

The sociality, ontogeny, and function of



corvid post-conflict affiliation

PhD Dissertation 2011

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DECLARATION

The following work was carried out at the Department of Experimental Psychology and the Sub-Department of Animal Behaviour at Madingley, University of Cambridge, between October 2008 and November 2011 under the supervision of Professor Nicola S. Clayton FRS. I hereby declare that this dissertation has not been submitted, in whole or in part, for any other degree, diploma or qualification at any other university.

This dissertation is the result of my own work and includes nothing that is the outcome of work done in collaboration, except where specifically indicated in the text and as described here:

- Chapter 2: I collaborated with Ljerka Ostojic and Gabrielle Davidson to collect data on the social behaviour of rooks, jackdaws, and jays. Both researchers are PhD candidates in my lab: Ljerka studies jay cognition and Gabrielle investigates jackdaw cognition. This data was collected jointly (77% by me, 16% by Ljerka, and 6% by Gabrielle), however each of us analysed the data independently for our own specific purposes.
- Chapter 5: Ljerka Ostojic assisted with the experimental design for the stress section (study 2) and one of the analyses therein (affiliation buffers aggression via contact).
- Chapter 6: I consulted with Dr Sonja Koski at the University of Zürich to develop the relationship quality hypothesis described in this chapter. Sonja did her PhD on post-conflict affiliation in chimpanzees and her in depth comments contributed to the clarification of ideas and broader scope of the chapter. In most cases, I integrated her comments into the text, and in a couple of instances she contributed to the crafting of the text, which I edited. This chapter has been submitted to *Biological Reviews*.

I have attempted to reference appropriately any idea or finding that is not my own. This dissertation does not exceed the limit of length specified by the Degree Committee for Biology.

Corina J. Logan

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SUMMARY

Humans and non-humans alike seek support after conflicts by making up with their former opponent (former opponent affiliation) or by affiliating with a bystander (third-party affiliation). Post-conflict behaviour has been studied in many mammals but only in two bird species: rooks and ravens. Consequently, the prevalence and function of avian post-conflict affiliation is unknown. My objectives were to expand the study of post-conflict affiliation to more bird species and examine two potential functions of this behaviour. I hypothesised that differences in sociality would influence corvid post-conflict affiliation, and that this behaviour would change as individuals developed from juveniles to adults. I predicted that social rooks (*Corvus frugilegus*) and jackdaws (*C. monedula*), but not the less social Eurasian jays (*Garrulus glandarius*), should have post-conflict affiliation because this behaviour should be dependent on the presence of high quality social bonds. Affiliation should only occur with their mate because they are monogamous; the pair-bond being by far the highest quality relationship in the group. My results showed that the social species have third-party affiliation with their mate, while the less social jays have third-party affiliation with anyone. This behaviour became more frequent and lasted longer as jackdaws went from the pair formation stage to sexual maturity. Exploring the function of third-party affiliation, I found that it decreased the likelihood of receiving non-conflict aggression, thus buffering post-conflict aggression for jackdaw and rook aggressors, as well as for rook victims. Hypotheses about post-conflict affiliation primarily concern former opponent affiliation and primates. I reviewed post-conflict affiliation across taxa and proposed a broad hypothesis that includes all forms of post-conflict affiliation: former opponent, third-party, quadratic, inter-group, and inter-species.

PUBLICATIONS

The publications listed here have resulted from the research carried out for this thesis.

Part of chapter 2 and all of chapter 3:

Logan CJ, Emery NJ, & Clayton NS. (*Submitted*). Testing alternative behavioral measures of post-conflict affiliation. *Behavioral Ecology*.

Part of chapter 2 and all of chapters 3 and 4:

Logan CJ, Emery NJ, & Clayton NS. June 2011. Squabbles and snuggles: how corvids handle conflict. *Natural History Magazine*, pp. 18-19.

Logan CJ. 7 July 2010. Settling arguments, the corvid way. *New Scientist*.

Chapter 3:

Logan CJ, & Clayton NS. (*In prep.*). Developmental effects on corvid post-conflict third-party affiliation.

Chapter 4:

Logan CJ, Ostojic L, & Clayton NS. (*In prep.*). Corvid post-conflict third-party affiliation buffers aggression.

Chapter 5:

Logan CJ, Hoppitt WJE, & Clayton NS. (*In prep.*). Does corvid post-conflict third-party affiliation reduce stress?

Chapter 6:

Logan CJ, Koski SE, & Clayton NS. (*In prep.*). A broad hypothesis for post-conflict affiliation.

Additionally, I published a theoretical paper based on previous field work combined with ideas I developed while working with Nicky Clayton:

Logan CJ, O'Donnell S, & Clayton NS. (*In press*) A case of mental time travel in ant-following birds? *Behavioral Ecology* 22:1149-1153. DOI: 10.1093/beheco/ARR104.

CONTENTS

Declaration.....	2
Acknowledgements.....	3
Summary.....	4
Publications.....	5
Chapter 1: Why be social?.....	7
Chapter 2: The social lives of three corvids.....	17
Chapter 3: How does sociality influence post-conflict affiliation in corvids?..	36
Chapter 4: Developmental effects on post-conflict third-party affiliation in rooks and jackdaws.....	64
Chapter 5: Does post-conflict third-party affiliation reduce aggression and stress?.....	78
Chapter 6: A broad hypothesis for post-conflict affiliation.....	109
Chapter 7: Discussion.....	124
References.....	133

CHAPTER 1: Why be social?

When studying any behaviour, it is useful to take a comparative approach: examining a social behaviour in species that vary in their degrees of sociality allows one to determine whether sociality is required for the behaviour to evolve or if the behaviour is present independently of social system (Harvey & Pagel 1991). Because I study a social behaviour, namely how individuals affiliate with each other after fights (post-conflict affiliation), I used a comparative approach to determine whether sociality influences this behaviour by studying three species that vary in their levels of sociality. If post-conflict affiliation occurs only in the social species, then it may indicate that sociality is a selective agent to which this behaviour is a response. Alternatively, if post-conflict affiliation occurs in all three species, regardless of their level of sociality, then sociality may not be a limiting factor for this behaviour. I provide a base here by taking a broad view, discussing the selection pressures that drive sociality. This base will allow me to discuss the implications for how differences in sociality impact post-conflict affiliation behaviour in each of the three species I study later in this thesis. I consider the costs and benefits for being social, focusing on the benefits that post-conflict affiliation provides, and how the balance of costs and benefits varies according to a species' social system. I conclude by putting forth some of the outstanding questions in post-conflict affiliation research that this thesis addresses and outline the content of subsequent chapters.

WHY BE SOCIAL?

Why invest energy into interactions with others, when individuals could spend that time foraging or sleeping if they lived a solitary existence? Social and solitary lifestyles incur costs and benefits, each evolving if the benefits of that method of living outweigh the costs (Alexander 1974). Some of the defining factors that determine whether sociality arises include the availability of resources, the probability of disease transmission, and predation risk (Alexander 1974).

One of the costs of asociality is reduced access to potential mates, while being social increases the chance of encountering a suitable mate due to increased population density (Andrewartha & Birch 1954). Some solitary spiders may never find a mate, therefore

when a male encounters a female, he invests his entire life in this one chance to reproduce by offering himself to the female as nourishment after copulation (redback spiders: Andrade 2003). These spiders cannot be choosy, whereas individuals in social species can because the chance of encountering a mate is much higher and one individual may have many chances to reproduce within their lifetime (e.g., red-sided garter snakes: Shrine et al 2006).

One of the benefits of asociality is reduced competition for food. Sociality increases competition for resources since more individuals per area compete for the limited resources within that area (Alexander 1974, Waser 1977a & b, West-Eberhard 1983, Svanbäck & Bolnick 2007). However, sociality can include benefits to offset these costs, including a higher chance of encountering patchy food sources or the ability to obtain a food resource requiring cooperation among foragers (Alexander 1974). Social groups can minimise foraging competition through niche partitioning according to age and sex classes (e.g., van Schaik & van Noordwijk 1986). A study on long-tailed macaques found that larger foraging groups tended to split into smaller groups when food was scarce: males left the main group to meet their higher food intake requirements by foraging alone, while adult females stayed in the main group to reduce travel costs while they were carrying infants (van Schaik & van Noordwijk 1986).

When the benefits of group living outweigh the costs, sociality evolves. With sociality, there arises a number of costs to which certain adaptations to reduce these costs have evolved; I shall describe these below.

COSTS AND BENEFITS OF SOCIALITY

Higher risk of disease transmission

One cost of sociality is the increased risk of transmitting diseases among individuals because of living in more dense populations than solitary species (Alexander 1974, Arneberg et al. 1998, Altizer 2003). Pathogens can have many consequences from causing fatal diseases and miscarriages to being responsible for congenital defects and sickness (see review in Freeland 1976). There are a number of ways in which animals reduce their parasite loads, and most of them do not involve contact with other individuals (Arneberg et al. 1998). Aside from immune systems evolving to counteract

pathogens, some species reduce their risk of contracting diseases through behavioural mechanisms. Some animals avoid food patches containing faeces to prevent the acquisition of new parasites, others eat plants with toxins to cleanse their digestive tract (see review in Altizer et al. 2003) or rub toxic plants over their bodies as a kind of insect repellent (see review in Lozano 1998).

Lower predation risk

Living in more dense populations decreases the chance that any one individual will be predated because the number of individuals in the group is larger than the number of individuals a predator can kill (Bednekoff & Lima 1998). Indeed, evidence in starlings provides support for this as vigilance decreases with increasing group size (Powell 1974). There are also behavioural adaptations that decrease the risk of predation. Some individuals in a group may notice a predator and flee, thus causing others to either flee or to look up, detect the predator and then flee (see Bednekoff & Lima 1998 for review). Additionally, some individuals may give an alarm call after detecting a predator, causing group members to run to safety (Trivers 1971). Alarm call rates can be socially transmitted as in the case of reed warblers who increase mobbing of brood parasitic common cuckoos after seeing neighbouring reed warblers do so (Davies & Wellbergen 2009). When there is a high risk that a cuckoo will lay its eggs in a reed warbler nest, mobbing reduces this risk, which decreases predation of reed warbler chicks (Wellbergen & Davies 2009).

Greater success at rearing offspring

Living in groups allows the opportunity for the communal rearing of young to evolve. Some species have groups containing multiple breeding adults who assist with raising offspring other than their own (plural breeders; Lewis & Pusey 1977). South American coatis are one such species: adult females form a band with their juveniles and collectively chase off potential predators (including adult male coatis), which is more successful than a single adult female trying to protect her juveniles (Russell 1981). Another breeding system involves one breeding pair with reproductively suppressed subordinates that help raise offspring (singular breeders; Lewis & Pusey 1997). Though helpers have no offspring of their own, the costs of living alone are too high and the

habitat too saturated to establish their own breeding territory, therefore they invest in indirect fitness by assisting with raising the dominant's young (Clutton-Brock et al. 2001, see Lewis & Pusey 1997 for a review). Singular breeding meerkat females enlist babysitters, during the first month of her pups lives, to help guard the burrow while the rest of the group forages (Clutton-Brock et al. 2000).

Higher probability of social disagreements

Once it becomes beneficial to exist in a group, individuals having different needs must agree about daily decisions such as how to get from one place to another, where to stop and forage, when to move to the next location, and when to go to the sleeping site (see review in Boinski et al. 2000). White-faced capuchin monkeys negotiate navigation vocally by using trill calls from the leading edge of the group, indicating the proposed direction of movement (Boinski & Campbell 1995). Dominance hierarchies can structure social groups to minimise social disagreements and carry on with fitness-enhancing activities (Maynard Smith 1974, see Preuschoft & van Schaik 2000 for review). In horses, males are dominant to females and one male maintains a harem of females (Rubenstein 1994). There is also a dominance hierarchy among the harem-holding males, which has advantages for the higher ranking individuals: lower ranking males direct their harems to avoid groups containing high ranking males who are aggressive, thus minimising conflict.

Higher probability of conflicts

When social disagreements do occur, they may escalate into a conflict. Conflicts take different forms in different species. Red-fronted lemur conflicts can be extremely subtle: the aggressor may lunge its upper body toward the victim who may sit still, neither aggressing nor submitting, and then one individual looks away ending the fight (Pereira & Kappeler 1997). Rhesus macaque conflicts can be much more aggressive, involving biting, slapping, and grabbing, resulting in the victim avoiding the aggressor while screaming (Thierry 1985). Conflicts come with their own costs: injury, death, damage to a valuable relationship, and stress (Cords and Killen 1998). However, it is in the interest of conflict participants, especially those that fight often, to reduce these costs by establishing dominance hierarchies, using signals to interact rather than

physical contact, and enlisting agonistic support (Maynard Smith 1974, see review in Preuschoft & van Schaik 2000). As such, many conflicts among conspecifics are limited in their intensity (Cords and Killen 1998).

Development of conflict management behaviour

Social species that have conflicts usually have some kind of conflict management behaviour (Aureli et al. 2002). These behaviours involve pre-conflict management (conflict avoidance, using greetings and grooming to reduce tension to make aggression less likely), third-party interventions during conflicts (agonistic support), post-conflict affiliation (friendly interactions between former opponents or a former opponent and a bystander after a conflict), and redirecting aggression at bystanders (to distract their opponent or manage dominance relationships; see reviews in Scucchi et al. 1988, Aureli et al. 2002, and Koyama & Palagi 2006). A study on macaques found a relationship between aggression intensity and dominance style: the more egalitarian species have less intense aggression and aggression management behaviours appear to be more developed (Thierry 1985). Individuals in a more egalitarian society have a greater ability to negotiate relationships and rank, which possibly acts as a selection pressure for a wider range of conflict management behaviours that are used more often.

In sum, there are a variety of advantages to being social, however there are also costs associated with sociality. Adaptations occur to make group living more beneficial than costly, but the balance of costs and benefits differ for each species. While behavioural repertoires tend to vary by species, the use of post-conflict affiliative behaviour appears almost ubiquitous across the social species, indicating a general selective pressure for the presence of this behaviour.

SOCIALITY AND POST-CONFLICT AFFILIATION

It is hypothesised that post-conflict affiliation occurs only in social species because conflicts of interest are a normal occurrence in the daily lives of group living species (Aureli et al. 2002). Individuals will work to maintain amicable group dynamics to continue to benefit from their membership in the group while minimising their costs through post-conflict behaviour (Aureli et al. 2002). However, this hypothesis has not

been tested: post-conflict affiliation has only been studied in social species, therefore we do not have evidence that this behaviour does not exist in asocial species. It does not seem likely that asocial species would have a need for conflict management behaviour, which is thought to be dependent on the need to invest in relationships with others. However, examining post-conflict affiliation in asocial species will allow us to confirm or reject this hypothesis based on evidence rather than assumptions. Variation in the use of post-conflict affiliation among social species appears to be partially due to dominance style and associated levels of aggression (Thierry et al. 2008), as well as the presence of high quality social bonds within the group (see Arnold et al. 2010 for a review). Therefore, it is important to examine how other factors involved in sociality influence post-conflict affiliation.

COSTS AND BENEFITS OF POST-CONFLICT AFFILIATION BY ROLE

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. 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 by their former opponent and by bystanders (see review in Arnold et al. 2010). Victims can offset these costs using post-conflict affiliation: initiating former opponent affiliation or affiliation with a bystander (third-party affiliation) 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). Victims are more commonly studied than aggressors, therefore it is unclear whether there are other functions of former opponent affiliation for aggressors or how these functions differ for aggressors and victims.

Post-conflict third-party affiliation is more complicated than former opponent affiliation because there can be a variety of functions for this behaviour which directly involves a

former opponent and a bystander, but it can also indirectly involve the other former combatant. Bystanders can benefit from initiating affiliation with conflict victims after conflicts to reduce their risk of receiving aggression if victims are agitated after fights (Fraser et al. 2009). Both bystanders and conflict victims can benefit from post-conflict third-party affiliation because it may reduce the stress caused by the conflict for both individuals (Fraser et al. 2009). 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 (Koski & Sterck 2009). Victims and aggressors may benefit from initiating third-party affiliation for stress reduction (Koski & Sterck 2009). It is not yet clear how third-party affiliation differs functionally for aggressors, especially outside of the primates, because studies often only investigate post-conflict affiliation for victims or they do not differentiate aggressors and victims or specify the initiator of the affiliation (Fraser et al. 2009). It is also common for investigations to study only former opponent affiliation and not third-party affiliation, which leaves gaps in understanding how and why third-party affiliation occurs.

There is another form of post-conflict affiliation called quadratic post-conflict affiliation, which has only been investigated in two species. A conflict between certain group members may increase the stress levels of other group members (bystanders). Quadratic affiliation is when bystanders affiliate with each other to reduce the stress induced by the conflict (Judge & Mullen 2005, de Marco et al. 2010).

OUTSTANDING QUESTIONS ON THE TOPIC OF POST-CONFLICT AFFILIATION

There are many questions about post-conflict affiliation that have yet to be answered, a few of which I shall address in this thesis:

- Is post-conflict affiliative behaviour restricted to social species? I will examine this by studying an species with very low levels of sociality in addition to two social species so I can compare the relative levels of post-conflict affiliation among species.

- Is post-conflict affiliation used by more corvids (birds in the crow family) than just rooks and ravens? Post-conflict affiliation has only been studied in three bird species (rooks: Seed et al. 2007, ravens: Fraser & Bugnyar 2010 & 2011, green woodhoopoes: Radford 2008), therefore, expansion of the evidence on birds is warranted. I study two new corvid species and replicate one other corvid species in the context of post-conflict affiliation.
- What are the functions of corvid post-conflict affiliation? Hypotheses about the functions of this behaviour exist and some have been tested in mammals (see review in Arnold et al. 2010), however there is only one functional study in birds (Fraser & Bugnyar 2010). I conduct experiments to determine whether post-conflict affiliation reduces stress or reduces aggression in corvids.
- How does corvid post-conflict affiliation develop as individuals grow from juveniles to adults? It is not known how this behaviour changes over the life course in birds. Indeed, only very few studies have explored the ontogeny of post-conflict affiliation in mammals (see review in Arnold et al. 2010). Therefore, I examine at what age post-conflict affiliation appears in relation to specific developmental stages (e.g., mated pair formation and sexual maturity).
- Does the number of high quality relationships individuals have influence post-conflict affiliation patterns? While the occurrence of post-conflict affiliation appears dependent on the presence of high quality relationships, it is not known whether the number of high quality relationships influences the use of particular post-conflict affiliative strategies. This study will allow an investigation of this question because the subjects were observed after pair formation had occurred, therefore they had only one high quality relationship, that with their mate. This is in contrast to the mammals and sub-adult ravens studied to date that have more than one high quality relationship. While the species in this study had already formed pairs by the time I began my research, two of these species (rooks and jackdaws) do have a stage before pair formation in which bonds are formed with multiple individuals (de Kort et al. 2006, Emery et al. 2007, von Bayern et al. 2007). This stage may influence post-conflict affiliation differently than in the older individuals, however investigation was beyond the scope of this study.

THESIS STRUCTURE

The purpose of this thesis is to examine post-conflict affiliation in three species of corvid to enhance our understanding of how sociality influences this behaviour, how it develops as individuals grow from juveniles to adults, and what the potential functions might be. In chapter 2, I discuss my study species in light of their natural history and their similarities and differences in social behaviour to provide information about how these species vary and how this variation is predicted to affect post-conflict affiliation behaviour. This data was collected over a three-year period to compliment the post-conflict affiliation data and provide background information on the study subjects, including identifying mated pairs and when these partnerships developed, and how the dominance interactions and hierarchies changed over time. I emphasise differences in their rates of affiliation and aggression, particularly regarding their mates, and provide information about conflict patterns that will inform the rest of this thesis.

Chapter 3 presents data from a three-year study of post-conflict affiliation in three corvids that vary in their levels of sociality. This data allows me to compare among the species regarding how their variation in social behaviour impacted post-conflict affiliation. This study began when subjects were juveniles (age one) and ended after they had become sexually mature adults (age three), which lets me examine when post-conflict affiliation behaviour appears in each species, which I address in chapter 4.

In chapter 5, I explore two functions of post-conflict affiliative behaviour. First, I conduct additional analyses on the data from chapter 3 to determine whether one of the functions of post-conflict affiliation is to reduce aggression. I investigate whether aggressors or victims experience different rates of aggression after conflicts, who initiates the aggression, and if affiliation reduces the likelihood of further aggression. Second, I examine whether post-conflict affiliation functions to reduce the stress induced by the conflict by determining whether affiliation frequencies differ after conflicts of high or low intensity.

After increasing the number of bird species in which post-conflict affiliation behaviour has been studied by 100%, I address the impact of my research to the field of post-

conflict affiliation in chapter 6. Consequently, I developed a hypothesis to explain broad patterns in post-conflict affiliation across taxa for which I created a model to test the quantitative validity of my ideas.

Finally, I discuss my key findings in the context of future directions for the field of post-conflict affiliation in chapter 7. I consider two new methods for studying post-conflict affiliation: one that was proposed by Radford (2008) and one that I developed which incorporates two additional measures into post-conflict affiliation analyses. I conclude with a broad summary of the main results in this thesis.

CHAPTER 2: The social lives of three corvids*

*Note: part of this chapter has been submitted for publication as:

Logan CJ, Emery NJ, Clayton NS. (*Submitted*). Testing alternative behavioral measures of post-conflict affiliation. *Behavioral Ecology*.

ABSTRACT

Rooks, jackdaws, and Eurasian jays are a good model system for comparative research because of their range of social systems, which will allow me to determine the influence of sociality on post-conflict affiliation. I examined the social behaviour of the subjects in this study to compare rates of affiliative and aggressive behaviour as well as dominance patterns and, in particular, the relationship with the mate. I also compared conflict rates and examined sex differences and seasonality. I found that rook and jackdaw mates stayed together year-round and were almost always monogamous. Jays were monogamous for shorter time periods and primarily affiliated with their mate during the breeding season. All three species had linear dominance hierarchies, but there was variation in hierarchy fluidity (the number of rank changes over time) with jackdaws being the most fluid and jays the least. All three species affiliated mostly with their mates, but rooks and jackdaws had much stronger pair-bonds than jays. Rooks had the highest frequency of aggression, and rooks and jays dispersed aggression across many dyads while jackdaws had particular enemies. Aggression rarely, if ever, occurred between mates. Conflict rates were higher in rooks and jackdaws than in jays, involved more males in jackdaws and jays, and were primarily over unknown causes (likely dominance relations), food, and nest material. Conflicts were fought between individuals regardless of rank distances, and occurred more during the pre-breeding season (all species) and the breeding season (rooks). I predict that variance in social behaviour will influence post-conflict affiliation: the weak partner bonds and lack of conflicts in jays should result in no post-conflict affiliative behaviour, and rooks and jackdaws should have post-conflict affiliation because they have strong partner bonds and many conflicts with other group members.

INTRODUCTION

Rooks (*Corvus frugilegus*), jackdaws (*C. monedula*), and Eurasian jays (*Garrulus glandarius*; hereafter ‘jays’) are common corvids in the United Kingdom. They are members of the bird family Corvidae, which includes more than 110 adaptable and successful species including the jays, ravens, crows, and magpies, which are distributed nearly worldwide (Snow & Perrins 1998). They tend to be foraging generalists, having many different foraging techniques (innovations), and are long-lived with part of their developmental period spent with their parents (Snow & Perrins 1998, Emery et al. 2007). These features indicate that learning may be important and profitable because their long-life spans allow ample opportunity to use the acquired information.

Corvids, with their large brains and high rates of innovation, are one of the most likely non-human taxonomic groups to exhibit complex cognition (Emery & Clayton 2004, Clayton & Emery 2005). Innovation rates are positively correlated with relative brain size (the ratio of brain weight to body weight; Lefebvre et al. 2002, Lefebvre et al. 2004, Overington et al. 2009), and *Corvus* is the most innovative genus in North America (Lefebvre & Sol 2008). Indeed, there is evidence of advanced cognitive capabilities in many corvids: western scrub jays can remember a past event to plan for the future (Raby et al. 2007) and their thieving is sensitive to who is watching (Dally et al. 2005); rooks and New Caledonian crows drop stones into water to raise the level to reach a food reward (Bird & Emery 2009b, Taylor & Gray 2009) and they manufacture and use hook tools to pull food out of cavities (Hunt 1996, Bird & Emery 2009a).

Why study post-conflict affiliation in corvids?

Only two bird species have been studied in the context of intra-group post-conflict affiliation and both are corvids (rooks: Seed et al. 2007, ravens: Fraser & Bugnyar 2010 & 2011; a special case of inter-group post-conflict affiliation in birds will be discussed later), while post-conflict affiliation behaviour has been studied in many mammals. Mammals tend to make amends with former opponents after fights (former opponent affiliation) as well as sometimes affiliating with a bystander (third-party affiliation; see review in Arnold et al. 2010). However, the recent studies on corvids are showing

different post-conflict affiliation patterns: they use only (rooks) or mostly (ravens) third-party affiliation. Seed and colleagues (2007) suggested that patterns may differ because of the differing number of valuable relationships between mammals and birds. Mammals tend to form many social bonds while corvids usually form only one social bond: that with their mate. Studying post-conflict affiliation in corvids is facilitating our understanding of how variance in social structure, namely the number of valuable relationships, promotes post-conflict former opponent affiliation, third-party affiliation, or both.

Corvids exhibit a range of social structures, making them amenable to a comparative study on how sociality influences a particular behaviour. I chose to replicate and expand the post-conflict affiliation study on rooks (Seed et al. 2007), and to study a new species of corvid, jackdaws, because of their similar social structure to rooks to determine if the peculiar post-conflict affiliation findings are unique to rooks or if they are due to the particular type of social system. I also chose to study jays which are not social outside of the breeding season (Snow & Perrins 1998) to determine whether post-conflict affiliation is restricted to social species. All three species form bonds with their mate, which is by far their strongest social bond (Röell 1978, Snow & Perrins 1998). Comparing these species allows for a straightforward investigation of the influences of sociality on post-conflict affiliation and provides an excellent system in which to begin examining the function of this behaviour in birds.

Natural history

Rooks

Living in the greater Europe-Asia area (as far south as Iran, as far as east as Japan, with southern Norway and Sweden at the northern edge, and the UK to the west of their range), and primarily in agricultural regions, rooks forage by digging into the ground with their bills to access invertebrates (Coombs 1978). They also eat plants (including cereal crops) and vertebrates (Snow & Perrins 1998). A highly gregarious species, rooks are famous for their rookeries: places where sometimes thousands of birds converge to roost in treetops (Coombs 1978, Cocker 2007), often in association with jackdaws (Coombs 1960). Rooks are socially, but not genetically, monogamous since males (often

the more dominant older males) sneak copulations with already-mated neighbouring females (Røskaft 1983). Mated pairs remain in close contact year-round, quite possibly for many years at a time, young are dependent on their parents for food for the first 4 months of life, and wild rooks can live up to 22 years of age (Coombs 1978, Goodwin 1986, Fransson et al. 2010). Territoriality is restricted to the area around the nest site during the breeding season, however nest-defence behaviours rarely escalate into fights (Coombs 1960). Males are the primary nest builders, making them out of twigs, bark, leaves and other materials, which are set on top of tree branches (Coombs 1960). Females lay on nests and brood nestlings, while males stand guard and provision the female during incubation and then provision the female and nestlings once the eggs hatch (Coombs 1960).

Jackdaws

Gregarious jackdaws range across the greater European area, extending as far south as Morocco, to the north into Norway, Sweden and Finland, with the UK at the western edge and western China on the eastern edge of their range (Coombs 1978). Though they often forage with rooks (Coombs 1960), jackdaws occupy a different foraging niche. They feed on grain in open areas with rooks, but instead of digging in the ground for worms, they eat insects and seeds above ground (Coombs 1978). They also forage in tree canopies for larvae during the nesting season (Coombs 1978). Jackdaws are highly genetically monogamous: one study found no extra-pair copulations in a colony with a high density of nests (Henderson 2000). Mated partners stay in close contact year-round for many years at a time, young are dependent on parents for 2 months after hatching, and wild jackdaws can live to 19 years of age (Röell 1978). Their territoriality centres around the nest site and fights are a common defence behaviour (Röell 1978). Jackdaws of both sexes build nests inside existing cavities (e.g., tree holes and chimneys) using sticks and soft fibres (Röell 1978). Males provision the female and young (Coombs 1978).

Eurasian jays

Jays live in forest canopies (particularly in oak forests) across Europe and Asia in a similar range as the rooks, but extending farther south to Morocco (Goodwin 1986,

Coombs 1978). They eat primarily acorns as well as other nuts, insects, and fruit from trees, shrubs, and on the ground (Goodwin 1986). Not much is known about wild jay behaviour because they flee from human observers and live in dense forests, however, in terms of their sociality, mated pairs are seen together from a couple of months before incubation, which occurs in March, through the end of summer or early autumn (Goodwin 1951). While it is stated that breeding pairs remain together on their territory year-round (Goodwin 1986), I can find no evidence of this. Jays are known to live up to 17 years of age in captivity (Carey & Judge 2000). Unlike rooks and jackdaws who are almost always in close contact with their partners, jay partners rarely come within a metre of each other (Goodwin 1986). There are annual social events called ‘spring gatherings’ involving many vocalising jays displaying at each other, which may function as a way for unpaired jays to find mates (Goodwin 1951). Young are dependent on parents for 2 months (Goodwin 1951). Jays are thought to maintain territories which are defended except during the winter when territorial behaviour is less intense (Coombs 1978, Bossema 1979), however there is no actual evidence for this. Nests are made out of sticks and roots and placed in trees at forks (Goodwin 1956). Males provision females during incubation, and then they provision the female and young during the nestling stage (Goodwin 1951, 1956).

A comparative study on the social behaviour of rooks, jackdaws, and jays

To determine how variance in social behaviour influences post-conflict affiliation in the subjects in this thesis, I collected detailed information about their social interactions across the same three-year period as the post-conflict affiliation study. The objectives of this study are to examine differences in the amounts of affiliation and aggression, compare dominance and conflict patterns, determine whether mates are monogamous, and investigate how the social bond with the mate differs from bonds with other group members.

METHODS

Study site

I observed 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) 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 (17 x 9 x 3m) and jays in an adjacent aviary (17 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 which 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. While sexing of the birds could be carried out partially through behavioural observations, it was important to sex the birds using genetic methods to confirm behavioural sexing for paired birds and to determine sexes for those individuals that did not find mates and thus did not show breeding behaviour (many of the jays and rooks and some of the jackdaws). Two jays (Rome and Caracus) had been previously sexed by DNA from their blood (0.15 ml taken from the ulnar vein) for animal management purposes by Greendale Veterinary Diagnostics Limited (www.greendale.co.uk) in December 2008 (pressure was applied to the vein afterward to avoid haematoma formation, and birds were monitored carefully afterward for signs of bleeding/haematoma). All other birds were sexed by DNA from breast feathers (three to four feathers per bird) by Avian Biotech International (www.avianbiotech.com) in May and June 2011. Breast feathers were chosen over wing or tail feathers because Avian Biotech International specifically requested these for the DNA analysis. Feather pulling was conducted by a veterinarian and in accordance with the Home Office licence for the jays and for animal welfare reasons for the rooks and jackdaws (knowing the sex of the birds allows technicians to separate birds appropriately during the breeding season if problems between certain individuals arise). Birds were hatched in March-May 2007, caught in the wild as nestlings, and hand-raised under a Natural England permit. Jays were included on the Home Office Project Licence (80/1975) and rooks and jackdaws were kept under a University of Cambridge non-regulated

procedures licence. Upon conclusion of this study, all subjects remained in the aviaries for further study by other researchers.

