

The quality of social relationships in ravens

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The quality of a social relationship represents the history of past social interactions between two individuals, from which the nature and outcome of future interactions can be predicted. Current theory predicts that relationship quality comprises three separate components, its value, compatibility and security. This study is the first to investigate the components of relationship quality in a large-brained bird. Following methods recently used to obtain quantitative measures of each relationship quality component in chimpanzees, *Pan troglodytes*, we entered data on seven behavioural variables from a group of 11 ravens, *Corvus corax*, into a principal components analysis. The characteristics of the extracted components matched those predicted for value, compatibility and security, and were labelled as such. When the effects of kinship and sex combination on each relationship quality component were analysed, we found that kin had more valuable relationships, whereas females had less secure and compatible relationships, although the effect of sex combination on compatibility only applied to nonkin. These patterns are consistent with what little knowledge we have of raven relationships from aviary studies and show that the components of relationship quality in ravens may indeed be analogous to those in chimpanzees.

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For many animals, observable social interactions between group members do not represent random patterns of association, but rather reflect a pattern of interactions whereby the occurrence and outcome of any one interaction between two individuals affect the occurrence and outcome of their subsequent interactions. In such cases, those individuals can be said to share a social relationship, which can be characterized by the relative quality and distribution of those interactions (Hinde 1976, 1983). The unique history of interactions between individuals may lead to a broad variation in the quality of social relationships within groups, and as group structure is determined by the sum of the social relationships within a group, heterogeneity in social relationships ultimately results in variation at the group level (Kutsukake 2009). Variation in relationship quality within and between groups has been suggested to account for the pattern, distribution and functions of many behaviours, such as vigilance behaviour (Kutsukake 2006), the likelihood of aggressive conflict (de Waal 2000; Wittig & Boesch 2003), postconflict behaviour (Cords & Aureli 2000; Aureli et al. 2002; Fraser et al. 2009; Arnold et al., In press), mother–infant interactions (Schino et al. 1995; Maestripietri 1998; Weaver & de Waal 2002), novel object exploration (Stöwe et al. 2006),

reciprocity (Cords 1997; Watts 2002; Romero & Aureli 2008), helping behaviour (Griffin & West 2003), tolerance to inequity (Brosnan et al. 2005) and social learning (Coussi-Korbel & Fragaszy 1995; Chapman et al. 2008; Pongrácz et al. 2008; Schwab et al. 2008). Understanding the nature and source of variability in social relationships is thus a critical factor in our understanding of how animals behave.

The quality of a relationship is likely to be composed of a number of different dimensions. Cords & Aureli (2000) proposed that relationship quality comprises three separate components, relationship value, compatibility and security. The value of a relationship refers to the direct benefits gained as a result of the relationship, such as agonistic support or food sharing. The compatibility of a relationship is a measure of the level of tolerance between individuals and the general tenor of social interactions. Relationship security describes the predictability of interactions between partners, or the consistency of their interactions over time. The differential influence of each of these components has been used to explain variation in patterns of behaviour, most notably postconflict behaviour (e.g. Cords & Aureli 2000; Fraser et al. 2009; Arnold et al., In press). However, most research on social relationships has thus far focused on primates and, although we know that relationship quality in general is important in the social organization of many species (Connor 2007; Emery et al. 2007; Holekamp et al. 2007; Silk 2007), no study has yet investigated the individual components of relationship quality in a nonprimate

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species. Moreover, even within the primates, the existence of three separate dimensions of relationship quality reflecting the value, compatibility and security of the relationship has thus far only been investigated, and demonstrated, in chimpanzees, *Pan troglodytes* (Fraser et al. 2008). Thus, although Cords & Aureli (2000) did not limit their proposal to primate species, it is as yet unknown whether relationships in other species also comprise the same components, and in particular whether avian relationship quality components, at least in some species, are indeed comparable with those found in chimpanzees, and more broadly in primates.

