). Jackdaws had a fluid dominance hierarchy with dominant and subordinate individuals changing rank throughout the study. The rook hierarchy was slightly fluid, with individuals moving up or down a couple of ranks from year to year, and jay dominance ranks were relatively stable across years.

Conflicts

Sixty-two rook dyads engaged in conflicts out of 78 possible dyads (1.74 ± 1.24 conflicts per dyad), 63 out of 91 dyads fought in jackdaws (1.84 ± 1.47 conflicts per dyad), and 16 out of 36 dyads fought in jays (1.13 ± 0.34 conflicts per dyad). Conflicts were initiated and/or won regardless of their dominance status in relation to the other opponent: aggressors were not more dominant than their opponent and victims not more subordinate than their opponent (rooks: $X^2_{1df}=0.01$, $p=0.92$; jackdaws: $X^2_{1df}=0.55$, $p=0.45$; jays: $X^2_{1df}=0.56$, $p=0.45$).

Post-conflict former opponent affiliation

Affiliation after conflicts between former opponents rarely occurred: 11 out of 108 rook PCs (10%), 11 out of 116 jackdaw PCs (9%), and 1 out of 18 jay PCs (6%). Similar levels of affiliation occurred in controls: 10%, 16%, and 6% respectively, indicating neither an affinity for nor an avoidance of former opponents after conflicts.

Corrected conciliatory tendencies

CCTs do not indicate the presence of former opponent affiliation in any of the species in this study. Rook, jackdaw, and jay CCTs were approximately zero for all affiliation categories meaning third-party affiliation occurred at about the same time after conflicts as in matched controls, resulting in no former opponent attraction or avoidance (rook mean CCT: all affiliation=0.01, active affiliation=0.03, passive affiliation=-0.004; jackdaw mean CCT: all=-0.06, active=-0.02, passive=-0.05;

jay mean CCT: all=0.02, active=there were no attracted PC-MC pairs in this category, passive=0.02).

First affiliation latencies

There was no post-conflict former opponent affiliation as evidenced by the similar proportions of attracted and dispersed PC-MC pairs (Figure 1A; Wilcoxon signed rank test: rook proportion attracted=0.09, proportion dispersed=0.07, $V=12$, $N_1=N_2=13$, $p=0.83$, 95% confidence interval=-0.11-0.14; jackdaw proportion attracted=0.09, proportion dispersed=0.13, $N_1=N_2=14$, $V=8$, $p=0.10$, 95% CI=-0.16-0.05; jay proportion attracted=0.06, proportion dispersed=0.06, $V=1.5$, $N_1=N_2=2$, $p=1.00$, 95% CI=NA). This indicates that former opponents were not more likely to affiliate after conflicts than in matched controls when examining the latency to first affiliative contact.

Frequency of affiliation

There was no evidence of former opponent affiliation according to the frequency of affiliation. When analysing the frequency of affiliation in PCs compared with MCs, the GLMM null model was no different from the test models for rooks, and the jackdaw and jay models of best fit did not include treatment, only age (mean frequency of affiliation per session \pm sd: rook PCs=0.33 \pm 0.71, MCs=0.30 \pm 0.56; jackdaw PCs=0.40 \pm 1.04, MCs=0.68 \pm 1.11; jays PC=0.11 \pm 0.33, MCs=0.11 \pm 0.33; Table 2).

Duration of affiliation

There was no evidence of former opponent affiliation when analysing the duration of affiliation for rooks: their model of best fit showed that affiliation durations were shorter between former opponents after conflicts than in matched controls (mean duration of affiliation in seconds \pm sd: PCs=8 \pm 26, MCs=13 \pm 37; Table 3). However, there was some evidence of former opponent affiliation according to affiliation durations for jackdaws and jays: the duration of affiliative events in-

creased after conflicts relative to matched controls (jackdaw PCs=18±58, MCs=42±109; jay PC=0.4±1, MC=3±12; Table 3). Though the jay model of best fit showed that affiliation durations increased in PCs, the standard error associated with this estimate was massive, thus this result is not reliable and we conclude that in reality there was no former opponent affiliation in the jays.

Since the GLMM analysis tables are becoming more complicated, we describe how to read and interpret these results using the rook results in Table 3 as an example. The first line of the ‘Null Model’ (intercept only) regresses the response variable (in this case, the duration of affiliation per PC or MC) against 1 instead of against any explanatory variables. This provides a model to compare test model results with: if test models are a better fit than the null model, then the test model is more parsimonious (as indicated by the lower AIC value). The second rook model is the ‘Full and Best Fit’, which means that it is the full model, including all of the factors of interest, and it was also the model of best fit. The intercept in this model represents the base model, which includes MCs and the lowest age (1 year). The second line, ‘Treatment: PC’, compares the two factor levels of this one explanatory variable ‘PC’ with ‘MC’. Since the estimate for this line is a negative number (-1.53), this indicates that the duration of affiliation decreases in PCs relative to the estimate for the intercept (3.38) which represents the duration of affiliation in MCs. The standard error for the PC estimate (0.25) is smaller than the estimate, indicating that this is a reliable result. Subject and treatment were random factors and the variance and standard deviation are reported under the Estimate and Standard Error columns respectively. When looking at the AIC value for the ‘Full and Best Fit’ model (836), it is lower than that for the null model (868), which indicates that the ‘Full and Best Fit’ model is the model of better fit. When comparing models, it is important to note that, for the most parsimonious model, each factor within the model is an important contribution to the low AIC value, thus it is the model as a whole and not just a few key variables that are ‘significant’. Therefore, the results for whether post-conflict former opponent affiliation occurs according to af-

filiation durations show that it did not occur in rooks due to the negative PC estimate which was in the model of best fit.

Post-conflict third-party affiliation

Third-party affiliation after conflicts was common in rooks (97 of 108 PCs; 90%) and jackdaws (103 of 116 PCs; 89%), but less common in jays (10 of 18 PCs; 56%), though it is important to note that the jays had so few conflicts that there may not be enough data to make a robust conclusion. However, rook and jackdaw affiliation in MCs was also high (83% and 86% respectively), indicating the need to examine the data in more detail to determine if post-conflict third-party affiliation occurred. Baseline jay affiliation remained lower than that for rooks and jackdaws with affiliation occurring in 38% of matched controls. Rook and jackdaw post-conflict first affiliative contacts occurred significantly more with partners than with all other relationship categories combined, while jays affiliated with partners and others indiscriminately (Mann-Whitney U test: rook: $W=121$, $N_1=N_2=8$, $p=0.05$; jackdaw: $W=166$, $N_1=N_2=12$, $p=0.002$; ; jay: $W=15$, $N_1=N_2=6$, $p=0.40$; analysis restricted to paired birds). While the rook and jackdaw pattern is consistent with their general behavior, this shows that the jays, while more affiliative with their partners in general, are not more affiliative with partners after conflicts.

