



Reciprocity of agonistic support in ravens

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Cooperative behaviour through reciprocation or interchange of valuable services in primates has received considerable attention, especially regarding the timeframe of reciprocation and its ensuing cognitive implications. Much less, however, is known about reciprocity in other animals, particularly birds. We investigated patterns of agonistic support (defined as a third party intervening in an ongoing conflict to attack one of the conflict participants, thus supporting the other) in a group of 13 captive ravens, *Corvus corax*. We found support for long-term, but not short-term, reciprocation of agonistic support. Ravens were more likely to support individuals who preened them, kin and dominant group members. These results suggest that ravens do not reciprocate on a calculated tit-for-tat basis, but aid individuals from whom reciprocated support would be most useful and those with whom they share a good relationship. Additionally, dyadic levels of agonistic support and consolation (postconflict affiliation from a bystander to the victim) correlated strongly with each other, but we found no evidence to suggest that receiving agonistic support influences the victim's likelihood of receiving support (consolation) after the conflict ends. Our findings are consistent with an emotionally mediated form of reciprocity in ravens and provide additional support for convergent cognitive evolution in birds and mammals.

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Whether truly altruistic behaviour (a behaviour that benefits the recipient but exerts a net cost on the actor over the course of its lifetime; Hamilton 1964; West et al. 2007) exists in nonhuman animals is a matter for debate (Hammerstein 2003; Silk et al. 2005; Stevens et al. 2005; de Waal 2008). Cooperative behaviour (initially costly to the actor but ultimately beneficial to both actor and recipient), however, manifests itself frequently in many different guises, from food sharing to cooperative breeding, hunting and agonistic support (Clutton-Brock 2009). Ultimate explanations for cooperative behaviour include kin selection, group selection, mutualism and reciprocal altruism (Trivers 1971; Axelrod & Hamilton 1981; Stevens et al. 2005; Brosnan & Bshary 2010). Reciprocal altruism, or reciprocity, is by definition not actually altruistic in ultimate terms as the initial cost to the actor is later rewarded. However, to assume that the animal's motivation in such cases is not altruistic is to infer that an actor is aware of the future net benefits of his/her initial investment and risks conflating proximate and ultimate explanations for the behaviour (Schino & Aureli 2009; de Waal & Suchak 2010). There is, in fact, very little evidence that animals are able to keep track of individual cases of cooperation received from various partners and reciprocate

accordingly (calculated or contingent reciprocity: Stevens et al. 2005; Brosnan et al. 2009; but see Dufour et al. 2009; Cheney et al. 2010). In many cases, reciprocated cooperation received is so far temporally removed from the initial event that the recipient is unlikely to associate the reward with its initial investment (de Waal & Suchak 2010).

Agonistic support (defined here as a third party intervening in an ongoing dyadic conflict to attack one of the conflict participants, thus supporting the other) is an ideal behaviour for studying the proximate and ultimate causes of cooperation because it entails a single clearly defined event with a clear net benefit to the recipient and a cost (risk of injury, cost of time and energy) to the actor. Agonistic support has been shown in nonhuman primates to be reciprocated within dyads and exchanged for other services ('interchange') such as grooming or access to food (Silk 1982, 1992; Hemelrijk & Ek 1991; Noë & Hammerstein 1995; Watts 2002; Schino 2007). Most research in this field has thus far been conducted on nonhuman primates, partially because their advanced cognitive abilities enable such cooperative acts to occur (Brosnan et al. 2010) but also because the structure of their relationships, frequently characterized by multiple high-value partners, may make such behaviours more likely (Harcourt 1992; but see Marino 2002; Seed et al. 2009). However, a recent review of patterns of agonistic support across all species studied so far found that even though primates were more likely to form intragroup coalitions than nonprimates (possibly owing to a literature bias), there was no

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support for any differences in the evolutionary forces favouring agonistic support in primates and other animals (Smith et al. 2010).