The corvids represent a family of large-brained birds that are phylogenetically distant from the primates, but with whom they show striking similarities in many aspects of their behaviour and cognition (e.g. episodic-like memory: Clayton & Dickinson 1998; planning for the future: Raby et al. 2007; cooperative problem solving: Seed et al. 2008; creating novel tools to solve problems: Weir et al. 2002; tactical deception: Bugnyar & Kotschal 2002). The social intelligence hypothesis (Humphrey 1976) and the social brain hypothesis (Dunbar 1998) predict that the evolution of cognitive intelligence is driven by social complexity. Thus, individuals living in large groups are expected to have larger relative brain size and perform better in cognitive tasks. However, although this pattern works well for primates (Dunbar 1992) and some other classes (bats: Barton & Dunbar 1997; carnivores, insectivores: Dunbar & Bever 1998; cetaceans: Marino 2002; Connor 2007; but see Schultz & Dunbar 2006 for ungulates), whether such a relationship exists for birds is as yet unclear (Emery 2004). It has been suggested, however, that the evolution of the high levels of social intelligence for which there is an ever-increasing wealth of evidence in corvids (and parrots) may be the result of the cognitive skills required to deal with the complexity of their relationships, rather than the number of social interaction partners (Emery et al. 2007; but see Scheiber et al. 2008). Emery et al. (2007) have shown that rooks, *Corvus frugilegus*, share valuable relationships that appear to resemble those found in primates, at least among pair mates, but little is yet known about the complexity and variety of other corvid relationships, or the existence of other relationship quality components and whether they resemble those that comprise ape and other primate relationships.

Ravens, *Corvus corax*, are members of the corvid family, characterized by long-term monogamy with mates remaining together throughout the year. Although classified as a territorial species, mating pairs are not socially isolated and prior to becoming territorial may be highly social (Heinrich 1999). Ravens have one of the longest periods of sociocognitive development of any avian species, often not becoming reproductively successful until their fifth year, and in some cases delaying reproduction until at least their 10th year (wild ravens; T. Bugnyar, unpublished data). Once independent from their parents at about 6 months of age, juvenile ravens join nonbreeder groups (Glutz von Blotzheim & Bauer 1993; Ratcliffe 1997). Group formation may provide nonbreeders with a competitive advantage when competing with territorial pairs over limited food resources in discrete patches (Marzluff & Heinrich 1991). Ravens may deal with strong competition at feeding sites by carrying off consecutive loads of food for caching, varying their caching behaviour according to the presence and the knowledge of conspecifics by hiding food away from others (Lorenz 1935; Heinrich & Pepper 1998), caching food behind objects that might obstruct the others' view (Bugnyar & Kotschal 2002), and even taking into account conspecifics' knowledge of cache location when protecting and pilfering caches (Bugnyar & Heinrich 2005).

Apart from these sophisticated social skills during foraging, there is a growing body of evidence that ravens' social relationships are similarly complex. In support of this, factors such as kinship, sex combination and levels of affiliation have been shown to influence

social learning (Schwab et al. 2008), individual learning (Range et al. 2006), novel object exploration (Stöwe et al. 2006) and attention (Scheid et al. 2007). How these factors relate to each other and to other aspects of raven behaviour, however, is as yet unknown. We believe, therefore, that ravens present us with an ideal model to investigate whether current theory on the components of relationship quality transcends the primate order, while a much more detailed understanding of raven relationships is also key to furthering our knowledge of raven behaviour and cognition.

The first aim of this study was to investigate the components of relationship quality in ravens using principal components analysis to extract key components of relationship quality from a number of behavioural variables, a method recently used to investigate relationship quality in chimpanzees (Fraser et al. 2008). Using this method, we could obtain composite, quantitative measures of each relationship quality component, specific to the study group, and draw comparisons between primate and corvid relationships. Our second aim was to investigate the effects of sex combination and kinship on each of the relationship quality components to determine the sources of variation therein.