Triadic contact tendencies

Rook TCTs were negative for all affiliation and passive affiliation, but positive for active affiliation (mean TCT: all affiliation=-0.10, active affiliation=0.11, passive affiliation=-0.01). Jackdaw TCTs were around zero, meaning third-party affiliation occurred at about the same time after conflicts as in matched controls (mean TCT: all=-0.03, active=-0.002, passive=0.05). The jays had TCTs around zero, indicating they affiliate at the same time in PCs as in MCs, if they affiliate at all (mean TCT: all=0.04, active=0.04, passive=0.04).

First affiliation latencies

Post-conflict third-party affiliation was not shown in rooks when analysing first affiliative contacts in PCs versus MCs. There were no significant differences between the proportion of attracted and dispersed PC-MC pairs (Figure 1B; Wilcoxon signed ranks test: all affiliation: proportion attracted=0.44, mean proportion attracted per bird \pm sd=0.03 \pm 0.03, proportion dispersed=0.51, mean \pm sd=0.04 \pm 0.01, $V=25.5$, $p=0.30$, 95% confidence interval=-0.02-0.01; active affiliation: proportion attracted=0.40, mean \pm sd=0.03 \pm 0.03, proportion dispersed=0.24, mean \pm sd=0.02 \pm 0.02, $V=24$, $p=0.11$, 95% CI=-0.005-0.06; passive affiliation: proportion attracted=0.44, mean \pm sd=0.03 \pm 0.02, proportion dispersed=0.46, mean \pm sd=0.04 \pm 0.02, $V=37$, $p=0.91$, 95% CI=-0.02-0.02).

A GLMM analysis was performed to determine whether a subset of the data from the proportion of attracted PC-MC pairs had shorter latencies to first affiliation. Rook and jackdaw results show that there is still no post-conflict third-party affiliation according to first affiliation latencies, regardless of the initiator of affiliation, relationship with the affiliator, or sex of the subject (Table 4, null model is the model of best fit). Jay results were not analyzed due to lack of data ($N=4$ attracted PC-MC pairs).

Jackdaws did not show post-conflict third-party affiliation according to the latency of affiliation in PCs and MCs. There was no difference between the proportion of attracted and dispersed PC-MC pairs (Wilcoxon signed rank test: all affiliation: proportion attracted=0.45, mean proportion attracted per bird \pm sd=0.03 \pm 0.02, proportion dispersed=0.48, mean \pm sd=0.03 \pm 0.02, $V=33$, $p=1$, 95% confidence interval=-0.03-0.03; active affiliation: proportion attracted=0.40, mean \pm sd=0.03 \pm 0.02, proportion dispersed=0.39, mean \pm sd=0.03 \pm 0.01, $V=27$, $p=0.63$, 95% CI=-0.02-0.02; passive affiliation: proportion attracted=0.50, mean \pm sd=0.04 \pm 0.02, proportion dispersed=0.47, mean \pm sd=0.03 \pm 0.02, $V=68.5$, $p=0.33$, 95% CI=-0.02-0.03). Results from the GLMM analysis

showed that no particular types of affiliation occurred more during attracted PC-MC pairs because the model of best fit was the null model (Table 4). Therefore, there was no post-conflict third-party affiliation even when examining affiliation at a finer level than the broad categories of affiliation type as with the Wilcoxon signed rank test.

Jays did not show post-conflict third-party affiliation according to affiliation latencies in PCs versus MCs. There was no difference between the proportion of attracted and dispersed PC-MC pairs (Wilcoxon signed rank test: all affiliation: proportion attracted=0.39, mean proportion attracted per bird±sd=0.05±0.06, proportion dispersed=0.22, mean±sd=0.03±0.03, V=4.5, p=0.59, 60% confidence interval=-0.06-0.17). The jay sample size was so small (only four attracted PC-MC pairs) that a GLMM could not be prudently applied to the data to determine whether particular categories influenced those instances in which attraction occurred.

Frequency of affiliation

A different analysis of the data follows, which examines the frequency of affiliation rather than the latency of first affiliative contact in PCs and MCs. This analysis includes all affiliative interactions from each 10-minute PC and MC (Figure 2), rather than just the first affiliative contacts from each.

Rooks had a higher frequency of affiliation in PCs compared with MCs according to the GLMM analysis (mean frequency of affiliation±sd: PCs=5.10±3.86, MCs=4.19±3.84; Table 5). Because the model of best fit for rooks involves interactions among variables, we will describe how to read and interpret these results. In the 'Full and Best Fit' model (Table 5), the first line is the intercept, or base model, which includes MCs, aggressors, and females. Each term, or interaction among terms, below this first line compares that specific element to its corresponding element in the base model. The estimate on the second line (Treatment: PC, -3.87) shows that the frequency of affiliation decreases in PCs compared with MCs (in the base model) for aggressors that are female. The eighth

line (PC*victim, 5.22) indicates that the frequency of affiliation in PCs increases for victims, relative to aggressors, that are female. In this case, the male value (on line nine, 38.99) had an even stronger effect than the female value, thus we added a line stating the male values. When male and female values were similar, we included only the female value for brevity. Summarising the results from the model of best fit, the frequency of post-conflict third-party affiliation increased for female victims relative to aggressors and this effect was even stronger for male victims. After conflicts, subjects tended to initiate affiliation with their partners, more than receiving affiliation or affiliating with non-partners, and affiliation increased with age. These results show that when the frequency of affiliation across the entire 10-minute period of PCs and MCs is considered, rooks have post-conflict third-party affiliation.

Jackdaw victims had a significantly higher frequency of affiliation in PCs than in MCs relative to aggressors; an effect that was stronger for females (mean frequency of affiliation \pm sd: PCs=5.29 \pm 3.30, MCs=4.47 \pm 3.05; Table 5). After conflicts, relative to matched controls, females also affiliated more with their partner than with others, initiated this affiliation more than being the recipient of it, and the frequency of affiliation increased with age.