Data collection

Baseline data on social behaviour were collected to determine dominance hierarchies and mated pairs. All behaviours in the ethogram (Table 2.1) were recorded *ad libitum* (Altmann 1974) during observation sessions between 10:00 and 17:00 hours from 1 November 2008 through 5 April 2011 by Corina Logan in collaboration with Ljerka Ostojic and Gabrielle Davidson (data collection effort was distributed 77%, 16%, and 6%, respectively). Social behaviours (affiliation and aggression) were prioritised over other behaviours if multiple types occurred simultaneously.

We observed the birds for 324 hours in total. However, I chose 16 random hours per season 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).

Data analysis

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 behaviours were recorded, particular attention was given to affiliative and aggressive interactions: if these interactions were observed, they were recorded with priority over other behaviours that might be happening at the same time. Proximity measures were coded using the nearest neighbour. Dominance hierarchies were determined for each species according to the number of aggressive interactions an individual initiated or received (Martin & Bateson 2007). 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 MatMan 1.1.

Table 2.1. Ethogram used to identify and record behaviour for rooks (R), jackdaws (JD), and jays (J).

Category	Behaviour	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 sitting	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 within one body length of each other, but more than 5 cm apart. 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 pulling	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 displacement	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

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, I inferred that those birds that could be housed together and those that shared food with each other were partners (only partners are tolerated for both of these activities).

To determine relative pair-bond strengths among the three species, sociograms (diagrams indicating the amount of affiliation or aggression exchanged between individuals) were created based on the frequency of all affiliative and aggressive interactions (including bidirectional and unidirectional behaviours) between all dyads in the group at ages one, two, and three. Sociograms were made using UCINET V6.216 (Borgatti et al. 2002) and NetDraw V2.084 (Borgatti 2002). Species were set to the same scale to make them comparable: maximum line widths were set according to the individual with the highest frequency of interactions (aggressive or affiliative) in each species and at each age. If the highest frequency of interactions was below 100, then the maximum line width was set at 1; for frequencies in the 100s, the maximum line width was 2; for 200s the line width was 3; 300s was 4; and 400s was 5.

Conflicts and seasonality

Seasonality was determined as follows: off season preceded the jay pair-formation stage (pre-breeding season) when little or no affiliative interactions took place (rooks and jackdaws engage in affiliative behaviours year-round, thus never have an off season); pre-breeding season occurred when active food sharing was consistently observed; and breeding season was determined as the time at which birds actively interacted with introduced nesting material (sticks and soft material), nesting platforms (rooks), and nest boxes (jackdaws), or when the jays needed to be separated due to increased aggression (Table 2.2).

Table 2.2. The study period was divided into distinct seasons, which included the first breeding season for all three species of birds.

Season	Age	Rooks	Jackdaws	Jays
Off 1	1	-	-	5 Nov 2008-9 Mar 2009
Pre-breeding 1	1	1 Nov 2008-23 Feb 2009	1 Nov 2008-23 Feb 2009	10 Mar-26 Apr 2009
Breeding 1	2	24 Feb-17 May 2009	24 Feb-17 May 2009	27 Apr-1 Jun 2009
Off 2	2	-	-	17 Jun 2009-1 Feb 2010
Pre-breeding 2	2	18 May 2009-25 Feb 2010	18 May 2009-23 Mar 2010	2 Feb-12 Apr 2010
Breeding 2	3	26 Feb-31 May 2010	24 Mar-31 May 2010	13 Apr-29 Jun 2010
Pre-breeding 3	3	1 Jun 2010-20 Feb 2011	1 Jun 2010-20 Feb 2011	30 Jun 2010-23 Mar 2011
Breeding 3	4	21 Feb-May 2011	21 Feb-May 2011	24 Mar 2011

RESULTS

Timing and stability of pairing with mates

Most individuals from all three of the species developed a pair-bond during the first year (Table 2.3; rooks: 4 pairs out of 13 birds, 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 less so. This indicates that rooks and jackdaws are monogamous, and that there may be some level of monogamy in the jays who affiliate with their mate mostly during the breeding season and often re-pair with the same individual every year.

Dominance hierarchies

There was a significant linear dominance hierarchy within each species for each year and when all years were combined (Table 2.3; Landau's linearity index for all years combined: rooks $h=0.88$, $N=13$, $P=0.0001$; jackdaws $h=0.62$, $N=14$, $P=0.0001$; jays $h=0.93$, $N=9$, $P=0.0001$). 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.

Table 2.3. Dominance rank and mated partner for all individuals in this study by year and from all years combined (overall). - = unpaired, N/A = subject died.

Subject	Sex	Overall		Age 1		Age 2		Age 3	
				Partner	Rank	Partner	Rank	Partner	Rank
		No. Conflicts	Rank						
Rooks									
Cassandra	Female	6	1	Leonidis	2	Leonidis	2	Leonidis	1
Arthur	Male	10	2	Hector	1	Hector	4	Hector	3
Beowulf	Male	19	3	Remus	3	Remus	1	Remus	4
Leonidis	Male	10	4	Cassandra	5	Cassandra	3	Cassandra	2
Hector	Female	6	5	Arthur	4	Arthur	8	Arthur	5
Remus	Female	6	6	Beowulf	6	Beowulf	5	Beowulf	7
Zara	Female	8	7	-	7	Merlin	7	Merlin	9
Chasca	Female	7	8	-	8	-	9	-	10
Thierry	Female	5	9	-	12	-	11	-	6
Merlin	Female	9	10	-	11	Zara	6	Zara	12
Romulus	Female	7	11	-	9	-	12	-	11
Ticci	Female	7	12	-	10	-	10	-	13
Loki	Female	8	13	-	13	-	13	-	8
Jackdaws									
Celli	Male	11	1	Claude	1	Claude	3	Claude	1
Munch	Male	12	2	Picasso	7	Picasso	1	Picasso	7
Raffa	Male	13	3	Dom	2	Dom	4	Dom	6
Will	Male	10	4	Pedro	8	Pedro	2	Pedro	4
Claude	Female	6	5	Celli	3	Celli	9	Celli	2
Dom	Female	5	6	Raffa	6	Raffa	5	Raffa	5
Escher	Male	9	7	-	14	Vasco	10	-	3
Jo	Male	6	8	-	5	-	11	N/A	N/A
Ivo	Female	7	9	Gaudi	10	Gaudi	12	Gaudi	9
Gaudi	Male	8	10	Ivo	4	Ivo	7	Ivo	11
Picasso	Female	7	11	Munch	13	Munch	6	Munch	8
Pedro	Female	5	12	Will	11	Will	8	Will	10
Dali	Female	7	13	-	9	-	14	Vasco	13
Vasco	Male	10	14	-	12	Escher	13	Dali	12
Jays									
Lisbon	Male	2	1	Rome	1	Rome	1	Rome	1
Rome	Female	3	2	Lisbon	2	Lisbon	2	Lisbon	2
Caracus	Male	1	3	Wellington	3	Wellington	3	Wellington	4
Tripoli	Female	-	4	-	4	N/A	N/A	N/A	N/A
Lima	Male	3	5	Quito	5	Quito	5	Jerusalem	3
Dublin	Male	3	6	Jerusalem	6	Jerusalem	4	Quito	5
Wellington	Female	2	7	Caracus	7	Caracus	6	Caracus	6
Jerusalem	Female	-	8	Dublin	8	Dublin	7	Lima	8
Washington	Female	3	9	-	9	-	8	-	7
Quito	Female	1	10	Lima	10	Lima	9	Dublin	9

Sociality influences affiliation

Compared to the rooks (Figure 2.1, A-C), jackdaws had slightly weaker pair-bond strengths (Figure 2.1, D-F), and the jays had almost non-existent pair-bonds compared to rooks and jackdaws (Figure 2.1, G-I). In all three species, the bonds between mates were much stronger than the bonds with others (Figure 2.1). 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. Overall,

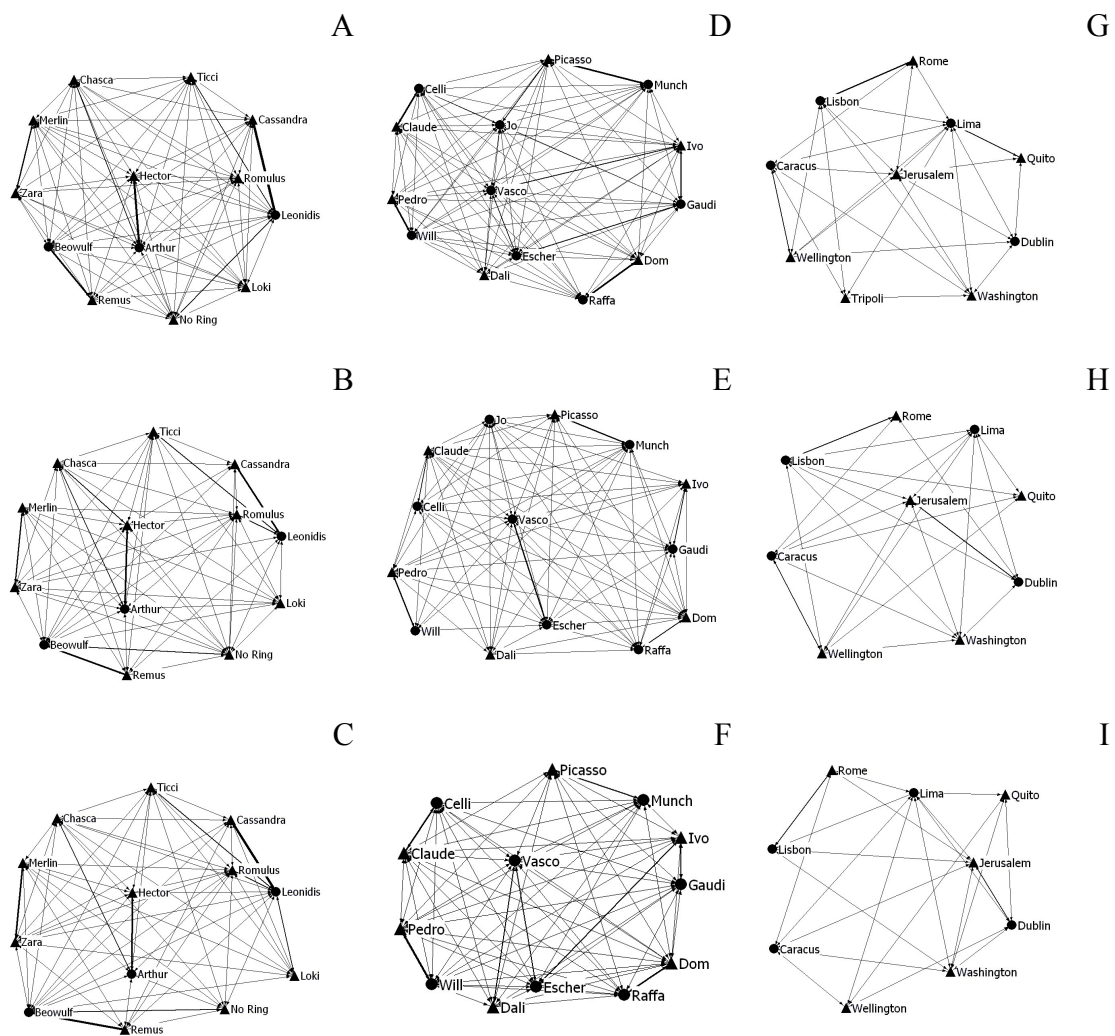


Figure 2.1. Sociograms showing the frequency of affiliative exchanges among the rooks (A-C), jackdaws (D-F), and jays (G-I) in this study at ages 1 (A, D, G), 2 (B, E, H), and 3 (C, F, I). Range of the frequency of interactions per dyad: A=62-480, B=43-259, C=58-451, D=101-246, E=65-189, F=99-237, G=4-164, H=5-92, I=9-25. Triangles=females, circles=males.

the total frequency of affiliation per bird across all years was similar for rooks and jackdaws (data were normal according to the Anderson-Darling normality test; t-test: $t=-1.26$, $df=15$, $p=0.23$, 95% confidence interval= $-298.71-76.89$), and significantly less for jays when compared with jackdaws ($t=9.16$, $df=21$, $p=0.000000008$, 95% confidence interval= $261.31-414.61$) who had less affiliation than rooks, thus the difference also applies to rooks and jays.

Sociality influences aggression

Rooks (Figure 2.2, A-C) had a higher total frequency of aggression per bird than jackdaws (data were not normally distributed according to the Anderson Darling normality test; Mann Whitney U test: $W=27.5$, $N=13$ rooks, $N=14$ jackdaws, $p=0.002$, 95% confidence interval= $-90.00-(-21.00)$) and similar frequencies as jays ($W=52$, $N=13$ rooks, $N=9$ jays, $p=0.44$, 95% confidence interval= $-89.00-45.00$), while jackdaw (Figure 2.2, D-F) and jay (Figure 2.2, G-I) aggression frequencies were similar to each other ($W=46$, $N=14$ jackdaws, $N=9$ jays, $p=0.17$, 95% confidence interval= $-98.00-7.00$). The pattern of aggressive interactions was much different from affiliation patterns, which occur primarily with one or two individuals. Aggression occurs between many dyads in rooks and jays. In the rooks, aggression occurred more between dominant males and between males and single females who often tried to affiliate with them, particularly during the breeding season. Since many jay dyads had similar amounts of aggression, this may indicate that they are generally less tolerant. There was aggression between many jackdaws at age one, but at ages two and three there were only one or two dyads that were particularly aggressive and these involved males defending their nest sites. Mates rarely or never exchanged aggression in all three species.

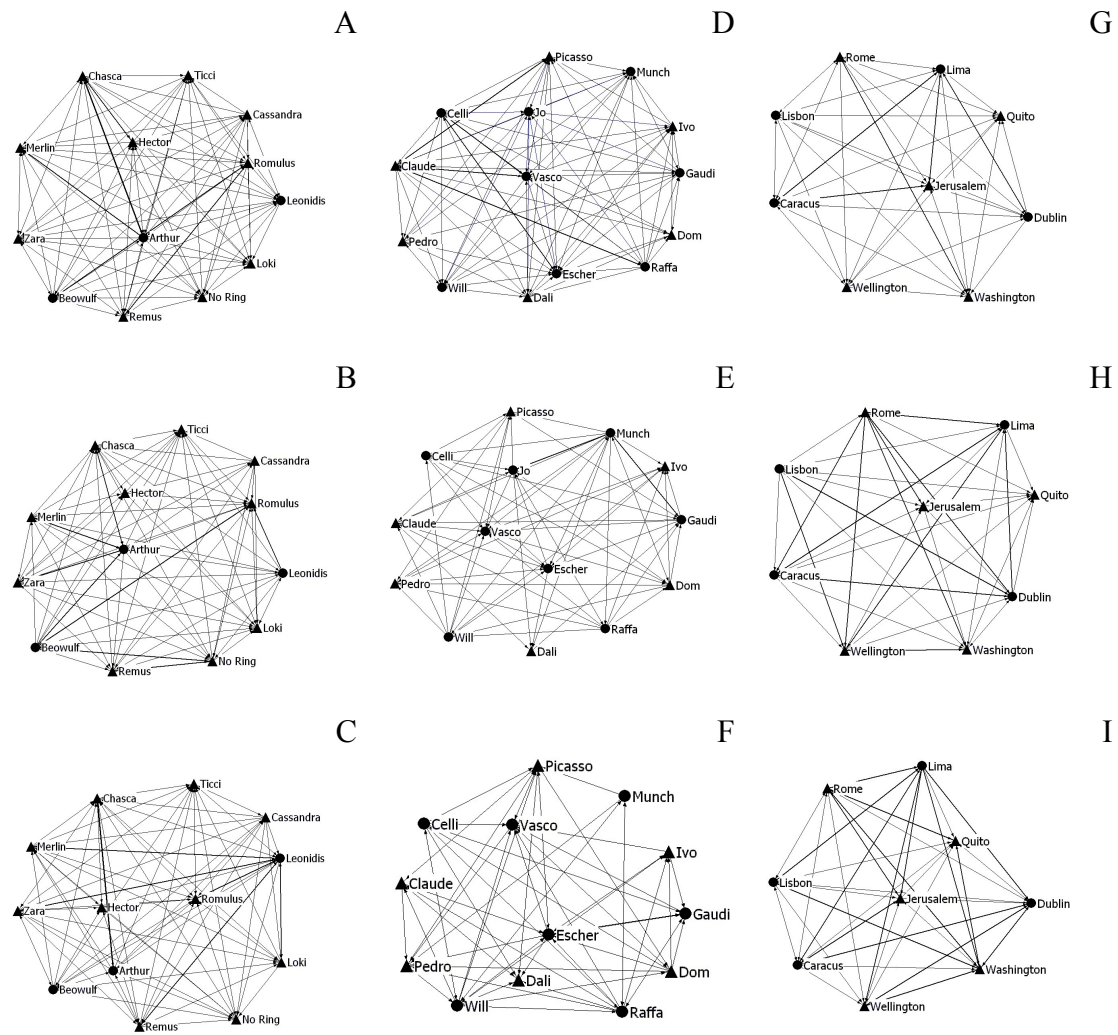


Figure 2.2. Sociograms showing the frequency of aggressive exchanges among the rooks (A-C), jackdaws (D-F), and jays (G-I) in this study at ages 1 (A, D, G), 2 (B, E, H), and 3 (C, F, I). Range of the frequency of interactions per dyad: A=3-149, B=4-56, C=9-130, D=3-32, E=1-57, F=0-55, G=2-82, H=0-52, I=3-52. Triangles=females, circles=males.

Sociality influences conflicts

Since jays are territorial and widely dispersed in the wild, I presumed their wild conflict rates would be very low. However, I expected that by exposing them to an artificially social environment in the aviary, they would either maintain low conflict rates by avoiding each other, or experience increased conflict rates through territory defense within the aviary. I found that jays had significantly lower conflict rates per bird than rooks (data were normal according to the Anderson Darling normality test; t-test: $t=-3.25$, $df=18$, $p=0.004$, 95% confidence interval= $-0.000007-(-0.000002)$) and

jackdaws ($t=3.12$, $df=21$, $p=0.005$, 95% confidence interval=0.000001-0.000007); and rooks and jackdaws had similar conflict rates ($t=-0.40$, $df=24$, $p=0.69$, 95% confidence interval=-0.000004-0.000003; Figure 2.3). Data for jays come from the non-breeding season because breeding season conflict intensities increased to an injurious level and birds had to be separated for ethical reasons. Therefore, the artificial social setting in the aviary appeared to result in low conflict rates outside of the territorial breeding season.

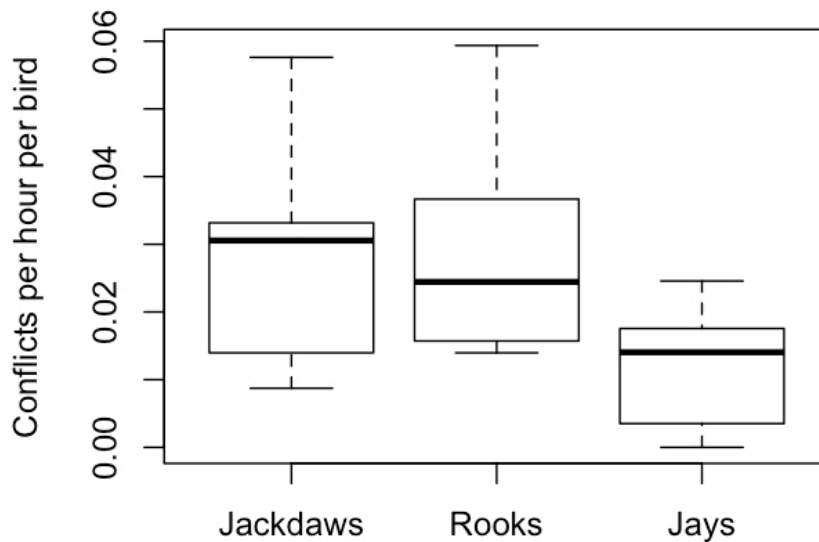


Figure 2.3. Comparison of conflict rates across species.

Conflicts were primarily over unknown causes, which I assume involved dominance relationships, however there was no objective way to code fights over dominance thus I left this category as unknown (Figure 2.4). The other most common sources of conflict were food (for all three species) and nest material (for rooks and jackdaws).

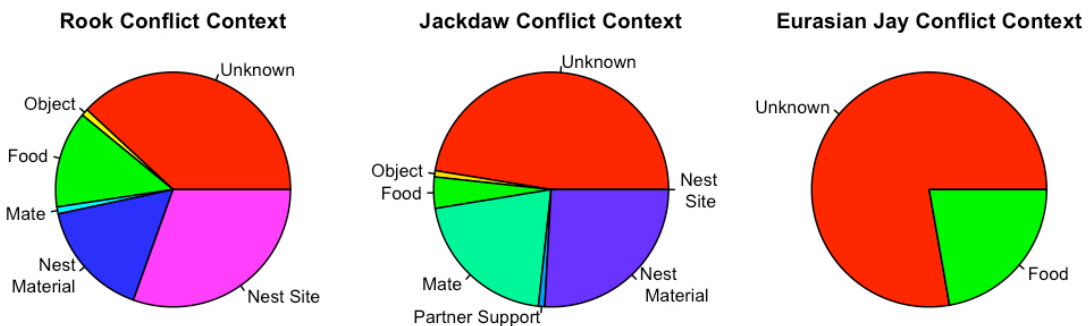


Figure 2.4. Breakdown of the context in which conflicts occurred for rooks, jackdaws, and jays.

Males primarily engaged in conflicts, except in rooks, but this was likely because there were 10 females to only 3 males thus increasing the probability of female involvement in fights such that it could mask natural behaviour if sex ratios were matched (Figure 2.5).

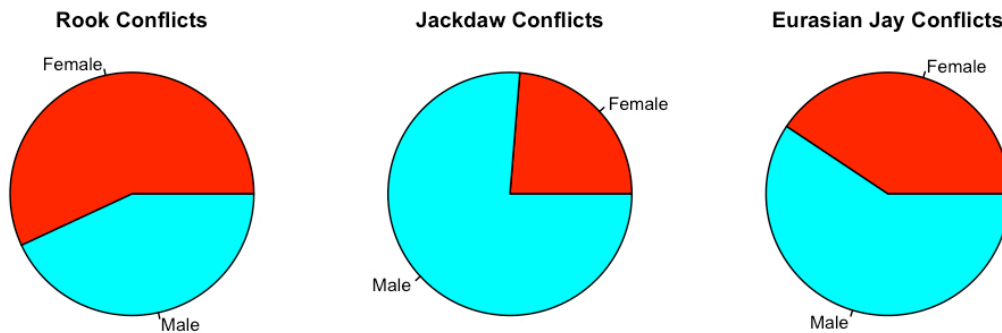


Figure 2.5. Examining sex differences in conflict participation for rooks, jackdaws, and jays.

Anecdotally, it appeared that higher ranking individuals fought more with each other than with lower ranks in rooks and jackdaws. Therefore, I expected a positive correlation between ranks of aggressors and victims. There was a trend toward this prediction in rooks (Spearman's Rank Correlation Coefficient: $\rho=0.18$, $N=13$ birds, $p=0.07$) and jackdaws (Pearson's Product Moment Correlation: $r=-0.19$, $N=14$ birds, $p=0.06$), but no correlation between dominance ranks when examining aggressor rank versus victim rank in jays (Spearman's Rank Correlation Coefficient: $\rho=0.29$, $N=9$ birds, $p=0.24$).

Conflicts and seasonality

Conflicts were differentially distributed throughout the year with most conflicts occurring during the pre-breeding season for all three species, and also during the breeding season for rooks (Table 2.4). Rooks and jackdaws had many more conflicts than jays, indicating that jays tend to avoid conflict outside of the breeding season when their territoriality is not as pronounced.

Table 2.4 Conflicts per species and season.

Species	Total conflicts	Conflicts per season			Average conflicts per subject
		Off	Pre-Breeding	Breeding	
Rooks	108	-	PB1=18 PB2=23 PB3=7	B1=21 B2=11 B3=28	8
Jackdaws	116	-	PB1=13 PB2=26 PB3=41	B1=14 B2=14 B3=8	8
Jays	18	O1=7 O2=0 O3=0	PB1=4 PB2=4 PB3=1	-	2

DISCUSSION

There were clear differences in social behaviour among the species in this study (see Table 2.5 for an overview). Consistent with previous research on their natural history, rooks and jackdaws were more similar to each other, being gregarious and in close contact with their mate year-round, while jays were much less affiliative, often not showing a strong pair-bond outside of the breeding season. Rooks and jackdaws kept the same mates throughout the study, with only one or two partner changes in jackdaws, therefore they exhibit a high degree of social monogamy. The jays showed monogamy over the short-term, with half the pairs remaining together over the course of the study. This was particularly interesting in the jays because they did not often affiliate with their mate unless it was the breeding season, however, they often reunited with the same individual each breeding season.

Table 2.5. Comparison of social behaviour among rooks, jackdaws, and jays.

Species	Sociality	Socially Mono-gamous?	Affil-iation Frequency	Agg-ression Fre-quency	Conflict Rate	Linear Dominance Hierarchy?	Dominance Rank Changes?
Rook	High	Yes	High	High	High	Yes	Few
Jackdaw	High	Yes	High	Medium	High	Yes	Some
Jay	Low	Yes	Low	Medium	Low	Yes	Rare

Sociality influenced affiliation rates, with rooks having the highest exchange of affiliation, jackdaws slightly less, and jays had much less as was expected due to their less social nature. Higher frequencies of affiliation were expected for rooks and jackdaws since they live in groups and therefore should engage in one of the benefits of sociality (social support) to offset some of the costs associated with sociality (chapter 1). Specifically, social life affords the opportunity to form alliances with others to acquire resources. The bond between mated pairs is an example of a social bond that can form such alliances, and this bond was apparent in all three species in this study.

Pair bond strengths differed in a similar way as affiliation rates: pair bonds were by far the strongest affiliative bonds in the group for rooks and jackdaws (jackdaws had slightly weaker pair bonds than rooks), and they were the most obvious bonds for jays, but jay bond strengths were much weaker than those of rooks and jackdaws. While rooks and jackdaws are gregarious species, the partner bond stands out as the main unit within the group. Perhaps because of the extensive amounts of affiliative interactions between partners, they are able to cooperate with each other to solve tasks (Seed et al. 2008). Social rooks cooperate with an affiliate to acquire food by coordinating their efforts of pulling each end of a string to drag a food tray into reach (Seed et al. 2008). In contrast, in the same kind of task, the less social jays, where partners are only weakly bonded, if at all, will not cooperate with a conspecific to solve it, but they will cooperate with a human to gain access to the food (Ostojic & Clayton in prep.). The jays ability to solve the task with a human, rather than with their conspecific partner, shows that they have the capacity to carry out the task but that conspecific social bonds may not be strong enough induce cooperation. Perhaps a strong enough social bond was formed with the familiar human experimenter who exhibited consistent behaviour that usually resulted in a food reward, thus inducing the motivation to cooperate.

The frequency of aggression also differed among species. Rooks had the highest exchange of aggression of all three species, while the jackdaws and jays had similar amounts to each other. Aggression was rarely, and sometimes not at all, exchanged between mates, regardless of the species, indicating the unique quality of this relationship when compared with other relationships in the group. Rooks and jackdaws

had higher conflict rates than the jays who had very few conflicts. The lack of jay conflicts indicates that they avoid each other outside of the breeding season rather than fight to maintain their territory. Their territoriality may decrease outside of the breeding season as well which could cause the lack of aggression, however territoriality was not examined in this study so I cannot determine whether or how aggression and territoriality are related. As predicted, the social species had relatively high conflict rates, likely due to their close contact with many individuals which increases the probability of disagreements over the distribution of resources (chapter 1).

All three species had linear dominance hierarchies that varied in their level of fluidity. Jackdaws were the most fluid, having more rank changes throughout the study than the other two species. Rooks had some fluidity: they had less rank changes than the jackdaws, but there were still some changes in the dominance hierarchy over the course of the study. Jays were less fluid: dominance patterns were relatively stable with almost no rank changes. Perhaps the stability of the jay hierarchy is due to their avoidance of conflicts outside of the breeding season: if no one challenges the hierarchy, then there is no chance to change rank. As well, it could be more dangerous for subordinates to challenge dominants since fights are more often injurious in this species.

I predict that differences in the social behaviour of the three species will influence post-conflict affiliation in the following ways:

1. Jays should have less, if any, post-conflict affiliation due to weak or non-existent pair-bonds outside of the breeding season (when these data were collected).
2. Jays may not have post-conflict affiliation because of the lack of conflicts, which could indicate they usually avoid each other rather than engage in physical contact.
3. Jackdaws and rooks should have post-conflict affiliation because they engage in many conflicts.
4. Jackdaws and rooks should have post-conflict affiliation with their mates because the existence of this high quality relationship could reduce some of the costs of having a high frequency of interactions with other individuals.

CHAPTER 3: How does sociality influence post-conflict affiliation in corvids?*

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ABSTRACT

Many mammals and two species of birds are known to affiliate after conflicts instead of avoid each other. Affiliative contact can occur between the former opponents or between a former opponent and a bystander (or ‘third-party’), and occurs most often between individuals that share a valuable relationship. Post-conflict affiliation is generally analysed using the latency to first affiliative contact, however this method has limitations. Therefore, I explore two different measures of post-conflict affiliation: the frequency and duration of affiliation across each observation session. I compare the results between methods to determine which are most appropriate for corvids. I conduct a comparative study of three corvid species to examine the influence of sociality on post-conflict affiliation using affiliation latencies, frequencies, and durations to examine post-conflict behaviour. I hypothesised that 1) there will be no former opponent affiliation because in these species the most valuable relationship individuals form is with their mate and mates never fight, therefore eliminating the need to repair other relationships when conflicts occur; and 2) colonial rooks and jackdaws will show third-party affiliation with partners, but the less social jays will not due to their lack of a valuable relationship outside of the breeding season when their data were collected. As predicted, the results showed that none of the three species displayed former opponent affiliation. Furthermore, both colonial species showed third-party affiliation with their mates when examining affiliation frequencies and durations, whereas the less social jays showed third-party affiliation with anyone (not just mates) according to the duration of affiliation. Comparing post-conflict affiliation analysis methods, I suggest that this behaviour is best investigated using more than just affiliation latencies, and that the frequency and duration of affiliation may indicate whether affiliation is used to address post-conflict stress for former combatants.

INTRODUCTION

Post-conflict affiliation usually occurs between individuals that share a valuable relationship (one that provides fitness benefits; see review in 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 (Aureli et al. 2002). The use of post-conflict affiliation strategies varies across taxa. Species in which individuals have many stable, and therefore important, relationships use both former opponent and/or third-party affiliation depending on how willing the former opponent is to affiliate and which bystanders are available. Some of the species that use both strategies are humans (Fujisawa et al. 2006), non-human primates (see Das 2000; Koski & Sterck 2007), domestic dogs (Cools et al. 2008), wolves (Cordoni & Palagi 2008; Palagi & Cordoni 2009), horses (Cozzi et al. 2010), and sub-adult ravens (Fraser & Bugnyar 2010; Fraser & Bugnyar 2011). Alternatively, some species have been found to only use former opponent affiliation (brown lemurs: Roeder et al. 2002; red-fronted lemurs: Kappeler 1993; black lemurs: Roeder et al. 2002; ring-tailed lemurs: Rolland & Roeder 2000; rhesus macaques: Matheson 1999; olive baboons: Castles & Whiten 1998a). However, many studies do not examine whether third-party affiliation occurs, therefore it is unknown how prevalent this behaviour is (goats: Schino 1998; dolphins: Weaver 2003; spotted hyenas: Wahaj et al. 2001; and many primate species: see chapter 6). By contrast, rooks use only third-party affiliation (Seed et al. 2007). It was suggested that this situation might arise because of the limited number of valuable relationships resulting from their long-term monogamous mating strategy (Seed et al. 2007). The rook findings raise the interesting question of whether other corvid species with a similar social structure only show third-party affiliation or whether this is peculiar to rooks.