Although the field has recently benefited from an expansion of studies on nonprimate species such as ring-tailed coatis, *Nasua nasua* (Romero & Aureli 2008), bottlenose dolphins, *Tursiops truncatus* (Connor 2007), fallow deer, *Dama dama* (Jennings et al. 2009) and spotted hyaenas, *Crocuta crocuta* (Smith et al. 2010), little is known about patterns of agonistic support in birds. Moreover, what we do know suggests that most support occurs among kin or pair partners (Scheiber et al. 2005; Emery et al. 2007), whose support is likely to be associated with inclusive fitness benefits for the actor and is not likely to be dependent on reciprocation, although reciprocal patterns may emerge (Emery et al. 2007). Ravens, *Corvus corax*, have recently been shown to share what are considered to be 'valuable' relationships (defined as those who spend time together, preen each other and support each other in aggressive conflicts: van Schaik & Aureli 2000) with individuals who are neither kin nor pair partners (Fraser & Bugnyar 2010a). Ravens sharing valuable relationships have also been shown to engage in postconflict bystander affiliation, functioning as consolation (Fraser & Bugnyar 2010b). Furthermore, ravens are members of the corvid family famed for their 'primate-like' cognitive abilities (Clayton & Emery 2005; Heinrich & Bugnyar 2007; Seed et al. 2009). Among the corvids, ravens are characterized by a particularly long period of social development, with territorial pair formation occurring as late as their fourth year (Boarman & Heinrich 1999), and occasionally up to 10 years after hatching (T. Bugnyar, unpublished data). Following independence from their parents and prior to territorial pair formation, ravens form large nonbreeder flocks (Glutz von Blotzheim & Bauer 1993; Ratcliffe 1997), enabling unpaired birds to compete with territorial pairs for access to monopolizable food sources (Heinrich 1989; Marzluff & Heinrich 1991). During this time, agonistic support may play a pivotal role in the establishment and maintenance of valuable relationships with other flock members, enabling the ravens to secure access to resources and progress up the dominance hierarchy (Gwinner 1964; Heinrich 1999).

We tested a number of predictions about patterns and determinants of agonistic support in a group of aviary-housed ravens to understand why agonistic support occurs, how the ravens decide whom to support, and whether patterns differ from those observed in primates. First, we investigated whether ravens simply follow a rule of thumb when offering support such as 'always support the aggressor' or 'always support the dominant opponent'. Second, we examined a range of factors that might predict the level of agonistic support exhibited within each dyad in the group. We predicted that if kin selection were the primary explanation for agonistic support, such support would only occur among kin. However, if empathy for a conflict opponent, the most likely basis for altruism, were the underlying mechanism, we predicted that the ravens would support kin as well as other individuals with whom they share valuable relationships, as these individuals are most likely to be responsive to each other's needs. We predicted that the ravens would support those who supported them if they were reciprocating agonistic support. However, for this to be calculated or short-term reciprocity, we expected provision of support in individual cases to be contingent on the recent receipt of support from that party (if support had been required). If ravens use agonistic support to their own advantage to cement or develop potentially valuable alliances, we predicted that they would be more likely to support ravens who were higher ranking than themselves.

Finally, as consolation (postconflict affiliation from a bystander to the conflict victim) in ravens is provided by bystanders with whom the victim shares a valuable relationship (Fraser & Bugnyar 2010b), we investigated whether dyadic levels of agonistic support predicted levels of postconflict consolation. We predicted that if consolation

and agonistic support were provided by the same individuals, the two interactions would become interdependent. Thus, we examined whether a victim's receipt of support during a conflict influenced the likelihood of receiving consolation afterwards.

METHODS

Study Subjects

We used 13 hand-reared ravens (seven males, six females) at the Konrad Lorenz Forschungsstelle, Austria as subjects for this study. Eleven subjects were in their first year at the start of the study; the other two subjects were a 4-year-old female and a 9-year-old male. All subjects were housed together in a large aviary (ca. 240 m²) situated in the Cumberland Wildpark. The study population included three sibling groups, consisting of two males and two females, two females and one male, and two males and one female. All other subjects were unrelated. During the study, two subjects died as a result of predation at the end of 2004 and the two adult subjects were removed from the group from August 2005. The aviary was enriched with trees, branches, stones, tree trunks and shallow pools for bathing. The ravens were fed twice per day with meat, milk products and kitchen leftovers and always had access to water.