Jays showed no post-conflict third-party affiliation according to the frequency of affiliation: their model of best fit included only age as an explanatory variable, and not treatment, therefore there were no differences in the frequency of affiliation between PCs and MCs (mean frequency of affiliation \pm sd: PCs=3.28 \pm 4.43, MCs=1.89 \pm 3.12; Table 5).

Duration of affiliation

All three species showed post-conflict third-party affiliation according to the duration of affiliation per 10-minute observation session (Figure 3). Rook victims had longer durations of affiliation in PCs relative to MCs, which increased with age, occurred more with partners, and were self initiated

(the latter two effects were stronger for males; mean duration of affiliation in seconds per session \pm sd: rook PCs=190 \pm 163, MCs=126 \pm 138; jay PCs=62 \pm 104 MCs=47 \pm 130; Table 6).

Jackdaw victims that were female had longer affiliation durations in PCs than in MCs relative to aggressors and males, but males did show longer affiliation durations in PCs relative to MCs overall (mean duration of affiliation in seconds per session \pm sd: PCs=248 \pm 185, MCs=257 \pm 187; Table 6). The duration of affiliation tended to decrease with age for both sexes.

Jays showed post-conflict third-party affiliation according to affiliation durations, which increased in PCs relative to MCs and decreased with age (mean duration of affiliation in seconds per session \pm sd: PCs=62 \pm 104 MCs=47 \pm 130; Table 6).

Interaction between third-party affiliation frequency and duration in PCs versus MCs

Affiliation frequency and duration were not independent of each other because they were positively correlated for all three species in PCs and in MCs (Spearman's rank correlation: rooks: PCs $S=5445003$, $p<0.001$, $\rho=0.54$, MCs $S=47819.6$, $p<0.001$, $\rho=0.77$; jackdaws: PCs $S=97184.4$, $p<0.001$, $\rho=0.63$, MCs $S=131861.2$, $p<0.001$, $\rho=0.49$; jays: PCs $S=44.1$, $p<0.001$, $\rho=0.95$, MCs $S=24.1$, $p<0.001$, $\rho=0.97$). While affiliation frequency and duration are not independent, they may show different patterns throughout post-conflict sessions, thus we explore these patterns below.

Rooks had lower affiliation frequencies in the first five minutes versus the last five minutes of PCs (Mann-Whitney U test: $N_1=N_2=105$ PCs: $W=3543$, $p=0.000003$, 95% CI=-3.00-(-1.00)) and MCs ($N_1=N_2=105$ MCs: $W=3747$, $p=0.00002$, 95% CI=-2.00-(-1.00)). Affiliation durations were shorter in the first five minutes of PCs ($N_1=N_2=105$ PCs: $W=4118$, $p=0.0008$, 95% CI=-92.00-(-20.00)) and longer in the first five minutes of MCs ($N_1=N_2=105$ MCs: $W=4157$, $p=0.001$, 95% CI=-58.00-

(-11.00)). We are unable to explain why MCs showed differences in the frequency and duration of affiliation between the first and last five minute periods. This is unexpected because MCs are the baseline behavior for which no affiliation patterns are predicted. Perhaps analyzing a different window of time would remove the patterns, or maybe a longer observation period (i.e., more than 10 minutes) is necessary to show these large scale differences. Regardless, after conflicts it appears that affiliation is delayed in terms of the frequency and duration of events until the latter five minutes of the 10-minute observation session. This indicates that the post-conflict observation period should be at least this length to account for the post-conflict affiliative response.

For jackdaws, affiliation frequencies increased in the first five minutes relative to the last five minutes of PCs (Mann-Whitney U test: $N_1=N_2=113$ PCs: $W=8198.5$, $p=0.0001$, 95% CI=0.99997-1.00) and MCs ($N_1=N_2=113$ MCs: $W=7622$, $p=0.007$, 95% CI=0.00003-1.00). Again, we are unable to explain the increase in affiliation frequencies in the first half of MCs, which is the baseline behavior. More experimentation would be needed to understand what causes this natural variation. There were longer affiliation durations in the first five minutes relative to the last five minutes of PCs ($N_1=N_2=113$ PCs: $W=7340$, $p=0.04$, 95% CI=-0.00004-39.00), and no difference in MCs ($N_1=N_2=113$ MCs: $W=6480.5$, $p=0.75$, 95% CI=-10.00-16.00). The results indicate that conflicts immediately increase the length of affiliative events.

There were no differences in the frequency or duration of affiliation for jays between the first five minutes and last five minutes of PCs (Mann-Whitney U test, $N_1=N_2=15$ PCs: frequency $W=121.5$, $p=0.83$, 95% CI=-2.00-1.00; duration: $W=134.5$, $p=0.80$, 95% CI=-13.00-27.00) or MCs ($N_1=N_2=15$ MCs: frequency: $W=139.5$, $p=0.63$, 95% CI=-0.00003-1.00; duration: $W=138.5$, $p=0.67$, 95% CI=-5.00-5.00). This result would be expected when no post-conflict affiliative behavior is predicted, as is the case for this species.

Post-conflict aggression

There was no difference in the probability of aggression between PCs and MCs for former opponent-former opponent aggression or former opponent-third-party aggression in any species when comparing aggression survival distributions (Wald test: former opponent-former opponent aggression: rooks $X^2_{11}=0.14$, $p=0.71$, $N=66$, jackdaws $X^2_{11}=0.90$, $p=0.34$, $N=78$, jays $X^2_{11}=0.55$, $p=0.46$, $N=12$; former opponent-third-party aggression: rooks $X^2_{11}=0.11$, $p=0.74$, $N=343$, jackdaws $X^2_{11}=2.44$, $p=0.12$, $N=11$, jays $X^2_{11}=0.18$, $p=0.67$, $N=56$). Therefore, post-conflict aggression does not appear to be one of the post-conflict interactions used by these species.