I investigated the influence of sociality on corvid post-conflict affiliation by studying colonial rooks and jackdaws, which have similar social structures, and the less social Eurasian jays. 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. They argued that these findings are in line with the valuable relationship hypothesis which posits that former

opponents will engage in former opponent affiliation if they have a valuable relationship (van Schaik & Aureli 2000, Aureli et al. 2002). If the valuable relationship hypothesis is extended to include third-party affiliation, then this hypothesis applies to rooks as well: the most important relationship rooks form is with their long-term mate and, since mates never fight with each other, the need to repair this relationship is eliminated. When one partner fights with another group member, this relationship may not be important enough to repair through former opponent affiliation or the conflict may not have damaged the relationship. Based on previous findings by Seed and colleagues (2007) on rooks, I hypothesised that there would be no former opponent affiliation in any of my species because they all form monogamous pair bonds which are the core units in the group (hypothesis 1; note that this is only true for jays during the breeding season; Goodwin 1951; Röell 1978; Goodwin 1986; Snow & Perrins 1998; Emery et al. 2007; chapter 2).

Furthermore, I hypothesised that jackdaws, which live in colonies and have a similar social structure to rooks, would also demonstrate third-party affiliation with their mates (hypothesis 2). Territorial jays, in contrast, were expected not to show any signs of post-conflict affiliation outside of the breeding season when this study was conducted because partners only affiliate with each other during the breeding season (chapter 1). Their lack of a valuable partner to go to after a fight outside of the breeding season would eliminate the option of having post-conflict third-party affiliation. While post-conflict affiliation is predicted to only occur in social species (Aureli et al. 2002), this prediction has not explicitly been tested in a species lacking sociality such as the jays. Therefore, this will be an investigation of the post-conflict affiliative behaviour in the least social species studied so far.

If jackdaws and jays behave as predicted, then these results would support the hypothesis that the differential use of post-conflict affiliative strategies between these corvids and the other species studied so far is due to the difference in social structure: having one main valuable relationship rather than many in the case of the rooks and jackdaws, or no valuable relationships as with the jays. Although another corvid, the raven, was found to use both former opponent affiliation and third-party affiliation, the

individuals under study were sub-adults which form several important bonds with group members before they pair as adults (Fraser & Bugnyar 2011). Adult ravens form a similar social structure to that of rooks and jackdaws and it would be expected that adult ravens would show only third-party affiliation as do the rooks.

An additional aim of this study is 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 timing of the first affiliative interaction in matched controls. If the first affiliative behaviour occurs sooner after conflicts than in matched controls then post-conflict affiliation is thought to occur (de Waal & Yoshihara 1983). However, there are a number of reasons to look beyond the first affiliative contact to all of the data in the observation sessions to understand the broader pattern of post-conflict affiliation. For instance, some species might be aggressive just after conflicts, delaying their time to first affiliative contact such that it occurs later than in the matched control, thus appearing as if they did not show post-conflict affiliation. In this case, there exists a possibility that they used affiliation after aggression subsided. 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 if using analysis methods involving only the first affiliative contact.

An alternative method for analysing post-conflict affiliation data is to examine the frequency of affiliation after conflicts versus the frequency in matched controls. One might expect the frequency of affiliation to increase after conflicts if conflicts are stressful. Stress has been shown to positively correlate with an increase in activity levels in great tits (Carere et al. 2003). If conflicts increase stress, then the frequency of affiliation and other behaviours should also increase after conflicts in response to the stress. If the frequency of affiliation increases more than other behaviours then the subjects could be using affiliation as way to reduce the stress induced by the conflict. Additionally, the duration of affiliation may play a role in post-conflict affiliative behaviour: if affiliative events last longer after conflicts than in matched controls, perhaps the subjects are using the extended contact to reduce stress. If the frequency of

affiliation increases, but duration decreases after conflicts relative to matched controls, then the conflict will have increased activity levels and it will be important to determine if affiliation is the preferred activity (which would allow the possibility for it to reduce stress) or if activity in general increased (which would not be an indicator 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 which lends more support to the hypothesis that affiliation functions to reduce stress (though it would not be a direct test of this hypothesis). I will explore alternative measures for analysing post-conflict affiliation using the frequency and duration of affiliation.

METHODS

Study site

See chapter 2 for details.

Data collection

I collected data from 1 November 2008 to 22 April 2011 between 09:30 and 17:15 from observation huts next to the aviaries using the Post-Conflict-Matched Control (PC-MC) method (de Waal & 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 rooks, 116 jackdaws, and 18 jays). 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 could be injurious) 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 hurt 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, a 10-minute post-conflict (PC) observation session began in which either the victim or aggressor was the focal subject and all behaviours were recorded as well as who initiated and terminated each interaction (Altmann 1974). Observations were equalised between victims and aggressors while those individuals least represented were prioritised to ensure at least five PC-MC pairs per subject. 10-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 behaviour 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 baseline stress levels for comparison with the PC that was assumed to involve elevated stress levels due to the conflict.

Data analysis

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 data (the proportion of attracted versus dispersed PC-MC sessions, 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 data for consistency and comparability.

Aggressors and victims of conflicts were classified as such according to the initiator of the fight (aggressors were the initiators). In some cases, I was 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, I relied on information regarding the outcome of the fight (winner or loser) to assign the role of aggressor or victim. 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: $X^2_3=14.6$, $P=0.002$; jays: $X^2_3=7.3$, $P=0.06$). 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).

Corrected conciliatory 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 behaviour occurred sooner in the PC than the MC, 'dispersed' if affiliative behaviour occurred sooner in the MC than the PC, and 'neutral' if no affiliative behaviour 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 (attracted+dispersed+neutral). 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).

Selective attraction

Wilcoxon signed rank tests were used to determine whether the proportion of attracted PC-MC pairs was higher than the proportion of dispersed PC-MC pairs (selective attraction) for active affiliation, passive affiliation, and all affiliation (active and passive combined). Selective attraction indicates a shorter latency to first affiliation after fights than in matched controls. 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. The response variable was the proportion of attracted PC-MC pairs, and the explanatory variables were 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). Subject was considered a random factor because observations from the same individual could be correlated. Aside from affiliation type and subject, 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 base model (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 factors included in the test model. The most parsimonious model (model of best fit) was selected according to the lowest AIC value (Akaike 1981). Jay models were GLMs and not GLMMs because only the ‘all affiliation’ category was analysed due to the small sample size, thus only one data point occurred per individual, eliminating the ability to run subject as a random factor.

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 according to the lowest AIC value (Akaike 1981). Using the GLMMs, I examined the influence of the following explanatory variables on the frequency of affiliation (the response variable which was

continuous): 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 included as a random factor and 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 increased or specifically affiliation, aggression rates were analysed for comparison using paired t-tests on aggression frequencies per bird in PCs versus MCs (these 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 (Poisson distribution and log link). The model of best fit was selected according to the lowest AIC value, as above. I investigated whether the total duration of affiliation per 10-minute session (0-600, response variable) was influenced by the treatment (MC`, PC), with treatment and subject as random factors for reasons stated above. 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 if longer durations of affiliation occurred later in PCs and to confirm that similar mean durations occurred in both halves of MCs.

Inter-observer reliability

I collected all data on the post-conflict affiliation study. To determine within-observer consistency, a second observer was trained and inter-observer reliability analyses conducted on rooks and jackdaws in April 2011. Ljerka Ostojic and I conducted 10-minute focal follows on the same subject for a total of 50 follows (25 per observer), recording the data in The Observer V9.0 on separate computers. Subjects were randomly chosen according to their position on the subject list, starting with birds at the top of the list. If the next bird on the list was not visible it was skipped and the next bird listed was observed. Skipped birds were sought again the next session. Ljerka was trained by me for 2-hr before collecting the data since Ljerka had extensive experience observing the three species.

The two data sheets for each session were examined for temporal matching (recorded within 5-sec of each other) and behaviour matching between the two observers using the inter-observer reliability analysis in The Observer V9.0 (Jansen et al. 2003). There were 448 agreements and 195 disagreements between observers, showing fair to excellent agreement between the two observers (average Pearson's product moment correlation: $r=0.96$, range: 0.69 to 1.00; average Cohen's Kappa: $k=0.63$; range: 0.42 to 1.00; Landis & Koch 1977, Fleiss 1981).

RESULTS

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 around 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 affiliation=-0.06, active affiliation=-0.02, passive affiliation=-0.05; jay mean CCT: all affiliation=0.02, active affiliation=there were no attracted PC-MC pairs in this category, passive affiliation=0.02).

Selective attraction?

There was no post-conflict former opponent affiliation in any species as evidenced by the similar proportions of attracted and dispersed PC-MC pairs (Figure 3.1; Wilcoxon signed rank test: rook proportion attracted=0.09, proportion dispersed=0.07, $V=13$, $N_1=N_2=13$, $P=0.67$, 95% confidence interval=-1.00-1.50; jackdaw attracted=0.09, dispersed=0.13, $N_1=N_2=14$, $V=13.5$, $P=0.28$, 95% CI=-2.00-1.00; jay attracted=0.06,

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.

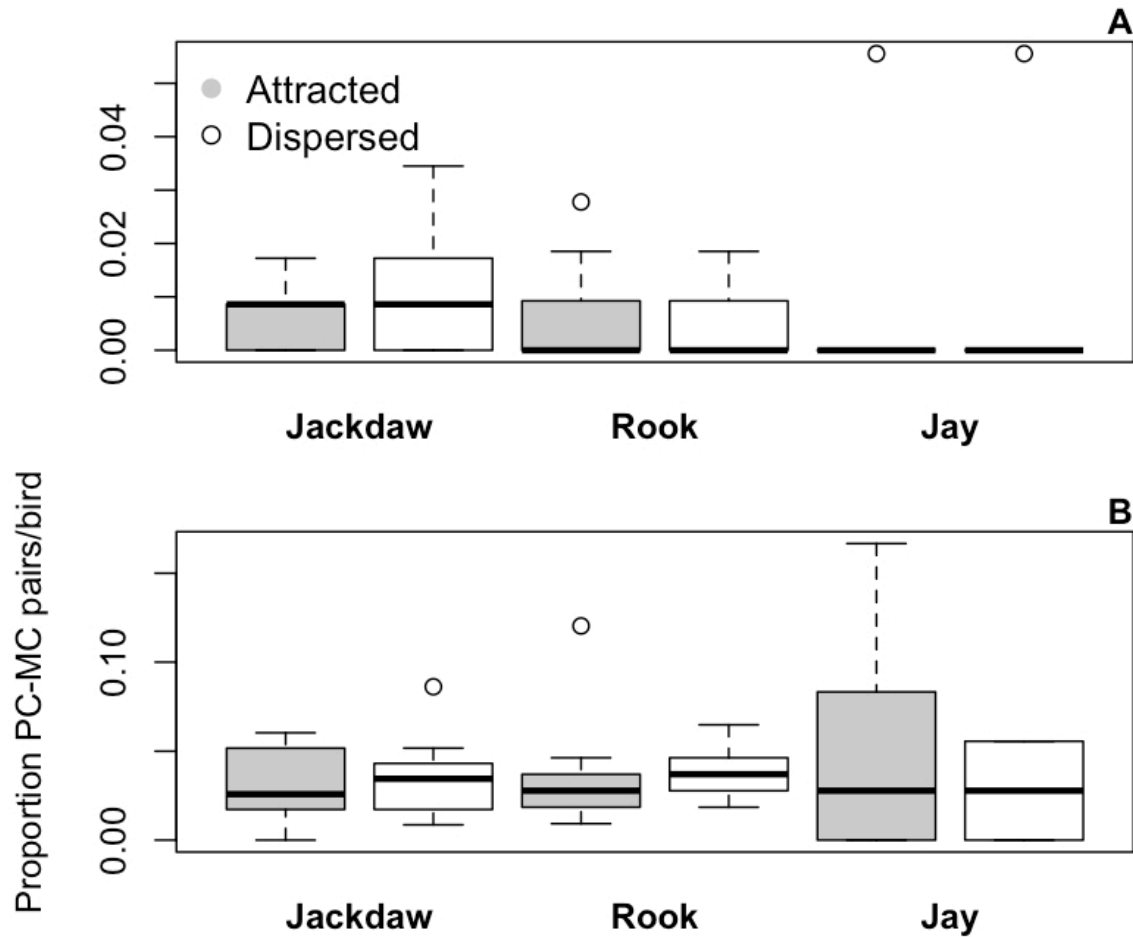


Figure 3.1. The proportion of PC-MC pairs that were attracted (active or passive affiliation occurring sooner after conflicts) or dispersed (active or passive affiliation occurring sooner in matched controls) per bird for each species for former opponent affiliation (A) and third-party affiliation (B).

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 or 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).

Triadic contact tendencies

Rook TCTs were negative for all affiliation and passive affiliation, but positive for active affiliation (mean TCT: all=-0.10, active=0.11, passive=-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).

Selective attraction?

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 3.1, Table 3.1; Wilcoxon signed ranks test: all affiliation: $V=25.5$, $N=14$ birds, $p=0.30$, 95% confidence interval=-0.02-0.01; active affiliation: $V=24$, $N=14$ birds, $p=0.11$, 95% CI=-0.005-0.06; passive affiliation: $V=37$, $N=14$ birds, $p=0.91$, 95% CI=-0.02-0.02).

A GLMM analysis was performed on the rook data from Table 3.1 to determine whether selective attraction may have occurred more for particular categories of affiliation (affiliation that was combatant initiated, for aggressors, males, or with partners). Since this is the first time I present GLMM results, I will describe how to read and interpret

Table 3.1. Third-party affiliation in rooks: the proportion of attracted PC-MC pairs per bird (sessions in which affiliation between a former opponent and a third party occurred sooner in the PC than in the MC) and the proportion of those attracted sessions that had affiliation initiated by former combatants, aggressors, males, and involved partners.

Subject	Proportion Attracted	Proportion Combatant Initiated	Proportion Aggressor	Proportion Male	Proportion of Interactions with Partner
<i>All Affiliation</i>					
Arthur	0.02	0	0.04	0.04	0.02
Beowulf	0.12	0.23	0.13	0.27	0.25
Cassandra	0.02	0.04	0	0	0.04
Chasca	0.04	0.06	0.02	0	0
Hector	0.03	0.06	0.04	0	0.06
Leonidis	0.03	0.06	0.04	0.06	0.04
Loki	0.02	0	0.02	0	0
Merlin	0.05	0.04	0.02	0	0.08
NoRing	0.03	0.04	0.04	0	0
Remus	0.01	0	0	0	0.02
Romulus	0.02	0.04	0	0	0
Ticci	0.03	0.06	0	0	0
Zara	0.05	0.10	0.02	0	0.02
Total	0.44	0.75	0.38	0.38	0.54
Mean	0.03	0.06	0.03	0.03	0.003
<i>Active Affiliation</i>					
Arthur	0.06	0.02	0.14	0.14	0.14
Beowulf	0.12	0.23	0.19	0.30	0.30
Cassandra	0.03	0.07	0.02	0	0.07
Chasca	0.01	0.02	0	0	0
Hector	0.03	0.07	0.05	0	0.07
Leonidis	0.05	0.09	0.02	0.12	0.12
Loki	0				
Merlin	0.04	0.02	0.02	0	0.09
NoRing	0				
Remus	0.03	0.05	0.05	0	0.07
Romulus	0				
Ticci	0.02	0.05	0	0	0
Zara	0.03	0.05	0	0	0.07
Total	0.40	0.67	0.49	0.56	0.93
Mean	0.03	0.07	0.05	0.06	0.09
<i>Passive Affiliation</i>					
Arthur	0.02	0	0.04	0.04	0.02
Beowulf	0.10	0.21	0.08	0.23	0.17
Cassandra	0.05	0.04	0.02	0	0.06
Chasca	0.04	0.06	0.02	0	0
Hector	0.04	0.04	0.06	0	0.06
Leonidis	0.03	0.04	0.06	0.06	0.02
Loki	0.02	0	0.02	0	0
Merlin	0.04	0.04	0	0	0.06
NoRing	0.03	0.04	0.04	0	0
Remus	0.01	0	0	0	0.02
Romulus	0.02	0.04	0	0	0
Ticci	0.03	0.06	0	0	0
Zara	0.04	0.08	0.02	0	0
Total	0.44	0.67	0.38	0.33	0.42
Mean	0.03	0.05	0.03	0.03	0.03

the table. The first line of the first rook model is the null model, which regresses the response variable (in this case, the proportion of attracted PC-MC pairs) against 1 instead of against any explanatory variables. This provides a model to compare actual test results: if test models are of 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 a test model. The intercept in this model represents the base model which includes self-initiated affiliation, active affiliation, affiliation with non-partners, and affiliation involving victims. The second line in this model compares the two factor levels of this one explanatory variable “Combatant-initiated” with “Third-party initiated”. Since the estimate for combatant-initiated is a positive number (26.92), this indicates that the affiliation estimate (i.e., affiliation) increases when former combatants initiate third-party affiliation relative to the estimate for the intercept (-5.24) which represents third-party initiated affiliation. However, the standard error (42.36) is larger than the estimate, indicating that this is not 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 test model, it is higher than that for the null model, which indicates that the null 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 valuable and contributes to the low

AIC value, thus it is the model as a whole and not just a few key variables that are “significant”. Therefore, results for selective attraction show that no category significantly influenced the occurrence of attraction because the model of best fit was the null model (Table 3.2). Thus, there is no selective attraction in rooks.

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 (Table 3.3; Wilcoxon signed rank test: all affiliation: $V=33$, $N=14$ birds, $p=1.00$, 95% confidence interval=-0.03-0.03; active affiliation: $V=27$, $N=14$ birds, $p=0.63$, 95% CI=-0.02-0.02; passive affiliation: $V=68.5$, $N=14$ birds, $p=0.33$, 95% CI=-0.02-0.03). Results from

Table 3.2. GLMM results for rooks and jackdaws to determine whether selective attraction (affiliating sooner in PCs rather than MCs) occurred more for particular classes of affiliation. Note: some interactions were omitted for brevity.

Model	Form	Estimate	Standard Error	delta AIC [AIC]
Rook	Intercept only Subject (random factor)	-3.54 0.00	1.01 0.00	0 [4]
	Intercept` Combatant-initiated Affiliation type: all Affiliation type: passive Partner Aggressor Subject (random factor)	-5.24 26.92 1.15 1.23 24.49 24.49 0.00	18.15 42.36 25.07 25.89 268.40 1176.00 0.00	46 [50]
Jackdaw	Intercept only Subject (random factor)	-3.41 0.00	0.88 0.00	0 [4]
	Intercept` Combatant-initiated Affiliation type: all Affiliation type: passive Partner Male <i>Note: interactions omitted</i> Subject (random factor)	-3.54 -40.70 -28.85 -31.59 -9.45 -9.24 0.00	28.06 137.90 29.52 32.51 688.80 432.80 0.00	46 [50]

Table 3.3. Third-party affiliation in jackdaws: the proportion of attracted PC-MC pairs per bird and the proportion of those attracted sessions that had affiliation initiated by former combatants, aggressors, males, and involved partners.

Subject	Proportion Attracted	Proportion Combatant Initiated	Proportion Aggressor	Proportion Male	Proportion of Interactions with Partner
<i>All Affiliation</i>					
Celli	0.05	0.02	0.12	0.12	0.12
Claude	0.04	0.04	0.06	0	0.08
Dali	0.02	0.02	0	0	0
Dom	0.02	0.02	0.02	0	0.04
Escher	0.04	0.08	0.06	0.10	0.02
Gaudi	0.02	0.02	0	0.03	0.04
Ivo	0.02	0	0.02	0	0.02
Jo	0.02	0.02	0.02	0.04	0
Munch	0				
Pedro	0.02	0.04	0.04	0	0.04
Picasso	0.03	0.08	0.08	0	0.06
Raffa	0.05	0.08	0.06	0.12	0.10
Vasco	0.06	0.08	0.06	0.13	0.06
Will	0.06	0.13	0.02	0.13	0.12
Total	0.45	0.62	0.54	0.67	0.67
Mean	0.03	0.05	0.04	0.05	0.05

Subject	Proportion Attracted	Proportion Combatant Initiated	Proportion Aggressor	Proportion Male	Proportion of Interactions with Partner
<i>Active Affiliation</i>					
Celli	0.05	0.04	0.11	0.13	0.13
Claude	0.02	0.02	0.02	0	0.04
Dali	0				
Dom	0.02	0	0.02	0	0.04
Escher	0.03	0.09	0.07	0.09	0.04
Gaudi	0.03	0.02	0.02	0.07	0.07
Ivo	0.02	0.02	0	0	0.02
Jo	0.009	0.02	0.02	0.02	0
Munch	0.05	0.09	0.09	0.13	0.11
Pedro	0.03	0.02	0.04	0	0.07
Picasso	0.03	0.09	0.09	0	0.04
Raffa	0.04	0.04	0.04	0.11	0.09
Vasco	0.02	0	0.04	0.04	0.02
Will	0.05	0.11	0.02	0.13	0.13
Total	0.40	0.57	0.59	0.72	0.80
Mean	0.03	0.04	0.05	0.06	0.06
<i>Passive Affiliation</i>					
Celli	0.03	0.03	0.05	0.07	0.07
Claude	0.04	0.03	0.05	0	0.07
Dali	0.02	0.02	0	0	0
Dom	0.02	0.02	0.02	0	0.03
Escher	0.04	0.07	0.03	0.09	0
Gaudi	0.05	0.05	0.05	0.10	0.07
Ivo	0.03	0	0.05	0	0.05
Jo	0.02	0.02	0.02	0.03	0
Munch	0				
Pedro	0.02	0.03	0.03	0	0.03
Picasso	0.04	0.07	0.09	0	0.07
Raffa	0.07	0.10	0.07	0.14	0.09
Vasco	0.05	0.07	0.03	0.10	0.05
Will	0.06	0.10	0.03	0.12	0.10
Total	0.50	0.62	0.53	0.66	0.64
Mean	0.04	0.05	0.04	0.05	0.04

the GLMM analysis on data from Table 3.3 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 3.2). 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 the Wilcoxon signed rank test did.

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 (Table 3.4; Wilcoxon signed rank test: $V=4.5$, $N=8$ birds, $p=0.59$, 60% confidence interval= $-0.06-0.17$). The jay sample size was so small (only

four attracted PC-MC pairs) that a GLM could not be prudently applied to the data to determine whether particular categories influenced those instances in which attraction occurred.

Table 3.4. Third-party affiliation in jays: all affiliation (active and passive combined). The proportion of attracted PC-MC pairs per bird (sessions in which affiliation between a former opponent and a third party occurred sooner in the PC than in the MC) and the proportion of those attracted sessions that had affiliation initiated by former combatants, aggressors, males, and involved partners.

Subject	Proportion Attracted	Proportion Combatant Initiated	Proportion Aggressor	Proportion Male	Proportion of Interactions with Partner
Caracus	0				
Dublin	0.17	0.14	0.29	0.43	0.14
Lima	0.11	0.14	0.29	0.29	0
Lisbon	0.06	0.14	0.14	0.14	0.14
Quito	0				
Rome	0.06	0.14	0.14	0	0
Washington	0				
Wellington	0				
Total	0.39	0.57	0.86	0.86	0.29
Mean	0.05	0.14	0.21	0.21	0.07

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, 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 (Figure 3.2). Because the model of best fit for rooks involves interactions among variables (Test model 2 in Table 3.5), I will describe how to read and interpret these results. In test model 2, the first line is the intercept, or base model, which includes MCs, females, aggressors, combatant-initiated affiliation, and affiliation with non-partners. Each term, or interaction among terms, below this first line compares that specific element to its corresponding element in the base model. The second line (Treatment: PC) shows that the frequency of affiliation increases in PCs compared with

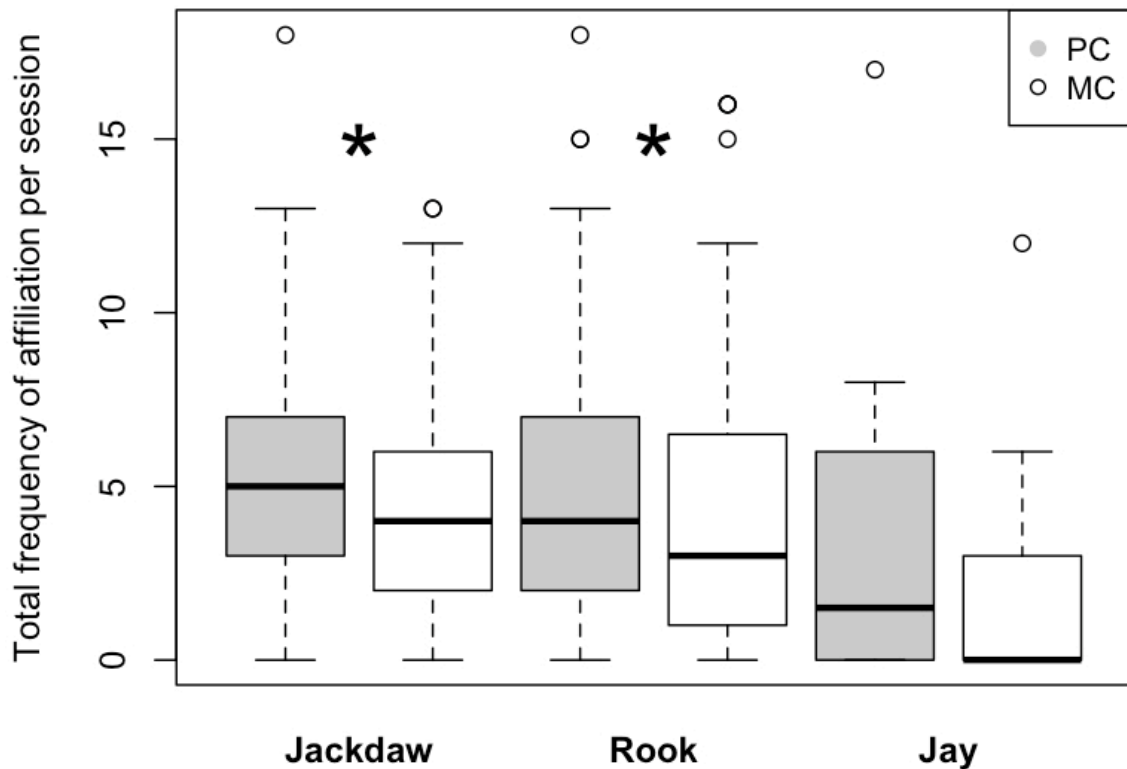


Figure 3.2. The total frequency of affiliation per session (PC or MC) by species.

MCs (in the base model). The third line (PC*third-party) indicates that the frequency of affiliation increases even more when third-parties initiate post-conflict affiliation and in brackets I note some of the base model terms to keep in mind, specifically that this result relates to female aggressors. The sixth line (PC*partner*victim) shows that the frequency of affiliation increases after conflicts (relative to matched controls) for victims (rather than aggressors) when this affiliation involves partners (rather than non-partners) for females (because this is part of the base model). Other intermediate test models were also included in the model selection process, but were excluded from the tables because they were not the model of best fit, which makes the tables clearer. Summarising the results from the model of best fit, the frequency of post-conflict third-party affiliation increased for victims and aggressors when affiliating with partners (Test model 2 in Table 3.5). Affiliation was third-party initiated for male and female victims, as well as for female aggressors, and self-initiated by male aggressors. This shows that when the frequency of affiliation across the entire 10-minute period of PCs and MCs is considered, rooks show post-conflict third-party affiliation. The increase in activity levels as shown by the increase in the frequency of affiliative interactions was not a

general increase in activity levels because there was no difference between aggression frequencies between PCs and MCs (paired t-test: $t=0.77$, $df=12$, $p=0.45$, 95% confidence interval= $-0.05-0.10$). Therefore, the rise in activity was specific to affiliation, indicating that it is a post-conflict behaviour.

Jackdaws had a significantly higher frequency of affiliation in PCs than in MCs regardless of the initiator of affiliation, relationship with the third-party, role in the conflict, or sex of the former combatant (Table 3.5). Age was a factor in their model of best fit, and I will discuss this in detail in chapter 4. As with the rooks, when examining the frequency of affiliation after conflicts, post-conflict third-party affiliation occurs. While the frequency of affiliation significantly increased after conflicts, there was no difference between the overall frequencies of non-conflict aggression in PCs versus MCs (paired t-test: jackdaws: $t=1.24$, $df=13$, $p=0.24$, 95% confidence interval= $-0.01-0.05$). Therefore, the increase in activity levels was restricted to affiliation and not a general increase in activity, which indicates that affiliation is a post-conflict behaviour.

Jay results from the GLMM analysis of the frequency of affiliation were severely restricted due to the lack of data. Since I primarily wanted to know if this species showed any post-conflict third-party affiliation, treatment was the most important explanatory variable and the only one analysed (subject and treatment were included as a random factor as in the other models). Consistent with results from the latency of first affiliative contacts in which jays lacked selective attraction, none of the models were better than the null model according to AIC values, therefore there was no increase in affiliation after conflicts when compared with matched controls, indicating that post-conflict third-party affiliation did not occur (Table 3.5). Aggression frequencies were also similar between PCs and MCs (paired t-test: $t=1.05$, $df=7$, $p=0.33$, 95% confidence interval= $-0.06-0.15$), therefore there was no increase in activity levels in general after conflicts.

Table 3.5. GLMM analysis of the frequency of affiliation in rooks, jackdaws, and jays. Note that interactions not discussed in the text are omitted for brevity. Beowulf was removed from the rook models because he was an outlier.