Ethical Note

Raven chicks were collected from the wild with permission from the Ministerium für Landwirtschaft, Umweltschutz und Raumordnung des Landes Brandenburg, Germany. Munich, Wuppertal and Schönbrunn Zoos provided raven chicks from captive breeding pairs. The study subjects remained in captivity at the Cumberland Wildpark after the completion of this study for further research.

Data Collection

Data were collected by T.B. from June 2004 to May 2006. Ninety-six 30 min all-occurrences group samples were taken, distributed evenly across the study period and always taken between 0700 and 1100 hours, with no more than one sample taken per day, and never during feeding times. During these samples all instances of preening and aggressive conflict were recorded, along with the identities of the victim (defined as initial recipient of aggression) and aggressor (defined as initiator of aggression). For each aggressive conflict, all instances of agonistic support (defined as a third party joining a dyadic conflict and attacking one of the conflict opponents, thus providing support to the other opponent) were recorded along with the identities of the supporter and recipient of support. The first affiliative contact (defined as preening, contact sitting or briefly touching another's body or beak with own beak) from a bystander (any group member other than the conflict opponents) to the conflict victim (initial recipient of aggression) in the 10 min following the cessation of aggression (known as 'consolation'; see Fraser & Bugnyar 2010b for further details) was also recorded.

Data Analysis

To investigate the influence of rank hierarchy on a third party's decision to offer agonistic support, the relative rank of each raven in the study group was calculated using David's scores (David 1987; Gammell et al. 2003). As a major rank change occurred in October 2005 (T. Bugnyar, unpublished data), David's scores were calculated separately for June 2004–October 2005 and November 2005–May 2006. The David's scores were used to categorize the relative rank of opponents with each other and third parties (dominant/subordinate).

An index of level of agonistic support provided for each dyad was calculated using the following formula: frequency of support provided/opportunity to provide support (i.e. for ravens 'A' and 'B', this would be the frequency with which A supported B divided by the number of conflicts that B was involved in, excluding conflicts between A and B). A similar index was calculated for counter-intervention (defined as intervening in a conflict to support a particular individual's opponent; de Waal & Luttrell 1988) as follows: the frequency with which raven A supported raven B's conflict opponent, divided by the number of conflicts involving B, excluding conflicts between A and B. An index of consolation (as per Fraser et al. 2008) was devised by calculating the frequency with which one individual consoled another relative to their opportunity to do so (i.e. the frequency with which raven A consoled raven B, divided by the number of times B was a conflict victim, excluding cases where A was the aggressor).

Linear mixed models (LMMs) were used to investigate simultaneously the effects of kinship (sibling/nonsibling), sex of the supporter, sex of the recipient of support, average rate at which the supporter received preening from the recipient of support (seconds of preening per minute of observation), index of support received, index of counterintervention provided and relative rank of the recipient of support (dominant/subordinate) on the index of agonistic support provided for all possible supporter–recipient combinations. The identities of the supporters and recipients of support were entered as random factors. LMMs enable the effects of each of a number of independent variables on the dependent variable to be ascertained while controlling for the effects of the other variables in the model. Thus, reciprocity of support, or interchange between support and preening, can be examined while controlling for symmetrical features of the relationship such as kinship and sex. A further LMM was run to determine whether the index of victim agonistic support provided (independent variable) significantly predicted dyadic values for the consolation index (dependent variable). Kinship, sex of the supporter and of the recipient of support and relative dominance rank were also included in the model to control for their effects. The identities of the supporter and recipient of support were entered as random factors. A generalized linear mixed model (GLMM) with binomial error structures and a logit link function was used to see whether providing support to a conflict victim during the conflict (yes/no; independent variable) influenced the likelihood of providing consolation during the postconflict period (yes/no; binomial dependent variable). All continuous variables were subject to square-root transformations to improve normality. Maximum likelihood estimation methods were used for all LMMs and Akaike's information criterion (AIC) values were used to evaluate the best (most parsimonious) model.