METHODS

Study Subjects and Housing

The study subjects were 11 hand-reared ravens (five males, six females) at the Konrad Lorenz Forschungsstelle, Austria. In 2004, 11 ravens were taken from four nests (two from the wild, two from zoos). The ravens were reared in sibling groups in artificial nests but were free to move between nests and interact with other nonkin nestlings as soon as they were physically able to do so (at 5 weeks of age). The birds fledged in May 2004, at which point they were housed together in one social group with two previously raised unrelated adult ravens (a 5-year-old female and a 9-year-old male) in a large outdoor aviary (ca. 240 m²), situated in the Cumberland game park in Grünau, Austria. Although data were collected on all 13 ravens, two juveniles died towards the end of 2004 as a result of predation, and thus were not subjects in this study. The two adult subjects were separated from the rest of the group from August 2005. Birds were marked with coloured leg-rings for individual identification. The aviary contained trees, branches, stones, tree trunks and shallow pools for bathing. The ravens were fed twice per day with meat, milk products and kitchen leftovers. Water was provided ad libitum.

Wild ravens were collected with permission of the Ministerium für Landwirtschaft, Umweltschutz und Raumordnung des Landes Brandenburg, Germany. The zoos in Munich and Wuppertal, Germany and Schönbrunn in Vienna, Austria provided raven chicks from captive breeding pairs. The study subjects remained in captivity at the Cumberland game park after this study for further research.

Data Collection

Data were collected by T.B. over 93 30 min observational samples from August 2004 to May 2006. Samples were collected between 0730 and 1100 hours (no more than one 30 min sample per day) and were spread evenly across the data collection period. During each sample, all occurrences of social interactions between any study subjects were recorded. We defined aggressive interactions as any interactions involving a threat (noncontact threat display or physical hitting from one individual), fight (contact aggression involving both individuals hitting each other), forced retreat (approached bird retreats after being threatened) and/or chase flight (one individual flies in pursuit of another following

a threat, forced retreat or fight). For all instances of aggression, the identities of the primary opponents and any supporters of either party were recorded. The duration of all instances of preening and contact sitting (defined as sitting within one body's length of a partner) within a sample was also recorded along with the identity of the partners involved. All approaches to within a body's length of another subject were recorded along with the approached bird's response. A negative response was recorded if the approached bird retreated, or chased or attacked the approaching bird. If no interaction occurred between the partners following an approach, a neutral response was scored. An affiliative response was recorded if the approached bird was handling food or an object prior to the approach and both partners subsequently handled the item, or the item was successfully transferred to the approached bird. An affiliative response was also recorded if the partners engaged in contact sitting or allopreening.

Data Analysis

Following Fraser et al. (2008), we used principal components analysis (PCA) to obtain composite measures of relationship quality. PCA is a statistical technique that can be used to identify underlying factors, or principal components, that explain the pattern of correlations within sets of variables (Tabachnick & Fidell 2007). The main advantages of this over previous methods used to measure relationship quality, such as using individual behavioural variables or relying on broad demographic categories such as age and sex combination or kinship, are two-fold. First, the assessment of relationship quality is based on multiple behavioural variables, which allows the full degree of variation in relationship quality to be quantified and, although the PCA approach does not protect researchers from missing important variables, also lessens the impact of such an event occurring. Second, the PCA enables those variables to be grouped objectively into components of relationship quality that reflect the animals' own appraisals of their relationships. The PCA provides coefficients of correlation between each behavioural variable and each extracted component and relative scores for each dyad for each component. As extracted components are by definition uncorrelated with each other, the total variance explained is the sum of the variance explained by each extracted component. We considered coefficients of correlation greater than 0.5 or less than -0.5 to be high loadings. A varimax rotation, an orthogonal rotation method that minimizes the number of variables that have high loadings on each component, was used to simplify the interpretation of the components. We used a minimum eigenvalue of 1.0 to determine the number of components extracted from the PCA (Tabachnick & Fidell 2007).

We entered seven behavioural variables into the PCA (Table 1). As assessment of the quality of a relationship is not necessarily symmetrical between partners, for example a relationship between