Model	Model Type	Form	Estimate	Standard Error	delta AIC [AIC]
Rook	Null	Intercept only Subject (random factor) Treatment (random factor)	0.47 0.13 0.00	0.12 0.36 0.00	15 [410]
	Test 1	Intercept` Treatment: PC Subject (random factor) Treatment (random factor)	0.47 0.01 0.13 0.00	0.13 0.11 0.36 0.00	17 [412]
	Test 2	Intercept` Treatment: PC PC*third-party (female, aggressor) PC*male (aggressor) PC*third-party*victim (female) PC*partner*victim (female, aggressor) PC*partner*male (aggressor) PC*third-party*victim*male PC*partner*victim*male Subject (random factor) Treatment (random factor)	0.54 0.06 0.18 0.29 0.04 1.86 0.07 1.42 0.19 0.06 0.00	0.32 0.41 1.21 0.71 1.26 1.33 1.04 1.96 1.71 0.25 0.00	0 [395]
	Test 2 + age	Intercept` Treatment: PC Initiator: third-party Relationship: partner Role: victim Sex: male Subject (random factor) Treatment (random factor)	0.95 -0.31 0.11 -0.38 -1.39 0.70 0.17 0.03	18.31 55.31 1.23 18.37 19.11 18.34 0.42 0.16	17956 [18351]
Jackdaw	Null	Intercept only Subject (random factor) Treatment (random factor)	1.61 0.03 0.005	0.07 0.16 0.07	2 [415]
	Test 1	Intercept` Treatment: PC Subject (random factor) Treatment (random factor)	1.53 0.15 0.02 0.00	0.06 0.06 0.15 0.00	1 [413]
	Test 1 + age	Intercept` Treatment: PC Age PC*Age Subject (random factor) Treatment (random factor)	1.70 0.07 -0.01 0.007 0.03 0.00	0.10 0.12 0.007 0.009 0.17 0.00	0 [412]
	Test 2	Intercept` Treatment: PC Initiator Relationship: partner Role: victim Sex: male Subject (random factor) Treatment (random factor)	1.55 0.60 -0.25 0.12 -0.28 -0.03 0.01 0.00	0.19 0.25 0.32 0.28 0.32 0.24 0.12 0.00	12 [425]

Model	Model Type	Form	Estimate	Standard Error	delta AIC [AIC]
Jay	Null	Intercept only Subject (random factor) Treatment (random factor)	0.08 3.83 0.03	0.76 1.96 0.17	0 [77]
	Test 1	Intercept` Treatment: PC Subject (random factor) Treatment (random factor)	-0.09 0.33 3.76 0.00	0.76 0.22 1.94 0.00	0 [77]
	Test 1 + age	Intercept` Treatment: PC Age PC*Age Subject (random factor) Treatment (random factor)	-0.48 0.59 0.07 -0.05 3.74 0.00	0.96 0.64 0.11 0.11 1.93 0.00	3 [80]

Duration of affiliation

The duration of affiliation per 10-minute observation session differed between PCs and MCs for all species (Figure 3.3). Rooks and jays had significantly longer affiliation durations in PCs than in MCs as shown in the model of best fit, which was more parsimonious than the null model (Table 3.6). In contrast, jackdaws had significantly shorter affiliation durations in PCs than in MCs in their model of best fit (Table 3.6). Age was a factor in the models of best fit for each species and will be discussed in chapter 4.

Combining the affiliation duration results with results from the frequency of affiliation models, indicates that rooks have a higher frequency and longer duration of affiliation after conflicts when compared with matched controls. When examining the mean affiliation duration in the first five minutes versus the last five minutes of PCs, rooks had significantly longer durations in the second five minutes as would be expected if higher frequencies of affiliation do indeed reduce stress and, thus, activity levels such that they stay in contact longer later in the session (Mann Whitney U test: $W=3985$, $N=108$ PCs, $p=0.0007$, 95% confidence interval= $-60.00-(-14.00)$). There was no difference between the duration of affiliation in the first versus the last five minutes in MCs, showing that this effect is restricted to the post-conflict session ($W=5196$, $N=108$ MCs, $p=0.54$, 95% CI= $-17.00-5.00$).

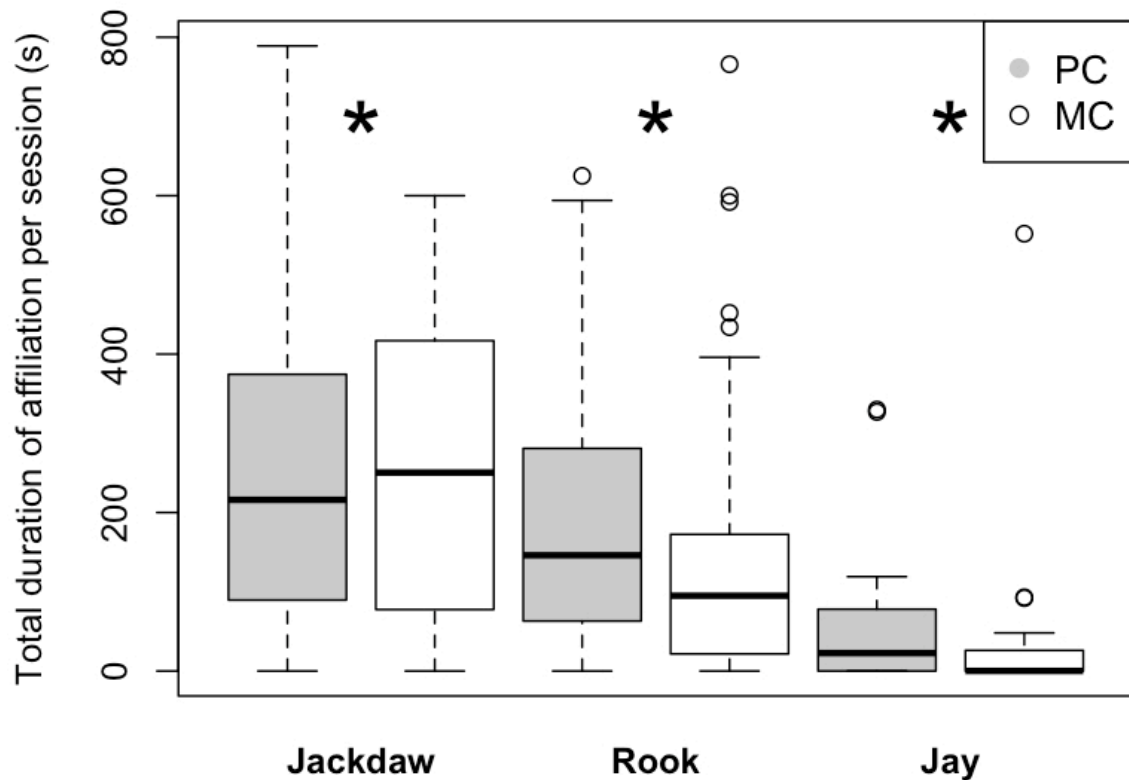


Figure 3.3. The total duration of affiliation per session (PC or MC) by species. Note that totals can add up to more than the observation session length (600s) because multiple affiliative states could occur at one time.

Jackdaws had a higher frequency of affiliation after conflicts which were of shorter duration than affiliation in matched controls. There was no difference in mean affiliation duration between the first and last five minutes of PCs ($W=5859$, $N=116$ PCs, $p=0.40$, 95% CI=-40.00-12.00), which shows that the higher frequency of affiliation during PCs does not change their activity levels such that they are maintaining longer contact. Perhaps jackdaw stress levels remain high for longer than 10 minutes after conflicts, which could explain why affiliation frequencies, but not durations, are higher in PCs. However, jackdaws had significantly longer mean durations in the last five minutes of MCs when compared with the first five minutes of MCs ($W=4283.5$, $N=116$ MCs, $p=0.00004$, 95% CI=-105.00-(-29.00)). I am unsure of how to interpret this result as I would predict there would be no difference in affiliation durations across time in MCs since this is the baseline behaviour. This result likely would require further experimentation to understand the reason for the difference.

Table 3.6. The effect of treatment on the duration of affiliation.

Model	Form	Estimate	Standard Error	delta AIC [AIC]
Rook	Intercept only Subject (random factor)	5.04 0.20	0.12 0.44	976 [19895]
	Intercept` Treatment: PC Subject (random factor) Treatment (random factor)	4.85 0.34 0.19 0.00	39.70 30.07 0.44 0.00	6 [18979]
	Intercept` Treatment: PC Age PC*age Subject (random factor) Treatment (random factor)	4.64 0.49 0.02 -0.01 0.19 0.00	0.12 0.02 0.001 0.002 0.44 0.00	0 [18973]
Jackdaw	Intercept only Subject (random factor)	5.51 0.11	0.09 0.34	42 [25094]
	Intercept` Treatment: PC Subject (random factor) Treatment (random factor)	5.54 -0.06 0.11 0.00	0.09 0.01 0.34 0.00	324 [25052]
	Intercept` Treatment: PC Age PC*age Subject (random factor) Treatment (random factor)	5.46 -0.18 0.007 0.009 0.10 0.00	0.08 0.02 0.0009 0.001 0.31 0.00	0 [24728]
Jay	Intercept only Subject (random factor)	4.31 0.60	0.35 0.78	647 [1024]
	Intercept` Treatment: PC Subject (random factor) Treatment (random factor)	4.24 0.12 0.61 0.00	0.35 0.05 0.78 0.00	644 [1021]
	Intercept` Treatment: PC Age PC*age Subject (random factor) Treatment (random factor)	0.71 2.50 0.62 -0.35 0.15 0.00	0.25 0.19 0.03 0.03 0.39 0.00	0 [377]

Jays had no difference between PCs and MCs in terms of the frequency of affiliation, however the duration of affiliation was longer in PCs than MCs, indicating the presence of post-conflict third-party affiliation. When examining the mean duration of affiliation, there were no significant differences between the first five versus the last five minutes of PCs ($W=230$, $N=18$ PCs, $p=0.78$, 95% CI=-30.00-18.00) or MCs ($W=121.5$, $N=18$ MCs, $p=0.82$, 95% CI=-8.00-0.00002). Therefore, mean durations of affiliative events

were similar in PCs and MCs and, while not significant, the slight increase in affiliation frequency in PCs interacted with mean durations such that durations became significantly longer in PCs.

DISCUSSION

Former opponent affiliation

Consistent with my hypotheses, none of the corvids under study engaged in former opponent affiliation after conflicts. This finding is consistent with the valuable relationship hypothesis which states that those individuals sharing an important relationship will have former opponent affiliation which most likely repairs the damage caused by the conflict (de Waal and Aureli 1997; Aureli et al. 2002). The social structure of the corvids in my study places the mated pairs as the strongest relationship in the group (chapter 2). Mated partners did not engage in any conflicts with each other, therefore I did not expect to see, and I did not find, former opponent affiliation.

Third-party affiliation

All three species showed post-conflict third-party affiliation according to affiliation frequencies and durations, but not latency to first affiliation. Rooks showed a higher frequency and duration of affiliation in PCs compared with MCs, jackdaws showed a higher frequency in PCs, and jays longer durations in PCs. The presence of post-conflict third-party affiliation was predicted for the social rooks and jackdaws who engaged in this behaviour with their mates, however it was unexpected in the less social jays who performed this behaviour with anyone who was not the former opponent. I hypothesised that jays, being less social than the rooks and jackdaws, would not have sufficiently, or possibly even any, important relationships to engage in post-conflict affiliation with. I found that the jays rarely had important relationships outside of the breeding season when these data were collected (chapter 2), yet they did engage in third-party affiliation. Their pattern of affiliation matches their bonding pattern: the absence of particularly strong bonds produced no bias in whom to affiliate with. The jay evidence does not support the valuable relationship hypothesis (expanded to include third-party affiliation) because post-conflict affiliation is only expected to occur when individuals have important social bonds, as in the rooks and jackdaws.

Rooks showed post-conflict third-party affiliation primarily with their partners when analysing the frequency of affiliation. Affiliation for victims of both sexes and female aggressors was primarily partner-initiated, which is sometimes called consolation, while male aggressors initiated affiliation after conflicts, sometimes called solicited consolation. Victims may experience more stress from the conflict than aggressors, thus resulting in more post-conflict affiliation if indeed the function of such behaviour is to reduce stress. Perhaps males initiated more affiliation because they often fought with unpaired females during nesting season when they were picking up nesting material. There were so few males that they were highly sought after by unpaired females who occasionally gained extra pair copulations from them. Males tolerated advances by unpaired females to a degree, however they often chased these females away when they were gathering nesting material, which often resulted in conflicts (initiated by the male). Soon after these conflicts, males would re-gather their nesting material and take it back to the nest where their partner was, thus resulting in combatant-initiated affiliation after conflicts by male aggressors. 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 also showed post-conflict affiliation according to affiliation durations: they engaged in longer durations of affiliation after conflicts, particularly in the last five minutes, than in matched controls. Higher frequencies of affiliation combined with longer mean durations of affiliation later in post-conflict sessions indicate that affiliation is used as a post-conflict behaviour, and suggest that it may serve a stress reducing function.

Jackdaws showed a general increase in post-conflict third-party affiliation according to the frequency of affiliation analysis. There were no particular categories of affiliation that increased more than others, therefore it appears to be a behaviour that is independent of sex, role in the conflict, and initiator of the affiliation. However, almost all jackdaws in this study were paired, in contrast with the rooks in which only half of the individuals had mates. Therefore, I would expect less variation in post-conflict affiliative behaviour in the jackdaws than in the rooks in this study because third-party affiliation occurs primarily with mates. That both aggressors and victims experienced

third-party affiliation equally may indicate that conflicts increase stress equally for both conflict participants, therefore there is no differential need to reduce the stress of one role over the other. As with the rooks, the increase in activity after conflicts was limited to affiliation because there was no difference in aggression frequencies between PCs and MCs. This suggests that affiliation was used as a post-conflict behaviour, possibly to reduce stress that may have arisen from the conflict. In contrast with the rooks, jackdaws had longer affiliation durations in MCs rather than in PCs, which indicates they do not increase the length of time spent in social contact after conflicts when compared with matched controls. This could result if jackdaws had higher stress levels throughout the 10 minute post-conflict session such that activity levels (frequencies of affiliation) had not subsided to the point that durations of affiliation would increase. A longer observation session would clarify whether this is the case.

Jays showed post-conflict third-party affiliation in the form of longer durations of affiliation after conflicts when compared with matched controls. Outside of the breeding season there were no strong social bonds, making it unlikely for post-conflict affiliation to occur. Similar to some macaques, jays are despotic with a rigid dominance hierarchy (chapter 2), 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 invest in the maintenance of social relationships, the presence of post-conflict affiliation shows that even the least social species studied so far in this context can produce this behaviour.

Consistent with findings from a different population of rooks, the rooks and jackdaws in the current study affiliated more with their mate than with non-mates, which is further evidence that mated partners have the most valuable relationship in the group (Seed et al. 2007). This indicates that third-party affiliation 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 & Sterck 2009; Wittig & Boesch 2010).

None of the species in this study showed post-conflict third-party affiliation when analysing the data according to the latency with which they affiliate in PCs versus MCs. However, rooks and jackdaws had high baseline levels of affiliation, especially with their partners (chapter 2), which 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 sometimes duration, of affiliation throughout each 10-minute observation period was a better indicator 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 the same results as in my study (i.e., consolation, solicited consolation, and third-party affiliation for aggressors that was initiated by both former combatants and third parties). 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 my study were juveniles in the beginning and adults in the end, thus, third-party affiliation may change over the developmental period with frequency of affiliation being important in the juvenile years and latency of first affiliation in the adult years. Alternatively, Seed and colleagues' (2007) rooks may also have had a higher frequency of affiliation after conflicts. A year-by-year analysis of my rook (and jackdaw) data using both latency and frequency methods will clarify if this is indeed the case (chapter 4).

For jackdaws, their failure to show post-conflict third-party affiliation using the latency to first affiliation could be due to their post-conflict aggression patterns. Jackdaws generally delayed their time to first affiliation after conflicts when compared with matched controls possibly because heightened agitation after conflicts led to non-conflict aggression after fights. Perhaps jackdaws were too busy aggressing against others soon after conflicts, which delayed their time of first affiliation relative to matched controls which, by definition, did not have the agitation of a conflict.

Methodology

The alternative methods for analysing post-conflict affiliation behaviour involving the frequency and duration of affiliation after conflicts when compared with matched controls proved useful. The frequency of affiliation was a good indicator of post-conflict third-party affiliation when compared with other behaviours 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 used as a post-conflict behaviour, and this was found in both rooks and jackdaws. This method of 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). Analysing the duration of affiliation in PCs versus MCs was also useful, especially when considering frequencies and durations of affiliation together since an increase in both after conflicts, as occurred with the rooks, provides even more evidence that affiliation is used in a post-conflict context, which may potentially reduce stress. Had I simply relied on the latency of affiliation methods, I would have missed the fact that rooks and jackdaws do have post-conflict affiliative behaviour when looking at all of the data across the 10-minute observation sessions. Therefore, I conclude that it is important to examine all of the data available when investigating post-conflict affiliative behaviour.

Conclusion

Research on corvid post-conflict affiliation has facilitated our understanding of how social structure influences the use of different post-conflict affiliation strategies. The social structure of rooks and jackdaws, having one main valuable relationship and no fights in this relationship, appears to produce third-party affiliation with mates, whereas the lack of strong bonds in the jays outside of the breeding season (when these data were collected) results in third-party affiliation with anyone (not restricted to mates). It will be important to investigate species that are less social than the jays to determine whether post-conflict affiliative behaviour disappears at a certain threshold of sociality. Identifying how post-conflict affiliation strategies vary across different contexts will be key to understanding the underlying patterns in post-conflict affiliative behaviour, particularly regarding predictions about which species show such behaviour and the selective pressures by which this behaviour can evolve.

CHAPTER 4: Developmental effects on post-conflict third-party affiliation in rooks and jackdaws

ABSTRACT

I hypothesised that post-conflict third-party affiliation would have a stronger effect with increasing age as rook and jackdaw pairs solidify and reach sexual maturity, and that jay third-party affiliation would decrease with age due to the decrease in conflict frequency. Using the models from chapter 3, when analysing the frequency and duration of affiliation after conflicts versus in matched controls, age became the best explanatory variable for jackdaws for the increase in post-conflict affiliation frequencies. Age was not a factor in the rook and jay models of best fit, thus post-conflict behaviour is independent of age in these species. Total affiliation duration increased with age in jackdaws, and decreased over time for rooks and jays. As in chapter 3, affiliation latencies did not explain any differences between affiliation in PCs and MCs, while the frequency and duration of affiliation did. Rooks and jackdaws were already paired when this study began and post-conflict third-party affiliation was present from the beginning of the study. Therefore, post-conflict affiliative behaviour is likely dependent on the most valuable relationship in the group: that with the mate. Jays began pairing in their first year and showed more post-conflict affiliation at this time, which could indicate this is a behaviour important for pair formation in this species. While the frequency of affiliation in general remained the same across the three years of the study (chapter 2), post-conflict third-party affiliation became increasingly stronger with age in jackdaws, which may indicate that partner relationships increased in value (fitness benefits). If competition over resources becomes more intense jackdaws reach sexual maturity, post-conflict third-party affiliation with mates could be used as a signal to other group members that pairs are united when competing for limited resources.

INTRODUCTION

While post-conflict affiliation has been studied in a number of species, investigations of the ontogeny of this behaviour are rare. Former opponent affiliation is predicted to occur when one or more valuable relationships are present in a group (van Schaik & Aureli 2000, Aureli et al. 2002) and I would extend this prediction to include third-party

affiliation based on evidence in chapter 3. Therefore, the onset of post-conflict affiliative behaviour should coincide with the presence of valuable relationship(s) and this behaviour should become stronger as relationships increase in value.

There is evidence that former opponent affiliation occurs in juveniles when valuable relationships are present. Brown capuchin monkey infants who were aggressed upon by non-mother adults used former opponent affiliation, which was initiated by both infants and adults (Weaver & de Waal 2003). While the most valuable relationship for infants is that with the mother, this species shows allomaternal care after infants reach one month of age, thus making other adult relationships important as well (Valenzuela 1993). Weaver and de Waal (2003) began their study when infants were three months of age, therefore the presence of valuable relationships with adults was already established when post-conflict affiliative behaviour was found. Long-tailed macaque juveniles (three to five years old) who were the recipients of aggression showed former opponent affiliation with those individuals with whom they often engaged in affiliative behaviour (Cords & Aureli 1993). These studies confirm that post-conflict affiliative behaviour is present in juveniles who have valuable relationships, though there have been no studies examining the onset of post-conflict affiliation to determine at what stage in the development of valuable relationships this behaviour appears.

There is also evidence that post-conflict affiliative behaviour becomes stronger with increasing relationship value. Long-tailed macaque affiliates increased their rates of former opponent affiliation after participation in a task in which cooperation between the two was necessary to receive a food reward (Cords & Thurnheer 1993). The cooperation task was presumed to increase their relationship value, and, consequently, strengthen their post-conflict affiliative behaviour, which it did. While this is the only study to experimentally manipulate relationship value to evaluate its influence on post-conflict affiliation, it might be possible to use naturally developing relationships to evaluate how changes in relationship value influence post-conflict affiliative behaviour.

There is some research on the ontogeny of post-conflict former opponent affiliation (see Arnold et al. 2010 for a review), however there is none regarding third-party affiliation.

This chapter examines the development of post-conflict third-party affiliation. I hypothesised that third-party affiliation would be present after mated pairs form because the pair is the most valuable relationship in the group (chapter 2) and the primary relationship that engages in post-conflict third-party affiliation (chapter 3). Rooks, jackdaws, and jays were studied from one year of age through four years of age, which included the age at which they reached sexual maturity (at age two in jackdaws [Röell 1978] and jays [Snow & Perrins 1998], and at age three in rooks [Coombs 1978]). Sexually immature and mature stages differ in that immature individuals choose mates and establish pair bonds using behaviours different from those behaviours used to maintain the pair bond after a pair is established (Emery et al. 2007). In rooks, sharing food with each other is important for establishing the pair bond; after the bond is established, allopreening becomes important to maintain the bond (Emery et al. 2007). Jackdaw nestlings share food with many affiliates when they are younger, slowly reducing the number of individuals they share food with as they age and seek their mate (de Kort et al. 2006, von Bayern et al. 2007). Because rooks and jackdaws have one main important relationship (with their mate), it seems likely that post-conflict affiliation would coincide with the timing of mate acquisition when this valuable relationship becomes the most important in the group, making post-conflict affiliation worth engaging in. The jays surprisingly showed post-conflict affiliation according to affiliation durations (chapter 3), therefore I will apply the post-hoc hypothesis that this behaviour would be present earlier in the study when they were forming pairs and engaging in more conflicts, and would decrease in strength with age as conflicts became rare (chapter 2).

I also hypothesised that post-conflict third-party affiliation would become stronger as rooks and jackdaws reach sexual maturity. It is plausible that mated partners experience an increasing need to coordinate with each other, thus forming a strong social bond, to successfully raise offspring. This is the case with jackdaws where paired birds outrank unpaired birds because of their ability to ally to defend each other and their nest site (Röell 1978). Only the more dominant pairs obtain the best nest sites and, thus, have the best chance of reproductive success (Röell 1978). As well, rank increases with age, which may be evidence that the social bond between mates continues to strengthen

through adulthood (Röell 1978). Mated partner bonds may undergo the greatest change in strength in the developmental stage after pair formation until around the stage of sexual maturity when mates likely experience the largest amount of pressure to establish themselves as a breeding pair. Strengthening the social bond between mates potentially represents an increase in relationship value over this key developmental period because this bond should ultimately incur fitness consequences.

METHODS

Study site

See chapter 2 for details.

Data collection

These data were collected as part of the main post-conflict affiliation study in chapter 3.

Data analysis

Post-conflict affiliation

See chapter 3 for details on post-conflict affiliation analysis for TCTs and selective attraction.

Frequency of affiliation

I examined all third-party affiliative interactions in PCs and MCs to determine whether the frequency of affiliation after conflicts increased at particular ages which may allow me to determine the onset of post-conflict affiliative behaviour. Since I used the same data set in chapter 3, I refer to the GLMM analysis in chapter 3 to discuss the role age played in the models of best fit (Table 3.5).

Duration of affiliation

This analysis was the same as stated above for the frequency of affiliation, using the data presented in Table 3.6 in chapter 3 to discuss the role of age on the duration of affiliation.

RESULTS

Triadic contact tendencies

To investigate the ontogeny of third-party affiliation using affiliation latencies, I compared TCTs at ages one, two, and three for rooks and jackdaws. Jays were excluded from this analysis, as they were in chapter 3, because there were only four attracted PC-MC pairs, which is too small of a sample size to further break down by age, affiliation initiator, affiliation type, and relationship with the individual one is engaging in affiliation with. Rook TCTs were zero (indicating neither avoidance nor attraction between former combatants and third-parties) or negative (indicating avoidance) at age one; even more negative at age two (avoidance), however a very positive TCT occurred for active affiliation showing attraction between former combatants and third-parties; and around zero or slightly positive at age three (no avoidance or attraction; Table 4.1). If post-conflict third-party affiliation occurs in rooks, I would expect it to happen at age two involving only close contact (active affiliation), which will be confirmed if selective attraction is shown (below). Examining the jackdaw TCTs showed values around zero at ages one and three, indicating neither attraction nor avoidance between former combatants and third-parties, however age two showed very negative TCTs for all and active affiliation (avoidance), yet a positive TCT (attraction) for passive affiliation which may indicate some post-conflict third-party affiliation according to affiliation latencies (Table 4.1).

Table 4.1. Mean triadic contact tendencies per bird across ages for rooks and jackdaws. Bold text indicates that post-conflict third-party affiliation may occur.

Age	Affiliation Type	Rook	Jackdaw
1	All	-0.17	0.06
	Active	-0.01	-0.07
	Passive	0.02	0.09
2	All	-0.26	-0.37
	Active	0.35	-0.16
	Passive	-0.26	0.15
3	All	0.00	0.009
	Active	0.11	0.07
	Passive	0.004	-0.03

Selective attraction?

Post-conflict third-party affiliation was not shown in rooks when analysing first affiliative contacts in PCs versus MCs by age and affiliation type. There were no significant differences between the proportion of attracted and dispersed PC-MC pairs (Figure 4.1; Bonferroni correction applied to 9 tests, therefore a result would be significant at the $\alpha=0.05$ level if $p<0.006$; Wilcoxon signed ranks test: *age 1* all affiliation: $V=13.5$, $N=10$, $p=0.30$, 95% confidence interval= $-0.05-0.03$; active affiliation: $V=19$, $N=6$, $p=0.43$, 90% CI= $-0.03-0.06$; passive affiliation: $V=21$, $N=11$, $p=0.90$, 95% CI= $-0.05-0.03$; *age 2* all affiliation: $V=21.5$, $N=6$, $p=0.31$, 95% CI= $-0.07-0.02$; active affiliation: $V=15$, $N=6$, $p=0.05$, 60% CI= $-0.04-0.07$; passive affiliation: $V=21.5$, $N=6$, $p=0.31$, 95% CI= $-0.07-0.02$; *age 3* all affiliation: $V=24.5$, $N=11$, $p=0.80$, 95% CI= $-0.04-0.05$; active affiliation: $V=21.5$, $N=9$, $p=0.67$, 95% CI= $-0.04-0.07$; passive affiliation: $V=27.5$, $N=11$, $p=0.58$, 95% CI= $-0.02-0.04$). These results are consistent with those found in chapter 3 when all age data were lumped together and selective attraction was investigated at the broader level.

There was no post-conflict third-party affiliation according to the latency of first affiliation for jackdaws. There were no significant differences between the proportion of attracted and dispersed PC-MC pairs (Bonferroni correction applied to 9 tests, therefore a result would be significant at the $\alpha=0.05$ level if $p<0.006$; Wilcoxon signed ranks test: *age 1* all affiliation: $V=36$, $N=9$, $p=0.82$, 95% confidence interval= $-0.04-0.06$; active affiliation: $V=36.5$, $N=7$, $p=0.78$, 95% CI= $-0.04-0.06$; passive affiliation: $V=26.5$, $N=10$, $p=0.96$, 95% CI= $-0.06-0.06$; *age 2* all affiliation: $V=28$, $N=6$, $p=0.22$, 95% CI= $-0.05-0.02$; active affiliation: $V=14$, $N=6$, $p=0.33$, 90% CI= $-0.05-0.03$; passive affiliation: $V=50$, $N=9$, $p=0.78$, 95% CI= $-0.05-0.05$; *age 3* all affiliation: $V=42.5$, $N=10$, $p=0.41$, 95% CI= $-0.02-0.04$; active affiliation: $V=30.5$, $N=10$, $p=0.36$, 95% CI= $-0.02-0.04$; passive affiliation: $V=31.5$, $N=10$, $p=0.71$, 95% CI= $-0.04-0.04$). These results are consistent with those found in chapter 3 when all age data were lumped together.

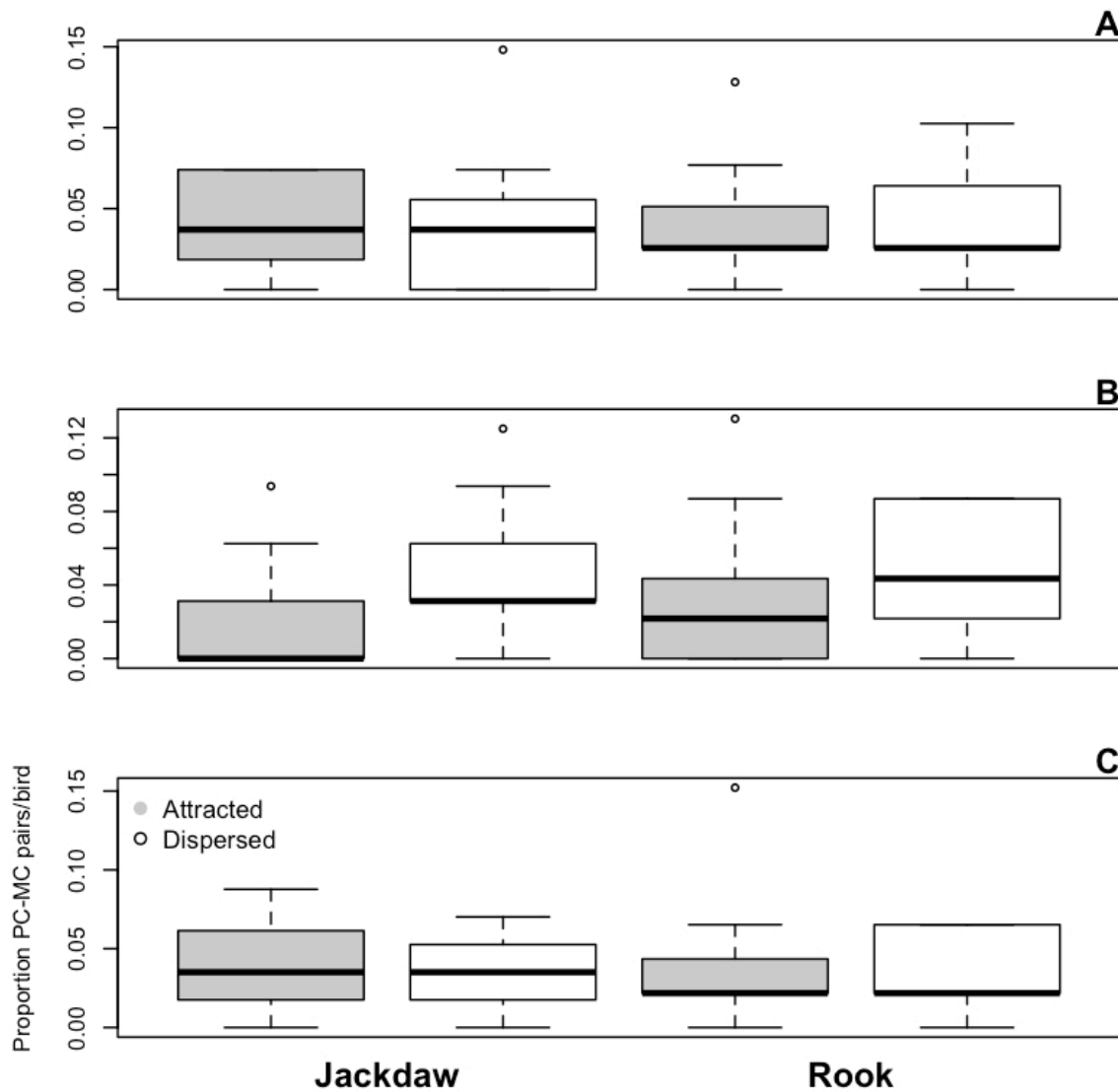


Figure 4.1. The proportion of attracted and dispersed PC-MC pairs at ages 1 (A), 2, (B), and 3 (C) for jackdaws and rooks.