To investigate whether provision of support was contingent on short-term reciprocation, we recorded for each case of agonistic support, the frequency with which the supporter was subsequently

involved in another conflict (as a victim or aggressor) within 1 week of the original conflict (excluding conflicts in which the original supporter and supported party were now opponents), and the proportion of those conflicts in which the original supported party now offered their support to the individual who had previously supported them. Using a paired *t* test, we then compared for each dyad the chance of the subject supporting a partner when the subject had received support from that partner within the preceding week with the chance of providing support when the subject had been involved in a conflict in the preceding week but had not received support from the partner. Only dyads with a minimum of three conflicts in each condition were included in the analysis ($N = 11$). To control for the possibility that support was not provided because it was not necessary, for these analyses we only considered conflicts with agonistic support ($N = 118$).

All analyses were conducted in SPSS version 17 (SPSS Inc., Chicago, IL, U.S.A.), with the exception of the GLMM analyses, which were conducted in R, using the lme4 package (Bates & Sarkar 2007).

RESULTS

Agonistic support occurred during 23% of aggressive conflicts. Data were collected on 139 cases of agonistic support during 118 conflicts, with each individual providing support on average \pm SE 12.64 ± 2.33 times to 3.83 ± 0.64 different individuals.

Third parties were more likely to support aggressors (mean individual proportion aggressor support \pm SD = 0.69 ± 0.22) than victims (Wilcoxon signed-ranks test: $T = 2.490$, $N = 9$, $P = 0.037$) and trends were found towards supporting the more dominant of the two opponents (proportion dominant support = 0.69 ± 0.08 ; $T = 2.245$, $N = 9$, $P = 0.055$) and towards targeting opponents who were subordinate to themselves (proportion subordinate targets = 0.75 ± 0.34 ; $T = 2.215$, $N = 9$, $P = 0.058$).

Determinants of Level of Agonistic Support Provided

Ravens were significantly more likely to support those ravens who supported them (LMM: $F_{1,152.6} = 5.690$, $P < 0.001$), demonstrating a reciprocation of agonistic support (see Table 1, Fig. 1). Furthermore, ravens were also more likely to support those who preened them ($F_{1,146.4} = 5.690$, $P = 0.018$), their siblings ($F_{1,144.4} = 5.582$, $P = 0.019$) and higher-ranking individuals ($F_{1,62.5} = 5.574$, $P = 0.021$; Table 1, Fig. 1).

Short-term Reciprocity?

We found no significant difference between the tendencies for a particular third party to provide support to an individual involved in a conflict when that third party had been involved in a conflict within the preceding week and either had or had not received support from that individual (paired *t* test: $t_{11} = 1.367$, $P = 0.199$).

Table 1
Predictors of agonistic support provided at the dyadic level

Independent variables	Full model (AIC = -413.833)					Best model (AIC = -419.386)				
	Estimate	SE	df	t	P	Estimate	SE	df	t	P
(Intercept)	0.041	0.02	105.27	2.02	0.046	0.036	0.02	128.19	1.95	0.053
Kinship	0.038	0.02	143.96	2.37	0.019	0.038	0.02	144.38	2.36	0.019
Supported dominant over supporter	0.023	0.01	94.58	1.82	0.072	0.026	0.01	62.49	2.36	0.021
Preening received	0.080	0.03	146.09	2.39	0.018	0.079	0.03	146.36	2.39	0.018
Support received	0.537	0.07	153.06	7.94	<0.001	0.541	0.07	152.60	8.03	<0.001
Counterintervention against recipient of support	0.001	0.05	151.51	0.02	0.983					
Sex of supporter	0.009	0.01	20.12	0.67	0.512					
Sex of recipient of support	0.000	0.01	26.62	0.03	0.976					

Supporter and recipient identities were included as random factors.