individuals A and B might be more valuable to A than to B, data were analysed at the individual rather than the dyadic level, with the exception of contact sit, which necessarily provided identical values for each partner in a dyad. To calculate the variation in response to approach over time we calculated the absolute difference in the proportion of negative responses to approaches in two periods (August 2004–August 2005 and May 2005–May 2006). As the ravens' behaviour may vary seasonally (T. Bugnyar, unpublished data), it was important to include a full 12 months in each period to control for any such variation across periods, but as the full data collection period did not span 2 whole years there was some overlap in these periods. An index of agonistic support was created by calculating the frequency of support as a function of the opportunity to support (i.e. the number of conflicts where A supported B or B supported A divided by the total number of conflicts involving A or B, excluding those in which A and B were opponents). We calculated a similar index for counter-intervention (agonistic intervention against a partner: de Waal & Luttrell 1988), that is, the number of conflicts in which A supported B's opponent, or B supported A's opponent, divided by the total number of conflicts involving A or B, excluding those in which A and B were opponents. Dyads for which no data were available for one or more of the behavioural variables (e.g. the individuals did not approach each other, so the proportion of negative responses to approaches could not be calculated) were excluded from the analysis ($N = 17$).

The behavioural variables entered into the PCA analysis were chosen to reflect as many aspects of the ravens' interactions as possible within the bounds of the data available. As one of the aims of this study was to provide a direct comparison with the findings of a similar study on chimpanzees (Fraser et al. 2008), the variables chosen were as similar as possible to those used in that study with the exception of two variables, which were omitted from the current study. Food sharing (recorded as the proportion of successful begging attempts in chimpanzees; Fraser et al. 2008) was not included here as this behaviour is particularly complex in juvenile ravens and may be confounded with their manipulation and sharing of nonfood objects (Stöwe et al. 2006; Bugnyar et al. 2007). Whether food and object 'sharing' is consensual may also be difficult to perceive. As the functions of different forms of sharing (object, food) are not yet clear in ravens, we refrained from making predictions about the quality of the relationship between 'sharing' partners and thus did not include this variable in our analyses. Symmetry in proportion of preening (grooming in chimpanzees; Fraser et al. 2008) provided between partners was not included because data for this variable could only be calculated for those dyads in which at least one preening bout took place, and as a result would have led to an excessive reduction in sample size.

We assessed the effects of sex combination (male–male, female–female or male–female) and kinship (kin or nonkin), and the interaction between sex combination and kinship, on each of the extracted relationship quality components (Value, Compatibility and Security) using within-subject general linear models (GLMs). Kin were defined as siblings (20 of 93 dyads) and were reared together until fledging. All other dyads were unrelated and classified as nonkin. Subject identity was included in all models to control for between-subject variation and nonindependence of data points. The dependent variables used in the analysis were the scores obtained for each dyad for each of the components extracted from the PCA. Value and Compatibility were subject to cube-root transformations to improve normality. We selected the best model using Akaike's information criteria (AIC), which compares the adequacy of several models and identifies the model that best explains the variance of the dependent variable as that with the lowest AIC value (Burnham & Anderson 2004; Tabachnick & Fidell 2007). Only the effects of those variables

Table 1
Variables entered into the principal components analysis

Variable name	Variable description
Contact sit	Duration of contact sitting/h
Preening	Duration of preening/h
Agonistic support	Index of agonistic support (frequency of support/opportunity to support)
Tolerance to approaches	Proportion of positive and neutral responses to approaches
Aggression	Frequency of aggressive interactions/h
Counter-intervention	Index of counter-intervention (frequency of counter-intervention/opportunity to counter-intervene)
Variation in response to approach over time	Difference in the mean proportion of negative responses to approaches in year 1 and year 2

present in the best model are presented. If sex combination was a significant predictor of the dependent variable in the best model, we used pairwise comparisons with Bonferroni adjustments for multiple comparisons to detect differences between male–male, male–female and female–female dyads. To aid interpretation of interaction terms, when a significant interaction between sex combination and kinship was observed, we split the data according to kinship and then re-ran the model, thus enabling the influence of sex combination on the dependent variable to be detected separately for kin and nonkin. An alpha level of 0.05 was adopted for all tests. All analyses were conducted in SPSS version 14.0 (SPSS Inc., Chicago, IL, U.S.A.).