A GLMM was applied to those PC-MC pairs that were attracted to determine whether certain types of affiliation might increase the number of attracted pairs such that post-conflict third-party affiliation might be exhibited and further explored. However, the model of best fit for both rooks and jackdaws was the null model, meaning that the most parsimonious model was the one without any explanatory variables, thus none of the explanatory variables significantly increase the proportion of attracted PC-MC pairs (Table 4.2). Therefore, post-conflict third-party affiliation was not found in any category of affiliation when comparing latencies of first affiliation in PCs and MCs across ages. This is the same result as in chapter 3 which omitted the age variable.

Table 4.2. GLMM results for rooks and jackdaws to determine whether selective attraction (affiliating sooner in PCs rather than MCs) occurred more for particular classes of affiliation. Interactions were omitted for brevity from models that were not the most parsimonious.

Model	Form	Estimate	Standard Error	delta AIC [AIC]
Rook	Intercept only Subject (random factor)	-3.55 1.28e-21	0.60 3.58e-11	0 [7]
	Intercept` Age Subject (random factor)	-3.28 -0.14 0.00	1.54 0.73 0.00	2 [9]
	Intercept` Age Combatant-initiated Affiliation type: all Affiliation type: passive Partner Subject (random factor)	-3.24 -0.49 -8.29 -0.32 -0.15 5.12 0.00	27.49 12.59 372.26 28.35 28.00 215.00 0.00	43 [50]
Jackdaw	Intercept only Subject (random factor)	-3.29 0.00	0.51 0.00	0 [8]
	Intercept` Age Subject (random factor)	-3.38 0.04 2.10e-16	1.38 0.63 1.44e-8	2 [10]
	Intercept` Age Combatant-initiated Affiliation type: all Affiliation type: passive Partner Aggressor Subject (random factor)	-2.17 -0.70 -4.16 0.07 -2.32 -21.23 -5.37 0.00	27.60 10.64 193.50 34.04 35.30 354.2 324.30 0.00	90 [98]

The lack of selective attraction in any species renders their TCTs insignificant: affiliation would need to have occurred sooner in a higher proportion of PCs for the TCTs to be functional indicators of post-conflict third-party affiliation.

Frequency of affiliation

Because the data used in this chapter are the same as that in chapter 3, age was included in the model selection process in chapter 3 (Table 3.5) to determine whether it played a role in the model of best fit. According to the model selection process in Table 3.5, the most parsimonious model for rooks and jays did not include age when examining the frequency of affiliation in PCs versus MCs across ages. Therefore, I conclude that post-conflict third-party affiliative behaviour is independent of age in these species.

In contrast, age was an important factor in the jackdaw model of best fit when examining the frequency of affiliation (Table 3.5 in chapter 3). Their most parsimonious model included treatment and age: as age increased, the frequency of affiliation in PCs increased relative to the frequency of affiliation in MCs (Figure 4.2, Table 3.5). Thus, post-conflict third-party affiliation becomes stronger as jackdaws go from the pair formation stage to sexual maturity.

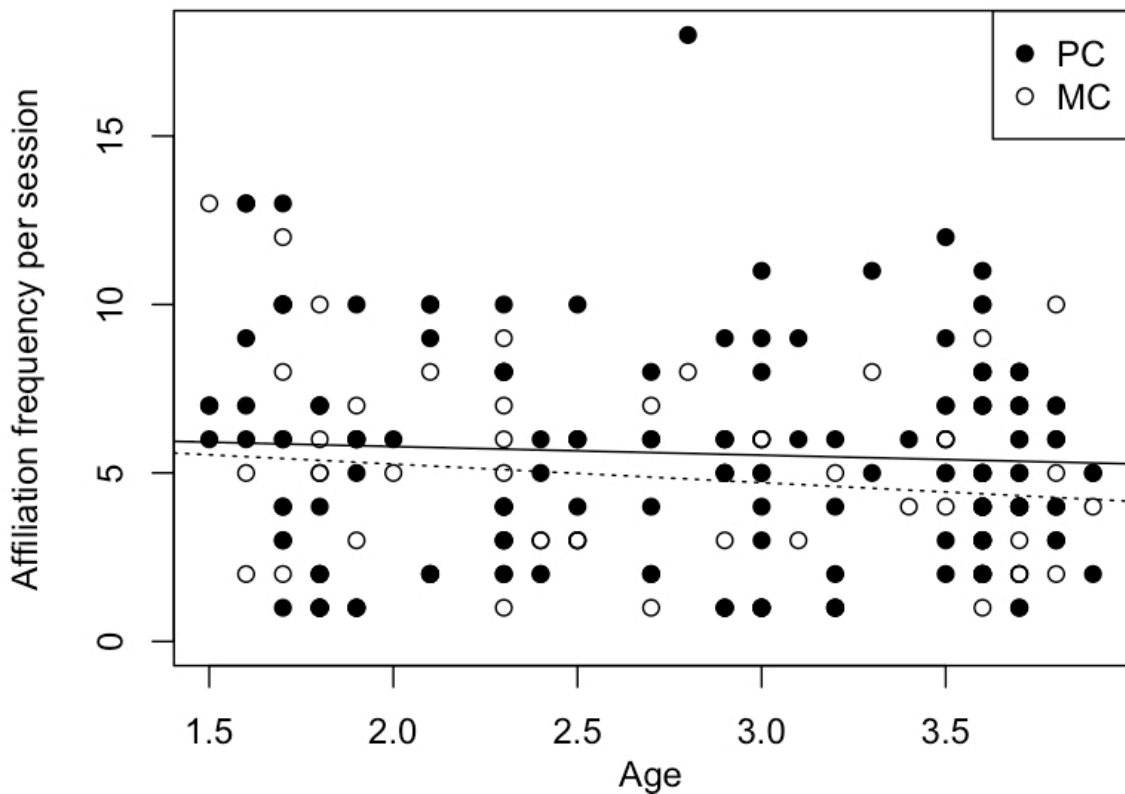


Figure 4.2. The total frequency of affiliation per session (PC or MC) across age for jackdaws.

Duration of affiliation

Using the models from chapter 3, which contain the model of best fit for the duration of affiliation in PCs versus MCs, age is a factor in the most parsimonious model for all species (Figure 4.3; Table 3.6 in chapter 3). While affiliation durations for rooks increased after conflicts versus in matched controls, the duration of affiliation slightly decreased over time when accounting for age relative to the equivalent interaction in MCs. This indicates that longer affiliative contact becomes less important as they develop from juveniles to adults.

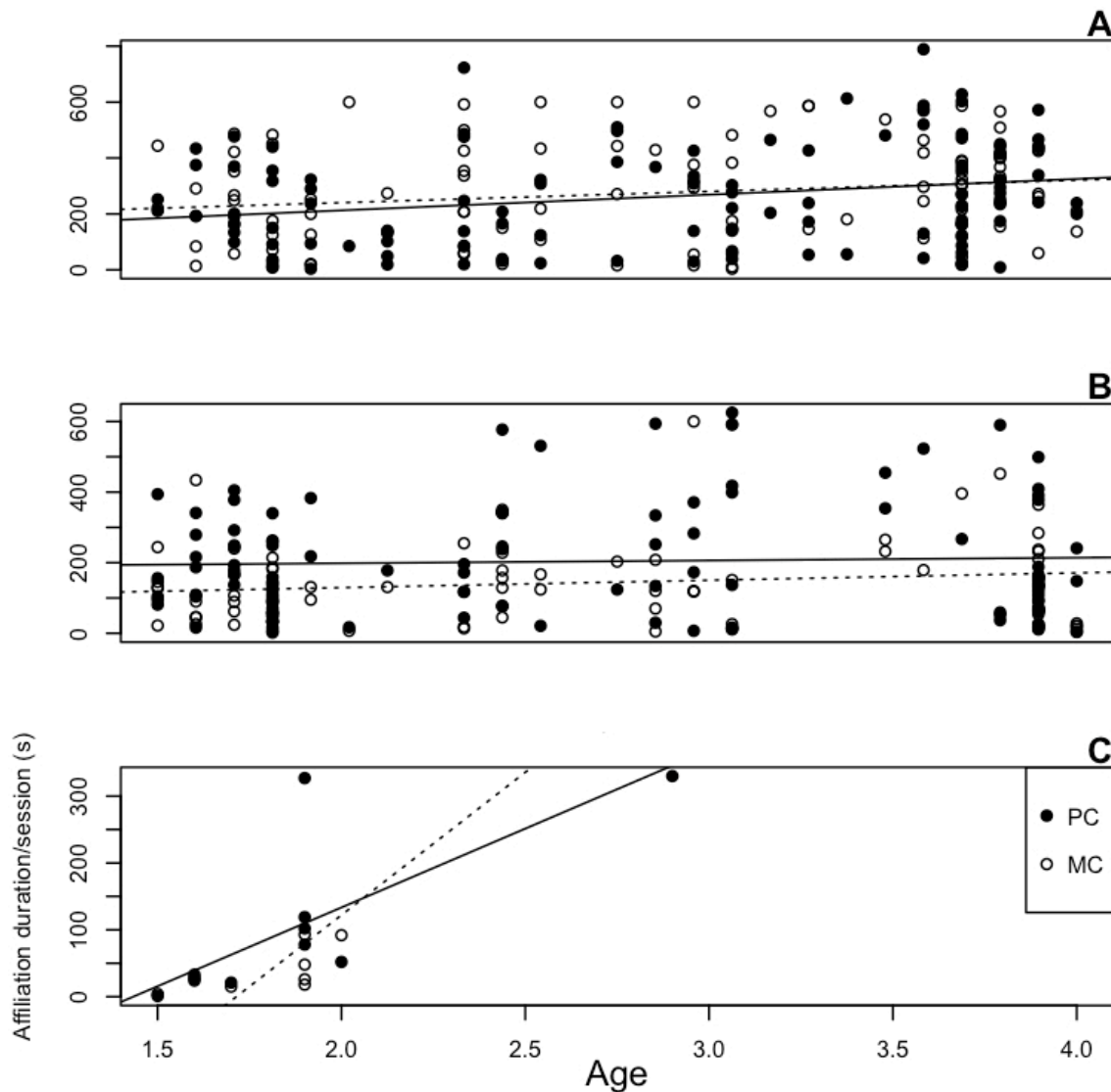


Figure 4.3. The total duration of affiliation per session (PC or MC) across age for jackdaws (A), rooks (B), and jays (C).

While jackdaw affiliation durations were shorter in PCs than in MCs, the duration of affiliation increased with age in both PCs and MCs (Figure 4.3, Table 3.6 in chapter 3). The increase in affiliation durations for PCs was more than the increase for MCs over time, indicating that longer affiliative contact becomes a more important post-conflict behaviour as juveniles develop into sexually mature adults.

Age was also an important factor in the jay model of best fit when examining the duration of affiliation in PCs versus MCs (Table 3.6 in chapter 3). The duration of affiliation after conflicts decreased with increasing age in their most parsimonious model. It is important to note that this decrease is relative to the duration of affiliation

across age in MCs. Therefore, relative to baseline behaviour, post-conflict affiliation durations decrease over time, indicating post-conflict third-party affiliation becomes less important with age (Figure 4.3).

DISCUSSION

Post-conflict third-party affiliation became stronger as the juvenile jackdaws in this study reached sexual maturity, both in terms of the frequency and duration of affiliation. The already higher frequency of affiliation after conflicts versus in matched controls in jackdaws increased with age. Age did not influence the frequency of affiliation in rooks or jays, and it appeared to decrease the duration of affiliation over time for both of these species.

In chapter 3, jackdaws had shorter durations of affiliative events in PCs when compared with MCs. However, when examining the ontogeny of this behaviour by including age as a factor in the GLMMs, it became clear that durations increased in PCs over time. The conclusion I reached in chapter 3 was that jackdaws may continue to experience stress for the 10-minute observation period and that PC affiliation durations might increase if this observation period is extended to allow time for the higher frequency of affiliation to reduce stress levels. The results from the ontogeny of post-conflict affiliation durations may suggest that post-conflict affiliation becomes more effective over time, requiring fewer events that more effectively reduce the stress induced by the conflict. Sexual maturity is likely a developmental period requiring intensive bonding and alliance formation to increase the pair's chances at reproductive success. Perhaps the increase in jackdaw post-conflict third-party affiliation (frequency and duration) with age was an indication of the pair's need to coordinate actions and enhance their bond to increase their chances of success (Coombs 1978). Nest defence in jackdaws is an extremely competitive activity requiring both partners (Röell 1978). Competition may become particularly intense after reaching sexual maturity when the importance of maintaining a viable nest increases.

The decrease in the duration of affiliation with age in rooks is perhaps due to the odd conflict pattern observed in year three when conflicts were rare outside of the breeding

season (chapter 2). Many conflicts occurred during the breeding season, which involved primarily unpaired females fighting with paired males. Since paired individuals are more likely to engage in post-conflict third-party affiliation (chapter 3), these paired males would be the former combatants that would be more likely to participate in this behaviour. However, paired males guarded their nests while their partners incubated the eggs during the breeding season, which meant that partners were often separated farther than the minimal distance for recording affiliative behaviour. Therefore, affiliative interactions between these paired males and their mates, perhaps decreased in frequency and duration due to his guarding behaviour.

The decrease in the duration of post-conflict third-party affiliation in jays is consistent with my post-hoc hypothesis that this behaviour would decline with age, which is likely due to the lack of conflicts as they aged. Most of the jay conflicts occurred at age 1 (chapter 2), 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.

The sociograms in chapter 2 indicate that the frequency of general affiliation (not specific to post-conflict situations) between mated jackdaw pairs remained constant across the three-year study period, however it is interesting that post-conflict affiliative behaviour became stronger (i.e., higher frequency and duration) for jackdaws over this same period of time. The frequency of general affiliation represents one aspect of relationship quality termed ‘compatibility’, while relationship ‘value’ is based on fitness benefits shared within the dyad (Cords & Aureli 2000). While compatibility remained constant, perhaps the value of the relationship increased over time as individuals approached sexual maturity, which could incur higher fitness benefits if the pair successfully raises offspring at an early age. It is also possible that the higher frequency of post-conflict affiliation indicates that conflicts were more stressful with increasing age as competition for resources (i.e., nest sites) becomes more intense. As well, perhaps there is more of an opportunity for pairs to advertise their alliance to others after conflicts occur if other individuals in the aviary are more attentive to the former

combatants because of the disturbance of the conflict. This could make post-conflict affiliative behaviour more important as juveniles reach sexual maturity if they are to ally to competitively raise their young.

If the presence of post-conflict third-party affiliation is dependent on individuals having a valuable relationship, then this behaviour should be present when mated pairs exist. The rooks and jackdaws were already paired with their mates from the beginning of this study (chapter 2) and post-conflict third-party affiliation with partners was present throughout the study (chapter 3). The prediction that third-party affiliation occurs when pairs are present is supported by the data in this chapter which showed third-party affiliation as increasing with age for jackdaws, and, while it decreased with age for rooks, that it existed at all is evidence that it was present at the beginning of the study. Future research could benefit from investigating the stage before pair formation to determine at what point in the developmental period post-conflict third-party affiliation begins. Post-conflict affiliation may occur in rooks and jackdaws before forming mated pairs at age one because both species form bonds with more than one individual at this stage (de Kort et al. 2006, Emery et al. 2007, von Bayern et al. 2007). The pre-pair developmental stage may show post-conflict former opponent affiliation as well as third-party affiliation since individuals form bonds with more than one individual. I would predict that if post-conflict affiliative behaviour is present at the pre-pair developmental stage, it will be weaker than that shown after mated pairs form since this relationship has more value in terms of direct fitness benefits. The subjects in my study were prevented from raising offspring (i.e., their eggs were pricked with a needle) so I cannot compare changes in post-conflict third-party affiliative behaviour regarding the presence of young and the consequential fitness variation due to these changes. However, this area of research will be an important avenue to pursue.

It is important to note that the presence of post-conflict third-party affiliation contradicts the hypothesis that valuable relationships are needed to produce this behaviour. Jays did not affiliate with former opponents to try to repair the relationship, likely because it was too risky to approach the former combatant. However, they did engage in third-party

affiliation with non-former combatants (though not specifically partners), which could indicate that affiliation may reduce stress.

This study examined the presence of post-conflict third-party affiliation in juveniles and showed that this behaviour strengthens in terms of both post-conflict affiliation measures as mated pairs approach sexual maturity in jackdaws, and weakens in terms of affiliation durations in rooks and jays. It will be important to continue research on the development of both post-conflict third-party and former opponent affiliation to understand what causes this behaviour to appear and how it changes as individuals develop into adults. This will help inform the main body of research on adult post-conflict affiliation through a deeper understanding of the mechanisms by which this behaviour is maintained.

CHAPTER 5: Does post-conflict third-party affiliation reduce aggression and stress?

ABSTRACT

I present two studies examining the potential functions of post-conflict third-party affiliation in rooks and jackdaws. Jays were excluded from this study because their small sample size lacked the power to subset their data. *Study 1* investigates whether conflicts increase non-conflict aggression and if affiliation also increases to potentially reduce this aggression. I hypothesised that non-conflict aggression will increase as a result of the conflict and third-party affiliation will also increase to reduce the aggression. Results showed that post-conflict aggression increased between rook former combatants, and between jackdaw conflict victims and bystanders. Rook aggressors directed aggression toward victims after conflicts, however there was no evidence that affiliation increased in response to the higher aggression levels. Jackdaw bystanders directed aggression toward conflict victims who also did not show an affiliative response. However, there is evidence that post-conflict affiliation functions to reduce aggression in rook aggressors and victims and in jackdaw aggressors: they had less aggression directed toward them when they were affiliating with another versus when they were alone after conflicts, and the frequency of aggression decreased as affiliation durations increased. *Study 2* examines whether high intensity conflicts are more stressful than conflicts of low intensity, and whether conflicts of high intensity have more post-conflict affiliation. Conflicts are known to increase stress in birds and mammals, and it has been shown in chimpanzees that post-conflict affiliation reduces this stress. In this study, bill wiping and self-preening were explored as behavioural indicators of stress to determine whether stress levels vary between high and low intensity conflicts. I induced conflicts to increase the sample size for this study by increasing the foraging competition in the aviary, which was successful for jackdaws, but not for rooks, which were excluded from this study. Results showed that bill wiping increased after conflicts when compared with baseline levels, but there was no difference in bill wiping frequencies after high or low intensity conflicts. Bill wiping appears to be an indicator of stress, but I could not validate whether there were differences in stress levels between high and low intensity conflicts. Post-conflict third-

party affiliation frequencies were also similar after high and low intensity conflicts, which could indicate that either high intensity conflicts do not increase stress or this behaviour has a threshold such that it is present or absent rather than continuous. The overall rate of aggression increased after conflicts in study 2, but not in study 1. Therefore, I conducted post-hoc analyses on the aggression data in study 2, which suggests that affiliation buffers post-conflict aggression for conflict aggressors. The results for both rooks and jackdaws from both studies indicate that post-conflict third-party affiliation may function to buffer post-conflict aggression directed toward conflict aggressors (and victims in the case of the rooks).

GENERAL INTRODUCTION

Because rooks and jackdaws show post-conflict third-party affiliation and have large enough sample sizes to further investigate (chapter 3), in this chapter I examined two of the functions of this behaviour, namely whether post-conflict third-party affiliation functions to reduce post-conflict aggression (study 1: post-conflict aggression), and whether it serves to reduce the stress induced by the conflict for former combatants (study 2: post-conflict stress). I have split this chapter into two parts, which correspond to study 1 and study 2, respectively. In study 1, I investigate the potential function of third-party affiliation to reduce post-conflict aggression using the data set from chapter 3, whereas in study 2, I collected a different set of data to examine the role of post-conflict third-party affiliation in stress reduction. Throughout this chapter, I refer to conflict aggressors (initiators and/or winners of conflicts) as ‘aggressors’ and individuals that initiate non-conflict aggression as ‘initiators of aggression’. In the latter case, non-conflict aggression could be initiated by conflict victims and could occur in MCs as well as PCs.

STUDY 1: POST-CONFLICT AGGRESSION

Introduction

There are several non-mutually exclusive hypotheses for the function of post-conflict third-party affiliation. Seed and colleagues (2007) suggested that there could be several functions for rook post-conflict third-party affiliation. One function might be to signal to other group members which birds are paired, which could assist the pair in

maintaining their dominance rank. Another function might be to maintain long-lasting partnerships: pairs that affiliate more after conflicts may have a longer and more stable relationship. It might also reduce the stress caused by the conflict itself. As well, post-conflict third-party affiliation may function to reduce post-conflict aggression (Fraser & Bugnyar 2010, see Koski & Sterck 2009). After conflicts, non-conflict aggression may be directed to others by former opponents, in which case third-party affiliation can be initiated by bystanders to reduce their chances of becoming a recipient of aggression. Alternatively, aggression can be directed to former opponents by others and here third-party affiliation initiated by the former combatant may reduce the likelihood of receiving this aggression. In either case, affiliation might buffer aggression. Post-conflict aggression between former opponents (renewed aggression) was reduced by combatant-initiated third-party affiliation in sub-adult ravens, indicating a self-protective function for third-party affiliation (Fraser & Bugnyar 2010). Although post-conflict aggression has not been studied in rooks or jackdaws, based on the results for ravens (Fraser & Bugnyar 2010), I predict an increase in renewed aggression between former combatants after conflicts, which may lead to an increase in post-conflict third-party affiliation initiated by former combatants if it is used for self protective purposes (Table 5.1, hypotheses 1 and 2). Third-party affiliation would only be protective if it buffered aggression (i.e., individuals receive aggression when they are alone rather than when they are affiliating with another), therefore I also predict that a reduction in post-conflict aggression will coincide with more post-conflict affiliation (Table 5.1, hypothesis 3).

Table 5.1. Hypotheses and predictions for rooks and jackdaws.

Hypothesis	Predictions
1. Renewed aggression post-conflict	More post-conflict aggression between former opponents
2. Post-conflict third-party affiliation reduces aggression (self protection)	More post-conflict self-initiated aggression before the first affiliative event
3. Post-conflict third-party affiliation buffers aggression	Less post-conflict aggression directed toward former combatants when affiliating with another Less post-conflict aggression when more affiliation

Study 1: Methods

Data were collected as part of the main post-conflict affiliation data set in chapter 3 (see chapter 3 for more details). Aggression data were normally distributed according to the Anderson-Darling normality test ($P > 0.05$), therefore parametric tests were used to analyse the data. To determine whether conflicts increased the rate of non-conflict aggression (displacements and threats) in PCs versus MCs, GLMM analyses were applied. The response variable was the frequency of aggression per session, and the explanatory variables included treatment (MC, PC), role in the conflict (aggressor, victim), as well as treatment and subject as random factors. Analyses were conducted separately according to the initiator of the aggression: combatant-initiated or third-party initiated. The degree to which the first affiliative contact after conflicts reduced the occurrence of aggression was also analysed with a GLMM examining how the frequency of aggression in PCs containing affiliation (total aggressive events per PC; response variable) was influenced by the first affiliative behaviour (after, before), the role in the conflict (aggressor, victim), and the total duration of affiliation for that session (0-600), including subject and affiliation duration as random factors. The base model is indicated by '' to which each other factor level is compared in the results. To test the affiliation buffers aggression hypothesis, two GLMMs were carried out. The first examined the frequency of aggression as influenced by whether the subject was affiliating with another (absent, present), treatment, and role, with subject and treatment as random factors. The second examined the frequency of aggression as influenced by the duration of affiliation, role, and treatment, with subject, treatment, and affiliation duration as random factors.

Study 1: Results

I present the descriptive statistics in Table 5.2 for reference throughout this section.

Table 5.2. Sample sizes for each analysis for PCs and MCs.

Variable	Rooks			Jackdaws		
	Subjects	MC	PC	Subjects	MC	PC
Conflicts	13	108	108	14	116	116
Conflict aggressors	12	-	42	14	-	61
Conflict victims	13	-	66	14	-	54
Sessions with no affiliation	-	-	6	-	-	5
Renewed aggression	13	-	14	14 (study 1) 10 (study 2)	-	18 10
Redirected aggression	13	-	55	14 (study 1) 10 (study 2)	-	49 23

Hypothesis 1: did non-conflict aggression increase after conflicts?

I examined post-conflict aggression rates between former opponents (renewed aggression) and former opponents and third-parties (redirected aggression) for rooks and jackdaws separately according to the initiator of the aggression (self or third-party).

Table 5.3. Rook renewed aggression. The frequency of non-conflict aggression between former combatants after conflicts as influenced by the initiator of aggression.

Model	Form	Estimate	Standard Error	delta AIC [AIC]
1a. Null	Intercept only Subject (random factor) Treatment (random factor)	-1.42 2.05 0.04	0.54 1.43 0.19	17 [70]
1b. Combatant initiated aggression	Intercept` Treatment: PC Role: victim PC*victim Subject (random factor) Treatment (random factor)	-1.04 1.39 -0.15 -19.54 0.12 0.00	0.61 0.65 0.79 3851.23 0.35 0.00	0 [53]
2a. Null	Intercept only Subject (random factor) Treatment (random factor)	-0.16 0.00 0.01	0.17 0.00 0.10	18 [81]
2b. Third-party initiated aggression	Intercept` Treatment: PC Role: victim PC*victim Subject (random factor) Treatment (random factor)	-2.08 0.37 2.00 0.15 0.00 0.00	1.00 1.22 1.04 1.27 0.00 0.00	0 [63]

When considering renewed aggression between former combatants, rook aggressors initiated more post-conflict aggression against conflict victims (Table 5.3, model 1b), which is reflected in the complimentary model that shows that victims received more aggression from former opponents (Table 5.3, model 2b). This shows that rooks have renewed aggression directed from aggressors toward victims (Figure 5.1 A and B).

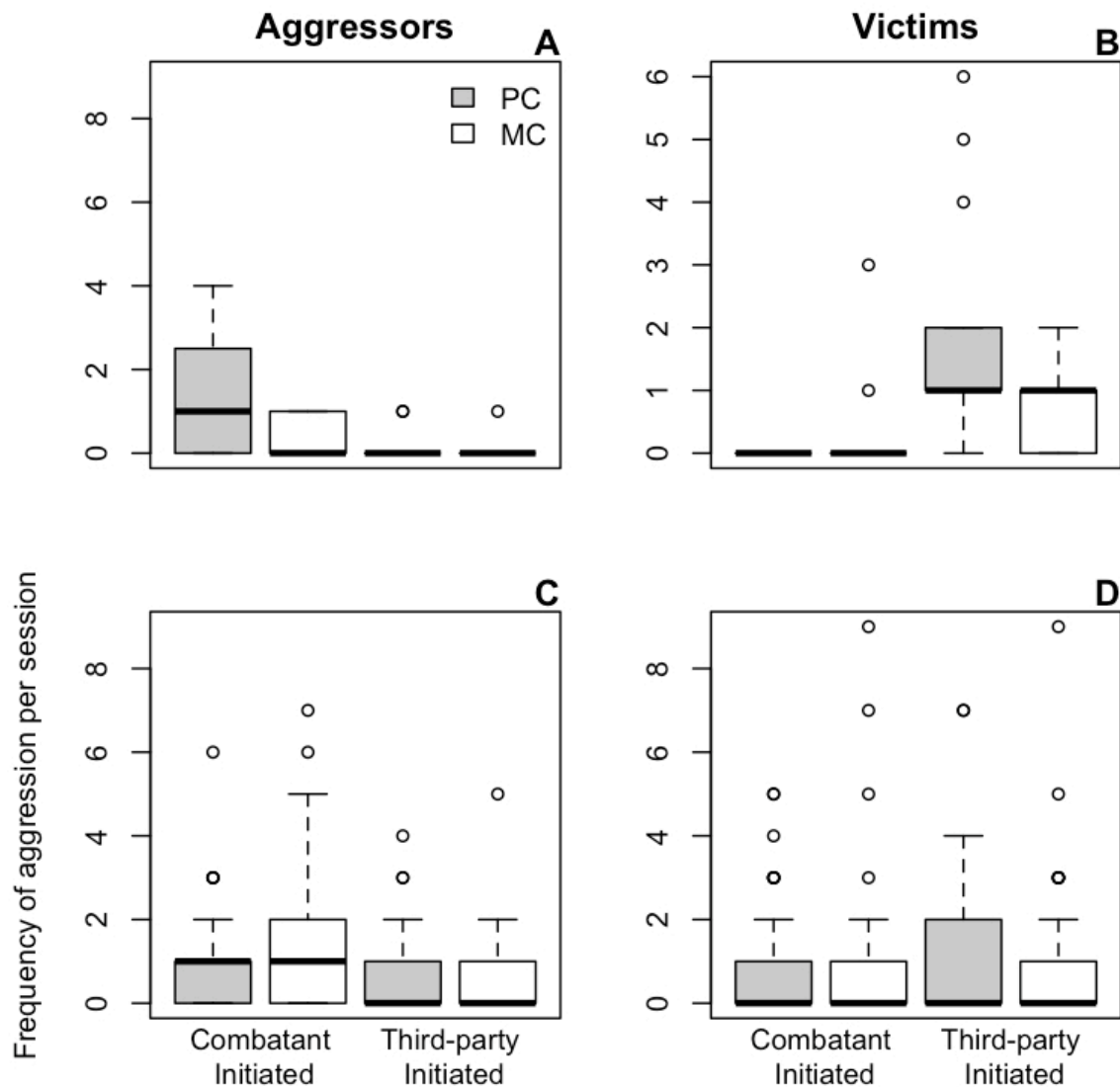


Figure 5.1. Rooks: renewed aggression between former combatants (A and B) and redirected aggression between a former opponent and a bystander (C and D) for aggressors (A and C) and victims (B and D).

Jackdaw former opponents did not have renewed aggression. There were no differences between aggression frequencies between former opponents in PCs versus MCs,

regardless of the role in the conflict or the initiator of aggression (Table 5.4, Figure 5.2 A and B).

Table 5.4. Jackdaw renewed aggression. The frequency of non-conflict aggression between former combatants after conflicts as influenced by the initiator of aggression.

Model	Form	Estimate	Standard Error	delta AIC [AIC]
1a. Null	Intercept only Subject (random factor) Treatment (random factor)	-1.23 0.70 0.20	0.46 0.84 0.45	0 [71]
1b. Combatant initiated aggression	Intercept` Treatment: PC Role: victim PC*victim Subject (random factor) Treatment (random factor)	-1.44 0.92 -0.59 -0.03 0.54 0.00	0.46 0.43 0.70 0.85 0.73 0.00	0 [71]
2a. Null	Intercept only Subject (random factor) Treatment (random factor)	-0.70 0.45 0.00	0.27 0.67 0.00	0 [102]
2b. Third-party initiated aggression	Intercept` Treatment: PC Role: victim PC*victim Subject (random factor) Treatment (random factor)	-0.65 -0.14 -0.57 1.11 0.42 0.00	0.37 0.43 0.56 0.70 0.65 0.00	2 [104]

Concerning redirected aggression, aggression between a former combatant and a third-party, there were no differences between treatments for the frequency of rook aggression, regardless of aggression initiator (Table 5.5, Figure 5.1 C and D). Thus, there is no redirected aggression in rooks.

For jackdaws, aggression did occur between bystanders and conflict victims: a higher frequency of aggression was directed from bystanders toward conflict victims after conflicts than was directed toward conflict aggressors (Table 5.6, model 2b, Figure 5.2 C and D).

Table 5.5. Rook redirected aggression. The frequency of non-conflict aggression between a former combatant and a bystander according to the initiator of aggression.