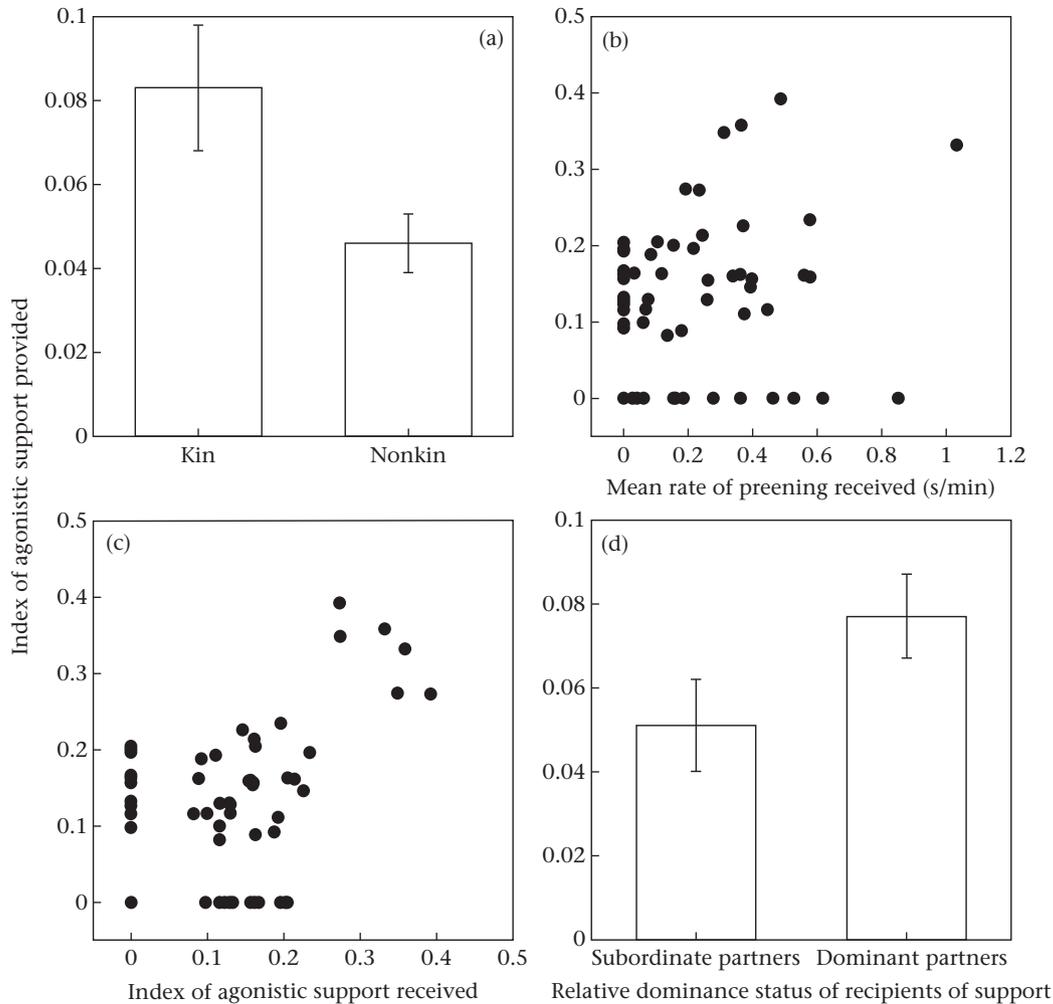


Figure 1. The influence of (a) kinship, (b) preening received, (c) support received and (d) relative dominance status on the tendency to provide agonistic support. Data in (a) and (d) represent estimated marginal means and SEs from the linear mixed models.

Interdependency between Support during and after Conflicts

The level of agonistic support provided at the dyadic level significantly predicted the level of consolation provided (LMM: $F_{1,115.4} = 4.825$, $P = 0.030$; Table 2). However, receiving support during a conflict did not influence the victim's likelihood of receiving consolation after a conflict (GLMM: $\beta \pm SE = 0.351 \pm 0.664$; $z = 0.529$, $P = 0.597$).