RESULTS

Relationship Quality Components

Three components were extracted from the PCA. Components 1, 2 and 3 explained 35.1%, 24.7% and 15.4% of the overall variance, respectively, totalling 75.2%. Loadings for each of the behavioural variables on each extracted component are presented in Table 2. Each behavioural variable loaded strongly onto a single component. The first component consisted of high loadings from contact sit, preening and agonistic support; these variables approximated Cords & Aureli's (2000) description of relationship value and Fraser et al.'s (2008) measure of relationship value in chimpanzees. Thus, we labelled the first extracted component 'Value'. The characteristics with high loadings on the second extracted component were aggression and counter-intervention, which both had positive loadings, and tolerance to approach, which had a strong negative loading on the component, suggesting that this component measures the lack of tolerance or incompatibility of the dyad. In concurrence with Fraser et al.'s (2008) measure of compatibility and Cords & Aureli's (2000) definition, however, we labelled this component 'Compatibility' for ease of interpretation. In all subsequent analyses involving the second component, we used inverse signs for each score for each dyad for that component, so that high values represented the compatibility, rather than incompatibility, of the dyad. The third and final component extracted included a high loading from only one variable, variation in response to approach over time. As high values of this variable indicate a high degree of variation in response to approaches, this component represents a lack of consistency in dyadic interactions, and thus, according to Cords & Aureli's (2000) definition, 'insecurity'. To simplify interpretation, however, we labelled the variable 'Security', and thus we used inverse signs for scores for each dyad for the component for all subsequent analyses involving the component. All variables loaded onto the same components in ravens as they did in chimpanzees (Fraser et al. 2008).

Table 2
Varimax rotated component matrix

Variable	Component		
	1	2	3
Contact sit	0.934	-0.176	-0.064
Preening	0.916	-0.183	-0.069
Agonistic support	0.827	0.000	0.059
Tolerance to approaches	0.187	-0.753	-0.268
Aggression	0.033	0.787	-0.257
Counter-intervention	-0.163	0.687	0.162
Variation in response to approach over time	-0.004	0.090	0.948

Values represent coefficients of correlation between each variable and each component. Values of >0.5 or <-0.5 (marked in bold) were considered high loadings.

Factors Influencing Relationship Quality

Kinship had a significant influence on Value (GLM: $F_{1,93} = 38.086$, $P < 0.001$), indicating that siblings have more valuable relationships than nonsiblings. For Compatibility, a significant interaction term between sex combination and kinship was observed ($F_{2,93} = 4.663$, $P = 0.012$), indicating that the effect of sex combination on Compatibility varied according to kinship classification. When we split the data into kin and nonkin, female–female dyads had less compatible relationships than male–male (pairwise comparison with Bonferroni correction: $df = 73$, $P < 0.001$) or male–female ($df = 73$, $P = 0.001$) dyads when the subjects were not related. Mixed-sex and male–male dyads did not differ in their compatibility ($df = 73$, $P = 1.000$). Among kin, however, we found no significant difference between the three sex combinations (female–female–male–female: $df = 20$, $P = 1.000$; female–female–male–male: $df = 20$, $P = 0.141$; male–female–male–male: $df = 20$; $P = 0.073$; Fig. 1).

Sex combination (but not kinship) had a significant effect on Security ($F_{2,93} = 8.688$, $P < 0.001$). Pairwise comparisons revealed that female–female dyads had less secure relationships than male–male dyads ($df = 93$, $P = 0.029$) or mixed-sex dyads ($df = 93$, $P < 0.001$), but that male–male dyads did not differ from male–female dyads ($df = 93$, $P = 1.000$).

DISCUSSION

Three components of relationship quality in ravens were extracted from seven behavioural variables. We labelled those components Value, Compatibility and Security, in concurrence with Cords & Aureli's (2000) theoretical proposal for relationship quality components and with the components of relationship quality recently determined in chimpanzees (Fraser et al. 2008). Thus, it appears that the demarcation of the quality of a relationship into its value, its compatibility and its security is not limited to chimpanzees, or indeed to primates or mammals, but that these components of relationship quality may also be applicable to corvids, and in particular to ravens. Moreover, although the labels given to the extracted components may be subjective, the methods used in this study allowed the components of relationship quality to be determined and quantified according to the subjects' interactions with each other. Thus, rather than representing arbitrary concepts of relationship quality as determined by the observer, the components represent the behavioural dimensions according to which