Model	Form	Estimate	Standard Error	delta AIC [AIC]
1a. Null	Intercept only Subject (random factor) Treatment (random factor)	-0.31 0.40 0.02	0.22 0.63 0.14	0 [342]
1b. Combatant initiated aggression	Intercept` Treatment: PC Role: victim PC*victim Subject (random factor) Treatment (random factor)	-0.08 -0.52 -0.17 0.42 0.40 0.00	0.23 0.21 0.20 0.29 0.63 0.00	1 [343]
2a. Null	Intercept only Subject (random factor) Treatment (random factor)	-0.57 0.80 0.05	0.31 0.89 0.23	0 [301]
2b. Third-party initiated aggression	Intercept` Treatment: PC Role: victim PC*victim Subject (random factor) Treatment (random factor)	-0.73 0.25 -0.07 0.23 0.76 0.00	0.34 0.31 0.29 0.37 0.87 0.00	2 [303]

Table 5.6. Jackdaw redirected aggression. The frequency of non-conflict aggression between a former combatant and a bystander according to the initiator of aggression.

Model	Form	Estimate	Standard Error	delta AIC [AIC]
1a. Null	Intercept only Subject (random factor) Treatment (random factor)	-1.15 0.20 0.00	0.17 0.44 0.00	0 [232]
1b. Combatant initiated aggression	Intercept` Treatment: PC Role: unknown Role: victim PC*unknown PC*victim Subject (random factor) Treatment (random factor)	-1.34 -0.14 -13.26 0.26 14.35 0.41 0.21 0.00	0.27 0.35 1227.05 0.33 1227.05 0.45 0.46 0.00	3 [235]
2a. Null	Intercept only Subject (random factor) Treatment (random factor)	-0.71 0.21 0.00	0.16 0.46 0.00	9 [290]
2b. Third-party initiated aggression	Intercept` Treatment: PC Role: unknown Role: victim PC*unknown PC*victim Subject (random factor) Treatment (random factor)	-0.81 -0.46 2.20 0.17 0.06 0.69 0.21 0.00	0.24 0.31 0.68 0.28 0.97 0.39 0.46 0.00	0 [281]

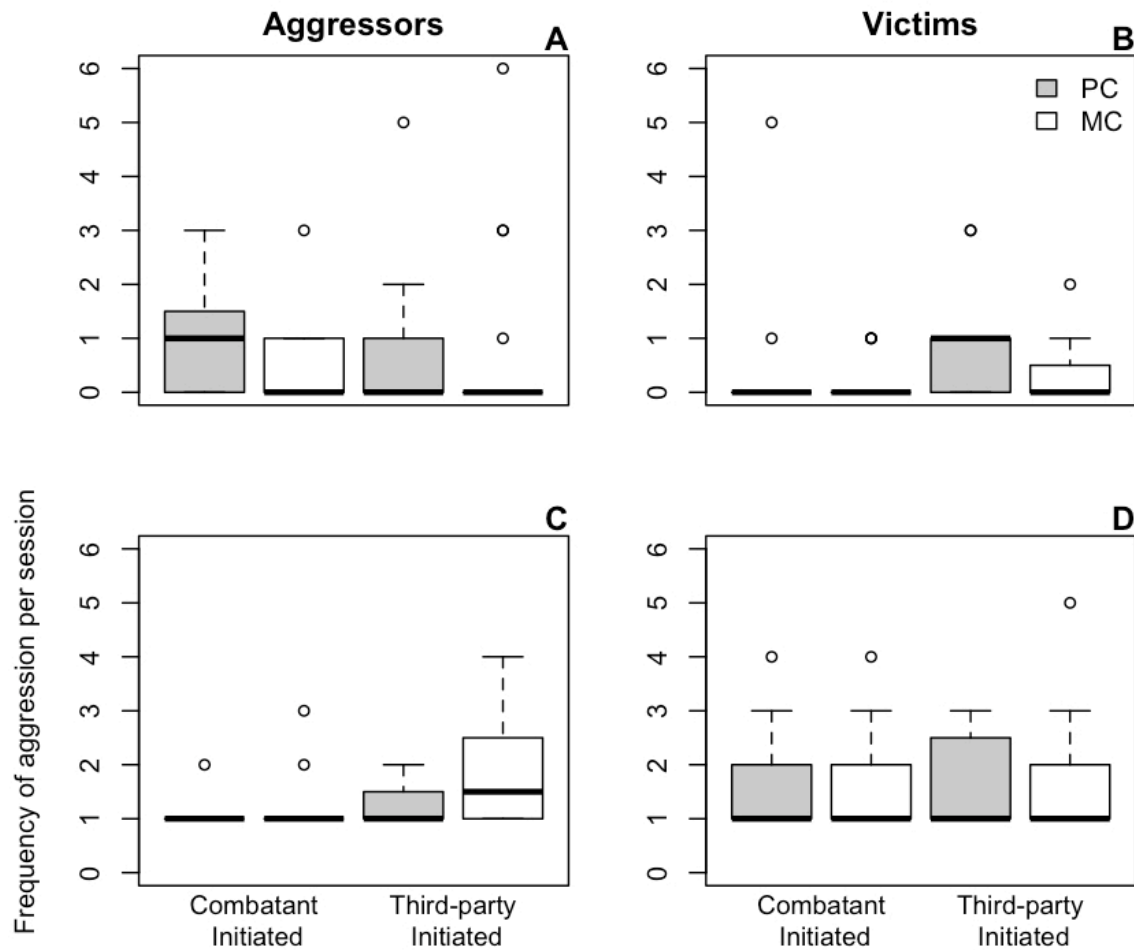


Figure 5.2. Jackdaws: renewed aggression between former combatants (A and B) and redirected aggression between a former opponent and a bystander (C and D) for aggressors (A and C) and victims (B and D). Note: zeros were excluded from C and D to show the GLMM effects which account for variation in subject and treatment.

A post-hoc analysis on the data set from study 2 was conducted on aggression to determine why overall rates of aggression increased after PCs when compared with MCs in study 2, but not in study 1. Part of this analysis included the exploration of whether there were increased rates of aggression between former opponents or between a former combatant and a bystander for comparison with study 1. I present this analysis here to facilitate the ease of making a direct comparison.

In study 2, renewed aggression between jackdaw former opponents occurred for conflict victims who received this aggression from their former opponent (the conflict aggressor; Table 5.7). However, the standard error for these terms in the model were

extremely high, so I conclude that this model is not different from the null model, and that no renewed aggression occurred.

Table 5.7. Jackdaw renewed aggression (data set from study 2). The frequency of non-conflict aggression between former combatants and bystanders according to the initiator of aggression.

Model	Form	Estimate	Standard Error	delta AIC [AIC]
1a. Null	Intercept only Subject (random factor) Treatment (random factor)	-0.83 2.39 0.19	0.83 1.55 0.44	0 [33]
1b. Combatant initiated aggression	Intercept` Treatment: PC Role: victim PC*victim Subject (random factor) Treatment (random factor)	-0.49 0.69 -18.62 18.07 1.09 0.00	0.79 0.62 9028.98 9028.98 1.04 0.00	0 [34]
2a. Null	Intercept only Subject (random factor) Treatment (random factor)	-1.38 0.00 2.21	1.23 0.00 1.49	1 [29]
2b. Third-party initiated aggression	Intercept` Treatment: PC Role: victim PC*victim Subject (random factor) Treatment (random factor)	-19.37 19.08 0.007 0.40 0.00 0.00	11350.00 11350.00 14630.00 14630.00 0.00 0.00	0 [28]

In study 2, there was redirected aggression in jackdaws. Conflict aggressors had higher frequencies of aggression in PCs when compared with MCs and this aggression was combatant initiated and therefore directed at bystanders (Table 5.8). Thus, there is the redirected aggression in this study as well as in study 1, but in this case, it is the conflict aggressor initiating aggression against bystanders, rather than aggression from bystanders to conflict victims.

Table 5.8. Jackdaw redirected aggression (data set from study 2). The frequency of non-conflict aggression between former combatants and bystanders according to the initiator of aggression.

Model	Form	Estimate	Standard Error	delta AIC [AIC]
1a. Null	Intercept only Subject (random factor) Treatment (random factor)	-0.36 0.22 0.17	0.37 0.47 0.41	1 [90]
1b. Combatant initiated aggression	Intercept` Treatment: PC Role: victim PC*victim Subject (random factor) Treatment (random factor)	-1.10 1.25 0.91 -0.56 0.26 0.00	0.54 0.57 0.61 0.68 0.51 0.00	0 [89]
2a. Null	Intercept only Subject (random factor) Treatment (random factor)	-0.17 0.77 0.11	0.40 0.88 0.34	0 [76]
2b. Third-party initiated aggression	Intercept` Treatment: PC Role: victim PC*victim Subject (random factor) Treatment (random factor)	-0.78 0.59 0.52 0.11 0.52 0.00	0.52 0.57 0.56 0.66 0.72 0.00	0 [76]

Hypothesis 2: did post-conflict aggression decrease after affiliation occurred?

I examined the frequency of non-conflict aggression in relation to affiliation by determining whether more aggression occurred before or after the first affiliative contact in PCs for former combatants that initiated the post-conflict aggression. If aggression after the first affiliative event is lower than before the first affiliative event, then it might suggest that affiliation acts to reduce this aggression. However, the effect of the first affiliative contact on aggression may not be enough to reduce aggression if the event is short or no further affiliation occurs in the PC. Results show that rook and jackdaw aggressors initiated more aggression after the first affiliative event rather than before (Tables 5.9 and 5.10).

Table 5.9. Rooks: frequency of former combatant initiated aggression before or after first affiliative contact in PCs.

Model	Form	Estimate	Standard Error	delta AIC [AIC]
Null	Intercept only Affiliation duration (random factor) Subject (random factor)	-1.78 1.25 0.90	0.32 1.12 0.95	140 [493]
Combatant initiated aggression	Intercept` Aggression before first affiliation Role: victim Affiliation duration Before*victim Before*affiliation duration Victim*affiliation duration Before*victim*affiliation duration Affiliation duration (random factor) Subject (random factor)	-1.04 -1.62 0.00 0.00 0.00 -0.003 0.00 0.00 1.20 1.00	0.42 0.58 0.27 0.001 0.81 0.003 0.001 0.004 1.09 1.00	0 [353]

Table 5.10. Jackdaws: frequency of former combatant initiated aggression before or after first affiliative contact in PCs.

Model	Form	Estimate	Standard Error	delta AIC [AIC]
Null	Intercept only Affiliation duration (random factor) Subject (random factor)	-2.63 3.35 0.59	0.31 1.83 0.76	144 [526]
Combatant initiated aggression	Intercept` Aggression before first affiliation Role: unknown Role: victim Affiliation duration Before*unknown Before*victim Before*affiliation duration Unknown*affiliation duration Victim*affiliation duration Before*unknown*affiliation duration Before*victim*affiliation duration Affiliation duration (random factor) Subject (random factor)	-2.38 -0.51 0.00 0.00 0.001 0.00 0.00 -0.007 0.00 0.00 0.00 0.00 3.30 0.58	0.50 0.61 0.36 0.36 0.001 0.84 0.84 0.003 0.001 0.001 0.004 0.004 1.82 0.76	0 [382]

Hypothesis 3: did post-conflict affiliation buffer aggression?

To examine whether post-conflict third-party affiliation might buffer aggression, I analysed whether aggression against former combatants occurred more when they were alone rather than when they were affiliating with another in both PCs and MCs. I also analysed the total duration of affiliation (affiliative behaviours are usually states) and the frequency of aggression (aggressive behaviours are usually events) per session to

determine whether an decrease in the frequency of aggression is correlated with an increase in the total amount of time spent affiliating in that session.

Both rook and jackdaw conflict aggressors received less aggression after conflicts when they were affiliating with another rather than when they were sitting alone (Figure 5.3, Tables 5.11 and 5.12). In contrast, victims of both species received more aggression when they were affiliating with another after conflicts than they did when they were sitting alone (Figure 5.3, Tables 5.11 and 5.12). Thus, affiliation appears to buffer aggression for conflict aggressors, but not for victims. The act of affiliating may reduce aggression such that post-conflict third-party affiliation could serve a self-protective function after conflicts.

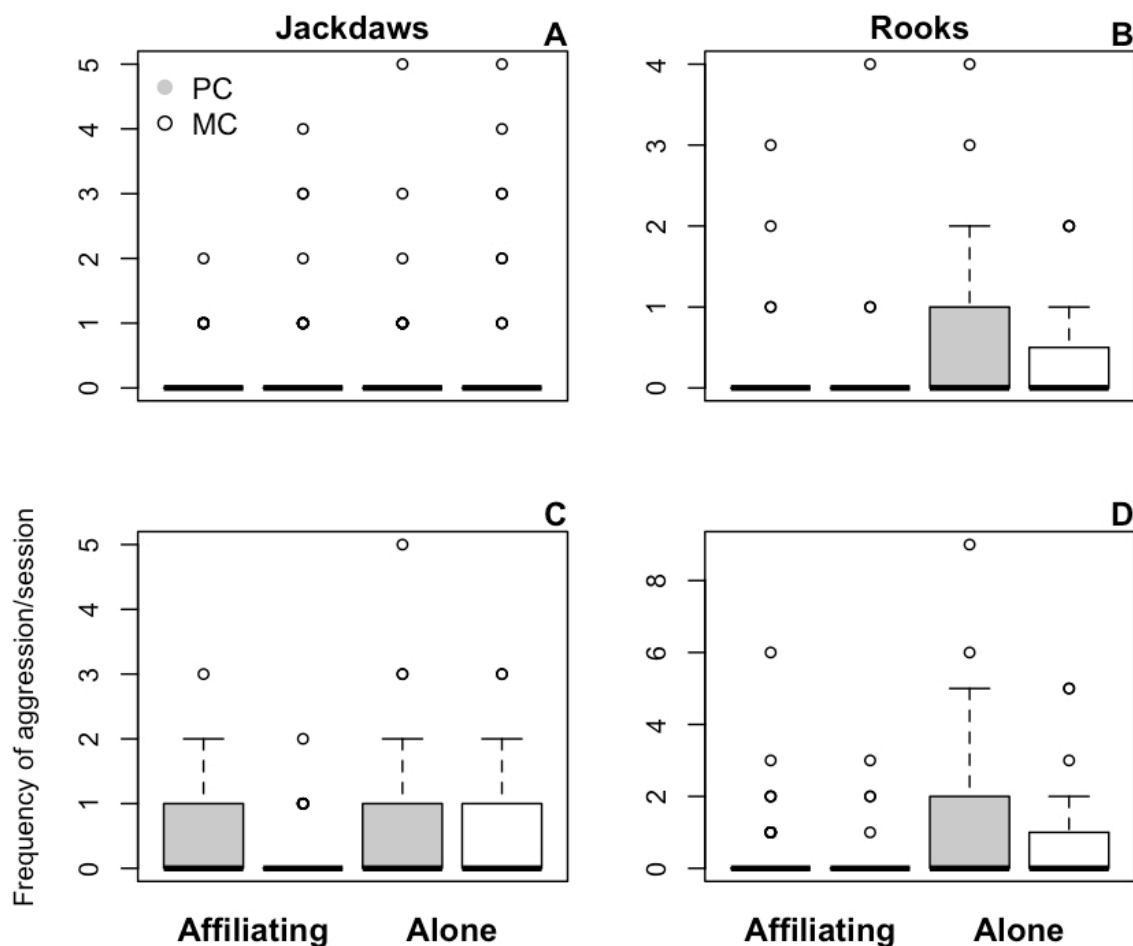


Figure 5.3. The total frequency of post-conflict third-party initiated aggression per session (PC or MC) for conflict aggressors (A and B) and victims (C and D) when jackdaw (A and C) and rook (B and D) former combatants were affiliating with another versus when they were alone.

Table 5.11. Rook frequency of aggression when affiliating with another (present) or alone according to treatment and role for former combatants that were recipients of aggression.

Model	Form	Estimate	Standard Error	delta AIC [AIC]
Null	Intercept only Subject (random factor) Treatment (random factor)	-1.03 0.52 0.12	0.33 0.72 0.34	40 [513]
Third-party initiated aggression	Intercept` Aggression when affiliating: present Treatment: PC Role: victim Present*PC Present*victim PC*victim Present*PC*victim Subject (random factor) Treatment (random factor)	-1.04 -0.77 0.33 0.17 -0.23 -0.55 0.40 0.46 0.44 0.00	0.34 0.50 0.36 0.34 0.66 0.34 0.42 0.81 0.66 0.00	0 [473]

Table 5.12. Jackdaw frequency of aggression when affiliating with another (present) or alone according to treatment and role for former combatants that were recipients of aggression.

Model	Form	Estimate	Standard Error	delta AIC [AIC]
Null	Intercept only Subject (random factor) Treatment (random factor)	-1.07 0.11 0.00	0.12 0.34 0.00	7 [516]
Third-party initiated aggression	Intercept` Aggression when affiliating: present Treatment: PC Role: victim Present*PC Present*victim PC*victim Present*PC*victim Subject (random factor) Treatment (random factor)	-0.97 -0.10 -0.17 0.23 -0.45 -1.00 0.33 1.11 0.10 0.00	0.23 0.31 0.32 0.29 0.49 0.50 0.41 0.69 0.31 0.00	0 [509]

Table 5.13. Rook frequency of aggression and duration of affiliation according to treatment for former combatants that were recipients of aggression.

Model	Form	Estimate	Standard Error	delta AIC [AIC]
Null	Intercept only	-0.73	0.26	23 [351]
	Affiliation duration (random factor)	0.85	0.92	
	Subject (random factor)	0.53	0.73	
	Treatment (random factor)	0.02	0.14	
Third-party initiated aggression	Intercept`	-0.90	0.58	0 [328]
	Role: victim	0.01	0.58	
	Affiliation duration	-0.002	0.003	
	Treatment: PC	0.23	0.69	
	Victim*affiliation duration	0.003	0.003	
	Victim*PC	0.60	0.76	
	Affiliation duration*PC	0.001	0.003	
	Victim*affiliation duration*PC	-0.003	0.004	
	Affiliation duration (random factor)	0.84	0.92	
	Subject (random factor)	0.45	0.67	
	Treatment (random factor)	0.00	0.00	

Table 5.14. Jackdaw frequency of aggression and duration affiliative contact according to treatment for former combatants that were recipients of aggression.

Model	Form	Estimate	Standard Error	delta AIC [AIC]
Null	Intercept only	-0.84	0.12	11 [330]
	Affiliation duration (random factor)	1.12	1.06	
	Subject (random factor)	0.00	0.00	
	Treatment (random factor)	0.00	0.00	
Third-party initiated aggression	Intercept`	-0.45	0.38	0 [319]
	Role: victim	0.26	0.50	
	Affiliation duration	-0.001	0.001	
	Treatment: PC	0.58	0.58	
	Victim*affiliation duration	-0.001	0.001	
	Victim*PC	-0.40	0.73	
	Affiliation duration*PC	-0.004	0.002	
	Victim*affiliation duration*PC	0.005	0.003	
	Affiliation duration (random factor)	0.87	0.93	
	Subject (random factor)	0.00	0.00	
	Treatment (random factor)	0.00	0.00	

The frequency of aggression and the duration of affiliation were inversely correlated for rook conflict victims and jackdaw conflict aggressors who received less aggression in PCs when there were longer durations of affiliation as predicted if affiliation serves to reduce aggression (Tables 5.13 and 5.14). In contrast, the frequency of aggression increased with increasing affiliation durations for rook aggressors and jackdaw victims.

Study 1: Discussion

The overall frequency of aggression between PCs and MCs was similar, however post-conflict aggression did increase for two categories of individuals. Aggression increased after conflicts when compared with matched controls for rook former opponents (directed from aggressors to victims) and for jackdaw victims (directed from bystanders to victims), therefore post-conflict third-party affiliation could have been used to reduce post-conflict aggression in these cases (Table 5.15).

Table 5.15. Study 1: does post-conflict third-party affiliation reduce post-conflict aggression? Hypotheses, predictions, and results for rooks and jackdaws.

Hypothesis	Predictions	Results	
		Rooks	Jackdaws
1. Renewed aggression post-conflict	More post-conflict aggression between former opponents	Yes aggressor to victim	X (yes redirected: bystander to victim, or aggressor to bystander)
2. Post-conflict third-party affiliation reduces aggression	Less post-conflict self-initiated aggression after the first affiliative event	X	X
3. Post-conflict third-party affiliation buffers aggression	Less post-conflict aggression directed toward former combatants when affiliating with another Less post-conflict aggression when more affiliation	Yes aggressor	Yes aggressor
		Yes aggressor/victim	Yes aggressor

Comparing this study to the one on ravens (Fraser & Bugnyar 2010), which my predictions for rooks and jackdaws were based on, rooks and ravens both have renewed aggression between former combatants (directed from aggressors to victims), but jackdaws do not. Raven conflict victims increased their probability of initiating post-conflict third-party affiliation after engaging in renewed aggression with former combatants, and post-conflict aggression decreased after initiating this affiliation (Fraser & Bugnyar 2010). This indicates that ravens may use post-conflict third-party affiliation for self protection. Rooks, however, did not have decreased frequencies of aggression after affiliation occurred. Instead, rook conflict aggressors decreased aggression after conflicts when they were affiliating with another individual, and both

aggressors and victims decreased aggression when the total amount of time spent affiliating increased. This suggests that rooks use affiliation for similar purposes as ravens: to buffer aggression. However, the first affiliative contact is not a good indicator of this buffer for rooks. Because victims received more aggression from conflict aggressors after fights, it is the victims that should be using third-party affiliation as a buffer to reduce aggression, however this does not occur. Instead, it is the aggressors to which the buffer hypothesis applies. This could indicate that aggressors have a stronger bond with their partners (with whom most of the affiliation is occurring) than victims do: if victims are more often single birds, then they would have no one to affiliate with. Aggressors and their partners may also outrank victims and the victims partner. Post-conflict third-party affiliation occurs more frequently in victims (chapter 3), thus perhaps third-party affiliation reduces their stress since they are not able to buffer the aggression. For the aggressors, who also had third-party affiliation, it may serve to maintain dominance status by reinforcing their rank through continued aggression against the victim and by affiliating with their mate to display this alliance.

There is also evidence that post-conflict affiliation buffers aggression in jackdaw conflict aggressors. However, aggression in jackdaws is different from rooks and ravens: instead of renewed aggression between former opponents, jackdaw aggressors direct higher rates of aggression to bystanders, and bystanders direct more aggression to victims after conflicts. Aggression rates before and after their first affiliative contact also do not show any differences. Evidence for the buffer hypothesis comes in the same form as in the rooks: there is less aggression directed toward conflict aggressors when they are affiliating with another. Again, this applies only to conflict aggressors when it is the victims that actually receive higher rates of aggression after conflicts. Post-conflict affiliation results from chapter 3 indicate that both aggressors and victims had similar amounts of third-party affiliation, suggesting that third-party affiliation could function differently for each role. Perhaps aggressors reduce their risk of attack to reinforce their win, while victims may reduce stress.

STUDY 2: POST-CONFLICT STRESS

Introduction

If a conflict is stressful, then former combatants can benefit from post-conflict affiliation if its function is to reduce stress. Social conflicts cause stress in great tits as shown through an increase in corticosterone from cloacal fluids after such conflicts (Carere et al. 2003). Corticosterone is a hormone that is released after stressful events, which acts to enable the animal to respond to the stress (Wingfield et al. 1995). Although studies are rare, post-conflict third-party affiliation has been shown to reduce post-conflict stress. Third-party affiliation reduces post-conflict stress for conflict victims in chimpanzees as shown by reduced self-directed behaviours indicative of elevated stress levels after affiliation (scratching and grooming; Fraser et al. 2008b). Chimpanzees also show bystander initiated third-party affiliation more frequently after conflicts of longer durations, which presumably increase stress levels more than shorter conflicts (Wittig & Boesch 2003). This suggests that chimpanzees use post-conflict third-party affiliation to reduce the stress that was induced by the conflict. While post-conflict third-party affiliation is usually only investigated for conflict victims, it is reasonable to assume that conflicts increase stress for both former combatants, thus both could benefit from stress reduction behaviour.

I investigate the role of conflict intensity on post-conflict affiliative behaviour in jackdaws in this study. Conflict intensity varies from low intensity (e.g., one bird pecks and chases another; a quick interaction) to high intensity (e.g., two birds wrestle on the ground while scratching, pecking, and vocalising, sometimes lasting around 20 seconds). It is possible that conflict intensities may differentially influence stress levels, with higher intensity conflicts being more stressful, as Wittig and Boesch (2003) found using conflict durations. To increase the number of conflicts for this study, I increased the foraging competition in the aviary to induce conflicts, which was successful in jackdaws, but not in rooks, thus only the jackdaws were included.

First, because it was not possible to collect physiological data on jackdaw stress levels, I investigated bill wiping and self-preening as potential behavioural indicators of stress to validate whether there were differences in stress between low and high intensity conflicts (Table 5.16, hypothesis 4). Bill wiping has been shown to increase in frequency in response to aversive conditions in chickens (Summers et al. 2003).

However, the frequency of bill wiping did not change with increasing corticosterone levels in zebra finches (Wada et al. 2008), which suggests there is variation regarding whether bill wiping is indicative of physiological stress. There is also evidence that the frequency of self-preening increases under stress (removal of eggs from the nest) in black-headed gulls (Moynihan 1953). While these behaviours may not be the most reliable indicators of stress, no other behaviours have been experimentally tested in this context in birds.

Second, I investigated whether post-conflict third-party affiliation varied with conflict intensity. If higher intensity conflicts are more stressful than those of lower intensity, I predict that post-conflict third-party affiliation frequencies will increase after conflicts of high intensity if the function of the affiliation is to reduce stress (Table 5.16, hypothesis 5).

Table 5.16. Hypotheses and predictions for jackdaws.

Hypothesis	Predictions
4. Self directed behaviour indicates stress	More bill wiping and/or preening after conflicts compared with matched controls More bill wiping and/or preening after high intensity conflicts
5. Post-conflict third-party affiliation increases with increasing stress	More post-conflict third-party affiliation after high intensity conflicts
6. Post-hoc: post-conflict third-party affiliation reduces aggression	Less post-conflict aggression before the first affiliative contact than after
7. Post-hoc: post-conflict third-party affiliation buffers aggression	Less post-conflict aggression directed toward former combatants when affiliating with another Less post-conflict aggression when more affiliation

Finally, there was a higher frequency of aggression in PCs when compared with MCs in this study, whereas there was no difference in study 1 when comparing overall rates. I conducted post-hoc analyses to explore why this might have occurred, hypothesising that aggression might have increased because of increased stress levels and that post-conflict third-party affiliation might reduce this aggression (Table 5.16, hypotheses 6 and 7).

Study 2: Methods

All data were collected outside of the breeding season (18 January-5 March 2010 and 11-30 October 2010) between 10:00 to 13:15 from observation huts adjacent to the aviaries. Data were collected using The Observer XT 7.0 and 9.0 (Noldus Information Technologies). Post-conflict affiliation data were collected using the PC-MC (Post-conflict-Matched Control) method (de Waal and Yoshihara 1983) with 27 PC-MC pairs (81 total hours of observation; see chapter 3 for more details on this method) distributed among 10 individuals (range: 1-7 PC-MC pairs per bird, mean: 2.4). Data were collected on all behaviours and their directions during PCs and MCs (see ethogram in chapter 2).

To induce conflicts and increase the sample size for the short duration of this study, I experimentally increased stress levels in the aviary by increasing foraging competition. To determine which high value foods would provoke the conflicts, a pilot project was conducted to examine the effect of high value food on conflict rates. High value food consisted of suet blocks filled with nuts, insects, or fruit (Dawn Chorus Wild Bird Fat Feast by Bulldog Products Ltd.). One block of suet was placed on or by the feeding table for one hour in which I observed subjects. Suet successfully increased conflict rates and aggression in jackdaws.

To increase foraging competition in the aviary during the course of this study, I placed one block of suet in the aviary for one hour after a period of food deprivation. Food deprivation lasted between one and three hours. At first, one hour of deprivation was used, then two hours, and then three hours. The three hour period was more effective at inducing conflicts and was used consistently after the first couple of days of the experiment. Observation sessions lasted one hour in the presence of the high value food. At the end of the hour, the experiment concluded and subjects were fed their regular maintenance diet. Post-conflict sessions were conducted during the one hour observation period in which there was increased foraging competition. Matched controls were conducted on days when there was no food deprivation or high value food item in the aviary: it was a day with regular maintenance diet dispersed throughout the aviary and available at all times.

All data were analysed with the statistical software R (R Development Core Team 2011). Data were Poisson distributed and a mix of normal and non-normal distributions according to the Anderson Darling normality test ($P > 0.05$ and $P < 0.05$ respectively), therefore non-parametric tests (two-tailed) were used for analyses to make results comparable. However, residuals were normally distributed, therefore GLMMs were applied in most cases. Akaike's Information Criterion (AIC) was used for model selection (Anderson and Burnham 2002). As in chapters 3 and 4, post-conflict affiliation data were analysed according to the frequency of affiliation in PCs versus MCs per individual using a GLMM with a log link. The timing (after or before first affiliative contact) and frequency of aggression were examined according to the influence of treatment (MC, PC), role in the conflict (aggressor, victim), affiliation duration, and initiator of the affiliation (self, third-party), as well as subject, affiliation duration, and treatment as random factors.

The frequency of bill wiping was also investigated using GLMMs. The response variable was the frequency of bill wiping per session, and explanatory variables included conflict intensity (high, low), timing around first affiliative contact (after, before), and timing before and after all affiliative contact (after last affiliative contact, before first affiliative contact) with subject and affiliation duration as random factors.

Study 2: Results

I present a summary of the sample sizes used in the analyses in this study (Table 5.17).

Table 5.17 Sample sizes for each analysis for baseline behaviour (MC) and post-conflict behaviour, categorised by PCs after conflicts of high and low intensity.

Variable	Birds	MC	PC		
			Total	High	Low
Conflicts	10	-	27	22	5
Conflict aggressors	7	-	12	11	1
Conflict victims	7	-	15	11	4
Bill wiping	6	1	23	20	3
Bill wiping before/after first affiliation	6	0 / 6	1 / 22	-	-
Bill wiping before first/after last affiliation	5	0 / 1	0 / 15	-	-
Aggression before/after first affiliation	10	1 / 16	6 / 47	-	-
Aggression before first/after last affiliation	2	0 / 0	4 / 1	-	-
Self-preening	1	1	0	-	-
PCs with no affiliation	-	-	5	-	-
Affiliation went through the end of the session	-	13	9	-	-

Did post-conflict affiliation occur?

Post-conflict third-party affiliation occurred as evidenced by the higher frequencies of affiliation after conflicts when compared with matched controls in the GLMM of best fit which included only treatment as an explanatory variable (Table 5.18). These results are consistent with those found in chapters 3 and 4 for jackdaws.

Does increased foraging competition induce conflicts?

The food competition condition, involving food deprivation followed by increased foraging competition, significantly induced conflicts in jackdaws. There were significantly higher conflict rates per subject in the food competition condition than in MCs (Mann-Whitney U test: $W=172$, $N=10$ birds, $p=0.00004$). This was not the case for rooks, which is why they were excluded from this experiment.

Table 5.18. Examining the frequency of affiliation in PCs versus MCs and the influence of the role in the conflict and the initiator of the affiliation.