DISCUSSION

Ravens were more likely to support the initial aggressor than the victim of the conflict. However, as support was nevertheless

provided to victims in a third of all cases, it seems unlikely that the ravens always supported the aggressor as a rule of thumb. Predominantly supporting the aggressor, and a tendency to support the dominant opponent and target subordinate individuals, suggests a strategy to minimize costs associated with becoming involved in an ongoing conflict. These patterns are also consistent with a strategy to reinforce the status quo and to aid group stability. Supporting aggressors and dominant opponents, however, also suggests that provision of agonistic support may not necessarily correlate with the recipient's need for support, as those individuals are generally predicted to be more likely to win conflicts than recipients of aggression (victims) or subordinate opponents. This is further reinforced by the finding that the ravens were more likely to

Table 2
Predictors of the level of consolation provided at the dyadic level

Independent variables	Full model (AIC=-99.697)					Best model (AIC=-105.565)				
	Estimate	SE	df	t	P	Estimate	SE	df	t	P
(Intercept)	0.193	0.05	111.99	3.93	<0.001	0.195	0.04	109.88	4.82	<0.001
Index of agonistic support	0.370	0.17	120.46	2.22	0.028	0.361	0.16	115.36	2.20	0.030
Kinship	0.174	0.04	125.91	4.38	<0.001	0.175	0.04	125.99	4.42	<0.001
Sex of supporter	0.008	0.03	23.54	0.25	0.806					
Sex of recipient of support	0.006	0.03	120.97	0.20	0.842					
Supporter dominant over recipient of support	0.000	0.03	65.06	0.01	0.996					

Supporter (consoler) and recipient identities were included as random factors.

support individuals who were dominant over themselves, for whom such support is likely to be less useful than for a subordinate bird. Providing support may thus represent a tactical way to reinforce a good relationship with a useful dominant group member.

Despite the ravens' propensity to support dominant group members, the level of support provided to an individual was most strongly predicted by the level of support received. However, recipients of support were not more likely to reciprocate support in conflicts involving the supporter up to a week later, suggesting that reciprocity of support in ravens is not based on short-term calculations on a tit-for-tat basis. The period of time following a specific interaction in which reciprocation should be considered short term is not always clear (Gomes et al. 2009). When reciprocation of grooming in primates is considered, short-term reciprocation is often limited to interactions occurring within a timeframe of only several minutes, or even seconds, following the initial interaction (e.g. Barrett et al. 1999; Schino et al. 2007; Gomes et al. 2009). Indeed, it is unclear whether some species are even cognitively capable of reciprocation over longer periods (Stevens & Hauser 2004). Agonistic support, however, is a much rarer occurrence than preening or grooming, and as such the opportunity to reciprocate is likely to be very low within a period of less than a day. Unfortunately, assessing reciprocation (or interchange) of specific individual acts over longer periods may provide less accurate results, as without continuous observation of the subjects, reciprocation of such acts may be missed. Our findings, however, show that ravens are more likely to reciprocate support over 2 years than within a week, mirroring recent findings in apes showing that the exchange and interchange of services is likely to be long term (Melis et al. 2008; Gomes & Boesch 2009; Gomes et al. 2009; Gilby et al. 2010).

As ravens were more likely to support those who preened them, they could be 'trading' preening for support. This scenario, however, is most likely in cases where subordinate individuals 'buy' the support of a valuable dominant group member in exchange for preening (or grooming in primates; Noë & Hammerstein 1995; Schino 2007). In this study, ravens were more likely to support dominant individuals, making such an exchange unlikely, as conflict opponents should have a preference for higher-ranking supporters, although further data are needed to rule out an interchange between preening and support. Neither were the observed patterns likely to have occurred as a result of symmetry of features within dyads, whereby the ravens supported or exchanged preening for support with similar group members, such as kin or those of the same sex or rank ('symmetry-based reciprocity': Brosnan & de Waal 2002), as our analyses controlled for such effects. Instead, the ravens may have supported individuals with whom they shared a good relationship. The reciprocal nature of such relationships is likely to lead to reciprocity in patterns of interactions between individuals, termed 'emotionally mediated' reciprocity (Schino & Aureli 2009). Emotion can be considered to be a temporary state brought about by external stimuli, leading to physiological and cognitive changes that reflect the individual's experience and cognitive assessment of the situation (de Waal 2011). Emotions may enable individuals to respond differently to different group members according to the quality of their relationship (representative of their history of interactions), but without the cognitively demanding task of keeping track of each interaction with each group member (Aureli & Schaffner 2002). As such, emotion may function as an intervening variable between sensory input and motor output, playing an important role in the modulation of flexible behavioural responses (Aureli & Whiten 2003; Aureli & Schino 2004). Ravens were found to reciprocate agonistic support for group members with whom they shared a valuable relationship in the long term but most likely did not reciprocate individual acts

of support in the short term. Thus, while reciprocity may explain the evolution of agonistic support in ravens in ultimate terms, at the proximate level, emotional mediation may explain how ravens choose when to intervene in a conflict, and whom to support.