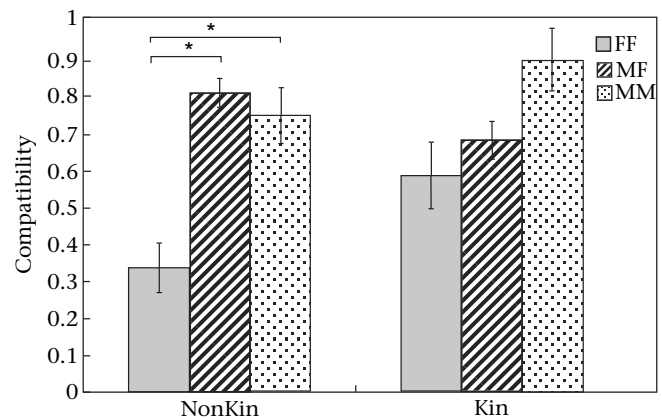


Figure 1. Mean \pm SE relative compatibility scores (estimated marginal means \pm SE from GLM analyses controlling for between-subject variation) for each sex combination for kin and nonkin. FF = female–female dyads, MF = mixed-sex dyads, MM = male–male dyads. * $P < 0.05$.

ravens assess their own relationships. Although we are already aware of the importance of relationship value in structuring some corvid interactions (Emery et al. 2007) and we know that certain relationship characteristics play an important role in cognitive task performance in ravens (e.g. Stöwe et al. 2006; Scheid et al. 2007; Schwab et al. 2008), demonstrating the true complexity of raven relationships and producing quantifiable measures of their Value, Compatibility and Security are significant steps towards furthering our understanding of raven, and corvid, behaviour. Furthermore, understanding the influence of sex combination and kinship on each of the relationship quality components may prove beneficial in any interpretation of patterns of behaviour observed across those demographic classes.

The value of a relationship is a measure of the direct benefits afforded by the relationship. Kin are therefore more likely to share valuable relationships than nonkin as any benefits provided to kin incur additional inclusive fitness benefits for the provider (Hamilton 1964). Accordingly, we found that raven siblings had more valuable relationships than nonsiblings, a finding that contrasts with the traditional view of kinship playing no or just a minor role in raven groups (Heinrich et al. 1994; Parker et al. 1994). While the aviary setting of this study may have been conducive to increased social interactions among kin as the subjects could not emigrate, valuable relationships among kin in ravens are likely to be associated with a number of benefits such as sharing information, as evidenced by enhanced social learning between raven siblings (Schwab et al. 2008). Agonistic support, one of the variables shown in this study to characterize valuable relationships, may also be more likely among kin in young ravens (Schloegl et al. 2008). Conversely, food sharing, a behaviour usually associated with valuable relationships, has not been found to occur more often between kin in ravens (Parker et al. 1994) or other corvid species (de Kort et al. 2006; von Bayern et al. 2007; Scheid et al. 2008).

Among nonkin, female–female raven dyads were found to have less compatible and less secure relationships than either male–male or mixed-sex dyads. This is likely to be because of the importance of coalition relationships between male–male dyads and the potentially reproductive importance of male–female relationships. When animals live in groups, individuals compete for access to limited resources. Where contest competition exists, dominance hierarchies are likely to form, and where there are dominance hierarchies, there is the potential for coalition formation (van Schaik et al. 2004). Individuals may thus increase their competitive ability for access to females and food resources by forming coalitions and supporting each other in agonistic conflicts. As males tend to have higher competitive abilities than females, maximum mutual benefit can be attained by forming male–male coalitions. In contrast with primates (Bercovitch 1988; Colmenares 1991; Chapais 1992; Harcourt & de Waal 1992; van Schaik et al. 2004) and other mammals (Packer & Pusey 1982; Zabel et al. 1992; Waser et al. 1994; Romero & Aureli 2008), little is known about corvid coalition relationships (Heinrich 1999; Schloegl et al. 2008), although in general coalition formation in corvids has been linked to an increase in social status for both partners (Lorenz 1931; Gwinner 1964; Emery et al. 2007). Although agonistic support is likely to be a valuable behaviour (Cords & Aureli 2000; van Schaik & Aureli 2000) and it loaded highly on the relationship quality component that we labelled Value in this study and in a previous study on chimpanzees (Fraser et al. 2008), those dyads that engage in frequent agonistic support are likely to share compatible and secure relationships as well, as a coalition partnership is unlikely to be as successful if the partners engage in frequent aggressive conflicts with each other. Conversely, among kin, we found no effect of sex combination. As animals typically show an aversion to mating with close relatives (Pusey & Wolf 1996), the potential