While the frequency of affiliation significantly increased after conflicts, there was no difference between the overall rates of non-conflict aggression in PCs versus MCs for rooks or jackdaws (paired t-test: rooks: $t=0.77$, $df=12$, $p=0.45$, 95% confidence interval=-0.05-0.10; jackdaws: $t=1.24$, $df=13$, $p=0.24$, 95% CI=-0.01-0.05). Thus, the increase in activity levels as shown by the increase in the frequency of affiliative interactions was not a general increase in activity, but rather the rise in activity was specific to affiliation indicating that it is a post-conflict behavior. Similar to their results for the frequency of affiliation, jay aggression rates were also similar between PCs and MCs (paired t-test: jays: $t=1.05$, $df=7$, $p=0.33$, 95% CI=-0.06-0.15), therefore there was no increase in activity levels specifically or in general after conflicts. While affiliation frequency and duration are not independent factors, they do show species specific patterns after conflicts.

DISCUSSION

In all three species mates had the highest quality relationships because mates had the greatest potential fitness benefits (value), exchanged more affiliation with each other than with others (compatibility), and additionally rook mates exchanged less aggression with each other than with others (security). None of the corvids under study engaged in former opponent affiliation (Table 7). We would expect that former opponent affiliation would be used after fights between mates because

this is the highest quality relationship in the group. Since there were no conflicts between mates in any of the species, former opponent affiliation should be absent, as was the case for rooks and jays. However, jackdaws showed some sign of former opponent affiliation according to affiliation durations. We think this may be due to the restrictions of behavioral coding: a jackdaw would often sit near their former opponent after fights, a behavior that was coded as proximity since there was no ruffling of feathers to indicate it was a threat. However, this behavior was often followed by an aggressive attempt, suggesting the behavior coded as proximity was actually not affiliation but rather some form of aggression. While we were aware of this issue, there were no observable differences between proximity and this agitative behavior, thus we could not justify coding these as two separate behaviors. Because of this confounding factor, we think the positive result for former opponent affiliation should be replicated before considering this a standard jackdaw post-conflict affiliative behavior.

All three species showed post-conflict third-party affiliation according to affiliation frequencies and/or durations, but not latency to first affiliation, and no species showed increases in post-conflict aggression. Rooks and jackdaws showed a higher frequency and duration of affiliation in PCs compared with MCs and jays had longer affiliation durations in PCs. The presence of post-conflict third-party affiliation was predicted for the colonial rooks and jackdaws who engaged in this behavior with their mates, however it was unexpected in the less social jays who performed this behavior with anyone who was not the former opponent. We hypothesised that jays, being less social than the rooks and jackdaws, would not have sufficiently, or possibly even any, high quality relationships to engage in post-conflict affiliation with. We found that the jays rarely had high quality relationships outside of the breeding season when these data were collected, yet they did engage in third-party affiliation. While they exchanged more affiliation in general with their partner than with non-partners, they did not preferentially affiliate with partners after conflicts, presumably because most

of the partner affiliation occurred near the breeding season while conflicts could occur at any time throughout the year, thus the probability that they would be partnered after a conflict was low.

Rooks and jackdaws showed post-conflict third-party affiliation when analysing the frequency of affiliation. Affiliation occurred more after conflicts for victims of both sexes and increased with age. Victims may experience more stress from the conflict than aggressors, resulting in more post-conflict affiliation if the function of such behavior is to reduce stress. The increase in post-conflict activity levels was specific to affiliation, providing stronger evidence that this result was not simply due to a general increase in activity after conflicts, which are presumably stressful. Rooks and jackdaws also showed post-conflict affiliation according to affiliation durations: they engaged in longer durations of affiliation after conflicts than in matched controls. This effect was stronger for victims (male rooks and female jackdaws) and changed with age (increased for rooks and decreased for jackdaws). Higher frequencies of affiliation combined with longer durations of affiliation indicate that affiliation is a post-conflict behavior, and suggest that it may serve a stress reducing function. Since rooks and jackdaws had post-conflict third-party affiliation primarily with their mates, this indicates that it was not used as a substitute for former opponent affiliation because former combatants did not affiliate with the former opponent's kin or partner to indirectly repair the relationship between the former opponents (Wittig et al. 2007; Koski and Sterck 2009; Wittig and Boesch 2010). This finding is consistent with what we would predict for these species who only fight with non-mates: in short, non-mate relationships are not of a high enough quality to necessitate repairing to maintain group dynamics.

Jays showed post-conflict third-party affiliation in the form of longer durations of affiliation after conflicts when compared with matched controls, an effect that decreased with age. Similar to some macaques, jays are despotic with a rigid dominance hierarchy, however even despotic macaques have conflicts and some levels of post-conflict affiliation (Petit et al. 1997). The main difference

between jays and macaques is that macaques are more social than jays. Therefore, while post-conflict avoidance is to be expected in jays because they do not need to continually invest in the maintenance of social relationships, the presence of post-conflict affiliation shows that even the least social species studied so far can produce this behavior. The decrease in the duration of post-conflict third-party affiliation with age is likely due to the decrease in the number of conflicts as they aged. Most of the jay conflicts occurred at age one, which could have resulted from the formation of pairs and the establishment of a dominance hierarchy. Once these dynamics had been established, perhaps conflicts were not needed to maintain partners and/or dominance rank, especially since there were so few rank changes throughout the study.

None of the species in this study showed post-conflict third-party affiliation when analysing the data according to the latency to first affiliation in PCs versus MCs. Rooks and jackdaws had high baseline levels of affiliation, especially with their partners. This could mask the presence of third-party affiliation when using latencies since MC latencies would likely occur near the beginning of the session, thus making it difficult to obtain a shorter PC latency. This is perhaps why the frequency and duration of affiliation throughout each 10-minute observation period were better indicators of the presence of post-conflict third-party affiliation. Studying a different group of adult rooks, Seed and colleagues (2007), using the latency to first affiliation method, found post-conflict third-party affiliation for both aggressors and victims, which was initiated by former combatants and bystanders. That two different methods were needed to show post-conflict third-party affiliation in two groups of rooks could be due to population differences or age. The rooks in this study were juveniles in the beginning and adults in the end, thus, third-party affiliation may change over the developmental period with frequency or duration of affiliation being important in the juvenile years and latency of first affiliation in the adult years. Alternatively, Seed and colleague's (2007) rooks may also have had a higher frequency and/or duration of affiliation after conflicts, however this analysis was not explored.