Model	Form	Estimate	Standard Error	delta AIC [AIC]
Null	Intercept only Subject (random factor) Treatment (random factor)	1.61 0.16 0.05	0.22 0.41 0.22	2 [79]
TPA	Intercept` PC Subject (random factor) Treatment (random factor)	1.40 0.43 0.15 0.00	0.16 0.11 0.39 0.00	0 [77]
+Role	Intercept` PC Role: victim PC*victim Subject (random factor) Treatment (random factor)	1.44 0.32 -0.10 0.21 0.16 0.00	0.19 0.16 0.19 0.23 0.40 0.00	3 [80]
+Role & Initiator	Intercept` PC Initiator: third-party Role: victim PC*third-party PC*victim Third-party*victim PC*third-party*victim Subject (random factor) Treatment (random factor)	1.52 0.31 -0.17 -0.06 0.07 0.12 -0.12 0.18 0.13 0.00	0.20 0.21 0.29 0.23 0.36 0.30 0.41 0.50 0.36 0.00	9 [86]

Hypothesis 4: do high intensity conflicts increase post-conflict bill wiping and self-preening frequencies?

There were almost no performances of self-preening, thus no data to compare between PCs and MCs or between conflicts of high and low intensity (N=0 PC, N=1 MC). That there was only one self-preening event in MCs, suggests its use does not increase after conflicts (regardless of the intensity), which are likely stressful. Therefore, I cannot use self-preening to determine whether stress increased after conflicts or between high and low intensity conflicts.

There was significantly more bill wiping in PCs when compared with MCs, however there were no differences within PCs when comparing high and low intensity conditions (Table 5.19). Therefore, bill wiping increases after conflict stress, which appears to indicate bill wiping can be used as a behavioural indicator of stress. However, either conflict intensity does not influence stress levels or there is not enough of a difference

to influence behaviour, which suggests that there will be no difference in post-conflict affiliative behaviour between high and low conflict intensity.

Table 5.19. The effect of conflict intensity and treatment on bill wiping frequency.

Model	Form	Estimate	Standard Error	delta AIC [AIC]
Null	Intercept only Subject (random factor) Treatment (random factor)	-1.27 1.09 0.45	0.64 1.05 0.67	3 [100]
Intensity	Intercept` Conflict intensity: low Treatment: PC Low*PC Subject (random factor) Treatment (random factor)	-1.65 -16.32 1.20 15.28 1.22 0.00	0.59 2259.83 0.47 2259.83 1.11 0.00	0 [97]

If bill wiping serves as an indicator of stress, it should be highest before affiliation and decrease after affiliation if affiliation reduces stress. Results from the timing of bill wiping indicate that it occurs more frequently after the first affiliative contact rather than before (Table 5.20). There was not much time before first affiliative contact in PCs and MCs, thus bill wiping was more likely to occur after the first affiliation if it was performed randomly.

Table 5.20. The effect of the timing of bill wiping events (before or after first affiliative contact) by treatment.

Model	Form	Estimate	Standard Error	delta AIC [AIC]
Null	Intercept only Subject (random factor) Treatment (random factor)	-1.96 1.09 0.45	0.64 1.05 0.67	30 [136]
Intensity	Intercept` Bill wiping before first affiliation Treatment: PC Before*PC Subject (random factor) Treatment (random factor)	-1.93 -17.80 1.30 14.71 0.94 0.00	0.55 3042.73 0.47 3042.73 0.97 0.00	0 [106]

Hypothesis 5: does affiliation increase with increasing conflict intensity?

Conflict intensity did not influence the frequency of post-conflict affiliation. There was no difference in the frequency of affiliation per conflict in PCs versus MCs because the

test model was as parsimonious as the null model (Table 5.21). This is consistent with the results from bill wiping in which there was no difference between conflict conditions and suggests that post-conflict third-party affiliation responds to stress in the same way.

Table 5.21. The effect of conflict intensity (high or low) on the frequency of affiliation by treatment.

Model	Form	Estimate	Standard Error	delta AIC [AIC]
Null	Intercept only	1.67	0.20	0 [78]
	Subject (random factor)	0.12	0.34	
	Treatment (random factor)	0.04	0.21	
Intensity	Intercept`	1.44	0.16	0 [78]
	Conflict intensity: low	0.03	0.27	
	Treatment: PC	0.38	0.12	
	Low*PC	0.15	0.31	
	Subject (random factor)	0.13	0.36	
	Treatment (random factor)	0.00	0.00	

Does aggression increase with food competition?

Unlike in chapter 3, there were significantly higher overall mean rates of aggression per bird after conflicts than in matched controls in this experiment (Wilcoxon signed rank test: PC-MC $V=45$, $N=10$ birds, $p=0.009$, 95% confidence interval: 0.17-0.35, 95% confidence interval=0.17-0.35). The increase in food competition must have elicited this increase in aggressive behaviour, but it is unclear why. I conduct an exploratory analysis here to better understand this result.

Hypothesis 6 (post hoc): does stress produce more aggression?

I hypothesise that an increase in stress may result in increased aggression. Therefore, aggression should occur more near the beginning of the PC, just after the conflict (i.e., the stressor) and before very much affiliation will have occurred (which may reduce stress). To test this, I examined whether former combatants initiated more aggression before or after the first affiliative event. I accounted for the total duration of affiliation per session which may affect the amount of aggression that occurs. GLMM results are not consistent with this prediction: there was more aggression after the first affiliative contact in PCs (Table 5.22).

Table 5.22. The effect of the timing of aggression (before or after first affiliative contact) on the frequency of aggression per session for initiators of aggression when accounting for treatment and the total duration of affiliation in each session.

Model	Form	Estimate	Standard Error	delta AIC [AIC]
Null	Intercept only Affiliation duration (random factor) Subject (random factor) Treatment (random factor)	-1.37 0.08 0.60 0.35	0.54 0.90 0.77 0.60	50 [185]
Before or after first affiliation/ aggression initiators	Intercept` Aggression before 1st affiliation Affiliation duration Treatment: PC Before*affiliation duration Before*PC Affiliation duration*PC Before*affiliation duration*PC Affiliation duration (random factor) Subject (random factor) Treatment (random factor)	-2.03 1.21 0.003 0.90 -0.02 -2.22 0.001 0.02 0.90 0.08 0.00	1.00 2.24 0.003 1.19 0.02 2.55 0.003 0.02 0.95 0.29 0.00	0 [135]

There is usually not much time before the first affiliative event in a PC, therefore limiting the amount of aggression that could occur before affiliation. As well, only examining the first affiliative contact may not have a significant impact on an individual's stress levels if the duration of the affiliation is short (which is why I also included the total duration of affiliation per session as a factor). I would expect that the combined influence of affiliative events on aggression should have more of an effect on aggression or stress levels, therefore I further tested this data set to examine the frequency of aggression before the first affiliative event and after the last affiliative event, while accounting for the total duration of affiliation, and excluding those PCs and MCs in which affiliation occurred until the end of the session (because there could be no aggression after the last affiliative event). If aggression frequencies increase in more stressful circumstances, then I would expect a higher frequency of aggression before the first affiliative contact than after the last affiliative contact, which may suggest that affiliation reduces aggression and/or stress. However, sample sizes were so small for each category that analysing this data would be inappropriate (PC aggressive events before first affiliation=4, PC aggressive events after last affiliation=1, and no aggression before first or after last affiliation in MCs).

Hypothesis 7: is affiliation a buffer for aggression?

Perhaps the act of sitting near or touching another individual (affiliating) prevents others from directing aggression toward either of these individuals because there are two potential adversaries rather than just one. Affiliation in this case could act as a buffer for aggression, which may be more likely to occur when individuals are alone. To test this, I investigated whether aggression against the focal subject occurred in the presence or absence of another individual. If affiliation acts as a buffer, then there should be less aggression in the presence of another. Results are similar to those in study 1. There was less aggression against conflict victims when they were affiliating in MCs, but the opposite for PCs, which had more aggression against conflict victims when they were affiliating, thus affiliation did not buffer conflict victims from aggression (Table 5.23). Conflict aggressors received more aggression in MCs, but less in PCs, when they were affiliating, thus post-conflict affiliation appears to buffer conflict aggressors from becoming targets of post-conflict aggression.

Table 5.23. The frequency of aggression against former combatants when the subject was alone or affiliating with another individual per session and according to treatment and their role in the conflict.

Model	Form	Estimate	Standard Error	delta AIC [AIC]
Null	Intercept only Subject (random factor) Treatment (random factor)	-0.73 0.53 0.25	0.45 0.73 0.50	2 [134]
Presence or absence of another	Intercept` Aggression when affiliating with another: present Treatment: PC (aggressor, alone) Role: victim (alone, MC) Present*PC (aggressor) Present*victim (MC) PC*victim (alone) Present*PC*victim Subject (random factor) Treatment (random factor)	-2.40 1.39 1.39 1.76 -0.69 -2.20 -1.02 2.07 0.27 0.00	1.03 1.13 1.13 1.08 1.29 1.28 1.21 1.47 0.52 0.00	0 [132]

I also tested whether a longer total duration of affiliation in a session was correlated with lower frequencies of aggression, which might further support the affiliation as a buffer for aggression hypothesis. However, the duration of affiliation did not influence

the frequency of aggression because the null model was the model of best fit (Table 5.24).

Table 5.24. The frequency of aggression against former combatants relative to the total amount of time spent affiliating with another individual per session and according to treatment and their role in the conflict.

Model	Form	Estimate	Standard Error	delta AIC [AIC]
Null	Intercept only Affiliation duration (random factor) Subject (random factor) Treatment (random factor)	-0.90 0.42 0.59 0.29	0.49 0.64 0.77 0.54	0 [131]
Presence or absence of another	Intercept` Affiliation duration Treatment: PC Role: victim Affiliation duration*PC Affiliation duration*victim PC*victim Affiliation duration*PC*victim Affiliation duration (random factor) Subject (random factor) Treatment (random factor)	-0.76 -0.002 0.56 0.94 0.0005 -0.004 -1.11 0.008 0.21 0.19 0.00	1.12 0.003 1.34 1.31 0.004 0.004 1.53 0.005 0.46 0.44 0.00	1 [132]

Study 2: Discussion

This study replicated that jackdaws show post-conflict third-party affiliation according to the frequency of affiliation using a different data set from that in chapters 3 and 4. Again, there was no difference in its occurrence between aggressors and victims: both participated in this behaviour.

The aims of this study were to 1) determine whether self directed behaviour indicates stress in jackdaws, 2) investigate whether high intensity conflicts were more stressful than low intensity conflicts using self directed behavioural indicators of stress (if any), and 3) examine whether post-conflict affiliation occurred more under more stressful conditions (Table 5.25).

Bill wiping increased after conflicts when compared with matched controls, but there was no difference in bill wiping frequencies between high and low intensity conflicts. Thus, while bill wiping appears to indicate conflict stress, it could not be used to

determine whether high intensity conflicts are more stressful than low intensity conflicts.

Post-conflict third-party affiliation followed the same pattern as bill wiping: affiliation increased after conflicts when compared with matched controls, but it did not differ according to conflict intensity. If higher intensity conflicts are indeed more stressful, then this may suggest that post-conflict affiliation is a response that varies according to a threshold rather than a continuous scale. The rule might be to use third-party affiliation if a conflict happens regardless of the level of stress induced, rather than adjust the amount of affiliative behaviour according to the amount of stress experienced. Alternatively, if post-conflict stress levels do not vary with conflict intensity, then I would expect the same result with post-conflict affiliation: no variance between conditions. To determine whether stress levels change with conflict intensity, a physiological measure is necessary, which was not possible in this study.

Table 5.25. Does post-conflict third-party affiliation reduce stress? Hypotheses, predictions, and results.

Hypothesis	Predictions	Results
4. Self directed behaviour indicates stress	More bill wiping and/or preening after conflicts compared with matched controls More bill wiping and/or preening after high intensity conflicts when compared with low intensity conflicts	Yes X
5. Post-conflict third-party affiliation increases with increasing stress	More post-conflict third-party affiliation after high intensity conflicts when compared with low intensity conflicts	X
6. Post-hoc: post-conflict third-party affiliation reduces aggression	More post-conflict aggression before the first affiliative contact than after	X
7. Post-hoc: post-conflict third-party affiliation buffers aggression	Less post-conflict aggression directed toward former combatants when affiliating with another Less post-conflict aggression when more affiliation	Yes aggressors X

The increase in overall aggression after conflicts versus matched controls was significant in this study, in contrast with the data set from chapter 3 (study 1 in this chapter) in which there was no difference in aggression frequencies between PCs and MCs. I explored two post-hoc hypotheses about why this might have occurred: that an

increase in aggression might occur when stress increases, and that post-conflict third-party affiliation might buffer aggression. There was no support for the former hypothesis which was examined using the frequency of aggression before and after the first affiliative event. However, there was evidence supporting the latter hypothesis. Conflict aggressors received less aggression when they were affiliating versus when they were alone after conflicts. As well, conflict aggressors received less aggression in sessions that had longer durations of affiliation. These results suggest that one of the functions of affiliation is to reduce aggression, which may be caused by stress.

The stress-reducing function of post-conflict third-party affiliation is still one of the most likely because both victims and aggressors engage in post-conflict affiliation which could indicate that conflicts are stressful for both combatants. These findings will provide some basis for future research to investigate the effect of conflicts, aggression, and affiliation on physiological stress levels.

GENERAL DISCUSSION

The main finding from both studies in this chapter supports the hypothesis that post-conflict third-party affiliation functions to buffer former combatants (mostly aggressors) from post-conflict aggression (Table 5.26). This may be why aggressors receive less aggression than victims after conflicts. The analysis that examined whether former combatants received less aggression when they were affiliating with another was a direct way of investigating this hypothesis and takes account all of the data in an observation session, rather than aggression before or after the first affiliative contact.

While the ‘affiliation as a buffer for aggression’ hypothesis applies to conflict aggressors, it is still unclear how conflict victims may be benefiting from post-conflict third-party affiliation. Victims receive more aggression after conflicts than aggressors, so the function is not to reduce aggression, however, it may still serve to reduce the stress induced by the conflict and by post-conflict aggression. Experiments that examine post-conflict affiliation in relation to physiological stress levels will be able to determine if this is the case.

Table 5.26. Summary of findings from study 1 and study 2.

Hypothesis	Predictions	Results		
		Study 1		Study 2
		Rooks	Jackdaws	Jackdaws
1. Renewed aggression post-conflict	More post-conflict aggression between former opponents	Yes aggressor to victim	X (yes redirected: bystander to victim)	X (yes redirected: aggressor to bystander)
2. Post-conflict third-party affiliation reduces aggression	More post-conflict aggression before the first affiliative contact than after	X	X	X (post hoc)
3. Post-conflict third-party affiliation buffers aggression	Less post-conflict aggression directed toward former combatants when affiliating with another Less post-conflict aggression when more affiliation	Yes aggressor Yes aggressor/victim	Yes aggressor Yes aggressor	Yes aggressor (post hoc) X (post hoc)
4. Self directed behaviour indicates stress	More bill wiping and/or preening after conflicts compared with matched controls More bill wiping and/or preening after high intensity conflicts when compared with low intensity conflicts			Yes X
5. Post-conflict third-party affiliation increases with increasing stress	More post-conflict third-party affiliation after high intensity conflicts when compared with low intensity conflicts			X

As a wider range of taxa are studied in the context of post-conflict affiliation and its potential functions, we become better able to predict the distribution of this behaviour across taxa. Since post-conflict affiliative behaviour has now been studied in four bird species, this data compliments the existing body of knowledge on mammals and allows us to make larger inferences about this behaviour regarding its use and prevalence. The differential post-conflict affiliation strategies used by rooks, jackdaws, and jays (chapter 3, Seed et al. 2007) present an opportunity to explore what drives these differences according to various aspects of sociality and natural history.

CHAPTER 6: A broad hypothesis for post-conflict affiliation

ABSTRACT

The recent expansion of post-conflict affiliation studies to include birds and fish allows for more accurate predictions about the prevalence of this behaviour across taxa. The valuable relationship hypothesis is the primary post-conflict affiliation hypothesis that accurately predicts the presence of former opponent affiliation. This hypothesis posits that individuals with valuable relationships, namely those that incur fitness benefits, will affiliate with these valuable partners after fights to reduce the cost of the conflict (e.g., damage to the relationship or increased stress). However, third-party affiliation is not included in this hypothesis, likely at least partially because of the lack empirical evidence on this form of post-conflict affiliation. I synthesize previous research to propose the relationship quality hypothesis, which states that all forms of post-conflict affiliation (former opponent, third-party, quadratic, inter-group, and inter-species) will vary across taxa according to the interaction of three relationship quality measures, namely value, compatibility, and security.

INTRODUCTION

My investigations of rook, jackdaw, and jay post-conflict affiliation (chapters 3, 4, and 5; Seed et al. 2007), as well as recent studies on ravens (Fraser & Bugnyar 2010 & 2011) have revealed that birds possess different inter-individual post-conflict affiliation patterns than mammals and fish. Mammals and fish make up with former opponents (also known as reconciliation) and affiliate with bystanders after fights, while the corvids use exclusively or mostly third-party affiliation. This provides an opportunity to further the existing theories for predicting which species will have post-conflict affiliation and to discuss the differential use of these two post-conflict affiliation strategies.

The various forms of post-conflict affiliation can serve one or many functions. Former opponent affiliation can function to repair the relationship after being damaged by the conflict; it can also reduce the stress induced by the conflict, and prevent further aggression (see Aureli & de Waal 2000 and Arnold et al. 2010 for reviews). Affiliating

with a bystander after fights can reduce stress (Fraser et al. 2008b), reduce further aggression between the combatants (Fraser & Bugnyar 2010), by the former combatant toward third-parties or by third-parties toward the former combatant (Das 2000, Call et al. 2002, Romero et al. 2009 & 2011, Koski & Sterck 2009), or it may serve as a replacement for former opponent affiliation if it is too risky (Judge 1991, Wittig et al. 2007; Wittig & Boesch 2010; see reviews for primates: Watts et al. 2000, Das 2000, Fraser et al. 2009). Though rarely studied, quadratic affiliation, when bystanders affiliate with other bystanders but not former combatants after fights, can also reduce stress among bystanders (Judge & Mullen 2005, de Marco et al. 2010). Quadratic post-conflict affiliation occurs in hamadryas baboons (Judge & Mullen 2005) and Tonkean macaques (de Marco et al. 2010), specifically among close affiliates and appears to reduce the tension that increases after fights. Post-conflict affiliation behaviour exists in different forms which vary by species, or even population.

Of the many hypotheses about the function of post-conflict affiliation, there is one that explains a great deal of the variation in post-conflict affiliation across taxa: the valuable relationship hypothesis (van Schaik & Aureli 2000, Aureli et al. 2002). The valuable relationship hypothesis posits that individuals will use former opponent affiliation with their valuable partner to reduce the damage caused by conflicts (de Waal & Aureli 1997). Valuable relationships are those that consist of repeated interactions resulting in higher fitness (Kummer 1978, Cords 1997, van Schaik & Aureli 2000, see review in Arnold et al. 2010). Former opponent affiliation is indeed best predicted by high relationship value (actually by high relationship quality; see below) among primates (see reviews for primates in Arnold et al. 2010, Watts et al. 2000; for other mammals and birds see below).

The valuable relationship hypothesis (in fact, most post-conflict affiliation hypotheses) has thus far only been applied to former opponent affiliation and not to third-party affiliation, quadratic affiliation, or inter-group post-conflict affiliation. This is because most theoretical and empirical work has concerned former opponent affiliation, thus less is known about the determinants of triadic post-conflict affiliation. However, it is important to develop hypotheses that recognise all forms of post-conflict affiliation if

we are to understand this complex behaviour. I propose a hypothesis to account for post-conflict former opponent affiliation, third-party affiliation (in its broad form, regardless of who initiates it or if it is directed toward the conflict victim or aggressor), quadratic affiliation, inter-group affiliation, and inter-species affiliation across taxa, the relationship quality hypothesis, based on work by Cords and Aureli (2000) and Fraser and colleagues (2009). The relationship quality hypothesis expands the valuable relationship hypothesis to include third-party affiliation, quadratic affiliation, and other components of relationship quality, besides just the value. It considers the interaction of three relationship quality components (value, compatibility, and security) to predict post-conflict affiliative strategies based on the associated benefits and risks.

Relationship quality is composed of three factors: value (direct fitness benefits), compatibility (the amount of affiliation exchanged), and security (variation in the response of an individual toward another; a larger variation in responses produces a less secure relationship; Cords & Aureli 2000). This three-component model is supported in chimpanzees (Fraser et al. 2008a), sub-adult ravens (Fraser & Bugnyar 2010), and Japanese macaques (Majolo et al. 2009), although a recent study on spider monkeys identified two, not three, relationship components: affiliation (which could be synonymous with value or compatibility) and risk (which could be security; Rebecchini et al. 2011). All three factors influence the likelihood of post-conflict affiliation. The basic pattern is that the higher the quality (value or compatibility or both), the higher the benefits of affiliation, and the lower the risks of it. High security, in contrast, decreases the benefits relative to costs because the conflict was unlikely to inflict considerable damage (Schaffner & Caine 2000, Schaffner et al. 2005, Koski et al. 2007; Fraser et al. 2009). Post-conflict affiliation for relationship repair (dyadic or triadic), bond strengthening, stress reduction, and bond advertising is more likely when relationships are highly valuable and/or compatible, while self-protective affiliation is more likely when the relationship of the affiliating dyad is of low value and/or compatibility (Arnold et al. 2010, Fraser et al. 2009). Thus, while post-conflict third-party affiliation has many functions, which can vary among and within species, one of the main underlying factors is high relationship quality shared by at least some of the interaction partners. For example, when former opponents fail to affiliate after conflicts, third-party

affiliation may be used as a substitute to indirectly repair the relationship between former opponents (chimpanzees: Wittig & Boesch 2010, chacma baboons: Wittig et al. 2007). A former combatant can affiliate with the former opponent's high quality relationship partners, or a bystander can affiliate with its friend (a former combatant) or its friend's former opponent on behalf of their friend to repair the relationship between the former opponents. In all scenarios, at least one high quality relationship is involved even when a low quality relationship is present (see Fraser et al. 2009 for review). In another example, former opponent and third-party affiliation used for stress reduction consistently occurs within high quality relationships (hamadryas baboons: Romero et al. 2009; chimpanzees: Romero & de Waal 2010, Fraser et al. 2008; barbary macaques: McFarland & Majolo 2011).

Relationship security is likely influenced by a species' dominance structure, which may influence post-conflict affiliation (Table 6.1). If aggression in a species is frequent and unilateral, competing for resources is more risky, therefore avoidance is more likely than confrontation (Thierry 1985). Such species can be characterised as despotic, having little leverage in conflicts and a strictly enforced, steep dominance hierarchy. If a species' aggression is bilateral and/or less frequent, the costs for competing are reduced, which may result in the development of behaviour to manage the aggression (i.e., redirected aggression, third-party interventions, and post-conflict affiliation; Thierry 1985). In such tolerant species conflict management is less risky and thus, more frequent. Evidence in macaques supports this notion: crested macaque (*Macaca nigra*) aggressive behaviour is not likely to inflict damage and they show more retaliation, third-party interventions during conflicts, and former opponent affiliation (Petit et al. 1997). In contrast, Japanese macaques have more injurious aggressive behaviour and are more despotic, with only occasional retaliation and former opponent affiliation, and no impartial third-party interventions during conflicts (Petit et al. 1997). Further evidence shows that rates of counter-aggression and former opponent affiliation both increased in macaques with less strict dominance styles when comparing nine species within the genus (Thierry et al. 2008). Macaques that have more despotic societies restrict former opponent affiliation to kin relationships (the most valuable and secure relationships), while less despotic species have more former opponent affiliation with

non-kin (Aureli et al. 1997).

Table 6.1. The strength of each relationship component predicts whether the benefits outweigh the risks of engaging in post-conflict affiliation (either former opponent or third-party affiliation). Dominance structure is incorporated into the component “security”, with tolerant indicating species with unclear dominance relationships and despotic referring to species that have clear dominance roles.

Value	Compatibility	Security	Security: Dominance	PCA	
				Benefit	Risk
High			Singular Breeder	Low (no conflict damage)	Low
High		Low-Med	Tolerant	Medium	Low
High	Med-High	Low-Med	Despotic Fluid	High	Med
Low &/or Med		High	Despotic Rigid	Medium	High
None			Asocial	None	High

To synthesise the literature on post-conflict affiliation, I discuss species in the context of their dominance style, based on the definitions from Sterck and colleagues (1997). Despotic species have clear dominance relationships and often a linear dominance hierarchy, while tolerant species have informal dominance relationships. I further defined the despotic category by the degree to which individuals change rank over time to account for the level of security. Those species in which individuals have few or no rank changes are considered despotic rigid, indicative of more secure (less variable) relationships that are less likely to have post-conflict affiliation because of their non-negotiable group status. For example, Japanese macaques fall into this category: they have a steep dominance hierarchy with unilateral aggression, and rank is maternally inherited resulting in few rank reversals (Aureli et al. 1997). Singular breeders are a special case in this category, even though they usually have extremely low levels of aggression. Singular breeding systems are characterised by a dominant breeding pair with subordinate offspring and helpers (Lewis & Pusey 1997). Helpers are reproductively suppressed, either behaviourally or physiologically, forgoing reproduction to assist with rearing the breeding pair’s offspring (which are usually siblings). Singular breeders have some or no post-conflict affiliation, presumably

because of high amounts of baseline affiliation and low levels of aggression (therefore low risk of approach), which creates high relationship value, compatibility, and security among group members (common marmosets: Westlund et al. 2000, red-bellied tamarins: Schaffner et al. 2005; see below).

Species that have clear dominance relationships, but change rank more often are categorized as despotic fluid and have less secure relationships (more variable) with more of an ability to negotiate these relationships. For instance, chimpanzees have some degree of tolerance, but existing dominance hierarchies and frequent but bilateral aggression (Goldberg & Wrangham 1997, Fraser et al. 2008b). These species tend to have more post-conflict affiliation than despotic rigid species because of the lower risk of approaching former combatants (Fraser et al. 2009). The despotic fluid styles have low to medium levels of security since dominance rank can be less obvious and more easily challenged, and relationships include a wider range of reactions from affiliation to aggression.

Tolerant species usually have less aggression and high compatibility, and are expected to vary in their levels of post-conflict affiliation because their high value relationships have varying levels of security: those with less security should have more post-conflict affiliation to reduce uncertainty in group dynamics or reduce stress. For example, red-fronted lemurs are a tolerant species with no dominance relationships, very high levels of compatibility, symmetrical aggressive outcomes, very low levels of aggression, and some post-conflict affiliation (Pereira & Kappeler 1997).

For some of the species I consider, my classification of dominance style differs from previous classifications. Specifically, I define humans as despotic fluid because of the presence of dominance hierarchies (as seen in kingdoms, states, families, in the workplace, etc.) in which rank changes are possible (Richerson & Boyd 1999). Bonobos are classed as tolerant because of their symmetrical distribution of aggression and, while dominance hierarchies have been found in captive populations, there are no identifiable hierarchies in wild populations (Furuichi 2011). Chimpanzees are despotic fluid because they have sex-specific linear dominance hierarchies (Goldberg & Wrangham 1997,

Wittig & Boesch 2003a) and aggression is often bidirectional, indicating that relationships are negotiable (Fraser et al. 2008b). Male gorillas have clear dominance relationships and rank reversals, and females sometimes form linear dominance hierarchies, therefore they are despotic fluid (Watts 1994 & 1996). Data on spectacled leaf monkeys is greatly lacking, however Arnold and Barton (2001a) found that one group had a linear dominance hierarchy, while another group did not. However, the group that did not have a linear hierarchy had recently acquired a new male, which caused an increase in aggression from all individuals as they worked to establish new relationships. Therefore, I classified this species as despotic fluid according to data from the group that had well-established relationships which, consequently, had a linear hierarchy.

In sum, the relationship quality hypothesis builds onto the valuable relationships, uncertainty reduction (former opponent affiliation and directing aggression at bystanders will decrease renewed conflict, thus increasing certainty in the relationship; Aureli & van Schaik 1991), and social constraints (bystanders will participate in third-party affiliation depending on the risks of receiving post-conflict aggression; de Waal & Aureli 1996) hypotheses to explain post-conflict affiliation broadly and comprehensively. The shared element in the prior work and in the available evidence is the relevance of high quality relationships in determining the relative costs and benefits of affiliative behaviour. Building on earlier hypotheses, it unites their common factors to a new hypothesis. The relationship quality hypothesis improves predictability of affiliation patterns across species by formulating a coherent and crystallised framework for all forms of post-conflict affiliation.

THE DIFFERENTIAL USE OF POST-CONFLICT AFFILIATION STRATEGIES

Many social species (mostly mammals have been studied thus far) use both former opponent affiliation and third-party affiliation to maintain amicable group dynamics. Among the species that use both former opponent and third-party affiliation are domestic dogs (Cools et al. 2008), wolves (Cordoni & Palagi 2008, Palagi et al. 2009), humans (Fujisawa et al. 2006), horses (Cozzi et al. 2010), and many non-human primates (Table 6.2; see reviews in Das 2000, Watts et al. 2000, Aureli et al. 2002,

Arnold et al. 2010). In all these species, individuals have multiple high quality relationships (see Table 6.2). Some species only use former opponent affiliation and not third-party affiliation, including dolphins (Weaver 2003), domestic goats (Schino 1998, Schino 2000), spotted hyenas (Wahaj et al. 2001) and some primates (see Table 6.2). Conversely, some species use only third-party affiliation, but not former opponent affiliation (rooks: chapter 3, Seed et al. 2007; jackdaws and Eurasian jays: chapter 3). Finally, some species use neither form of post-conflict affiliation (Eurasian jays: chapter 3; black lemur: Roeder et al. 2002, Fornasieri & Roeder 1992). In some of these cases, the absence of post-conflict affiliation may reflect false negatives due to methodological challenges (e.g., restricted access to third parties in goats and dolphins, too short of a post-conflict observation period in ring-tailed lemurs, or data on triadic interaction was not recorded in hyenas, cotton-top tamarins and lion-tailed macaques).

However, in most cases the absence of post-conflict affiliation can be explained by the relationship quality hypothesis. In black lemurs the main valuable relationships are between males and females. However, there are no conflicts in these relationships and consequently, no former opponent affiliation. Instead, females aggress against females and do not use former opponent affiliation. Former opponents often remain near after conflicts, indicating that the conflict did not damage the relationship in this species with medium relationship security. This may also explain why no third-party affiliation is used.

In singular breeders I observe several post-conflict strategies, presumably reflecting differences in the frequency of aggression. In singular breeder societies, all relationships are highly valuable, compatible, and secure. All individuals need the group because individuals cannot survive alone, creating valuable relationships that have direct fitness benefits for the dominant pair and indirect fitness benefits with occasional direct fitness benefits for subordinates (Kutsukake & Clutton-Brock 2006). They tend to be highly compatible, with high rates of affiliation, staying near each other almost constantly. These relationships are secure because subordinates rarely attain dominant status, therefore the hierarchy is rarely challenged and individual behaviour is highly consistent (i.e., dominants aggressively enforce the rules, but are otherwise tolerant).

In meerkats, a singular breeder, conflicts occur between dominants or a dominant against a subordinate, but post-conflict affiliation does not occur (Kutsukake & Clutton-Brock 2008). While meerkats have low rates of aggression in general, there is a high prevalence of renewed aggression after conflicts, increasing the risk of post-conflict affiliation. I hypothesise that the absence of post-conflict affiliation may be due to the increased risk of aggression, or that affiliating would have no effect on the relationship due to the high level of security (i.e., there are almost no changes in dominance rank), therefore post-conflict aggression was reduced by avoiding the dominant. An alternative explanation is that meerkats do not recognise individuals (Schibler and Manser 2007, Townsend et al. 2010, but see Townsend et al. in press) which is presumed to be a prerequisite for post-conflict affiliation (Aureli et al. 2002).