reproductive advantages of maintaining a compatible relationship with members of the opposite sex are not applicable to kin. Thus, male–female dyads are not expected, and were not found, to have more compatible relationships than other sex combinations. Furthermore, kin selection theory predicts that the escalation of conflicts of interest to aggressive conflicts is less likely to occur between kin as the costs of such escalation, and the benefits of its avoidance, are higher for kin than for nonkin (Hamilton 1964). Accordingly, levels of aggressive conflict have been found to be lower among relatives in several species, including birds (e.g. Butovskaya 1993; Sklepkovych 1997; Ensminger & Meikle 2005; but see Tóth et al. 2009), which may explain why kinship in ravens negates any variation in compatibility among sex combinations.

Relationship security has received considerably less attention than other aspects of relationship quality. Nevertheless it may be important when considering costs and benefits of particular behaviours. Reconciliation, the postconflict reunion between former opponents, does not appear to occur among cooperatively breeding primates, probably because the relationship between the opponents is so secure that aggressive conflict does not damage the opponents' relationship, and thus reconciliation is not necessary (Schaffner et al. 2005). Female olive baboons, *Papio hamadryas anubis*, however, showed an increase in self-directed behaviour when in proximity to dominant individuals, suggesting that the uncertainty about the dominant individuals' intentions, and thus the low degree of security that characterizes relationships between such partners, leads to an increase in anxiety (Castles et al. 1999). Investigating relationship security in birds for the first time, we found that the security of raven relationships was not influenced by kinship, but that female–female dyads had less secure relationships than male–male or mixed-sex dyads. As evidenced by their low degree of compatibility, female ravens tend not to develop strong bonds with each other (Gwinner 1964). Thus, the nature of their interactions is likely to be more unpredictable as the high level of reciprocity underlying tolerance and the exchange of valuable behaviours is unlikely to typify female–female relationships. Furthermore, coalition relationships among male–male dyads and pair bonds among male–female dyads represent long-term investments that are necessarily coupled to the consistency of interactions over time that characterizes relationship security.

The patterns observed in the variation in relationship quality according to sex combination and kinship are consistent with what little knowledge we have about raven relationship quality. It is important to bear in mind, however, that the subjects of this study were aviary birds, and that the findings presented here cannot be assumed to be representative of all other raven populations, either wild or captive. Indeed the plasticity of corvid behaviour makes it likely that the structure of social relationships within groups varies according to factors such as group composition, setting and other ecological determinants (Dall & White 2009). In addition, the majority of the subjects in this study were young birds and, as such, their behaviour and their relationships may not be representative of adult birds. Moreover, it is likely that their behaviour and the complexity of their relationships changed over the course of the study period. Nevertheless, as adult ravens are territorial and form monogamous pair bonds, the heterogeneity of their social relationships and the number of partners with whom they interact are likely to be considerably restricted compared with those of young ravens (Gwinner 1964; Heinrich 1999). Studying young ravens may thus offer a greater understanding of the potential of the complexity and diversity of relationships that characterizes raven sociality.

This study has shown that the components of relationship quality hitherto demonstrated only in chimpanzees (Fraser et al. 2008) and considered primarily only in studies of primate behaviour also form the core constituents of social relationships in

ravens. Numerous parallels have recently been made between corvid and primate (and particularly ape) behaviour and intelligence (Emery 2004; Seed et al. 2009). If indeed the complexity of social relationships is the key to higher intelligence (Byrne & Whiten 1988; Emery et al. 2007), a critical step has been taken in showing that relationship quality in both chimpanzees and ravens is composed of the same three components: value, compatibility and security. Many more studies, however, are needed before we can truly understand the consistency of the qualities of social relationships across and within corvid, primate and other species and the associated implications. Moreover, variation in relationship quality plays a key role in determining the function, patterns and distribution of social interactions and, as such, should be considered in all future studies concerning those interactions.

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