The alternative methods for analysing post-conflict affiliation behavior involving the frequency and duration of affiliation after conflicts when compared with matched controls proved useful. Affiliation frequency was a good indicator of post-conflict third-party affiliation when compared with aggressive behaviors to determine whether the increase in activity was general or specifically regarding affiliation. A specific increase in affiliation frequency would be expected if affiliation is a post-conflict behavior, and this was found in both rooks and jackdaws. This analysis may be useful in species for which conflicts are presumed to be stressful since stress is known to increase activity levels (Carere et al. 2003). Our results show an increase in affiliation across the 10-minute observation session, which indicates that affiliative events following the first affiliative event could be responding to the conflict and not just the previous affiliative event. Analysing the duration of affiliation in PCs versus MCs was also useful, especially since both frequencies and durations increased after conflicts in rooks and jackdaws, which provides more evidence that affiliation is used in a post-conflict context. Had we solely relied on the latency of first affiliation method, we would have missed the fact that rooks, jackdaws, and jays do have post-conflict affiliative behavior when looking at all of the data across the observation sessions. We highlight the importance of examining all available data when investigating post-conflict affiliative behavior, and suggest that the post-conflict response entails more than just the first affiliative event.

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Table 1. Ethogram used to identify and record behavior for rooks (R), jackdaws (JD), and jays (J).

Category	Behavior	Definition
Affiliative: active	Bill twining	“Two birds interlock the mandibles of their beaks. Often this is accompanied by simultaneous displaying” (Seed et al. 2007, p. 153). R
	Active food sharing	Placing a food item into the bill of another bird (Goodwin 1951, 1986). Rooks: the recipient emits a begging call while the giver uses a different vocalization before and during food transfer. R, JD, J
	Bow display	A rook synchronously bows its body and fans its tail while vocalizing (Coombs 1960). Coded as active affiliation when performed by two birds that alternate bows or when directed at another bird in proximity. R
	Contact sit	A bird sitting 5 cm or closer to another bird. R, JD, J
	Courtship display	A Eurasian jay moves in long hops along a branch and from perch to perch while leaning forward and fluffing out the belly and back feathers. Movement involves turning and swaying side to side. Often accompanied by active food sharing motions, but without exchanging food (Goodwin 1951). J
	Allopreening	A bird nibbles or strokes the feathers of another bird (Coombs 1960). R, JD
	Dual caching	Two individuals caching the same object, sometimes synchronously manipulating the same item. R, J
	Dual object manipulation	Two birds manipulating the same object. R, JD, J
	Dual nest building	Nest building with another individual present on the nesting platform or nest box. The other individual may arrange nest material and manipulate nest material in coordination with the subject. R, JD
	Mount	A crouched receiver is mounted by another bird that climbs on its back, oriented such that both birds’ heads face the same direction. Accompanied by growling vocalizations. R, JD, J
Affiliative: passive	Proximity	Individuals >5cm apart and closer than one body length of each other. R, JD, J
	Co-feeding	Foraging while in proximity (see above) of another. R, JD, J
	Tolerated theft	Taking material from another individual’s bill, feet, or nest that does not result in an aggressive response. R, JD, J
	Begging	“[F]luttering or flapping wings, juvenile-type begging calls and, usually, a somewhat hunched and crouching posture” (Goodwin 1986, p. 83). Occurs when requesting food from an affiliative partner or before and during egg incubation (Goodwin 1986). R
Aggressive: no contact and/or did not result in displacement	Displacement	One bird retreats at the approach of another bird who locates itself in the retreating bird’s original spatial position. R, JD, J
	Threaten	One bird makes a movement directly at, pecks at, flies at, or lunges at another bird without making contact, or fluffs feathers while in proximity of or sidling up to another bird. The aggressing bird does not occupy the exact location of the retreating bird as with displacements. R, JD, J
	Peck	Using the bill to peck and make contact with another bird. R, JD, J
	Feather pull	Grabbing onto the feather(s) of another bird and pulling on them. R
	Chase	A prolonged, continuous approach by one bird toward another while the other continuously moves away. The interaction has a longer duration than avoid, threaten, or displacement. R, JD, J
	Theft	Taking material from another individual’s bill, feet, or nest resulting in an aggressive response. R, JD, J
Aggressive: with contact and dis- placement	Conflict	Contact aggression resulting in the displacement of one individual. Can include: pulling a bird off a branch and dangling it by its wing, locking talons and pecking and wrestling on the ground or in the air, knocking a bird off a perch, pecking, vocalizations, and chasing. Could occur over access to food, nest sites, nesting material, or unknown causes (supposedly maintenance of dominance rank). R, JD, J

Table 2. GLMM results for rooks and jackdaws and GLM results for jays for the *frequency of former opponent affiliation* (note: because there were very few occurrences of former opponent affiliation, the full model is greatly reduced compared with the full model for third-party affiliation frequencies to accommodate the reduced sample size).

Species	Model	Form	Estimate	Standard Error	delta AIC [AIC]
Rook	Null and Best Fit	Intercept only	0.20	0.19	0
		Subject (random factor)	0.00	0.00	[12]
		Treatment (random factor)	0.00	0.00	
Jackdaw	Null	Intercept only	0.53	0.14	2
		Subject (random factor)	0.00	0.00	[28]
		Treatment (random factor)	0.00	0.00	
	Best Fit	Intercept [*]	-0.44	0.57	0
		Age	0.33	0.18	[26]
		Subject (random factor)	0.00	0.00	
		Treatment (random factor)	0.00	0.00	
Jay	Null and Best Fit	Intercept only	-2.20	0.71	1 [15]
		Intercept [*]	-0.11	1.45	0
		Age	-1.00	0.84	[14]

^{*} denotes the base model as described in the methods. Subject and treatment were random factors and the variance and standard deviation are reported under the Estimate and Standard Error columns respectively.

Table 3. GLMM results for rooks and jackdaws and GLM results for jays for the *duration of former opponent affiliation* (note: because there were very few occurrences of former opponent affiliation, the full model is greatly reduced compared with the full model for third-party affiliation durations to accommodate the reduced sample size).