In contrast to meerkats, general and post-conflict aggression is very rare in the despotic rigid red-bellied tamarin who is also a singular breeder, and these few conflicts are not followed by post-conflict affiliation (it is not known whether they have third-party affiliation; Schaffner & Caine 2000, Schaffner et al. 2005). A more fluid strategy (though they are still classified as despotic rigid) is shown by two other singularly breeding Callitrichids: common marmosets and cotton-top tamarins. In these species, aggression is more frequent than in red-bellied tamarins, and former opponent affiliation, but not third-party affiliation occurs. The presence of post-conflict affiliation is possibly because common marmoset subordinates have an internal dominance hierarchy, making a usually rigid system more fluid since rank is more negotiable (less security). Cotton-top tamarins also have former opponent affiliation, but they are not a strict singular breeder, sometimes exhibiting polygyny or polyandry which contributes to more relaxed dominance relationships (less security) relative to other singular breeders (Savage et al. 1996). These species may not show third-party affiliation because former opponent affiliation may be the more effective strategy for repairing these relatively secure relationships with low rates of aggression. Further, an elevated risk of renewed aggression or the inability to recognise individuals, a lack of damage inflicted by the conflict, and high relationship security have been proposed as explanations for low post-conflict affiliation in singular breeders (Schaffner et al. 2005,

Kutsukake & Clutton-Brock 2008).

Table 6.2. The presence or absence of post-conflict affiliation in all non-primate species studied to date and a representative sample of primate species. Third-party affiliation includes all interactions with a bystander without differentiating between aggressors and victims or bystander and opponent initiation. FOA=former opponent affiliation, TPA=third-party affiliation. Types of high quality relationships include: ff=female-female, fm=female-male, mm=male-male, dom-dom=dominant-dominant, dom-sub=dominant-subordinate. See the next section for a description of how the number of high quality relationships were chosen.

Common Name	Species	FOA	TPA	Dominance Structure	Number of High Quality Relations	Types of High Quality Relations	Citation
Human	<i>Homo sapiens</i>	Yes	Yes	Despotic Fluid	11.6	fm, ff, mm	Fujisawa et al. 2006, Richerson & Boyd 1999, Dunbar & Spoors 1995
Western lowland gorilla	<i>Gorilla gorilla gorilla</i>	Yes	Yes	Despotic Fluid	5.5	fm	Cordoni et al. 2006, Palagi et al. 2008b, Mallavarapu et al. 2006, Watts 1994, 1996, Maple & Hoff 1982
Mountain gorilla	<i>Gorilla gorilla beringei</i>	Yes	Yes	Despotic Fluid	5.5	fm	Watts 1995a,b, Watts 1994, 1996, Maple & Hoff 1982
Chimpanzee	<i>Pan troglodytes</i>	Yes	Yes	Despotic Fluid	5	*ff, mm	Wittig & Boesch 2003b, Arnold & Whiten 2001, Koski et al. 2007, Fraser & Aureli 2008, Koski & Sterck 2009, Romero et al. 2011, Wittig & Boesch 2005, Fuentes et al. 2002, Preuschoft et al. 2002, Lehmann & Boesch 2009, Goldberg & Wrangham 1997, Fraser et al. 2008b
Bonobo	<i>Pan paniscus</i>	Yes	Yes	Tolerant	6	ff, mother-son	Palagi et al. 2004, Hohmann et al. 1999, Furuichi 2011, but see Stevens et al. 2007
Spectacled leaf monkey	<i>Trachypithecus obscurus</i>	Yes	Yes	>Despotic Fluid	16	ff	Arnold & Barton 2001a & b, Nunn & Barton in press
Hamadryas baboon	<i>Papio hamadryas hamadryas</i>	Yes	Yes	Despotic Rigid	126.4	fm, ff (kin), mm	Romero et al. 2008 & 2009, Swedell 2002, Kummer 1968, Coelho et al 1983
Long-tailed macaque	<i>Macaca fascicularis</i>	Yes	Yes	Despotic Rigid	28.8	ff	Aureli & van Schaik 1991, de Waal & Aureli 1996, Das et al. 1997, Aureli et al. 1997, van Noordwijk & van Schaik 1987 & 1999
Japanese macaque	<i>Macaca fuscata</i>	Yes	?	Despotic Rigid	24.9	ff, mm	Koyama 2001, Majolo et al. 2009, de Waal & Aureli 1996, Aureli et al. 1997, Maruhashi 1982, Furuichi 1985
Lion-tailed macaque	<i>Macaca silenus</i>	Yes	?	Despotic Rigid	18.8	ff	Abegg et al. 1996, Kumar 1995, Singh et al. 2006
Stumptailed macaque	<i>Macaca arctoides</i>	Yes	Yes	<Despotic Fluid	24.3	non-kin friends	Call et al. 1999 & 2002, Fooden 1990, de Waal & Luttrell 1989

Common Name	Species	FOA	TPA	Dominance Structure	Number of High Quality Relations	Types of High Quality Relations	Citation
Common marmoset	<i>Callithrix jacchus jacchus</i>	Yes	No	+Despotic Rigid	7.7	dom-dom dom-sub	Westlund et al. 2000, Koenig 1995
Cotton-top tamarin	<i>Saguinus oedipus</i>	Yes	?	+^Despotic Rigid	4.8	dom-dom, dom-sub, mm	Penate et al. 2009, Savage et al. 1996
Red-bellied tamarin	<i>Saguinus labiatus</i>	No	?	+Despotic Rigid	6.5	dom-dom dom-sub	Schaffner et al. 2005, Buchanan-Smith 1991
Guyanese squirrel monkey	<i>Saimiri sciureus</i>	Yes	?	Despotic Rigid	20.5	mm	Pereira et al. 2000, Boinski et al. 2002
Verraux's sifaka	<i>Propithecus verreauxi</i>	Yes	?	Tolerant	7	fm	Palagi et al. 2008a, Kappeler 1999
Ring-tailed lemur	<i>Lemur catta</i>	Yes/ No	No	Despotic Fluid	12	fm, ff	Kappeler 1993, Rolland & Roeder 2000, Kappeler & Pereira 1997, Roeder et al. 2002, Pereira & Kappeler 1997, Palagi et al. 2005
Red-fronted lemur	<i>Eulemur fulvus rufus</i>	Yes	No	Tolerant	8.5	fm, ff	Kappeler 1993, Roeder et al. 2002, Pereira & Kappeler 1997, Overdorff et al. 1999, Pereira et al. 1990
Brown lemur	<i>Eulemur fulvus</i>	Yes	?	Tolerant	5.5	fm	Roeder et al. 2002, Kappeler 1993, Pereira & Kappeler 1997
Black lemur	<i>Eulemur macaco</i>	No?	No	Tolerant	8.75	fm	Roeder et al. 2002, Fornasieri & Roeder 1992
Dog	<i>Canis lupus familiaris</i>	Yes	Yes	Despotic Rigid	2	non-kin friends	Cools et al. 2008, Daniels & Bekoff 1989
Wolf	<i>Canis lupus</i>	Yes	Yes	+Despotic Rigid	6.9	dom-dom, dom-sub, foraging allies	Cordoni & Palagi 2008, Palagi & Cordoni 2009, Dekker 1998
Meerkat	<i>Suricata suricatta</i>	No	No	+Despotic Rigid	6.5	dom-dom	Kutsukake & Clutton-Brock 2008, Clutton-Brock et al. 1999
Spotted hyena	<i>Crocuta crocuta</i>	Yes	?	Despotic Rigid	19	matriline	Wahaj et al. 2001, Holekamp et al. 1997, Kruuk 1972
Horse	<i>Equus caballus</i>	Yes	Yes	Despotic Rigid	6.9	ff, fm	Cozzi et al. 2010, Berger 1977, McCort 1984
Goat	<i>Capra hircus</i>	Yes	?	Despotic Fluid	5	fm, mm	Schino 1998, Schino 2000, Schackleton & Shank 1984
Dolphin	<i>Tursiops truncatus</i>	Yes	?	§Despotic Fluid	3.3	mm, ff	Weaver 2003, Samuels & Gifford 1997, Wells 1991, Gibson & Mann 2008, Mann et al. 2000
Cleaner wrasse	<i>Labroides dimidiatus</i>	Yes	Yes	Despotic Rigid	% 100	cleaner-client	Bshary & Wurth 2001, Bshary & D'Souza 2005, Robertson 1972
Raven (subadult)	<i>Corvus corax</i>	Yes/ No	Yes	Despotic Fluid	8	kin	Fraser & Bugnyar 2010, 2011, Schwab 2008
Rook	<i>Corvus frugilegus</i>	No	Yes	Despotic Fluid	1	mate	Chapter 3, Seed et al. 2007
Jackdaw	<i>Corvus monedula</i>	No	Yes	Despotic Fluid	1	mate	Chapter 3
Eurasian jay	<i>Garrulus glandarius</i>	No	Yes	Despotic Rigid	0	none	Chapter 3
Green woodhoopoe	<i>Phoeniculus purpureus</i>	?	Yes	+Despotic Rigid	4	dom-sub	Radford 2008, Radford 2004

Common Name	Species	FOA	TPA	Dominance Structure	Number of High Quality Relations	Types of High Quality Relations	Citation
*ff post-conflict affiliation occurs in captivity, but is rare in the wild. >Not enough evidence for a firm conclusion about the dominance structure. <Though classed as tolerant (egalitarian) by Sterck et al. 1997, this species has a clear linear dominance hierarchy, thus is despotic, and, in the absence of information about rank reversals, I classed them as fluid because of their symmetrical conflict outcomes (de Waal & Luttrell 1989). +Singular breeder. ^Not a strict singular breeder, but also shows polygyny and polyandry. \$Females have a despotic rigid dominance hierarchy, however I chose the male dominance structure to represent this species since males are the dominant sex. %Cleaners can have up to 2000 client interactions per day and the same client might visit a cleaner 100 times per day, but there are no mean numbers of clients encountered reported, therefore I estimated.							

In contrast to mammals, birds tend to have one main high quality relationship because of their generally monogamous mating strategy which makes the pair bond by far the strongest bond in the group. The bird species studied for conflict management so far are all corvids. Rooks and jackdaws form long-term monogamous bonds with their mate while jays form short-term monogamous bonds, though in all three species mates do not fight with each other (chapter 3, Seed et al. 2007). Though rooks and jackdaws usually exist in groups, non-partner bonds are much weaker than partner bonds (Emery et al. 2007), therefore, I would not expect former opponent affiliation in these species since their highest quality relationship does not have conflicts and therefore does not need repairing. Indeed, only third-party affiliation was found in rooks (chapter 3, Seed et al. 2007) and jackdaws (chapter 3). This third-party affiliation was used specifically with mates: after one of the members of a pair has a conflict with another group member, they affiliate with their partner. Since jays do not form strong bonds with others outside of the breeding season when their data were collected, they engage in post-conflict third-party affiliation with anyone, not just mates, after fights. Sub-adult ravens exhibit third-party affiliation (Fraser & Bugnyar 2010) and former opponent affiliation was found in one population but not another (Fraser & Bugnyar 2011). Ravens present a unique opportunity for studying post-conflict affiliation because their social structure changes with developmental stage. Adult ravens have a social structure very similar to rooks and jackdaws in that the mated pair has the highest quality relationship in the group by far and mates do not fight with each other. Therefore, I would expect only third-party affiliation in adult ravens as was found in the rooks and jackdaws. However, before pairing with their mate, sub-adult ravens form groups. Individuals in these groups have many high quality relationships, these relationships have conflicts, and

former opponent affiliation appears.

Aureli and colleagues (2002) proposed that asocial species lack valuable relationships and therefore would not have post-conflict affiliation. The basic precondition for any post-conflict affiliation is living in societies in which individuals recognise and interact with each other. The least social species studied in the context of post-conflict affiliation so far is the jay, which engaged in post-conflict third-party affiliation (chapter 3). Jays are not very social outside of the breeding season: they lack high quality relationships expected to produce post-conflict affiliation, however their weak social bonds produced third-party affiliation with anyone rather than just in their high quality relationships as has been found in many other species. Perhaps sociality exists more on a continuum than being a quality that is present or absent, therefore the intermittent high quality relationships in jays may place them somewhere in the middle of this spectrum, rather than at the extreme asocial end.

There is a unique case of inter-species post-conflict affiliation which occurs in fish, between the cleaner wrasse and its reef fish clients (Bshary & Würth 2001, Bshary & D'Souza 2005). Client fish come to 'cleaning stations' where cleaner wrasse rid them of their parasites. However, sometimes the wrasse cheats the client and takes a bite out of the client itself, which causes the client to swim away or chase the cleaner. In the case of the clients who swim away, wrasse use former opponent affiliation by either following the client and providing tactile stimulation to get the client to stay for more cleaning, or by giving tactile stimulation at the beginning of their next encounter (Bshary & Würth 2001). They also use third-party affiliation: a wrasse female will often clean alongside her male partner, but she is less able to inhibit her bites than he. When she bites a client and it starts to swim away, sometimes the male will follow the client and provide tactile stimulation to entice it to stay for more cleaning (Bshary & D'Souza 2005). The cleaner wrasse-client relationship is valuable to both parties, but it is more in the interest of the wrasse to initiate post-conflict affiliation since the wrasse depends on repeat clients while the client can swim off to visit other cleaners if it has a large enough territory.

Post-conflict affiliation also occurs at a larger scale, after inter-group conflicts. Green woodhoopoes are a highly social, singular breeding bird that holds group territories. After inter-group conflicts, losing groups engaged in more within-group allopreening (one bird preening another), which increased in response to increased conflict durations (Radford 2008). This classifies as post-conflict third-party affiliation at the scale of the group, and it occurred with their high quality relationships: by the dominant pair to their subordinate helpers. This was thought to aid in increasing group cohesion such that all group members would participate in their next fight. Larger groups usually win conflicts, therefore it is beneficial to maintain high membership levels. As well, allogrooming has been shown to reduce self-directed behaviour which is thought indicative of physiological stress levels, thus the green woodhoopoes appear to use post-conflict third-party affiliation to reduce stress (Radford in press). This work expands the scale of post-conflict affiliation to include group-level interactions, which have never been considered before.

In sum, almost all species studied thus far exhibit some form of post-conflict affiliation. Factors common to all of these species involve living in individualised societies and the existence of (sometimes intermittent) high quality relationship(s). Exceptions can be explained by variation in three factors of relationship quality.

DISCUSSION

I have shown that similar predictors involving relationship quality can apply not just to former opponent affiliation, but also to third-party affiliation. The relationship quality hypothesis integrates many existing hypotheses and ideas to explain post-conflict behaviour, including former opponent affiliation, third-party affiliation, quadratic affiliation, inter-group affiliation, and inter-species affiliation across a broad range of taxa.

The current data stresses the overarching importance of high quality relationships in determining post-conflict affiliation across social taxa. Further empirical work is needed to confirm the robustness of this hypothesis. Particular emphasis should be placed on gathering more information on third-party affiliation, quadratic affiliation, inter-group

affiliation, non-primate post-conflict affiliation, the types of post-conflict affiliation strategies that occur in species with only one high quality relationship, and exploring what degree of sociality is required for post-conflict affiliation to exist.

One of the advantages of the relationship quality hypothesis is that it does not limit the occurrence of post-conflict affiliation to only those individuals that share a high quality relationship, but it expands the scale of the interaction, showing that when post-conflict affiliation occurs, it usually involves at least one high quality relationship, however this relationship need not be the one that was engaged in the conflict. Therefore, whenever high quality relationships exist, post-conflict affiliation can occur in some form or another. In this way, the relationship quality hypothesis can also apply to quadratic post-conflict affiliation when group members that were not involved in conflicts were disturbed by conflicts within the group and thus increase their levels of affiliation with other bystanders.

Another advantage of the relationship quality hypothesis is that it frees post-conflict affiliation from concepts of scale. Because a high quality relationship can occur between two individuals (e.g., mates or grooming partners) or among many (e.g., members of an alliance or a group), this allows for post-conflict affiliation to occur at these scales as well: among individuals after intra-group conflicts (as is usually studied) or inter-group conflicts (e.g., green woodhoopoes: Radford 2008), and even after inter-species conflicts (e.g., reef cleaner-client fish: Bshary & Würth 2001, Bshary & D'Souza 2005).

My study of post-conflict affiliation in species that have one or no high quality relationships (chapter 3) contributed to the development of the relationship quality hypothesis in part because the differential use of post-conflict affiliative behaviour for these categories was striking and provided much of the intellectual material for this chapter.

CHAPTER 7: Discussion

The purpose of this thesis was to investigate post-conflict affiliation in three species of corvid, namely rooks, jackdaws, and Eurasian jays, to understand how sociality influences this behaviour, how it develops across life stages, and what the potential functions might be. The rooks and jackdaws are social species that engage in daily conflicts. As such, they have developed conflict management behaviour to offset the costs of these conflicts (chapter 1). While the jays are not social outside of the breeding season, engaging in very few interactions with others and rarely in conflicts after age 1, they actually did show conflict management behaviour, which coincided with the pair formation stage and the establishment of dominance hierarchies. This indicates that they used some of the benefits of sociality to offset the costs of increased proximity to others (chapter 1). The balance of the costs and benefits of sociality is unique for each species, perhaps each population, and can fluctuate temporally. These variations make excellent natural experiments for the further study of conflict management behaviour.

In this thesis, I addressed some of the outstanding questions in the field of post-conflict affiliation behaviour, including whether this behaviour is restricted to social species, whether it is present in additional social corvids, how this behaviour changes with development, what purpose it might serve, and whether the number of high quality relationships influence post-conflict affiliation patterns. Here, I summarise the contribution of my work to this field and discuss research that will be beneficial for furthering our knowledge on this topic.

Is post-conflict affiliative behaviour restricted to social species? (Chapter 3)

The study in chapter 3 was the first to explicitly test this question by studying the less social jays. Jays showed post-conflict affiliation outside of the breeding season, even when they had weak social bonds when compared with the social rooks and jackdaws. Jays appear to be monogamous at least seasonally (short-term rather than for many years at a time), which should produce a seasonal high quality relationship during the breeding season when they affiliate with their mate. It is during the breeding season that I would expect post-conflict affiliation to occur if this behaviour is dependent on the

presence of a high quality relationship. However, jays affiliated with anyone after fights, not just partners as in the rooks and jackdaws, thus indicating that high quality relationships are not necessary for this behaviour to occur. It is unclear whether jays engage in post-conflict third-party affiliation because they have some degree of sociality (at least temporally) or whether they possess the capability to engage in this social behaviour regardless of whether they express it in the wild. It is difficult to hypothesise as to why the jays have post-conflict affiliation when almost nothing is known about their behaviour in the wild. Thus, investigations on natural social behaviour as well as post-conflict behaviour will need to be conducted to further elucidate the significance of this result. A study in the wild would allow jays to maintain territories and have enough space to retreat from opponents after conflicts to examine whether they use post-conflict affiliation when they are not in an artificially social condition as in the aviary. However, studying post-conflict affiliation in wild jays would not be feasible using the PC-MC method because jays are widely dispersed across the landscape and wary of humans, which makes observing a conflict and finding certain individuals at exact times to follow them for a specific duration in matched controls unlikely to happen. If it could be done, such a study in jays, or in another species that is not very social, would be an excellent demonstration of the flexibility of post-conflict behaviour. While it appears that post-conflict affiliation is not restricted to highly social species having at least one high quality relationship, the sample size for the less social species is small and must be increased to determine the reliability of this result.

Do other corvids use post-conflict affiliation as well? (Chapter 3)

Rooks and ravens are known to show post-conflict affiliation (Seed et al. 2007, Fraser & Bugnyar 2010 and 2011), therefore studying jackdaws and jays doubled the number of corvid species studied in this context. Jackdaws behaved as predicted: having a similar social structure to rooks with one high quality relationship between mates, they showed the same post-conflict affiliation pattern as the rooks. However, as just discussed, jays did not behave as predicted: they showed post-conflict third-party affiliation. Additionally, I replicated Seed and colleagues' (2007) study on rook post-conflict affiliation and found the same post-conflict affiliation pattern: third-party affiliation between mates.

All corvids in which post-conflict affiliation has been examined have demonstrated this behaviour. In the social corvids, post-conflict affiliation is sensitive to the number of high quality relationships individuals have, which can vary by species and developmental stage. The diverse social structures that corvids possess, both across and within species, have allowed the investigation of some of the basic principles of post-conflict affiliative behaviour, namely how variance in the number of high quality relationships produces different kinds of post-conflict affiliation.

How does corvid post-conflict affiliation change as individuals develop from juveniles to adults? (Chapter 4)

As soon as pairs form, a high quality relationship should be present and post-conflict affiliation should be able to occur. Both rooks and jackdaws were already paired from the beginning of the study and also showed post-conflict affiliative behaviour from the start of the investigation. The frequency and duration of post-conflict affiliative events increased with increasing age for jackdaws and decreased for rooks as they reached sexual maturity. This developmental period could show the most change in bond strength between partners since it coincides with a time when increasing dominance rank and establishing a nest site could result in higher reproductive success at an earlier age. The jays formed pairs at age one when their post-conflict affiliative behaviour was the strongest, indicating a potential role for this behaviour for solidifying the bond between mates.

In terms of general affiliative behaviour, the bond between mates did not become stronger over the course of this study (chapter 2). In contrast, jackdaw post-conflict affiliative behaviour did increase during the time between pairing and sexual maturity, which shows that one aspect of the pair bond did strengthen. Perhaps post-conflict affiliation can be used to signal alliances and assist with the maintenance of dominance rank such that it results in higher fitness benefits than general affiliation, which may not convey much information to other group members.

This was a useful first examination of the development of avian post-conflict affiliation behaviour. It will be beneficial for future research to track individuals from the nestling stage into the later years of adulthood to examine behavioural and physiological changes that influence the onset and occurrence of post-conflict affiliation. There has been no physiological study of the effects of post-conflict affiliation, which is an important step for examining the mechanisms underlying this behaviour, specifically to determine if it releases endorphins and reduces stress. Determining whether there are fitness consequences for the differential use of post-conflict affiliative behaviour is crucial to understanding the selective forces responsible for the maintenance of this behaviour. Additionally, understanding why post-conflict affiliation is used in different contexts by different individuals will illuminate the flexibility of this behaviour and the individuals who use it.

What is the function of corvid post-conflict affiliation? (Chapter 5)

One possible function of third-party affiliation is to reduce aggression after conflicts, either through bystanders appeasing aggressive combatants or combatants protecting themselves from being aggressed upon. While renewed aggression occurred between rook former opponents (directed from aggressors to victims), victims did not receive more affiliation after conflicts to reduce this aggression. Instead, aggressors appeared to use post-conflict third-party affiliation to reduce aggression directed toward them after conflicts. Victims had more post-conflict third-party affiliation (chapter 3), for which the function remains elusive. Perhaps victims use this behaviour to reduce stress, which may increase since they not only receive attacks, but also higher levels of aggression after conflicts.

Jackdaws had more post-conflict aggression between former combatants and bystanders, which was directed from bystanders to victims, and from aggressors to bystanders. Jackdaws showed the same pattern of post-conflict behaviour as rooks: aggressors used affiliation to buffer aggression. However, again it is the victims receiving more aggression after conflicts and again the function of post-conflict third-party affiliation for victims is unclear. It appears that rook and jackdaw aggressors use post-conflict affiliation to buffer themselves from post-conflict aggression. This may

also serve to display their alliance with their mate to assist in maintaining their dominance rank, which could be enforced through aggression.

Another function of third-party affiliation is to reduce stress. This function was also tested using variation in conflict intensity as a proxy for stress to investigate whether post-conflict third-party affiliation increases after conflicts of high intensity. Post-conflict-third party affiliation increased after conflicts when compared with matched controls, however there were no differences in this behaviour between conflicts of high and low intensities. Thus, either stress does not vary with conflict intensity, or post-conflict affiliation is a behaviour that is present or absent rather than varying in strength on a continuous scale. Post-conflict affiliation experiments that measure physiological stress are needed to distinguish whether this behaviour fits a threshold or continuous pattern.

Primate third-party affiliation is the most comprehensively studied and the most complex, showing many different functions within species, and these functions can vary among populations (see Fraser et al. 2009 for a review). However, it is unknown whether other species lack third-party affiliation complexity because it does not exist or because it has not been studied. Further testing is needed to determine which functions are acting under which circumstances, however, the work here illustrates that aggressors and victims in rooks and jackdaws appear to use post-conflict affiliation differently and, thus, may have multiple functions for this behaviour. This gives an indication that third-party affiliation may be as complex as it is in primates and that the absence of this complexity is simply due to a lack of examination of this behaviour. Continued research investigating post-conflict affiliation and its functions will elucidate the mechanisms and selective pressures driving it, which will allow for more powerful predictions about which species use this behaviour and why.

Does the number of high quality relationships individuals have influence post-conflict affiliation patterns? (Chapter 6)

Studying post-conflict affiliation in rooks and jackdaws was crucial to the development of the relationship quality hypothesis because no other studies had been conducted on

species or populations in which individuals have only one high quality relationship. This facilitated the observation that when only one high quality relationship is present, only third-party affiliation occurs, but once two or more high quality relationships are present, then former opponent affiliation can also occur. This led to the recognition that it is the spread of high quality relationships, not just the number of them, that is important in producing different post-conflict affiliation patterns. It is not clear yet how the jays fit the pattern since they had only weak high quality relationships when they engaged in post-conflict affiliation. This aspect will need to be explored more fully in future studies in jays, and in other less social or asocial species to determine what drives post-conflict affiliative behaviour in this context.

Perhaps it is because rooks and jackdaws only show third-party affiliation, which means that I only study third-party affiliation, that I place equal importance on this behaviour as I do on former opponent affiliation, the latter of which has been the focus of almost all literature on post-conflict affiliation. Following this trend, most post-conflict affiliation hypotheses concern only former opponent affiliation. However, some of these hypotheses can also be applied to third-party affiliation (i.e., the valuable relationship hypothesis: more former opponent affiliation will occur with relationships of higher value), which has not been explicitly implied. Third-party affiliation should be considered an equivalent post-conflict affiliation pattern to former opponent affiliation, therefore the development of a hypothesis that includes both former opponent and third-party affiliation is warranted. That is why I formed the relationship quality hypothesis, which is based on previous work on relationship quality (Cords & Aureli 2000, Fraser et al. 2009). The relationship quality hypothesis states that individuals with high quality relationships (friendly relationships that have direct fitness benefits and some consistency in their responses to each other) will have post-conflict affiliation (former opponent and/or third-party affiliation) to reduce the costs involved with conflicts (increased stress and relationship uncertainty, a declining dominance rank, etc.). This hypothesis integrates the valuable relationship hypothesis, the uncertainty hypothesis (former combatants will use former opponent affiliation and redirected aggression to reduce stress and uncertainty in the relationship), and the social constraints hypothesis

(bystanders will engage in third-party affiliation if it is not too risky), which are three of the main post-conflict affiliation hypotheses.

Relationship security is the most difficult element of the relationship quality hypothesis to model because of the paucity of empirical data on this component. I chose dominance style to represent security, however it is unknown whether this is an accurate measure. There is much empirical work that needs to be done on the different forms of post-conflict affiliation (presence and functions) and relationship quality components before a robust picture of post-conflict affiliation patterns emerge, however this broad hypothesis provides the context in which to carry out further research.

Another aspect that will be important to focus on to advance the field of post-conflict affiliation regards third-party affiliation, as this thesis has emphasised. This field will greatly benefit from detailed studies of the presence and function of third-party affiliation across taxa. This particularly applies to bird species in which many high quality relationships are maintained, to species that are not monogamous, and species that are not social to compliment the corvid research, which should illuminate whether predictions in the relationship quality hypothesis also apply to non-corvid bird species.

New methods for studying post-conflict affiliation

Rooks and jackdaws did not show third-party affiliation according to the standard method for calculating its occurrence (latency to first affiliation; chapters 3, 4, and 5). Instead, they showed a higher frequency of affiliation and sometimes also a higher duration of affiliation after conflicts. The high baseline levels of affiliation in rooks and jackdaws species may obscure clear results from methods using latency to first affiliative contact. Former combatants may have delayed their first affiliation after conflicts relative to matched controls due to a preoccupation of aggressing against others when stress was presumably the most elevated, and only affiliating with their mate after this activity had subsided. The delay in first affiliative contacts after conflicts resulted in triadic contact tendencies that showed more post-conflict third-party avoidance than attraction. However, the fact that affiliation was delayed after conflicts, does not mean that third-party affiliation did not occur. Indeed, it did when the

frequency and duration of affiliation were accounted for. Conflict stress may increase activity levels, requiring individuals to engage in a higher number of affiliative events to obtain a long enough duration of affiliation to reduce the stress, if that is one of the functions of post-conflict affiliation. Using the frequency and duration of affiliation to measure post-conflict affiliation may be particularly useful in cases where a stress reducing function is suspected due to the increase in activity levels that stress can cause.

Radford (2008) expanded the scale of post-conflict affiliation from looking at inter-individual behaviour to inter-group behaviour when he found third-party affiliation within groups of green woodhoopoes after fights with other groups. Looking at post-conflict affiliation at a larger scale will be particularly useful when investigating this behaviour in singular breeders (species where a dominant pair reproductively suppresses subordinates who help raise their offspring). Singular breeders often exhibit little or no inter-individual post-conflict affiliation, supposedly because their dominance hierarchies are rigid (opportunities to increase rank are rare), they are generally highly tolerant, and their fitness (direct or indirect) depends on remaining in the group. Singular breeder groups function more cohesively than groups in many other social species, and they share some traits with eusocial insects (reproductive suppression of subordinates and helpers raise the dominant's offspring). Singular breeding groups behave more like a superorganism than groups in a fission-fusion society, which can influence the scale at which they behave. Indeed, meerkats are singular breeders that do not show inter-individual post-conflict affiliation, however they rally each other in war dances before engaging another group in a conflict (as do green woodhoopoes). Perhaps meerkats also have intra-group affiliation after inter-group conflicts. Investigating post-conflict affiliation at this larger scale opens a new realm for the field and will require much empirical work to understand when and why it occurs.

Summary

Social system, particularly the number of high quality relationships, influences post-conflict affiliative behaviour. Studying this behaviour in rooks, jackdaws, and jays has elucidated specific post-conflict affiliation patterns because of their unique number of high quality relationships: one for rooks and jackdaws who show post-conflict

affiliation within their high quality relationship, and none for jays who show post-conflict affiliation with any of their relationships. Within the social corvids, jackdaw post-conflict third-party affiliative behaviour becomes stronger across the developmental period after pair formation through the age at sexual maturity when partner bonds appear to increase in terms of their relationship value. Post-conflict third-party affiliation appears to reduce aggression for rook and jackdaw aggressors because they receive less aggression when they are near another (likely their mate). However, the function of post-conflict third-party affiliation is less clear for victims of both species. Perhaps the most likely function is that it reduces the stress involved with being attacked in conflicts and receiving aggression afterward, however, experiments involving physiological measurements of stress will be necessary to determine whether this function applies. Data from this thesis provided sufficient information to begin analysing the spread of post-conflict affiliation across taxa according to the number of high quality relationships individuals have. This resulted in the formation of the relationship quality hypothesis as a broad hypothesis for the field of post-conflict affiliation that should prove useful for future research.

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