Emotions may also play an important role in what happens after the conflict. Bystanders may be empathically motivated to console victims of aggression, thus alleviating the victim's postconflict distress (de Waal & Aureli 1997; Fraser et al. 2008; Romero et al. 2010). Bystanders offering postconflict consolation are likely to share a valuable relationship with the victim (Fraser et al. 2009; Fraser & Bugnyar 2010b). Our results suggest that similarly valuable individuals provide agonistic support in ravens and, moreover, showed that levels of agonistic support provided correlated with levels of consolation provided. Thus, those who offered the victim support during a conflict were also likely to offer support (in the form of consolation) after aggression ceased. We found, however, no evidence to show that receiving agonistic support during a particular conflict affected the victim's likelihood of receiving consolation afterwards. Thus far, postconflict interactions between opponents and third parties have primarily been considered independently from those occurring during the conflict, despite the fact that they may involve the same individuals and may occur only seconds apart. These findings highlight the importance of further integration of research on behaviour before, during and after conflicts. Moreover, the association between agonistic support and consolation further suggests that agonistic support may form part of a larger network of cooperative behaviour in ravens, and shows that proactive, prosocial behaviour (Jaeggi et al. 2010) not only exists outside of the pair bond in a nonprimate species, but also that it occurs regularly under multiple guises. In the context of aggressive conflict, cooperative behaviour, such as the lateralization of aggressive displays in convict cichlids, *Amatitlania nigrofasciata* (Arnott et al. 2011), has been suggested to reduce the costs of fighting. In alleviating postconflict distress, consolation fulfils a similar function (Fraser et al. 2009). Agonistic support may therefore form part of a range of strategies to mitigate the negative consequences of aggressive conflict when conflicts of interest arise.

In hyaenas (Smith et al. 2010) and fallow deer (Jennings et al. 2009, 2011), two of the few other nonprimate species in which agonistic support has been studied in detail, agonistic support was found to reinforce existing hierarchies, thus maintaining the status quo. Furthermore, fallow deer appear to follow a 'random target model' (Dugatkin 1998), where the identity of the target of aggression is unimportant and the purpose of intervening in the conflict is to avoid the positive effect that winning a conflict has on the chance of winning subsequent conflicts ('winner effect'; Chase et al. 1994; Jennings et al. 2011). As ravens showed tendencies to support the dominant opponent and target opponents subordinate to themselves, impeding subordinate group members from rising up the hierarchy may play a role in why ravens intervene in aggressive conflicts, but as only nonsignificant trends were found in those directions, it is unlikely to represent the primary motivation behind the act. Rather, as ravens supported those who supported them, preened them and kin, it appears that for ravens, it is not the identity of the target, but the identity of the supported opponent and the relationship between the supporter and the recipient of support that are critical in predicting the occurrence of agonistic support.

Reciprocity of agonistic support and interchange of agonistic support and preening has previously been demonstrated in rooks, *Corvus frugilegus*, another corvid species, but was only found within pair partners, and is thus likely to be a product of their symmetrical and exclusive relationship (Emery et al. 2007). Reciprocity of agonistic support and interchange of support and grooming has also been demonstrated in ring-tailed coatis, a social carnivore, but

kinship was unknown, and thus kin selection cannot be ruled out as the driving force behind provision of agonistic support (Romero & Aureli 2008). Hence, here we present the first quantitative evidence of reciprocity and interchange of social interactions outside of a pair bond in a nonprimate species while controlling for kinship. Moreover, we show that relationships of the sort previously suggested to occur only among pair bonds outside of the primates (Dunbar & Schultz 2007) may also occur among unpaired ravens and provide additional support for convergent cognitive evolution in birds and mammals (Emery & Clayton 2004; Emery 2006).

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