Species	Model	Form	Estimate	Standard Error	delta AIC [AIC]
Rook	Null	Intercept only	3.16	0.41	32
		Subject (random factor)	0.75	0.86	[868]
		Treatment (random factor)	0.14	0.37	
	Full and Best Fit	Intercept`	3.38	0.36	0
		Treatment: PC	-1.53	0.25	[836]
		Age (MC)	0.05	0.07	
		PC*age	0.36	0.09	
		Subject (random factor)	0.68	0.83	
		Treatment (random factor)	0.00	0.00	
Jackdaw	Null	Intercept only	4.21	0.30	1120
		Subject (random factor)	0.92	0.96	[2239]
		Treatment (random factor)	0.009	0.09	
	Full and Best Fit	Intercept`	0.02	0.33	0
		Treatment: PC	1.25	0.24	[1119]
		Age (MC)	1.42	0.05	
		PC*age	-0.52	0.08	
		Subject (random factor)	0.87	0.93	
		Treatment (random factor)	0.00	0.00	
Jay	Null	Intercept only	0.77	0.16	49 [210]
	Full and Best Fit	Intercept`	2.61	0.33	0
		Treatment: PC	14.63	1188.74	[161]
		Age (MC)	-0.52	0.14	
		PC*age	-16.03	1188.74	

Table 4. GLMM results on the *proportion of attracted PC-MC pairs* for particular classes of *third-party affiliation*: combatant-initiated, male, partner, or affiliation type (active, passive, or all).

Species	Model	Form	Estimate	Standard Error	delta AIC [AIC]
Rook	Null and Best Intercept only		-3.54	1.01	0
	Fit	Subject (random factor)	0.00	0.00	[4]
Jackdaw	Null and Best Intercept only		-3.41	0.88	0
	Fit	Subject (random factor)	0.00	0.00	[4]

Table 5. GLMM results for the *frequency of third-party affiliation*.

Species	Model	Form	Estimate	Standard Error	delta AIC [AIC]	
Rook	Null	Intercept only	1.52	0.11	36	
		Subject (random factor)	0.11	0.33	[444]	
		Treatment (random factor)	0.003	0.06		
	Full and Best Fit	Intercept` (MC, aggressor, female) Treatment: PC Role: victim (MC) Sex: male (MC) Age (MC) Proportion affiliation with partner (MC) Proportion affiliation self initiated (MC) PC*victim (female) PC*victim*male PC*male PC*age PC*prop. aff. with partner PC*prop. aff. self initiated Subject (random factor) Treatment (random factor)		6.69	2.22	0
				-3.87	2.86	[408]
				-4.59	2.32	
				-0.03	3.23	
				-1.51	0.65	
				-2.70	2.70	
				-6.26	3.08	
				5.22	0.04	
				38.99	9.93	
				-6.90	4.70	
				1.25	0.98	
				4.20	3.88	
				4.57	4.03	
				0.03	0.16	
	0.00	0.00				
Jackdaw	Null	Intercept only	1.63	0.07	1	
		Subject (random factor)	0.02	0.13	[389]	
		Treatment (random factor)	0.005	0.07		
	Full and Best Fit	Intercept` (MC, aggressor, female) Treatment: PC (female) Treatment: PC*male Role: victim (MC, female) Role: victim*male (MC) Sex: male (MC) Age (MC, female) Age*male (MC) Proportion aff. w/ partner (MC, female) Proportion aff. w/ partner*male (MC) Proportion aff. self initiated (MC, female) Proportion aff. self initiated*male (MC) PC*victim (female) PC*male (similar for male victims) PC*age (female) PC*age*male PC*prop. aff. with partner (female) PC*prop. aff. with partner*male PC*prop. aff. self initiated (female) PC*prop. aff. self initiated*male Subject (random factor) Treatment (random factor)		3.86	1.70	0
				-0.63	2.04	[388]
				2.25	2.42	
				-7.02	3.00	
				8.55	3.43	
				-3.62	2.02	
				-0.90	0.56	
				1.50	0.69	
				-3.37	2.42	
				9.90	3.29	
				-1.11	2.06	
				3.51	2.40	
				11.21	5.02	
				2.25	2.42	
				0.43	0.66	
				-0.93	0.82	
				2.44	2.94	
				-8.77	4.02	
	1.59	2.83				
	-5.75	3.42				
	0.0001	0.01				
	0.00	0.00				
Jay	Null	Intercept only	1.55	0.26	4	
		Subject (random factor)	0.23	0.48	[49]	
		Treatment (random factor)	0.02	0.14		
	Best Fit	Intercept` Age Subject (random factor) Treatment (random factor)		0.66	0.34	0
				0.19	0.06	[45]
				0.03	1.17	
	0.02	0.13				

Table 6. GLMM results for the *duration of third-party affiliation*.

Species	Model	Form	Estimate	Standard Error	delta AIC [AIC]
Rook	Null	Intercept only	5.02	0.18	4155
		Subject (random factor)	0.20	0.45	[18985]
		Treatment (random factor)	0.04	0.19	
	Full and Best Fit	Intercept` (aggressor, female)	6.64	0.43	0
		Treatment: PC	-1.08	0.53	[14830]
		Role: victim (MC)	-2.96	0.43	
		Sex: male (MC)	5.43	0.67	
		Age (MC)	-0.33	0.11	
		Proportion affiliation with partner (MC)	-2.61	0.52	
		Proportion affiliation self initiated (MC)	-2.86	0.57	
		PC*victim	3.14	0.56	
		PC*male	-9.87	0.84	
		PC*age	0.18	0.17	
		PC*prop. aff. with partner (female)	1.58	0.69	
		PC*prop. aff. with partner*male	16.32	1.24	
		PC*prop. aff. self initiated (female)	2.64	0.72	
		PC*prop. aff. self initiated*male	16.28	1.34	
		Subject (random factor)	0.18	0.42	
		Treatment (random factor)	0.00	0.00	
Jackdaw	Null	Intercept only	5.51	0.09	4216
		Subject (random factor)	0.12	0.34	[25055]
		Treatment (random factor)	0.001	0.04	
	Full and Best Fit	Intercept` (aggressor, female)	3.97	0.54	0
		Treatment: PC	2.65	0.70	[17839]
		Role: victim (MC, female)	-0.87	0.62	
		Role: victim*male (MC)	4.37	0.70	
		Sex: male (MC)	-1.74	0.41	
		Age (MC)	0.50	0.11	
		Proportion aff. w/ partner (MC, female)	4.42	0.45	
		Proportion aff. w/ partner*male (MC)	-3.21	0.58	
		Proportion aff. self initiated (MC, female)	-0.67	0.40	
		Proportion aff. self initiated*male (MC)	2.75	0.49	
		PC*victim (female)	16.73	1.59	
		PC*victim*male	-22.71	1.66	
		PC*male	0.16	0.59	
		PC*age	-0.33	0.15	
		PC*prop. aff. with partner (female)	-5.27	0.60	
		PC*prop. aff. with partner*male	4.67	0.74	
		PC*prop. aff. self initiated	-0.73	0.74	
Subject (random factor)	0.81	0.90			
Treatment (random factor)	0.11	0.34			
Jay	Null	Intercept only	4.30	0.36	645
		Subject (random factor)	0.61	0.78	[1022]
		Treatment (random factor)	0.006	0.08	
	Full and Best Fit	Intercept`	0.71	0.25	0
		Treatment: PC	2.50	0.19	[377]
		Age (MC)	0.62	0.03	
		PC*age	-0.35	0.03	
		Subject (random factor)	0.15	0.39	
		Treatment (random factor)	0.00	0.00	

Table 7. Summary of whether former opponent or third-party affiliation occurred according to which method.

Species	Former Opponent Affiliation			Third-Party Affiliation		
	Latency	Frequency	Duration	Latency	Frequency	Duration
Rook	X	X	X	X	Yes	Yes
Jackdaw	X	X	Yes	X	Yes	Yes
Jay	X	X	X	X	X	Yes

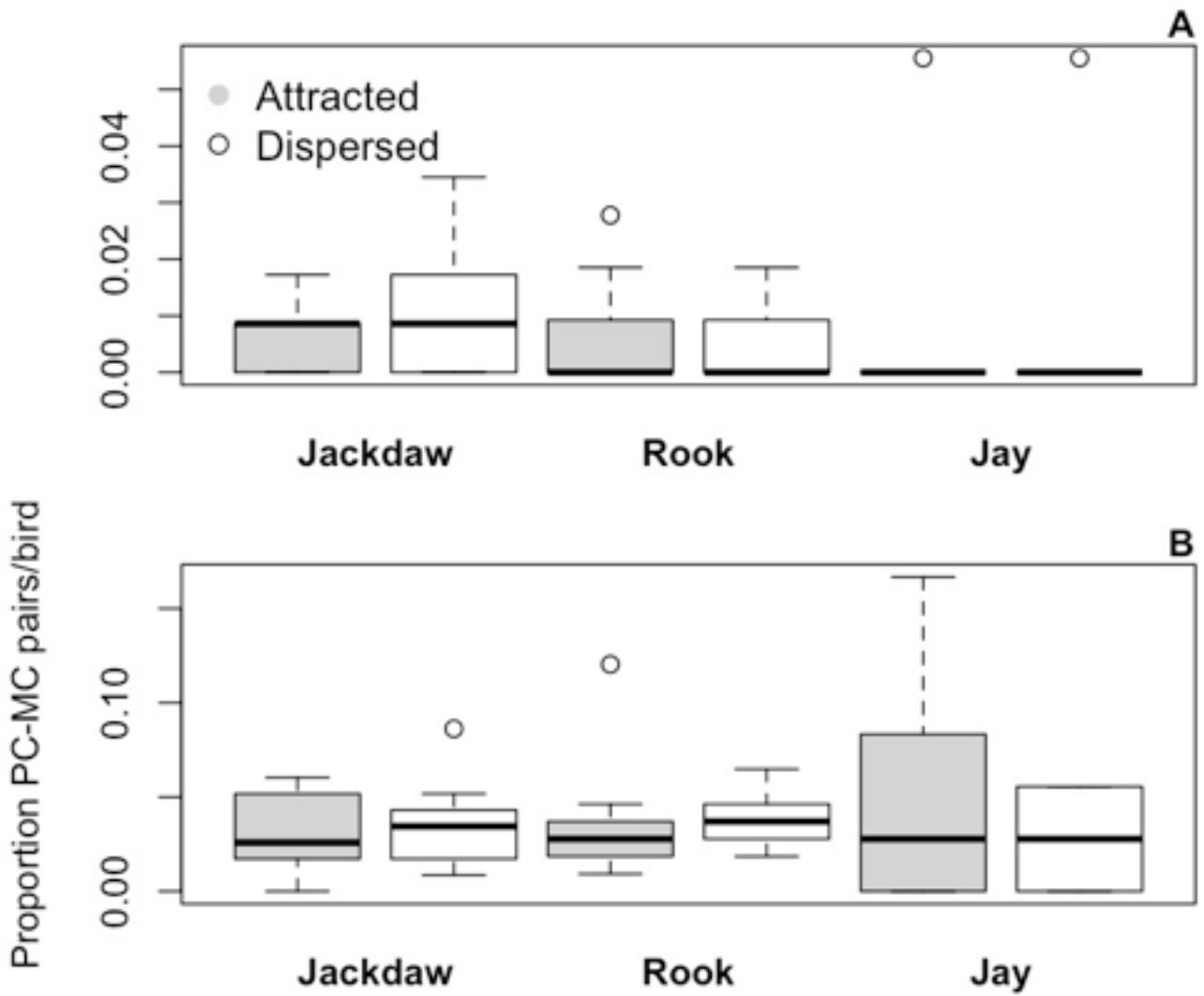


Figure 1 The proportion of PC-MC pairs that were attracted (active or passive affiliation occurring sooner after conflicts) or dispersed (active or passive affiliation occurring sooner in matched controls) per bird for each species for former opponent affiliation (A) and third-party affiliation (B).

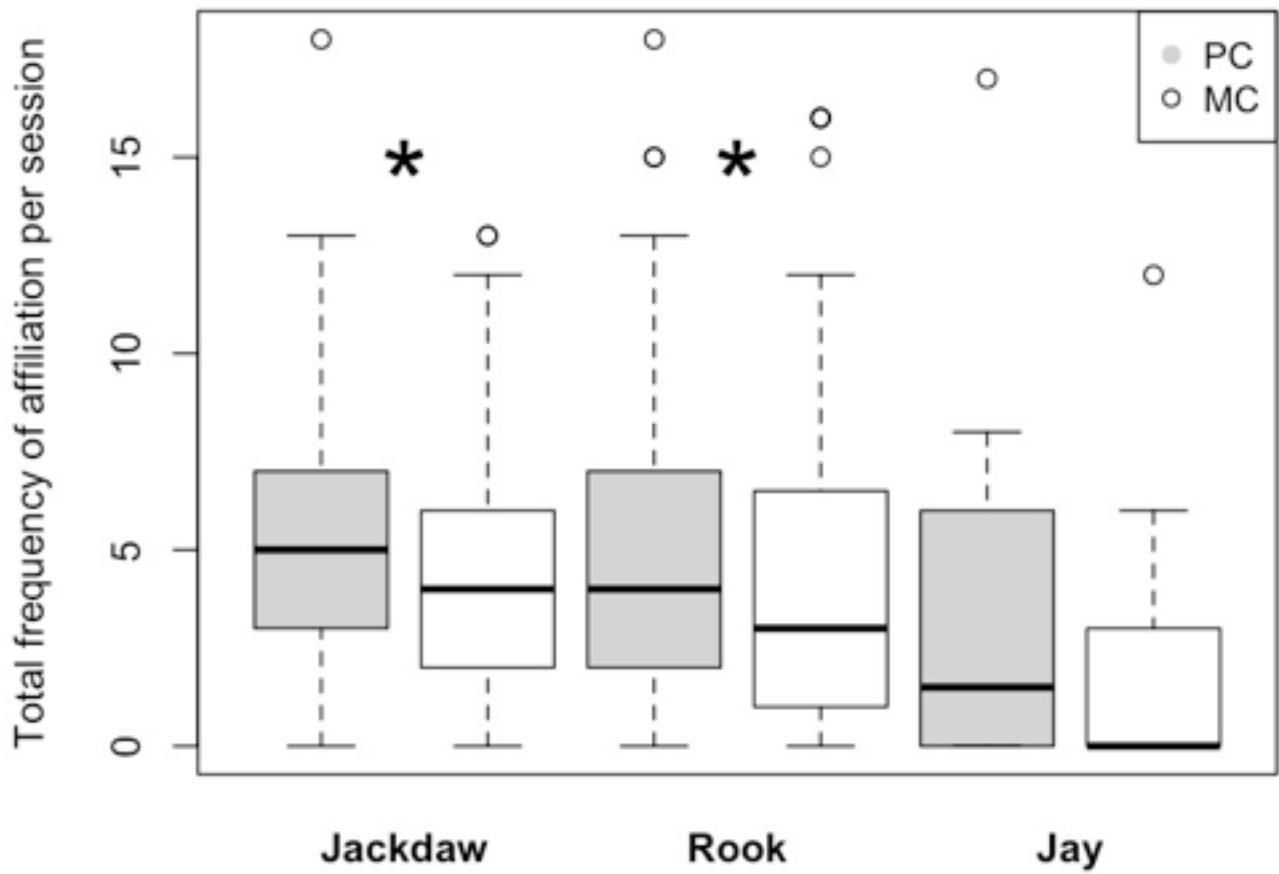


Figure 2 The total frequency of affiliation per session (PC or MC) by species.

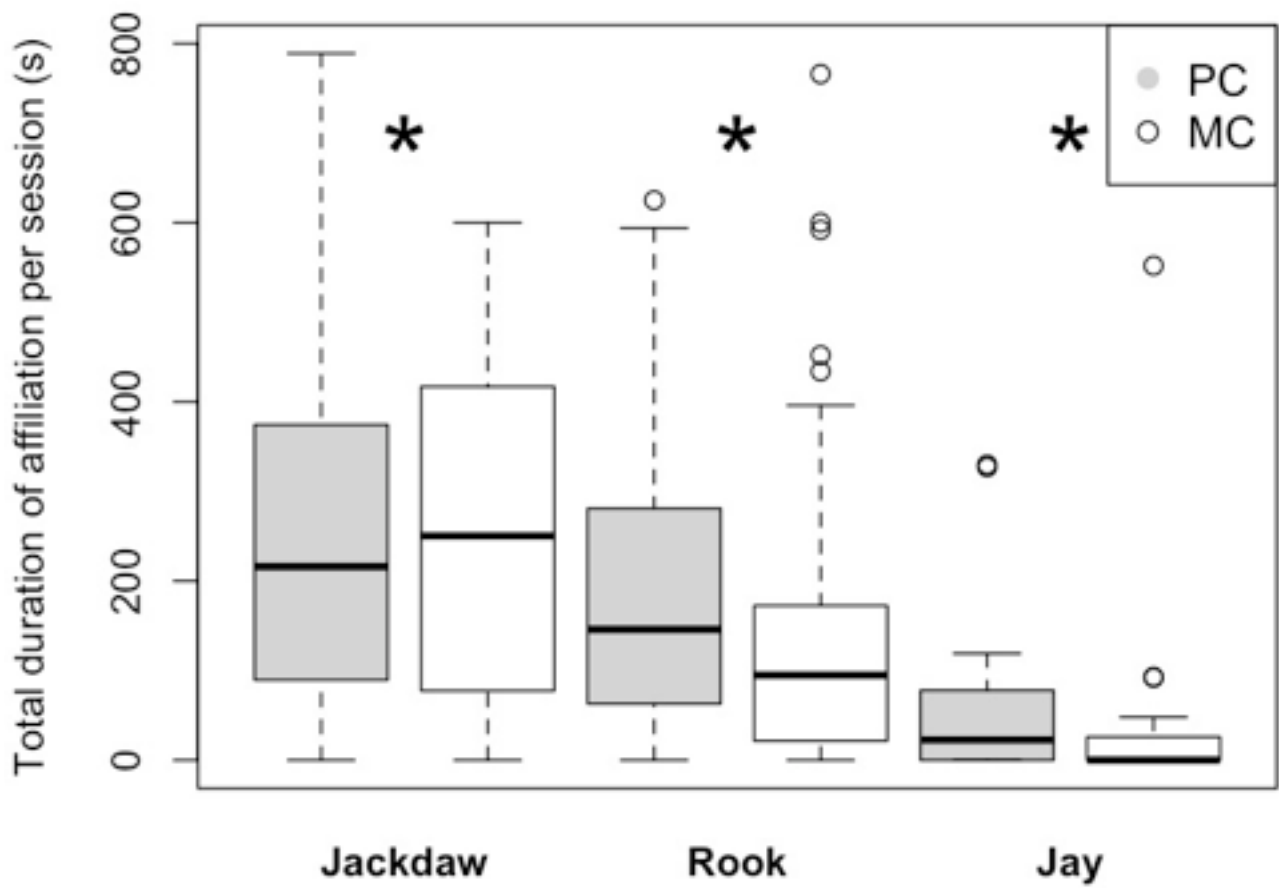


Figure 3 The total duration of affiliation per session (PC or MC) by species. Note that totals can add up to more than the observation session length (600s) because multiple affiliative states could occur at one time.